MODEL/REX WORKSHOP TO DEVELOP A MARINE ECOSYSTEM MODEL OF THE NORTH PACIFIC OCEAN INCLUDING PELAGIC FISHES

(Co-conveners: Bernard A. Megrey and Michio J. Kishi)

Summary

A 4-day MODEL/REX workshop made several significant achievements:

1. Assembled an international team of marine biologists, fisheries biologists, and physical oceanographers who collectively achieved a consensus on the structure and function of a PICES Climate Change and Carrying Capacity (CCCC) prototype lower trophic level (LTL) ecosystem model for the North Pacific Ocean that included pelagic fishes, and named it "*NEMURO.FISH*";
2. Developed a computer simulation model of fish bioenergetics and growth;
3. Coupled the fish model to the NEMURO lower trophic level model;
4. Adapted the fish bioenergetics model to Pacific herring (*Clupea harengus pallasi*) in the eastern North Pacific, and Pacific saury (*Cololabis saira*) in the western North Pacific;
5. Made recommendations for future modeling activities.

The significance of these achievements will ultimately be evaluated by how well the CCCC Program effectively utilizes and embraces these models as a basis of future modeling activity.

1.0 Workshop overview

Introduction

The North Pacific Marine Science Organization (PICES) organizes and promotes an international science program, CCCC, in the temperate and subarctic regions of the North Pacific Ocean. Ecosystem modeling is one of five key research activities defined by the CCCC Implementation Panel. The PICES CCCC MODEL Task Team is given the role to encourage, facilitate and coordinate modeling activities within the member nations with respect to the goals and objectives of the PICES-CCCC Program. At the 2000 Nemuro Workshop, the MODEL Task Team developed NEMURO, a lower trophic level marine ecosystem model. NEMURO has been internationally recognized, and recently, the Max Planck Institute has adopted the use of NEMURO.

At PICES IX in Hokkodate, the REX and MODEL Task Teams met and agreed it would be useful to extend NEMURO to include higher trophic level components. Based on some presentations there, we agreed to try Pacific herring as a candidate higher trophic level species and plans began for a joint workshop. Dr. Michio Kishi prepared a proposal to the Heiwa-Nakajima foundation of Japan to help fund attendance to the workshop. The proposal was successful and planning began to hold the next workshop in Nemuro, Japan in 2002.

Goals and objectives of the Workshop

The goals of the 2002 Nemuro PICES workshop were to (1) develop a bioenergetics-based fish model for Pacific herring (*Clupea harengus pallasi*) and Pacific saury (*Cololabis saira*) and (2) to couple this model with output from the NEMURO lower trophic level model developed at the 2000 Nemuro PICES workshop.

Organizing Committee, participants, sponsors and venue

Drs. Michio J. Kishi, Bernard A. Megrey and Francisco E. Werner organized the meeting. Drs. Megrey and. Kishi served as workshop co-chairmen. The Heiwa-Nakajima foundation of Japan, PICES, and the city of Nemuro provided financial support and access to excellent meeting rooms in the City Hall. The Nemuro Support Committee supplied local logistical support.

The venue was set at the Multi Purpose Hall, a large octagon-shaped room, in the Nemuro City Cultural Center. The hall had a local area network which included a server workstation, laser and color printers, and another personal computer connected to the Internet. A classroom style table was arranged in the center of the room for the plenary session. A set of LCD projectors and screens and AC power outlets for participants' laptop computers were available and were arranged in each work area to make group work more effective.

Twenty six scientists from China, Korea, Russia, Japan, Canada and the United States (Fig. 1) convened in Nemuro, Japan, between January 25 and January 27, 2002, to participate in a modeling workshop focused on developing a coupled lower trophic level-higher trophic level model of the marine ecosystem. Most scientists arrived with their own laptop computers. Participants (Appendix 1) consisted of plankton scientists, modelers, and individuals with biological knowledge of herring and saury. Key regional data sets were also provided by many workshop participants. The workshop was continued at the Frontier Research System for Global Change (FRSGC) facilities in Yokohama on January 29, 2002.

Fig. 1 Nemuro Workshop participants. Left to right –Top Row: Douglas Hay, Tomokazu Aiki, Masakatsu Inada, Daiki Mukai, Lan S. Smith, Vadim V. Navrotsky, Alexander V. Leonov, Francisco E. Werner, Robert A. Klumb, Bernard A. Megrey, Toshio Katsukawa, Takeshi Okunishi, Yasuhiro Yamanaka, Tomonori Azumaya. Bottom Row: Chul-hoon Hong, Sanae Chiba, Yuri I. Zuenko, Daji Huang, Masahiko Fujii, Kazuaki Tadokoro, Shin-ichi Ito, Shoichi Hamaya (Nemuro City Supporter), Michio J. Kishi, Makoto B. Kashiwai.

Workshop schedule

Date: January 25th-29th, 2002

Venue: Nemuro City Culture Center* (25-27 Jan. 2002), FRSGC (28,29 Jan. 2002)

Conveners: Michio J. Kishi (Hokkaido University), Bernard A. Megrey (NOAA), Francisco E. Werner (University of North Carolina)

Workshop Co-Chairmen: M. Kishi and B. Megrey

Agenda

January 25th, Friday

18:00	Opening ceremony
19:00	Welcome reception

January 26th, Saturday

09:00-09:10	Remarks by M. J. Kishi
09:10-09:30	Review of NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) developed by PICES MODEL Task Team in 2000 (Michio Kishi)
09:30-10:30	Review of NEMURO FORTRAN code (Yasuhiro Yamanaka)
10:30-11:00	Fish bioenergetics/biomass modeling: an application to Pacific herring (Bernard Megrey)
10:30-11:00	Review of NEMURO FORTRAN code (Yasuhiro Yamanaka)
11:00-11:30	Review of Clupeid biology with emphasis on energetics (Robert Klumb)
11:30-12:00	Analysis of change in Pacific herring distributions (Douglas Hay)
12:00-13:00	Lunch
13:00-13:30	Review of Pacific saury (*Cololabis saira*) study under VENFISH (Shin-ichi Ito)
13:30-17:00	Grouping of scientists ("team herring" and "team saury")

January 27th, Sunday

09:00-12:00	Continue working in teams
12:00-13:00	Lunch
13:00-15:30	Discussion on the results and modification of model
15:40-16:00	Closing ceremony
16:30-	Press conference (Megrey, Kishi, Werner)
18:30-20:30	Farewell party by Nemuro city (at hotel)

January 28th, Monday

Move to Frontier Research System for Global Climate Change

January 29th, Tuesday

09:00-12:00	Discussion on the results of new model and future strategy
12:00-13:00	Lunch
13:00-17:00	Seminar at FRSGC
13:00-13:30	Zuenko
13:30-14:00	Navrotsky
14:00-14:30	Huang
14:30-15:00	Klumb
15:00-15:30	Hong
15:30-16:00	Tea break
16:00-16:30	5-minute speech of Japanese participants
16:30-17:00	Discussion of future work

Workshop activity

After an opening ceremony with the people of Nemuro and a welcome party held the day before, the participants convened at the venue to start the workshop.

On the first day, the workshop officially opened with a welcome to all who had endured a long journey to come back to Nemuro. In the morning session, individual presentations were made on the NEMURO LTL model, a review of the FORTRAN program to execute NEMURO, the proposed fish bioenergetics model, and presentations on herring and saury biology as outlined in the agenda. During the afternoon session, the workshop participants split into two groups, to adapt the generalized fish bioenergetics model for Pacific herring ("team herring") and Pacific saury ("team saury").

The second day was taken up primarily with the two working groups dealing with their specific tasks. Results of the Pacific herring and saury

applications were presented for discussion in the afternoon. Also on the second day the coupled lower trophic level-higher trophic level model was named NEMURO.FISH (North Pacific Ecosystem Model for Understanding Regional Oceanography.For Including Saury and Herring). Robert Klumb suggested the name.

The participants received closing remarks from the vice-chairman of the Nemuro Supporting Committee where appreciation was extended to have brought into being such a productive workshop. These feelings were amplified during a Sayonara Party, which was full of warm hospitality by the people of Nemuro city.

The third session was held at the Frontier Research System for Global Change in Yokohama. The group discussed the structure and organization of the final report, made writing assignments, generated a list of workshop recommendations, discussed where the MODEL Task Team should be going next, and the possibility of holding future workshops. Several individual seminars were presented by workshop participants dealing with their personal research topics.

2.0 Workshop presentations

This section contains abstracts, extended abstracts, or fully prepared reports and workshop summaries given at the workshop. The reports that follow are organized by authors, according to the schedule provided in the agenda. The authors whose last name is in underline and bold font made the presentation. Model versions referenced in these reports are described in Megrey *et al.* (2000).

2.1 A generalized fish bioenergetics/biomass model with an application to Pacific herring

Bernard A. Megrey[1], Kenny Rose[2], Francisco E. Werner[3], Robert A. Klumb[4] and Douglas Hay[5]

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We chose to use bioenergetics/biomass modeling to represent fish growth because (1) the theory is based on the Law of Thermodynamics, (2) outputs must equal inputs, *ie.*, the energetic budget must balance (Law of Conservation of Mass), (3) terms in the equations are simple to biologically interpret, (4) fish physiological terms are well known and in general can be directly measured, and (5) this modeling approach allows users to focus on important external regulators such as temperature and diet composition. Model formulation and parameters for Pacific herring followed the approach used by Rudstam (1988) for Atlantic herring (*Clupea harengus*).

The growth rate of an individual Pacific herring (non reproductive) is calculated as weight increment per unit of weight per time and is defined by:

(2.1.1) $$\frac{dW}{dt} = \left[C - (R + S + F + E)\right] \cdot \frac{CAL_z}{CAL_f} \cdot W$$

where C is consumption (g prey·g fish^{-1}·d^{-1}), E is excretion or losses of nitrogenous excretory wastes (g prey·g fish^{-1}·d^{-1}), F is egestion or losses due to feces (g prey·g fish^{-1}·d^{-1}), R is respiration or losses through metabolism (g prey·g fish^{-1}·d^{-1}), S is specific dynamic action or losses due to energy costs of digesting food (g prey·g fish^{-1}·d^{-1}), W is the weight of the fish (g wet weight), t is time (days) CAL_z is the caloric equivalent of zooplankton (cal·g zooplankton^{-1}), and CAL_f is the caloric equivalent of fish (cal·g fish^{-1}). Note that (2.1.1) does not include energetic costs of reproduction (spawning).

If we define CAL_z as calories·g zooplankton^{-1}

$$CAL_z = \frac{2580\,joules}{gram\ \ zoop} \cdot \frac{1\ \ cal}{4.18\,joules} = 617.22$$

and CAL_f as calories·g fish^{-1}

$$CAL_f = \frac{5533\,joules}{gram\ \ fish} \cdot \frac{1\ \ cal}{4.18\,joules} = 1323.68$$

then once the change in weight from 2.1.1 is computed in terms of g zooplankton·g fish^{-1}·d^{-1}, we can multiply it by the weight of the fish (W, g) to get g zooplankton·d^{-1}, and finally convert g zooplankton·d^{-1} to g fish·d^{-1} by multiplying the change in weight (dW/dt) by the ratio CAL_z/CAL_f.

In the simulations described in this report, equation 2.1.1 was solved using an Euler numerical integration routine using a dt=0.01.

The formulation of the individual processes represented by the terms in equation 2.1.1 is described individually below. Consumption and respiration are nonlinear functions of fish weight and water temperature.

In addition to the physiological parameters, the model requires information about caloric content of herring (which can change seasonally), caloric content of the prey, diet composition, prey densities, and water temperatures.

Consumption

Consumption is estimated as the proportion of maximum daily ration for herring at a particular mass and temperature. Maximum daily consumption rate (g of prey per g body mass of herring per day) is estimated using an allometric function of mass from *ad libitum* feeding experiments conducted at the optimum temperature.

The basic form of the consumption function is

(2.1.2) $$C = C_{MAX} \cdot p \cdot f_C(T)$$

(2.1.3) $$C_{MAX} = a_C \cdot W^{b_C}$$

where C is the specific consumption rate (g prey·g fish^{-1}·d^{-1}), C_{MAX} is the maximum specific feeding rate (g prey·g fish^{-1}·d^{-1}), p is the proportion of maximum consumption, $f_C(T)$ is a temperature dependence function for consumption, T is water temperature (ºC), W is herring mass (g wet weight), a_c is the intercept of the allometric mass function (for a 1 g fish at 0°C), and b_c is the slope of the allometric mass function. The subscript C on the parameters refers to the consumption process.

In equation (2.1.2), the maximum specific feeding rate is modified by a water temperature dependence function described below and an additional proportionality constant that accounts for ecological constraints on the maximum feeding rate. The p can range from 0 to 1, with 0 representing no feeding and 1 indicating the fish is feeding at its maximum rate, based on its body mass and water temperature. The lower panel of figure 2.1.1 shows the relationship between fish weight and consumption from equation 2.1.3.

Temperature dependence for cool and cold water species (Thornton and Lessem 1978)

The Thornton and Lessem description of temperature dependence is essentially the product

of two sigmoid curves: one curve is fit to the increasing portion of the temperature dependence function (*gcta*), and the other to the decreasing portion (*gctb*). Four temperatures and percentages are needed. We used two sets of parameters, one for herring ages ≤1 year old, and one set for herring > 1 years old.

As an example, parameters for the second set are *xk1*=0.1, *xk2*=0.98, *xk3*=0.98, *xk4*=0.01, *te1*=1.0, *te2*=13.0, *te3*=15.0, and *te4*=23.0. For the increasing part of the curve, *te1* is the lower temperature at which the temperature dependence is a small fraction (*xk1)* of the maximum rate, and *te2* is the water temperature corresponding to a large fraction (*xk2)* of the maximum consumption rate. For the decreasing portion of the curve, *te3* is the water temperature (≥ *te2*) at which dependence is a fraction (*xk3)* of the maximum, and *te4* is the temperature at which dependence is some reduced fraction (*xk4)* of the maximum rate.

The temperature dependence model is given by

(2.1.4) $f_C(T) = gcta \cdot gctb$

where T is water temperature (ºC)

$$tt5 = \frac{1}{(te2 - te1)}$$

$$t5 = tt5 \cdot \ln\left[xk2 \cdot \frac{(1.0 - xk1)}{(0.02 \cdot xk1)} \right]$$

$$t4 = e^{[t5 \cdot (T - te1)]}$$

$$tt7 = \frac{1}{(te4 - te3)}$$

$$t7 = tt7 \cdot \ln\left[xk3 \cdot \frac{(1.0 - xk4)}{(0.02 \cdot xk4)} \right]$$

$$t6 = e^{[t7 \cdot (te4 - T)]}$$

$$gcta = \frac{(xk1 \cdot t4)}{(1.0 + xk1 \cdot (t4 - 1.0))}$$

$$gctb = \frac{(xk4 \cdot t6)}{(1.0 + xk4 \cdot (t6 - 1.0))}$$

Figure 2.1.2 shows an example of the Thornton and Lessem (1978) temperature adjustment function for a theoretical set of parameters. The upper panel of Figure 2.1.1 shows the Thornton and Lessem temperature adjustment function over a typical temperature range, and Figure 2.1.3 shows the flexibility of this curve by adjusting *te2* for a range of temperatures. Finally, Figure 2.1.4 shows the multi-dimensional relationship between consumption, body mass and water temperature from equation 2.1.2.

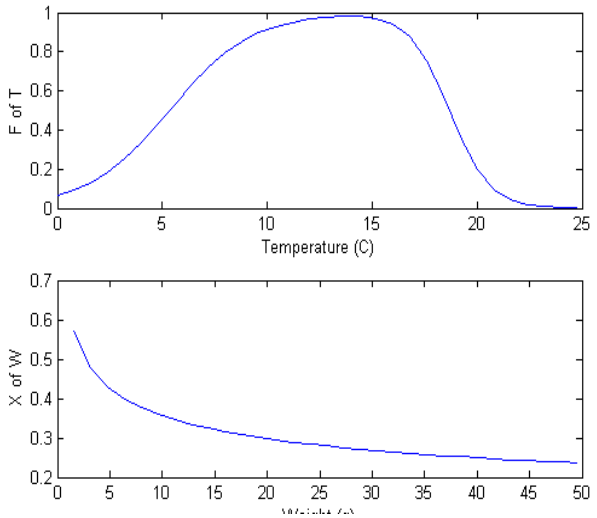

Fig. 2.1.1 Relationship between consumption and temperature from equation 2.1.4 (upper panel) and consumption and weight from equation 2.1.3 (lower panel).

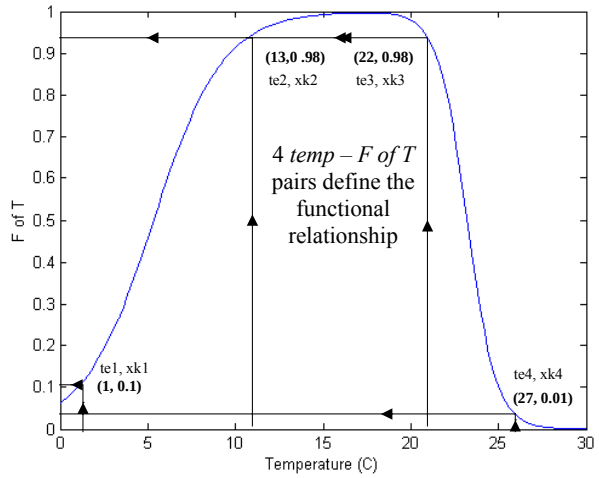

Fig. 2.1.2 Example of the Thornton and Lessem (1978) temperature adjustment curve for a theoretical set of parameters.

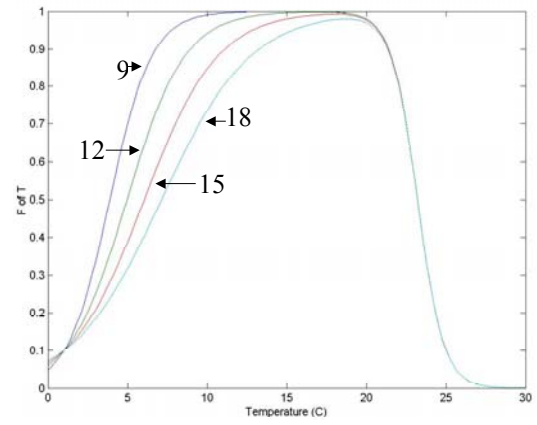

Fig. 2.1.3 Example of the Thornton and Lessem (1978) temperature adjustment curve from Figure 2.1.2 as a result of changing te2 from 9, 12, 15, 18.

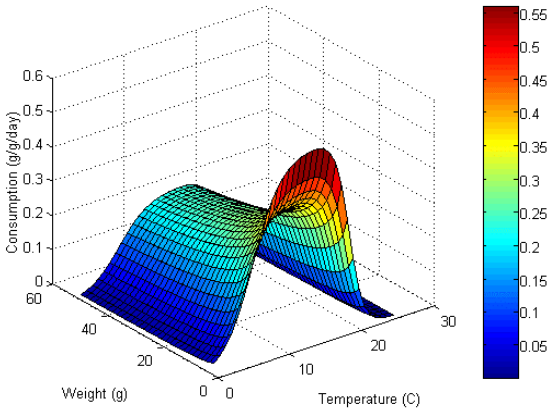

Fig. 2.1.4 Plot of the consumption, temperature and weight relationships from equation 2.1.2.

Respiration

The respiration or metabolic rate is dependent on body weight, ambient temperature and activity (swimming speed). Total metabolic rate is estimated by adding the costs of respiration to the costs of digestion, specific dynamic action (SDA).

Metabolism is modeled as

(2.1.5) $R = a_R \cdot W^{b_R} \cdot f_R(T) \cdot activity \cdot 5.258$

(2.1.6) $S = SDA \cdot (C - F)$

where R is resting respiration (*i.e.* standard metabolism) in (g O_2·g $fish^{-1}$·d^{-1}), W is wet weight in g, $f_R(T)$ is the temperature dependence function for respiration, T is temperature in ºC, a_R is the intercept of the allometric mass function and represents the weight specific oxygen consumption rate of a 1 g fish (g O_2·g $fish^{-1}$·d^{-1}) at 0ºC and no activity, b_R is the slope of the allometric mass function for standard metabolism, *activity* is the activity multiplier, S is the specific dynamic action, SDA is the proportion of assimilated energy lost to specific dynamic action, C is the specific consumption rate (g prey·g $fish^{-1}$·d^{-1}) and F is the specific egestion rate (g prey·g $fish^{-1}$·d^{-1}). The subscript R on the parameters refers to the respiration process. The coefficient 5.258 converts g O_2·g $fish^{-1}$·d^{-1} into g prey·g $fish^{-1}$·d^{-1} using the conversion

(2.1.7)

$$\left(\frac{13560\,joules}{gO_2}\cdot\frac{1\,cal}{4.18\,joules}\right)\div\left(\frac{2580\,joules}{g\ zoop}\cdot\frac{1\,cal}{4.18\,joules}\right)=5.258g\ zoop/g(O_2)$$

The temperature dependence function for respiration is a simple exponential relationship given by

(2.1.8) $f_R(T) = e^{(c_R \cdot T)}$

where c_R approximates the Q_{10} (the rate at which the function increases over relatively low water temperatures).

Activity is a power function of body weight conditioned on water temperature and is given by

(2.1.9) $activity = e^{(d_R \cdot U)}$

where U is swimming speed in cm·s^{-1} and d_R is a coefficient relating swimming speed to metabolism. Swimming speed is calculated as a function of body weight and temperature using

(2.1.10) $U = a_A \cdot W^{b_A} \cdot e^{(c_A \cdot T)}$

where $a_{A=}$ 3.9, b_A = 0.13 and c_A=0.149 if T <9.0 °C and $a_{A=}$ 15.0, b_A = 0.13 and c_A=0.0. if T ≥9.0 °C

Figure 2.1.5 shows the three dimensional relationship between respiration, water temperature and fish weight.

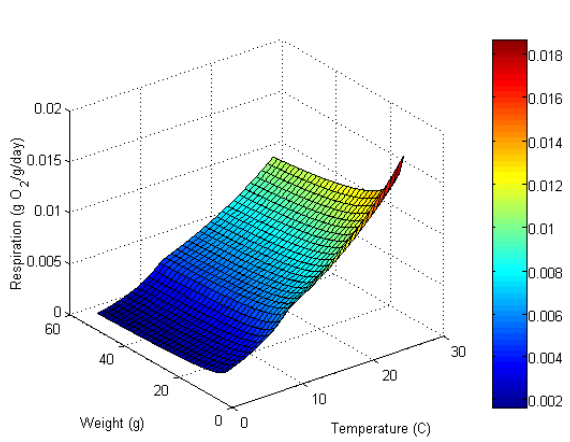

Fig. 2.1.5 Relationship between standard respiration, weight and temperature from equation 2.1.5.

Egestion and excretion

Egestion (F, fecal waste) and excretion (E, nitrogenous waste) can be computed as a constant proportion of consumption.

(2.1.11) $F = a_F \cdot C$

(2.1.12) $E = a_E \cdot (C - F)$

where a_F and a_E are constant proportions of consumption for egestion and excretion respectively. The subscript F and E on the parameters refers to the egestion and excretion process.

Multispecies feeding functional response

In most cases realized consumption is calculated by adjusting C_{MAX} from equation 2.1.2 by p, and this would be sufficient if there were only one prey type by using a Type II functional response equation (Fig. 2.1.6). When there are multiple prey types, realized consumption depends on prey densities, vulnerability of each prey item to herring (the predator), and half-saturation constants governing the rate of herring saturation. A Type II functional response equation for multiple prey types (after Rose *et al.* 1999) is used to compute realized daily consumption of each herring i (C_r, g prey·g fish^{-1}·d^{-1}) and the consumption of each prey type j (C_j, g prey·g fish^{-1}·d^{-1}) using

(2.1.13) $C_r = \sum_{j=1}^{n} C_j$

(2.1.14) $C_j = \dfrac{C_{MAX} \cdot \dfrac{PD_{ij} \cdot v_{ij}}{K_{ij}}}{1 + \sum_{k=1}^{n} \dfrac{PD_{ik} \cdot v_{ik}}{K_{ik}}}$

where C_{MAX} , which is dependent on the weight of an individual fish and water temperature, is the consumption rate (g prey·g fish^{-1}·d^{-1}) of individual herring i from equation 2.1.3, PD_{ij} is the density of prey type j (g wet weight/m^3), v_{ij} is the vulnerability of prey type j to herring i (dimensionless), and K_{ij} is the half saturation constant (g wet weight/m^3) for individual herring i feeding on prey type k ($k=1, 2, \ldots j, \ldots n$). Because the herring model is tracking one fish, there is only one predator.

A total of three prey types are represented in the current fish model, microzooplankton, copepods and euphausids. The prey densities are read in from the NEMURO model (µmole N/liter) and converted to g wet weight/m^3 using the conversion

$$\frac{14\mu g\ N}{\mu mole\ N} \cdot \frac{1.0e^{-6} g}{\mu g} \cdot \frac{1g\ dry\ weight}{0.07 g\ N\ dry\ weight} \cdot \frac{1g\ wet\ weight}{0.2g\ dry\ weight} \cdot \frac{1.0e^{3} liters}{m^3}$$

In Figure 2.1.7, the time-dependent solution to the NEMURO model for the three prey groups at the Station P location is shown. These data were used to drive herring consumption using the multiple species functional response model.

In the situation when there are multiple prey types, Figure 2.1.6 becomes more difficult to graphically represent. Figures 2.1.8 to 2.1.11 represent equations 2.1.13 and 2.1.14 for various parameter values.

In Figure 2.1.8, we represent fish consumption of three prey types from the NEMURO LTL model (small zooplankton, large zooplankton and predatory zooplankton) as stacked bars, where the height of the bar is cumulative consumption from equation 2.1.13, and the colored segments within a bar represent the consumption of each prey type.

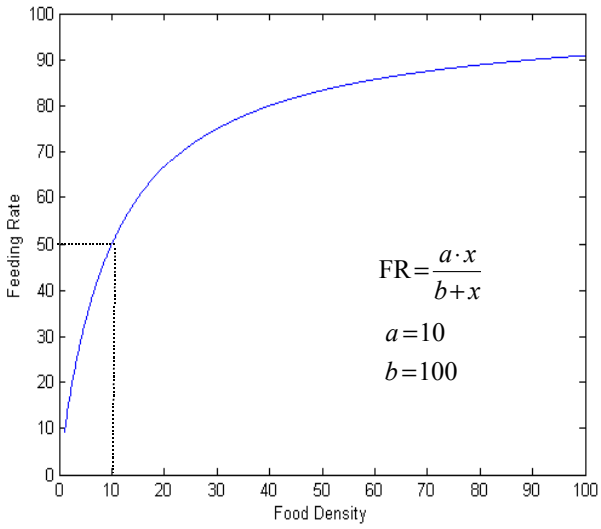

Fig. 2.1.6 Type II functional response describing the theoretical relationship between available food density and feeding rate when there is just one prey type.

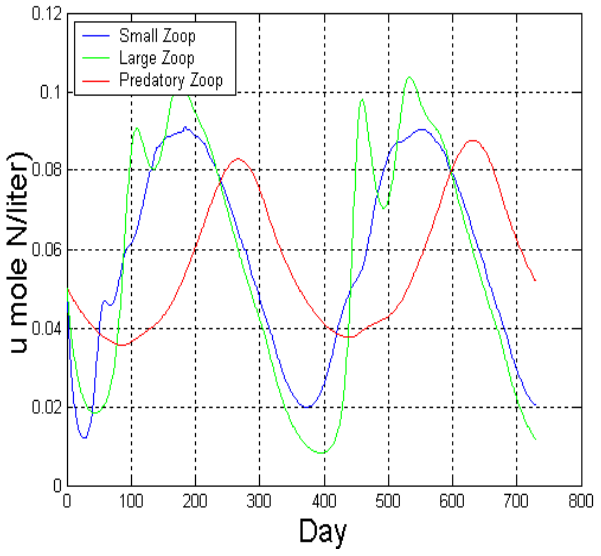

Fig. 2.1.7 NEMURO model output showing time-dependent dynamics of small, large and predatory zooplankton.

The parameters at the left of the figure were used in equations 2.1.13 and 2.1.14. For each panel within a figure, the vulnerability of one prey type was changed from 0 to 1, while keeping all other parameters the same and assigning the vulnerability parameter for the remaining two prey type to 1.0. For example, in the top panel of Figure 2.1.8, the vulnerability parameter for small zooplankton was varied from 0.0 to 1.0, while keeping the vulnerability parameter for large zooplankton and predatory zooplankton equal to 1.0 and using the parameters at the left of the figure in equations 2.1.13 and 2.1.14. In the middle panel, just the vulnerability for large zooplankton was varied from 0.0 to 1.0, while holding the vulnerabilities for small zooplankton and predatory zooplankton at 1.0. In the bottom panel, only the vulnerability for predatory zooplankton was varied from 0.0 to 1.0.

These results show that, for the prey whose vulnerability is changing (let us call it the target prey type), the contribution of the target prey type to total consumption ranges from 0.0 at 0.0 vulnerability, gradually increases as vulnerability increases, until a vulnerability of 1.0, where its contribution to total consumption is exactly one third. Also total consumption gradually increases as the proportion of the target prey type increases with increasing vulnerability to the predator.

Also note that the right-most bar in each panel is the same (height and contribution of each prey type) when vulnerability is 1.0 for all prey types.

Using Figure 2.1.8 as a base case, Figure 2.1.9 shows the change when the half saturation constant for large zooplankton (K_2) is changed from 100.0 to 10.0. Now each panel in Figure 2.1.9 is similar to the corresponding panel in Figure 2.1.8 (the base case), except that large zooplankton make up the bulk of total consumption regardless of which prey types vulnerability is changed.

Now using Figure 2.1.9 as a base case, Figure 2.1.10 shows the change when the density of predatory zooplankton (PD_3) is changed from 2.0 to 4.8. Now each panel in Figure 2.1.10 is similar to the corresponding panel in Figure 2.1.9, except that the contribution of predatory zooplankton to total consumption is higher in each case. Also, the height of each bar (total consumption) is higher in Figure 2.1.10 compared to Figure 2.1.19.

Figure 2.1.11 shows the results of the mutispecies feeding functional response for the parameter values used in the herring application.

PD_1=2.0
PD_2=2.0
PD_3=2.0
C_{MAX}=2.5

K_1=100.0
K_2=100.0
K_3=100.0

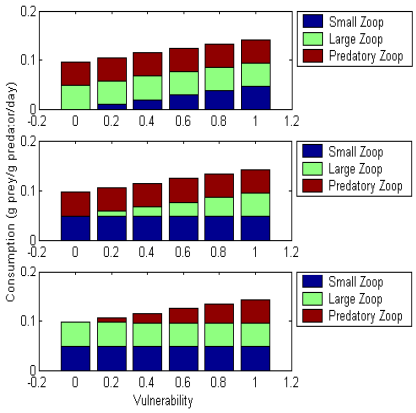

Fig. 2.1.8 An example of the mutispecies functional response formulation (equations 2.1.13 and 2.1.14) for three prey groups, varying the vulnerability of the target prey group one at a time.

PD_1=2.0
PD_2=2.0
PD_3=2.0
C_{MAX}=2.5

K_1=100.0
K_2=10.0
K_3=100.0

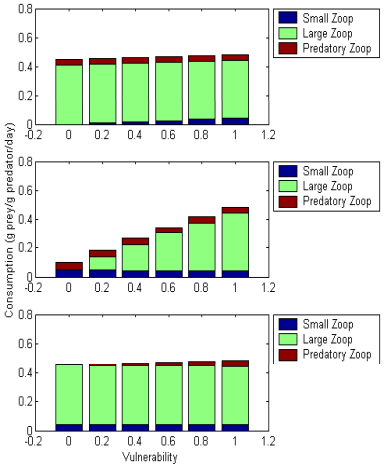

Fig. 2.1.9 An example of the multispecies functional response formulation (equations 2.1.13 and 2.1.14) for three prey groups, varying the vulnerability of the target prey group one at a time, and changing the half saturation constant for prey group 2 (K_2) from 100.0 to 10.0.

PD_1=2.0
PD_2=2.0
PD_3=4.8
C_{MAX}=2.5

K_1=100.0
K_2=10.0
K_3=100.0

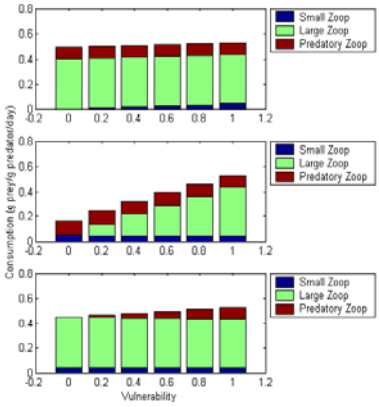

Fig.2.1.10 An example of the multispecies functional response formulation (equations 2.1.13 and 2.1.14) for three prey groups, varying the vulnerability of the target prey group one at a time, changing the half saturation constant for prey group 2 (K_2) from 100.0 to 10.0, and changing the density of prey group 3 (PD_3) from 2.0 to 4.8.

PD_1=1.8
PD_2=0.8
PD_3=4.8
C_{MAX}=2.5

K_1=100.0
K_2=10.0
K_3=100.0

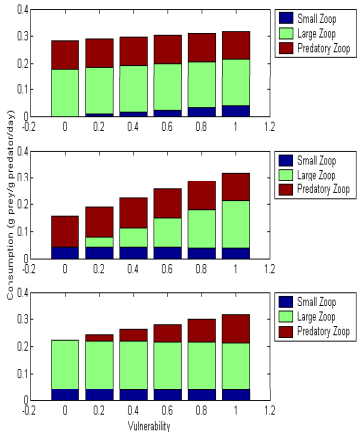

Fig. 2.1.11 An example of the multispecies functional response formulation (equations 2.1.13 and 2.1.14) for three prey groups, varying the vulnerability of the target prey group one at a time using the parameters in the herring model.

Linking a fish bioenergetics model to the NEMURO LTL model

The NEMURO LTL model and the fish bioenergetics model were developed independently. Linking the two models involves paying close attention and reconciling two important differences: 1) the way the two models account for time, and 2) the way NEMURO generates phytoplankton and zooplankton densities (mole N/liter), and the way the fish bioenergeticsmodel expects phytoplankton and zooplankton densities (μmole N/liter). These differences are presented in Table 2.1.1. Reconciling these differences requires the use of several conversion coefficients, which can be seen in the code presented in Appendices 4 and 5.

Table 2.1.1 Ways in which NEMURO and the fish bioenergetics model account for time and LTL densities.

Model	Time	LTL Density
NEMURO	seconds	mole N/liter
Fish Bioenergetics	day	μ mole N/liter

Linking the fish bioenergetics model to NEMURO can be done in two ways. In a static linkage (Fig 2.1.12), the NEMURO model is run and a time series of small, large and predatory zooplankton abundances are stored in an output file and used as an input file for the fish bioenergetics model where they influence the consumption term of the bioenergetics governing equation 2.1.1. The models are run sequentially and there is no feedback between the two models.

In the dynamic linkage (Fig 2.1.13), the models are run simultaneously, the zooplankton prey groups contribute to the consumption term of the fish bioenergetics governing equation 2.1.1, the ZOOS, ZOOL, and ZOOP state variables of NEMURO are reduced by the amount eaten by herring, fish excretion waste is added to the nitrogen pool of NEMURO, and fish egestion waste is added to the DOM pool of NEMURO.

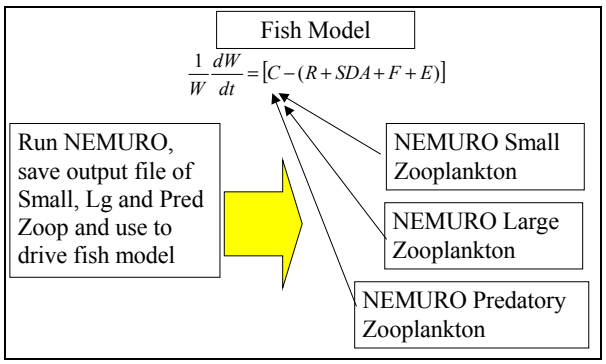

Fig. 2.1.12 Example of a static linkage between NEMURO and the bioenergetics fish model.

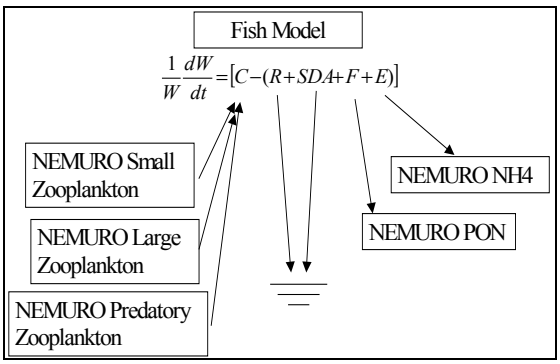

Fig. 2.1.13 Example of a dynamic linkage between NEMURO and the bioenergetics fish model..

Table 2.1.2 Summary of parameter values used in the generalized herring bioenergetics model from Rudstam (1988).

Symbol	Parameter description	Value	
Consumption, C_{MAX}			
a_C	Intercept for C_{MAX} at (te1+te3)/2		0.642
b_C	coefficient for C_{MAX} versus weight	-0.256	
te1	Temperature for xk1 (in ºC)		1[a] 1[b]
te2	Temperature for xk2 (in ºC)		15[a] 13[b]
te3	Temperature for xk3 (in ºC)		17[a] 15[a]
te4	Temperature for xk4 (in ºC)		25[a] 23[b]
xk1	Proportion of C_{MAX} at te1	0.10	
xk2	Proportion of C_{MAX} at te2	0.98	
xk3	Proportion of C_{MAX} at te3	0.98	
xk4	Proportion of C_{MAX} at te4	0.01	
Metabolism, R			
a_R	Intercept for R		0.0033
b_R	Coefficient for R versus weight		-0.227
c_R	Coefficient for R versus temperature		0.0548
d_R	Coefficient for R versus swimming speed	0.03	
S	Coefficient for Specific Dynamic Action		0.175

Table 2.1.2 (cont.)

Symbol	Parameter description	Value	
Swimming Speed, U			
a_A	Intercept U (< 9 ºC) (in cm/s)		3.9
a_A	Intercept U (≥ 9 ºC) (in cm/s)		15.0
b_A	Coefficient U versus weight		0.13
c_A	Coefficient U versus temperature (< 9 ºC)	0.149	
c_A	Coefficient U versus temperature (≥ 9 ºC)	0.0	
Egestion and Excretion, F and E			
a_F	Proportion of consumed food egested		0.16
a_E	Proportion of consumed food excreted		0.10

a - values for age 0 and 1herring
b - values for age 2 and older herring

2.2 Review of Clupeid biology with emphasis on energetics

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The general bioenergetics model based on the Law of Thermodynamics balances all consumed energy as follows: G = C – R – F – U, where G=growth, C=consumption, R=metabolism (respiration), F=egestion, and U=excretion. Consumed energy is first allocated to costs of metabolism and waste losses with the remainder available for somatic growth. Energy lost by the gametes released during spawning can also be included. Formulas and parameters provided below for the individual components in the bioenergetics model follow the terminology and symbols used in Hansen *et al.* (1997). Energy equivalent conversion factors for oxygen consumption, carbohydrates, fats, and protein can be found in Elliott and Davison (1975), with additional comments on the oxycalorific coefficient found in Brett (1985).

Consumption

Consumption (C) = C_{max}*P-value*f(T) and
C_{max}=CA*W^{CB}

Consumption (g prey·g^{-1}·d^{-1}), is generally modeled as an allometric (power) function of weight. Maximum consumption rates are determined in laboratory experiments by feeding fish a known (by weight) *ad libitum* ration and then subtracting uneaten food after a specified time interval. For adult alewife *Alosa pseudoharengus*, the specific slope for weight dependence on maximum consumption was -0.3 (Stewart and Binkowski 1986), a value intermediate to that found in studies of larval and juvenile clupeids (De Silva and Balbontin 1974; Theilacker 1987). The specific weight-dependent slope (CB) for maximum consumption of northern anchovy *Engraulis mordax* larvae (wet weight < 0.001 g) re-calculated from data in Theilacker (1987) was -0.367, while the slope for Atlantic herring (wet weight 8 – 15 g) was -0.256 (De Silva and Balbontin 1974). Rudstam (1988) used the slope and intercept derived by De Silva and Balbontin (1974) in the bioenergetics model for adult Atlantic herring *Clupea harengus* consumption. Due to a lack of data for larval and juvenile fishes, the same relations for maximum consumption of adult herring and alewives were applied to age-0 fish by Arrhenius (1998a) and Klumb *et al.* (in review), respectively.

The "P-value" in the bioenergetics model refers to the proportion of maximum consumption. This value is used to fit the bioenergetics model to observed growth or can be set constant to check resultant growth potential in varied environments.

Temperature dependence of consumption is usually modeled as simple or modified exponential functions (Hansen *et al.* 1997). For cool- and cold-water species, the temperature dependence of consumption is generally modeled using a curve proposed by Thorton and Lessem (1978), which modified the logistic equation. This function is the product of two intersecting sigmoid curves (one ascending and one descending) forming a "humped" curve across the entire temperature range inhabited by a given species.

Required parameters include the approximate temperatures for optimum consumption, and the high and low temperatures where consumption is dramatically reduced (~98%) compared to maximum consumption. Any temperatures derived from laboratory or field data showing maximum or reduced consumption levels can be used. If specific data relating consumption and temperature are lacking, the optimum of consumption is generally equated to the fish's thermal optimum for growth (Beitinger and Magnuson 1979), and the temperatures where consumption is dramatically reduced are derived from the thermal tolerances (survival limits) of a species.

Metabolism/respiration

Total metabolism = Respiration + specific dynamic action (SDA)

where

Respiration (R) = $RA*W^{RB}$ * f(T)*Activity and $f(T) = e^{RQ*T}$

Metabolism of fishes is determined by measuring oxygen consumption at various temperatures over a known time period, and generally modeled as an allometric function of weight and an exponential function of temperature. Brett and Groves (1979) distinguished three types of metabolism in fishes: standard, routine and active. By definition, standard metabolism is the minimum energy requirements needed by a fish at rest (also known as basal metabolism), and it is this metabolic state that is used in bioenergetics models. Measuring standard metabolism is difficult and requires use of anesthetized fish or fish with movements confined by small respirometers. Routine metabolism includes normal spontaneous activity, while active metabolism includes the cost for activity above the spontaneous activity level. Winberg (1956) stated that active metabolism was approximately twice standard metabolism (*i.e.* the "Winberg multiplier" of 2). However, Ware (1975) indicated active metabolism could range from 2 to 3 times standard rates. Bioenergetics models generally use allometric function parameters derived for standard metabolism multiplied by a temperature function and an activity factor to estimate total respiration costs.

Respiration (g oxygen$\cdot g^{-1}\cdot d^{-1}$) of adult fishes generally scales negatively with weight (*i.e.* negative slope), and ranges from -0.25 to -0.15 on a weight specific basis (Winberg 1956). For clupeids, slopes of the metabolism-weight relations ranged from -0.19 to -0.28 for Atlantic menhaden *Brevoortia tyrannus* (Hettler 1976), -0.215 for alewife (Stewart and Binkowski 1986), and -0.227 for Atlantic herring (De Silva and Balbontin 1974). Rudstam (1988) used -0.227 in the adult Atlantic herring bioenergetics model, and this value was also applied to age-0 herring (Kerr and Dickie 1985; Arrhenius 1998a). The slope for the metabolism-weight relation of *Maurolicus muelleri*, a mesopelagic planktivore, was -0.15 (Ikeda 1996).

The relation of respiration to weight of fishes has been found to change ontogentically, with isometric (mass independent) relations for larvae switching to negative allometries in adults (Post and Lee 1996). However, the variability of slopes found in the review of 31 species by Post and Lee (1996) highlighted the need to derive weight-metabolism relations for the larvae of individual species. The final weight-metabolism relation derived likely depends on the range of fish sizes used. Studies of larval fishes encompassing greater than three orders of magnitude in weight documented isometric relations between metabolism and weight for Clupeidae (Klumb *et*

al., in review), Cyprinidae (Kamler 1972), and Scombridae (Giguère *et al.* 1988).

Specific dynamic action (SDA)

$SDA = SDA*(C - F)$

Specific dynamic action, or more appropriately termed "apparent specific dynamic action" and also known as the "heat increment", is the energy allocated to the digestive processes of food, principally deamination of proteins but also includes energy costs of absorption, transportation and deposition of food (Beamish 1974). Oxygen consumption by fasting and fed fish in flow-through respirometers (where the fish is subjected to a known level of activity, *i.e.*, forced to swim against a known current) is required to measure SDA (Beamish and Trippel 1990). Beamish and Trippel (1990) found that SDA increased with meal size and body weight but declined with weight at fixed rations. However, in most bioenergetic models, SDA is considered a constant proportion of ingested energy with values for adult fish ranging from 10-29% (reviewed by Beamish and Trippel 1990). The SDA parameter in bioenergetics models is generally borrowed from non-related species because proper measurement requires strict laboratory experiments using specialized equipment. For adult alewife (Stewart and Binkowski 1986) and adult Atlantic herring (Rudstam 1988), SDA was assumed to be 17.5% based on data for aholehole *Kuhlia sandvicensis* (Muir and Niimi 1972). Arrhenius (1998a) lowered SDA to 15% for age-0 Atlantic herring. Larval clupeids have been found to assimilate food more efficiently than adults (Kiørboe *et al.* 1987). In energetic terms, Kiørboe *et al.* (1987) estimated SDA for larval Atlantic herring to be 10% of assimilated rations, and Limburg (1994) calculated the mean SDA for American shad *Alosa sapidissima* juveniles to be 13%.

Activity

$Activity = e^{RTO*VEL}$,
where $VEL = RK1*W^{RK4}$ for $T \geq RTL$
or $VEL = ACT*W^{RK4}*e^{BACT*T}$ when $T < RTL$

The energetic cost of activity is generally considered a multiple of standard metabolism. A simple constant, *i.e.* the "activity multiplier = 2" of Winberg (1956), can be used to accord increased (aerobic) metabolic costs due to swimming. Exponential functions have been used to model activity costs of adult alewife (Stewart and Binkowski 1986) and Atlantic herring (Rudstam 1988). The exponential model is composed of three components: 1) VEL which is the weight dependence of swimming speed (cm/s), 2) the temperature (T) dependence of swimming speed (BACT), and 3) the relation of respiration to swimming speed (RTO). The parameter ACT is the intercept (cm/s) for a 1-g fish at 0°C. Swimming speed can change from temperature dependence to independence (at T = RTL). Swimming speeds of Atlantic herring were only dependent on weight at temperatures > 9°C (Rudstam 1988), and alewife swimming speeds were independent at > 15°C. (Stewart and Binkowski 1986)

The coefficient for swimming speed dependence of metabolism (RTO) used in the adult alewife model was assumed constant (RTO = 0.03) and based on data in Muir and Niimi (1972). Data for Cape anchovy *E. capensis* found that coefficients before, during, and after feeding ranged from 0.01 to 0.04 (James and Probyn 1989). A coefficient relating respiration and swimming speed of 0.03 has also been reported for adult menhaden (Durbin *et al.* 1981), and the coefficient for adult coregonids was 0.02 (Dabrowski 1985). However, the coefficient relating respiration rate to swimming speed increased substantially in larval coregonids (Dabrowski 1986) and cyprinids (Kaufmann 1990); therefore, a constant relating metabolic cost to swimming speed is inappropriate for early life stages. Using an exponential activity function and a constant relating swimming speed to oxygen consumption resulted in essentially no energetic costs for the activity of YOY alewife (Klumb *et al.*, in review).

How to best model the activity costs of larval fish is uncertain since existing data from the few studies relating metabolism and swimming speeds at early life stages are equivocal. Because the slope of metabolism versus swimming speed varied with body size, Dabrowski *et al.* (1988) found active metabolic rates of coregonids to be 5 - 50 times standard metabolism. A size-effect on

the slope for the metabolism-swimming speed relation also existed for larvae of two cyprinid species (Kaufmann 1990); however, ratios of routine metabolism to standard metabolism were low (< 1.5) and essentially flat from 0.005 - 0.300 g (wet weight). In Kaufmann's (1990) study, ratios of active to routine metabolism (*i.e.*, the factorial scope) ranged from 2 - 4. These contrasting results may lie in the function chosen to describe the metabolism-swimming speed relation, *i.e.*, exponential (Dabrowski 1986; Dabrowski *et al.* 1988) or allometric (Kaufmann 1990). However, using an exponential model, Wieser and Forstner (1986) found the ratios of active to routine metabolism for larvae of three cyprinid species ranged from 1 - 4 and were independent of weight (0.01 - 0.3 g wet) and temperature (12 - 24°C). Activity rates of fishes can also vary widely with growth rate and food density (Ware 1975), while laboratory measurements of metabolism during activity may be higher than actual costs in the wild, since larvae are also passively moved by water currents. Klumb *et al.* (in review) used routine metabolism parameters without an activity multiplier in a bioenergetics model for age-0 alewife.

Clupeids have pronounced changes in activity patterns possibly due to circadian rhythms (Katz 1978; Batty 1987). Clupeids do not swim in schools during darkness (Limburg 1994). Accuracy of bioenergetic estimates of herring consumption were improved when including diel feeding cycles (Arrhenius 1998a).

Egestion

Egestion (F) = FA*C

Egestion is modeled as a constant proportion of consumption. Assimilation efficiency (in terms of energy) of adult menhaden ranged from 86 to 92% (Durbin and Durbin 1981). In the adult alewife (Stewart and Binkowski 1986) and Atlantic herring models (Rudstam 1988), egestion was assumed to be 16% of consumption.

Data for egestion processes and models are not common; most extensive studies have been done for brown trout *Salmo trutta* (Elliot 1976a, 1976b). Egestion has been found to be a function of temperature and ration (Elliott 1976a). However, Stewart and Binkowski (1986) found small changes in estimated consumption when making the simplified assumption of egestion being a constant proportion of consumption in the bioenergetics model for alewife.

The proportion of consumption egested has been found to be low in larval and juvenile clupeids (Kiørboe *et al.* 1987; Limburg 1994). Arrhenius (1998) used 16%, the value from the adult Atlantic herring (Rudstam 1988) and alewife (Stewart and Binkowski 1986) models for the proportion of assimilated ration egested by larval Atlantic herring. Both Kiørboe *et al.* (1987) and Limburg (1994) found the percentage of food egested was 10% (by mass). However, Klumpp and von Westernhagen (1996) found egestion for Atlantic herring larvae age 8 - 33 days averaged 17.6% (range 13.4 - 25.6%) of ration (*Artemia* sp. nauplii) energy content.

Based on the above three studies on larval and juvenile clupeids (Kiørboe *et al.* 1987; Limburg 1994; Klumpp and von Westernhagen 1996), Klumb *et al.* (in review) chose 0.125 as a first approximation for the proportion of consumption egested by larval and juvenile alewife.

Excretion

Excretion (U) = UA*(C – F)

Excretion is modeled as a constant proportion of assimilation (consumption minus egestion). In the adult alewife (Stewart and Binkowski 1986) and Atlantic herring models (Rudstam 1988), excretion was assumed to be 10% of assimilation based on rates measured for brown trout (Elliott 1976b).

Few studies on larval fish excretion have been conducted. For three species, *Blennius pavo*, plaice *Pleuronectes platesssa*, and Atlantic herring, Klumpp and von Westernhagen (1996) found the mean percent of the assimilated ration excreted was 6.0, 6.6 and 10.7%, respectively. Due to high mortality for Atlantic herring larvae in Klumpp and von Westernhagen's study, Klumb *et al.* (in review) used the average value of 7.8% for all three species as a first approximation of the

percent of assimilation excreted by larval and juvenile alewife.

Data requirements

There are four data requirements for the bioenergetics model: 1) diet (in proportions of prey types), 2) energy density of the predator fish, 3) energy density of the prey, and 4) water temperatures. The bioenergetics model is an individual based model but can incorporate populations by multiplying mean weight by population number.

Diet

Diet information was summarized by Douglas E. Hay (Pacific Biological Station, Fisheries and Oceans Canada) based on recent observations (Hay and McCarter 2001, and older literature such as Wailes 1936). Depending on the population, herring diets can be simple or complicated. The simple story is that herring eat mainly copepod eggs and nauplii as larvae, copepod adults and nauplii as juveniles and euphausiids as adults. This over-simplified` story gets messy when the smaller, non-migratory marginal populations are examined because they appear to eat a wider variety of taxa. Herring feed intensely in the summer months but they also eat during winter. In all areas, winter diets, although small in relation to total annual consumption, may be more variable than summer diets. Perhaps the main point to emphasize, however, is that in southern British Columbia, most herring feed in shelf waters where the main food items are euphausiids. Atlantic herring and sprat *Sprattus sprattus* diets consisted of 70 - 73% copepods, 12 - 14% *Oikopleura*, and 9 - 12% cladocerans (De Silva 1973).

Adult clupeids feed by filtering or particulate feeding (Blaxter and Hunter 1982; Janssen 1976). Janssen (1976) found for alewives that the filter feeding mode displayed by large alewives (total lengths > 170 mm) was not size-selective, while particulate feeders (total lengths 50 - 115 mm) selected zooplankton > 1.0 mm. Transition of larvae to adult body morphology and feeding modes occurs at metamorphosis (~35 mm) after gill rakers and the upper and lower jaws become developed (Blaxter and Hunter 1982). Although activity of clupeids may be lower at night (Katz 1978), filter feeders can still feed in darkness (Hettler 1976; Janssen and Brandt 1980; Grabe 1996).

Feeding activity of larval herring has been found to be dependent on densities of copepod nauplii (Munk and Kiorboe 1985) with success a function of prey size (Hunter and Blaxter 1982). Atlantic herring (length 25 mm) larvae were able to consume prey sizes ≥ 1.0 mm (Sherman and Honey 1971, cited in Hunter and Blaxter 1982). Foraging behavior of Altantic herring larvae changed with prey size and was related to larval length by the equation: prey length = 0.027*larval length (Munk 1992), and attack success was directly related to relative prey size. Fiksen and Folkford (1999) included the mouth size of herring larvae, perception (visual field and reaction distance), light intensity, and the length, width and density of plankton prey when modeling encounter rates and probabilities of successful strikes.

Energy density of predator and prey

Energy density, also called caloric content and energy content, in bioenergetics models is used in terms of wet weight. Dry-weight data are customarily converted (approximated) to wet weight assuming dry weight is 10 - 20% of total weight. Hartman and Brandt (1995) provided many equations for estimating energy density from the percent dry weight of various marine and freshwater fish species. Assuming constant energy densities or using values that are too high or low can greatly affect bioenergetics model consumption estimates (Stewart and Binkowski 1986).

Energy density (ED) of clupeids has been found to vary seasonally, peaking in fall and declining through winter (Arrhenius and Hansson 1996; Flath and Diana 1985; Paul *et al.* 1998). Age-0 EDs are lower than older fish (Arrhenius and Hansson 1996; Flath and Diana 1985; Paul *et al.* 1998). For age-1 alewife in Lake Michigan, ED in June and July was 4520 $J \cdot g^{-1}$, increased in August and September to 4729 and 5440, respectively, then declined to 4729 in April, and 4436 by May (Flath and Diana 1985). For age-0 Atlantic herring, Arrhenius and Hansson (1996) found ED

increased from 2600 $J \cdot g^{-1}$ in mid-July to 4500 $J \cdot g^{-1}$ in October. The ED of age-0 Baltic Sea sprat increased from 4000 $J \cdot g^{-1}$ in August to approximately 5250 $J \cdot g^{-1}$ by December (Arrhenius 1998b). October ED of alewife was 5020 $J \cdot g^{-1}$ (Flath and Diana 1985).

Higher energy densities were found for Pacific herring off Alaska (Paul *et al.* 1998; Foy and Paul 1999) compared to Great Lakes alewives and Baltic Sea clupeids. Age 2+ Pacific herring had EDs in fall that ranged from 9400 to 10200 $J \cdot g^{-1}$ and declined over winter to 5200 to 6300 $J \cdot g^{-1}$ by spring. Females had higher energy densities in both seasons than males by 200 - 400 $J \cdot g^{-1}$. Age-0 herring had EDs of 5700 $J \cdot g^{-1}$ in fall which declined to 4400 $J \cdot g^{-1}$ by the following spring (Paul *et al.* 1998). Equations to predict ED from standard length of juveniles by month are provided in Paul and Paul (1998a). The ED for age-0 captive fasting herring declined 23 $J \cdot g^{-1} \cdot d^{-1}$ from December to the end of January (Paul and Paul 1998b).

Energy densities of freshwater and marine invertebrates can be found in Cummins and Wuycheck (1971), while good tables of the caloric content of marine invertebrates (with references) are presented in Foy and Norcross (1999) and Foy and Paul (1999). Laurence (1976) provides energy densities for marine calanoid copepods in the Atlantic. Like fish, the energy density for invertebrates has been found to vary seasonally.

Table 2.2.1 Energy densities (jouls/gram) for main food items of Pacific herring.

Food Item	**$J \cdot g^{-1}$**
Copepoda	2580
Euphausiids (per gram wet weight)	5020
Fish eggs (per gram wet weight)	4520

Table 2.2.2 Existing bioenergetic models.

Reference	Comments
General models	
Winberg 1956	extensive early work but reference not that accessible
Kitchell *et al.* 1974	results of International Biological Program (IBP) workshops and first paper of the "Wisconsin" bioenergetics model – applied to bluegill sunfish (*Lepomis macrochirus*) in terms of mass balance
Elliott 1976b; 1979	general review of energetics resulting from his extensive work with brown trout (*Salmo trutta*)
Stewart *et al.* 1983	changed the Kitchell *et al.* 1974 model from mass to energy balance, for lake trout (*Salvelinus namaycush*)
Clupeid bioenergetics models	
Rudstam 1988	Adult Atlantic herring (*Clupea harengus*)
Kerr and Dickie 1985	Age-0 Atlantic herring
Arrhenius 1998	Age-0 Atlantic herring
Fiksen and Folkford 1999	Larval Atlantic herring– Individual based model, which includes metabolism, ingestion, prey encounter success, and multiple prey functional response
Stewart and Binkowski 1986	Adult alewife (*Alosa pseudoharengus*)
Hewett and Stewart 1989	Age-0 alewife: (only temperatures for the consumption component differed from the adult model)
Klumb *et al.* In review	Age-0 alewife
Durbin and Durbin 1983	Adult menhaden (*Breoortia tyrannus*):– in terms of energy and Nitrogen

2.3 Reflections of factors affecting size-at-age and strong year classes of herring in the North Pacific

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One approach to the investigation of linkages between oceanographic process and subsequent impacts on marine fish populations, is retrospective analyses of age-specific growth rates (size-at-age) from archive collections of scales or otoliths. This approach can be linked to independent observations on (1) temporal variation in abundance, (2) synchrony or asynchrony of year-class strength among different populations, or different species, and (3) habitat requirements of life history stages (eggs, larvae, juveniles, adults) that have different spatial and trophic characteristics.

Widespread geographic synchrony sometimes occurs in Pacific herring (Hollowed and Wooster 1995, Hay *et al.* 2001). An exceptionally strong year-class occurred in 1977 over a broad and geographic range (Fig. 2.3.1). It was strong in northern BC, parts of south-eastern and central Alaska and the Bering Sea (Hollowed and Wooster 1995). This 1977 year-class developed in different populations with different spawning times, with a range of about 3 months from the earliest to the latest mean spawning time. Pacific herring spawn in shallow, inshore inter-and subtidal waters. In many areas of the Pacific coast of North America, spawn deposition is monitored and quantified annually. Spawn deposition was not exceptional in 1977. Therefore, it follows that in 1977, survival from eggs to the juvenile and recruit stage, between 1977 and 1980, was relatively higher (or mortality was lower) than most other years. It also follows that the factor(s) that promoted the strong year-class were widely distributed in space and time.

Retrospective analysis of archived herring scales (Fig. 2.3.2) from northern BC populations, indicates that individuals of the 1977 year-class were of normal size, or slightly larger than normal, relative to samples from other years (Fig. 2.3.3).

After age 4, the relative size-at-age of individuals in the 1977 year-class declined, and was smaller than normal, which indicates that growth rate declined in older individuals. This retrospective analysis of growth from scale analysis was corroborated by analyses of catch-sampling data, collected routinely for the last 70 years. The size-at-age of 3-year-old members of the 1977 year-class was normal in most areas in 1980, but size-at-age of older individuals (*e.g.* age 6 fish collected in 1983) was smaller than normal (Fig. 2.3.4).

A strong 1977 year-class also occurred in several other species, including blackcod and lingcod (Hollowed and Wooster 1995). Climate-related changes, but not necessarily increases in abundance, also occurred in other marine species including salmonids (Beamish *et al.* 1999) and pollock *Theragra chalcogrammus* (Ohtani and Azumaya 1995). Further, there are periods when there has been synchrony of strong year-classes among different species in the North Pacific (Hollowed *et al.* 1987), which is evidence of environmental influence on the production of year-class strength.

The habitats occupied by age 1 and 2 herring are mainly inshore (Haegele 1997), whereas most of the older age groups (age 3 and older) tend to occupy shelf waters. During intensive summer feeding periods, juvenile herring are found mainly in shallow, nearshore waters of less that 50 m. In general, age 1 juveniles occur in shallower waters, closer to shore, than age 2 herring. In general, herring form shoals of similar-sized individuals so the two larger age groups do not mix, although both age groups of juveniles occur in the same vicinities, herring juveniles are widely dispersed through all BC coastal waters.

Over the last 70 years in British Columbia (BC), herring stomachs have been examined by different

people, in different years, at different places and at different herring life history stages. Wailes (1936) summarized the food of young herring mainly in the first summer of life. At very young stages, eggs (ova) and nauplii from various invertebrates are most important. Copepod nauplii seem to dominate the food but food composition varied with location. The youngest juveniles (age 1) fed mainly on copepods. Older, larger juveniles took various zooplankton, with euphausiids being common. More recent work examined gut data from herring juveniles in Georgia Strait, BC, Hecate Strait and Prince William Sound Alaska (Haegele 1997, Foy and Norcross 1999, Hay and McCarter 2001). In general the main food for herring at ages 1 and 2 is copepods. Therefore if the abundant 1977 year-class ate mainly copepods at ages 1 and 2, then copepods must have been abundant in nearshore northern waters, both in 1977 and 1978. From our present understanding of herring life history, there is little opportunity for trophic interaction (*i.e.* direct density-dependent competition for food) between age-classes: either among juveniles (ages 1 versus age 2) or between juveniles versus adults (age 3+ and older). In BC waters, probably the first opportunity for direct interaction occurs during the third winter of life, at age 2+, when (BC) herring start to mature sexually and join the adult stock. At this time, however, winter feeding is minimal and growth is slight.

The observations above can be summarized as follows. In 1977, and some other years, we see that strong year-classes can develop over broad areas of time and space. They develop in years when spawn deposition is normal, and sometimes even lower than normal. Further, sometimes they can be synchronous over broad areas of time and space. Synchrony may develop in other species. Retrospective analysis of herring scales indicates superior juvenile growth among strong cohorts, but decreased growth during older adult stages (in 1977). Strong year-classes can arise in years of normal or modest spawn deposition. These observations indicate that survival, between the egg and recruit stages, is enhanced. Such enhanced survival must occur during the juvenile stages that consume mainly copepods in nearshore habitats. Therefore strong year-classes may develop as a consequence of changes in these habitats.

If lower mortality of early life history stages is part of the explanation for the formation of the 1977 year-class - or other year classes, why did this happen? Presumably it must reflect decreases in mortality by starvation, disease or predation? In 1977, starvation seems unlikely, because juvenile growth was enhanced compared to other years. We have no evidence to suggest that disease routinely limits survival. Rather, outbreaks seem episodic, and this could explain years with exceptionally bad year-classes, but not the reverse. A decrease in predation, between the egg/larval stages and pre-recruit stage could occur if there were (i) fewer predators, or (ii) if the predators 'switched' or decreased predation on herring for a different prey species. Were predation rates on juvenile herring lower in 1977 and 1978? We have no data on this, but we observe that some common herring predators (lingcod and blackcod and some piscivorous salmon) also had strong 1977 year-classes. Therefore it seems improbable that there was a decrease in the potential community of herring predators between 1977 and 1980.

From the observations and reasoning above, we conclude that the most parsimonious explanation for the development of the strong 1977 year-class was a general decrease in predation of juveniles because the main herring predators had alternate prey. Such a reduction in predation could occur through predator switching during early life history stages - specifically, predators of herring chose to feed on an alternate food source. If this alternate food source was an unusually abundant supply of copepods, available both to the juveniles of herring and their predators, this could explain our observations. Specifically if predators preferentially switched to copepods, instead of herring juveniles, the consequence of a substantial increase in copepod availability would be both enhance survival and growth of juvenile herring.

If the cause(s) of the strong 1977 year-class was similar in all geographic areas where it occurred, from northern BC to the Bering Sea, and if the cause was from decreased predation associated with availability of an alternate food source, then clearly the factors which promoted this alternate food source were widespread. There have been

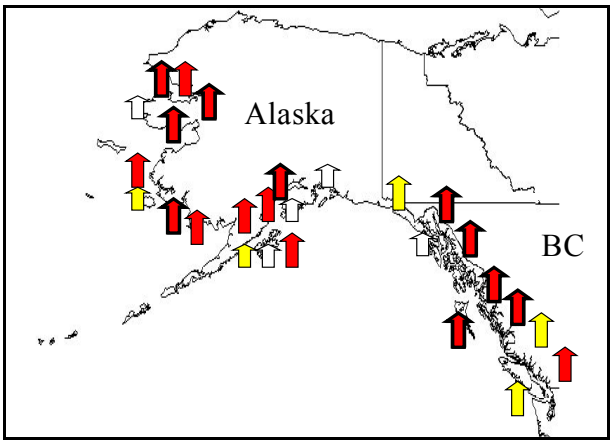

Fig. 2.3.1 Approximate locations of the strong 1977 year-class, indicated by arrows. Red arrows with dark outlines show locations where the 1977 year-class made up 70% or more of the spawning population as age 3 in 1980, or age 4 in 1981. Plain red and yellow arrows show populations where the 1977 year-class represented over 50% and 40% of the populations, respectively.

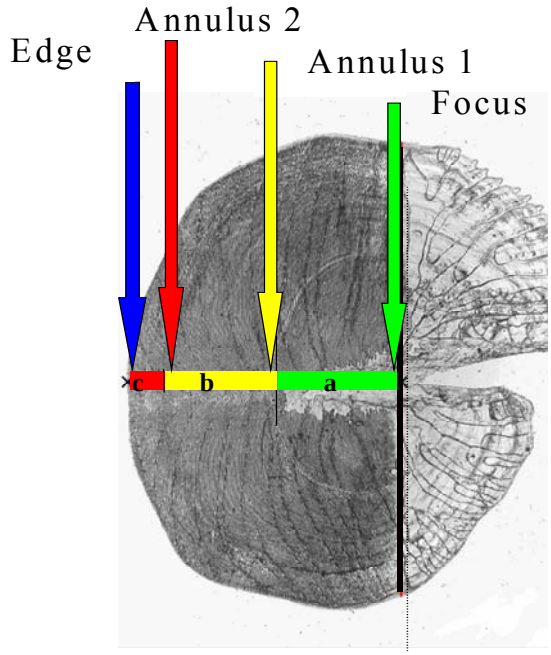

Fig. 2.3.2 A herring scale, showing the focus (start of growth) and the first and second annuli. Retrospective indices of age-specific growth rates during the first year (green bar a) and second year (yellow bar b) was determined by direct measurement of scales.

some suggestions (Hollowed and Wooster 1992; Polovina *et al.* 1995) that there can be such linkages between offshore oceanographic changes and changes in productivity or food abundance on shelf and inshore waters, resulting from mid-gyre changes, but these are not well understood. If there were such a relationship, the impact of an

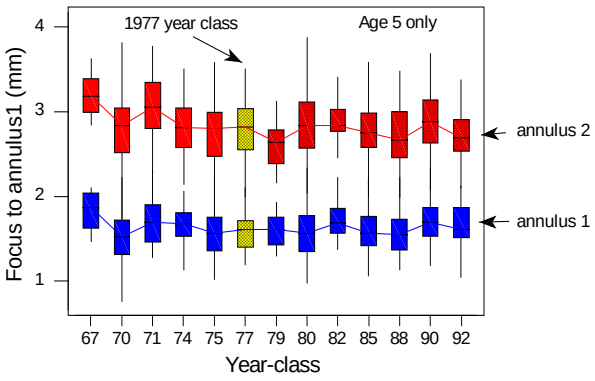

Fig. 2.3.3 Retrospective analyses of scale growth of 5-year-old-herring from archived collections of scales from northern BC. Scale growth, corresponding to juveniles at age 1 (blue rectangles) and age 2 (red rectangles), as estimated from comparison of focus: annuli distances, was normal in the 1977 year-class. The 1977 year-class is shown in yellow. The boxes and vertical lines represent the range and 95% confidence limits about the mean.

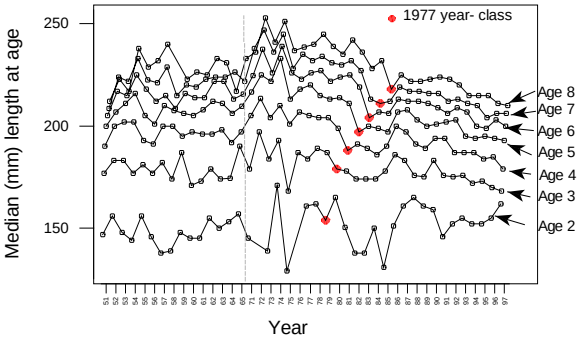

Fig. 2.3.4 Comparison of the size-at-age of the 1977 year-class with those of other years from catch sampling data collected in northern BC. The 1977 year-class (large dark circles) was normal (or slightly larger than normal at age 2). Thereafter, the relative size-at-age, relative to previous year-classes, decreased until age 8.

abundant production of zooplantion, specifically copepods, could explain both enhanced growth and year-class survival in herring and other species. There is a precedent for assuming that an abundant source of an alternate zooplankton prey species can reduce predation on herring. Ware and McFarlane (1995) showed that increased euphausiid production resulted in a decreased hake predation on adult herring off the west coast of Vancouver Island. Similar mechanisms mightoperate at the juvenile stages, so factors promoting a strong year-class of herring might also support strong year-classes of other species, leading to synchrony between unrelated species such as such as blackcod and lingcod. Again, the answer is a tentative yes. Both of these species have early life stages (first several years of life) in nearshore waters.

2.4 Review for Pacific saury (*Cololabis saira*) study under the VENFISH project

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VENFISH (Comprehensive study of the Variation of the oceanic ENvironment and FISH populations in the northwestern Pacific) project was started in April 1997 and will end in March 2002. This project has been supported by Japan Agriculture Forest Fisheries Agency. The aim of this project is clarification of bottom-up control process for Pacific saury and walleye pollock in the Northwestern Pacific. More than 20 scientists from National Fisheries Research Centers at Hokkaido, Tohoku, Yokohama and Shimizu, and Hokkaido University and Tohoku University joined this project.

The VENFISH team is composed of 5 teams and there are primary production, zooplankton and fish teams. The fish team is composed of Pacific saury and walleye pollock groups. Between these three teams there is a plankton ecosystem model team and a fish population model team. In this report we will note our studies of saury, which is only one portion of this project.

The main target area of the VENFISH project is east of 160ºE in the northwestern Pacific, and in that region there is a warm Kuroshio current and a cold Oyashio current. Between these two western boundary currents, there is a mixed water region, and in that area many eddies are detached from the Kuroshio and Oyashio and make very complicated environments. The saury spawning starts in the mixed water region in autumn, moves to the Kuroshio area in winter, and moves back to the mixed water region in spring (Fig. 2.4.1) (Odate 1977; Watanabe and Lo 1989; Watanabe *et al.* 1997). Juveniles are advected to the Kuroshio extension region, then grow and migrate to the Oyashio region through the mixed water region for feeding. After sufficient feeding they migrate back to the Kuroshio region for spawning. On the southward migration, they are fished in the Japanese coastal zone. We will briefly report the new findings for Pacific saury in the later sections.

Feeding habitat

The feeding habitat of Pacific saury (*Cololabis saira*) changes according to the life stage and the location. Larvae smaller than 15 mm mainly feeds on *Oncea* and *Oitona* sp. (Nakata and Koyama 2002), whereas larvae and juvenile larger than 15 mm prefer *Calanus* sp. Young saury which migrate to the mixed water region mainly feed on *Euphausia pacifica*. In the Oyashio region they feed mainly on *Euphausia pacifica* and *Neocalanus cristatus* and the ration becomes the

maximum in this season. On the way of their backward migration, they feed *Euphausia pacifica* and *Sagitta elegans*, but the ration decreases to the minimum. In the spawning area they feed on calanoid copepods and the ration is higher than in autumn (Sugisaki and Kurita, in preparation; Kurita and Sugisaki, in preparation).

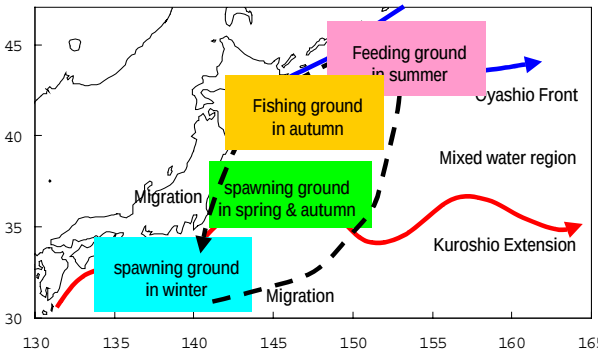

Fig. 2.4.1 Schematic picture of Pacific saury (*Cololabis saira*) life history. Spawning starts in September and continues until June, shifting location from the mixed water region and Kuroshio region. The main spawning season is winter. Juveniles are advected to the Kuroshio extension region and migrate to the Oyashio region through the mixed region for feeding. After sufficient feeding they migrate back to the Kuroshio region for spawning. On the southward migration, they are fished in the Japanese coastal zone.

Spawning density

Kurita and Sugisaki (in preparation) surveyed the seasonal change of the saury distribution and the ratio of mature stage in the three regions. In early autumn, half of the saury occur in the Oyashio region and they are immature. In winter almost all of the saury are in the Kuroshio and they are mature. In spring, half of the saury exist in the Kuroshio and most of them are mature. But the other half occurs in the mixed water region and only about 70% of them are mature. These results show that the most important area is the Kuroshio region and the most important season is winter for the saury spawning.

Kurita and Sugisaki (in preparation) estimated the spawning interval and batch fecundity. Using these values and ratio of mature saury to the total, they estimated the spawning density for each season. Their result showed that the most important season for spawning is winter.

Larvae and juvenile

Many studies have been done about larval and juvenile saury (Watanabe *et al.* 1997; Oozeki and Watanabe 2000; Oozeki and Watanabe, in preparation). Using widely sampled field data, Watanabe *et al.* (1997) and Oozeki and Watanabe (2000) estimated the production of hatched larvae in each season since 1990 to 1997. The average value for 8 years showed the highest value in autumn and the lowest value in spring. They also estimated the growth rate and mortality of larvae and production of juveniles. Growth rate showed a maximum in autumn and a minimum in spring. Mortality was highest in autumn and lowest in spring. As a result, the production of surviving juveniles showed a maximum in spring and a minimum in autumn. But the fluctuation of juvenile production in spring is very high and stable in winter. Watanabe *et al.* (1997) suggested that the stable winter juvenile might contribute to stable recruitment and middle size saury landings in autumn. Also Watanabe and Lo (1989) pointed out that winter was the most active spawning season using larval catch data during 1973-1986.

Oozeki and Watanabe (2000) conducted laboratory incubation experiments on saury eggs. They reared same age larvae at three different temperatures and observed growth rate. This was done for three different age larvae (9, 20, 30 days) and the dependency of growth rate on age was also tested. The result showed that the growth rate increased linearly with temperature and also increased with age. Analysis of the otolith increment and the knob length of the larvae showed the possibility of the estimation of growth rate of saury juveniles from the otolith field data. Then, they estimated the instantaneous growth rate from otolith field data and analyzed the relationship between the recent growth rate and oceanic environments (Oozeki and Watanabe: in preparation). Their result showed that the SST and food density affected larval growth during the early stages, and SST and chlorophyll become more important in the later stage.

Growth rate of adults

Suyama *et al.* (in preparation) analyzed the presence of a hyaline zone in the otoliths of Pacific saury. Usually the size decomposition is done by knob length, but sometimes it is difficult to divide them only from body length information. On the other hand, the otoliths of large size saury have the hyaline zone whereas the small and middle sizes do not. They analyzed the existence the hyaline zone and found out that the large and middle size cohort can be decomposed by the boundary of 50% existence ration of hyaline zone. Using this definition they decomposed the large and middle cohort and analyzed the inter-annual variability in the growth of each cohort. The middle size fluctuated between 264 and 286 mm, and the large size fluctuated between 303 and 314 mm, and the fluctuation was larger in the middle size.

For example, the growth increment of the large and middle cohort from July to November 1999, was 11.3 and 19.3 mm respectively. On the other hand, they increased to 12.5 and 31.3 mm respectively in 2000. This result suggests that the growth rate of the large size cohort is more stably estimated compared to the middle size cohort.

Growth rate between juvenile and large size

Using the hyaline zone information from the otolith it is possible to estimate the growth rate of young and adult saury, but the growth rate between juvenile and young saury is very difficult to estimate because of the existence of the hyaline zone. We cannot count the increment of the otolith because the increment is unclear in the hyaline zone. So, we cannot determine the age of adult saury.

For this problem, Kurita (personal communication) developed a new method to estimate the hatch date from the age at which the otolith increment width reached a second maximum. It became possible to estimate the age of saury using this method even if there is a hyaline zone. He estimated the hatch date of the large size saury and developed a new scenario of the life history of Pacific saury combined with the information of the growth of the saury with no hyaline zone. According to his scenario, saury which are born in the earlier season spawn in the first winter and also in the second winter. But the later spawned saury do not spawn in the first year and spawn in the second year.

Energy for migration and spawning

Kurita (personal communication) analyzed seasonal variation of lipid and protein content in 30 cm knob length saury. The protein content did not vary much but lipid variation showed very large variability. The average lipid content is about 40 g in summer. In winter, which is the active spawning season, mature saury contained little neutral lipid. Moreover, protein seemed to be utilized as energy sources because the sum of protein and water content was constant. From this result he concluded that saury need to feed in order to spawn eggs in the Kuroshio region.

Thus, the environment may be very important for the saury reproduction in the Kuroshio region. From the energy balance between the food nutrient and egg production, he estimated that about 35.6% of total assimilated energy was used for winter egg production in the Kuroshio.

Population dynamics model for Pacific saury

Tian *et al*. (2002b) analyzed the interannual variability of the saury stock using a population dynamics model. In his model there are two cohorts. One is a cohort spawned during autumn - winter and the other is spawned during winter - spring. The life span of the saury was assumed to be two years, and as a result the large size saury included both cohorts. The governing equations were growth rate, population, fishing effort and reproduction equations. In the population dynamics the mortality included environmental effects. As environment factors they adapted SST in the Kuroshio Extension zone (KE SST) and SOI (Southern Oscillation Index) according to the result of Tian *et al*. (2000a).

The results showed that the effect of KE SST was important to the longer-period variability, and the SOI effect was important to both the longer-period and inter-annual variability.

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

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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^{-1}).

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^{-1}; C_i is the concentration of concrete substratum, mg/l; K_m 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_m. 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,

nitrates, phosphates, silicates) 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) $UP = K(T, L) / (1 + K_m / C_i)$

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

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) $PoolF_N = d(1) * NH4 + d(2) * NO2 + d(3) * NO3$

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

or

(2.5.6a) $UP_{FN} = K(T, L) / (1 + B_N / (d(1)*NH4 + d(2)*NO2 + d(3)*NO3))$

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) $UP_{FN} = UP_{NH4} + UP_{NO2} + UP_{NO3}$

Let us write down the equations, which describe the consumptions of individual substrates (NH_4, NO_2 and NO_3) 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) $UP_{NH4} = K(T, L) * d(1) * NH4 / (PoolF_N + B_N)$

(2.5.9) $UP_{NO2} = K(T, L) * d(2) * NO2 / (PoolF_N + B_N)$

(2.5.10) $UP_{NO3} = K(T, L) * d(3) * NO3 / (PoolF_N + B_N)$

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

Here B_P is the biomass in units of P, mg P/l; $PoolF_p$ - 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) $PoolF_p = d(4)*DIP + d(5)*DOP$

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) $UP_{FN} = UP_{NH4} + UP_{NO2} + UP_{NO3}$

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

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) $UP_{NH4} = K(T, L) * d(1) * NH4 / MF$

(2.5.16) $UP_{NO2} = K(T, L) * d(2) * NO2 / MF$

(2.5.17) $UP_{NO3} = K(T, L) * d(3) * NO3 / MF$

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

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

where

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

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

where

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

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) $UP_{NH4} = K(T, L) * d(1) * NH4 / MF1$

(2.5.24) $UP_{NO2} = K(T, L) * d(2) * NO2 / MF1$

(2.5.25) $UP_{NO3} = K(T, L) * d(3) * NO3 / MF1$

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

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

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

where

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

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 (α) from the UP function:

(2.5.30) $L = \alpha * UP$

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

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

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

First phytoplankton group (F1-diatom algae) Maximum growth rate: K=2.5 *Preference coefficients for substrate uptake:* for Si-containing substrate: d_{DOSi}=0.3; d_{DISi}=0.7 for N-containing substrate: d_{NH4}=0.025; $_{NO2}$=0.025 d_{NO3}=0.9; d_{UR}=0.05 for P-containing substrate: d_{DOP}=0.3; d_{DIP}=0.7 *Excretion activity:* for Si substrate: a_{Si}=0.051; b_{Si}=0.052 for N substrate: a_N=0.05; b_N=0.053 for P substrate: a_P=0.05; b_P=0.065 *Mortality coefficients:* for Si substrate: $g(1)_{Si}$=0.0; $g(2)_{Si}$=0.08 for N substrate: $g(1)_N$=0.0; $g(2)_N$=0.02 for P substrate: $g(1)_P$=0.0; $g(2)_P$=0.02	**First phytoplankton group (F1-diatom algae)** Maximum growth rate: K=2.5 *Preference coefficients for substrate uptake:* for Si-containing substrate: d_{DOSi}=0.3; d_{DISi}=0.7 for N-containing substrate: d_{NH4}=0.2; d_{NO2}=0.05 d_{NO3}=0.7; d_{UR}=0.05 for P-containing substrate: d_{DOP}=0.05; d_{DIP}=0.95 *Excretion activity:* for Si substrate: a_{Si}=0.051; b_{Si}=0.052 for N substrate: a_N=0.05; b_N=0.052 for P substrate: a_P=0.05; b_P=0.055 *Mortality coefficients:* for Si substrate: $g(1)_{Si}$=0.04; $g(2)_{Si}$=0.03 for N substrate: $g(1)_N$=0.05; $g(2)_N$=0.049 for P substrate: $g(1)_P$=0.05; $g(2)_P$=0.07
Second phytoplankton group (F2-peridinium algae) Maximum growth rate: K=1.8 *Preference coefficients for substrate uptake:* for N-containing substrate: d_{NH4}=0.15; d_{NO2}=0.05 d_{NO3}=0.2; d_{UR}=0.6 for P-containing substrate: d_{DOP}=0.4; d_{DIP}=0.6 *Excretion activity:* for N substrate: a_N=0.049; b_N=0.0495 for P substrate: a_P=0.049; b_P=0.053 *Mortality coefficients:* for N substrate: $g(1)_N$=0.0; $g(2)_N$=0.05 for P substrate: $g(1)_P$=0.0; $g(2)_P$=0.1	**Second phytoplankton group (F2-green algae)** Maximum growth rate: K=2.5 *Preference coefficients for substrate uptake:* for N-containing substrate: d_{NH4}=0.2; d_{NO2}=0.05 d_{NO3}=0.7; d_{UR}=0.05 for P-containing substrate: d_{DOP}=0.05; d_{DIP}=0.95 *Excretion activity:* for N substrate: a_N=0.049; b_N=0.0495 for P substrate: a_P=0.049; b_P=0.052 *Mortality coefficients:* for N substrate: $g(1)_N$=0.04; $g(2)_N$=0.03 for P substrate: $g(1)_P$=0.04; $g(2)_P$=0.06
Third phytoplankton group (F3-green algae) Maximum growth rate: K=1.8 *Preference coefficients for substrate uptake:* for N-containing substrate: d_{NH4}=0.15; d_{NO2}=0.05 d_{NO3}=0.2; d_{UR}=0.6 for P-containing substrate: d_{DOP}=0.4; d_{DIP}=0.6 *Excretion activity:* for N substrate: a_N=0.049; b_N=0.0495 for P substrate: a_P=0.049; b_P=0.0523 *Mortality coefficients:* for N substrate: $g(1)_N$=0.0; $g(2)_N$=0.05 for P substrate: $g(1)_P$=0.0; $g(2)_P$=0.1	**Third phytoplankton group (F3-blue-green algae)** Maximum growth rate: K=2.5 *Preference coefficients for substrate uptake:* for N-containing substrate: d_{NH4}=0.2; d_{NO2}=0.05 d_{NO3}=0.7; d_{UR}=0.05 for P-containing substrate: d_{DOP}=0.05; d_{DIP}=0.95 *Excretion activity:* for N substrate: a_N=0.049; b_N=0.0495 for P substrate: a_P=0.049; b_P=0.052 *Mortality coefficients:* for N substrate: $g(1)_N$=0.04; $g(2)_N$=0.03 for P substrate: $g(1)_P$=0.04; $g(2)_P$=0.06
First zooplankton group (Z1-herbivorous) Maximum growth rate: K=1.5 *Preference coefficients for substrate uptake:* for Si-containing substrate: d_{DOSi}=0.15; d_{DISi}=0.02 d_{SiD}=0.77; d_{BSi}=0.01 d_{F1Si}=0.05 for N-containing substrate: d_{ND}=0.48; d_{F1N}=0.34 d_{F2N}=0.05; d_{F3N}=0.02	**First zooplankton group (Z1-herbivorous)** Maximum growth rate: K=0.75 *Preference coefficients for substrate uptake:* for Si-containing substrate: d_{DOSi}=0.15; d_{DISi}=0.02 d_{SiD}=0.77; d_{BSi}=0.01 d_{F1Si}=0.05 for N-containing substrate: d_{ND}=0.5; d_{F1N}=0.05 d_{F2N}=0.25; d_{F3N}=0.1

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; *Excretion activity:* 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 *Mortality coefficients:* 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 *Excretion activity:* 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 *Mortality coefficients:* 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
Second zooplankton group (Z2-predatory) Maximum growth rate: K=0.5 *Preference coefficients for substrate uptake:* 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 *Excretion activity:* for N substrate: a_N=0.0276; b_N=0.0287 for P substrate: a_P=0.0276; b_P=0.0287 *Mortality coefficients:* 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	**Second zooplankton group (Z2-predatory)** Maximum growth rate: K=0.75 *Preference coefficients for substrate uptake:* 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 *Excretion activity:* for N substrate: a_N=0.0276; b_N=0.03 for P substrate: a_P=0.0276; b_P=0.032 *Mortality coefficients:* 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 - day^{-1}, d_i, a_i, b_i - (undimension), $g(1)$ - day^{-1}, $g(2)_i$ - $[(mg\ Element/l)^{-1}\ (day^{-2})]$.

3.0 Herring group report and model results

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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

for consumption and cutoff temperature values, where swimming speed changes in the Rudstam model to describe the actual temperatures inhabited by Pacific herring, 2) accounting for known differences in larval and juvenile fish physiology (age-0) compared to adults, and 3) incorporating known seasonal changes in energy density of adult Pacific herring. Trends in size-at-age were discussed and potential hypotheses to be tested after completion of the model were proposed. In the application to Pacific herring our objectives were to model one fish, generate data to compare to observed size-at-age, follow one cohort through time, and provide a means to perform regional comparisons.

Temperature-dependence of consumption and swimming speed

Douglas Hay provided diet data for Pacific herring from near Vancouver, British Columbia, from which he and Robert Klumb tried to extract the temperature-dependence terms for the herring consumption equation. The original herring bioenergetics model was formulated for the Baltic Sea, but the Vancouver site has lower temperatures and less seasonal variation of temperature. Because temperature is one of the main process-mediating functions in the bioenergetics model, we had to modify the parameters for temperature dependence on consumption function to agree with the temperature ranges inhabited by Pacific herring off the coast of Vancouver. Vadim Navrotsky suggested that we formulate this temperature dependence in terms of DT = T - T_{opt} , where T_{opt} is the optimal temperature for consumption (depending upon location). One could also use the temperature of the waters in which the growth of herring is maximized as a proxy for the temperature at which their consumption rate is maximum (*e.g.*, 12°C, based on the data for peak growth versus abundance and temperature in Haist and Stocker (1985)).

As a preliminary approximation, Bernard Megrey normalized the Baltic Sea temperatures to a zero-one scale, based on the maximum and minimum temperatures observed for a location off the west coast of Vancouver Island, Amphitrite lighthouse (Fig. 3.1).

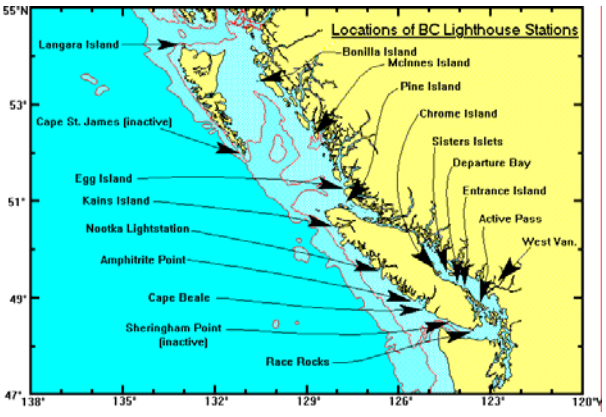

Fig. 3.1 Location of B.C. Lighthouse stations including Amphitrite Point Lighthouse, the source of the temperature data used in the model.

Values for the two temperature series were rescaled using the formula:

(3.1)

$$TA = \frac{(TB - TB_{\min}) \cdot (TA_{\max} - TA_{\min})}{(TB_{\max} - TB_{\min})} + TA_{\min}$$

where TB_{max}=30.0, TB_{min}=1.0, TA_{max}=14.0, TA_{min}=8.0, TA refers to temperatures from Amphitrite lighthouse, and TB refers to temperatures from the Baltic Sea.

The re-scaled temperatures used for the Thornton and Lessem (1978) temperature dependence function for consumption were as follows:

Age 0		**Age 1**		**Age > 1**	
Amphitrite	Baltic	Amphitrite	Baltic	Amphitrite	Baltic
8.0	1	8.0	1	8.0	1
10.897	15	10.897	15	10.483	13
11.31	17	11.31	17	10.897	15
12.552	23	12.552	23	12.553	23

Temperatures in the respiration model, where activity changed needed to be re-computed for age-0 and age-1 herring:

Old	▶	New
15°C		10.897°C
9°C		9.655°C

Finally the equation describing the annual temperature signal needed to be re-computed based on observed mean monthly sea surface temperature (SST) data from Amphitrite lighthouse. The following equation

(3.2)

$$T = 7.717 + \left(5.6796 \cdot 0.5 \cdot \left(1 - \cos\left(\frac{2 \cdot \pi \cdot (JDAY - 30)}{365} \right) \right) \right)$$

was fit to the observed data (Fig 3.2) where JDAY is Julian day and T is water temperature.

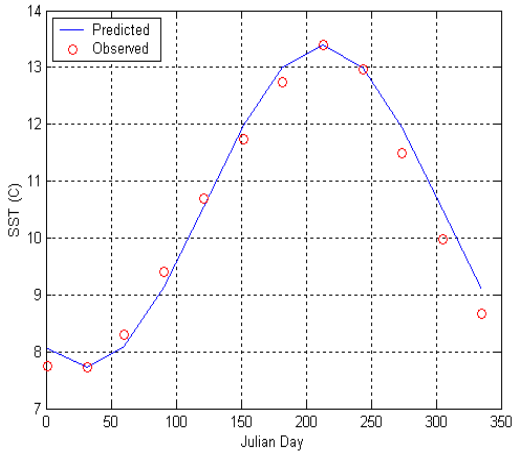

Fig. 3.2 Observed and predicted mean SST at Amphitrite Lighthouse.

Validation to Pacific herring

To validate the bioenergetics model to herring, we used model structure and parameters after Rudstam (1988) for Baltic Sea herring, but included no young-of-the-year (YOY) dynamics, no multispecies functional response, and no spawning (Rudstam model has spawning).

Results of the model (Fig 3.4) can be compared to the Rudstam results (Fig. 3.3) and good agreement in dynamical behavior can be noted.

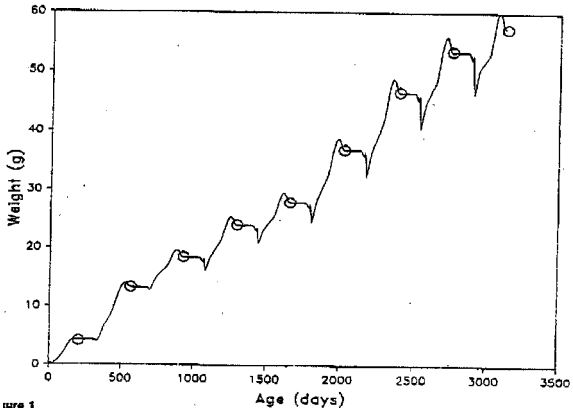

Fig. 3.3 Results of the Baltic Sea herring model from Rudstam (1988). The solid line represents model output and the open circles are weight-at-age values from field observations.

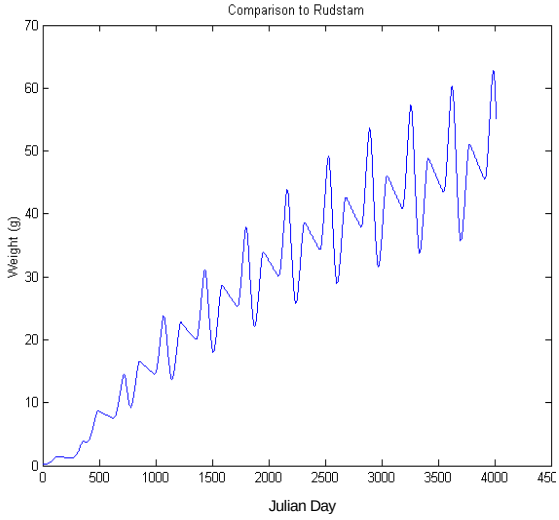

Fig. 3.4 Simulated growth from the herring bioenergetics model.

Separate age 0 and adult formulations

Describing the growth of a YOY fish involves more than just rescaling process equations derived for adult fishes. Often the process rates differ substantially between different life stages (Post and Lee 1996). Cisco Werner and Rob Klumb modified the Atlantic herring bioenergetics model for age-0 herring. Rob's parameters for respiration were based on his laboratory measurements from age-0 alewife, another clupeid, which used routine metabolism without an activity multiplier. Literature values for larval and juvenile clupeids

were also used that lowered SDA, egestion, and excretion parameters compared to the adult Atlantic herring parameters.

The YOY formulation for herring respiration proposed by Arrhenius (1998) along with our conversion factor from wet weight (g) to energy (J) was:

(3.5) $R = a_R \cdot W^{b_R} \cdot f_R(T) \cdot activity \cdot 5.258$

where the units are the same as in equation 2.1.5 and $a_{R=}$ 0.0033, b_R = -0.227.

The temperature dependence function for respiration

(3.6) $f_R(T) = e^{(c_R \cdot T)}$

for a age-0 herring was similar to equation 2.1.8.

Activity is a power function of body weight conditioned on water temperature and is given by

(3.7) $activity = e^{(d_R \cdot U)}$

where U is swimming speed in cm·s^{-1} and d_R is a coefficient relating swimming speed to metabolism. Swimming speed is calculated as a function of body weight and temperature using

(3.8) $U = a_A \cdot W^{b_A} \cdot e^{(c_A \cdot T)}$

Swimming speeds have been observed to switch from temperature dependence (at low temperatures) to temperature independence (at high temperatures). Formulations by life stage for changes in swimming speeds versus the adjusted temperatures from temperature-dependence of consumption and swimming speed section (given earlier) were:

if age=0 and T ≤10.897 °C then
$a_{R=}$ 0.0033, b_R = -0.227, $c_{R=}$ 0.0548,
$a_{A=}$ 5.76, b_A = 0.386, c_A=0.238 and d_R=0.03

if age=0 and T >10.897 °C then
$a_{R=}$ 0.0033, b_R = -0.227, $c_{R=}$ 0.0548, $a_{A=}$ 8.6,
b_A = 0.386, c_A=0.0 and d_R=0.03

if age≥=1 and T ≤9.655 °C then
$a_{R=}$ 0.0033, b_R = -0.227, $c_{R=}$ 0.0548, $a_{A=}$ 3.9,
b_A = 0.13, c_A=0.149 and d_R=0.03

if age≥=1 and T >9.655 °C then
$a_{R=}$ 0.0033, b_R = -0.227 $c_{R=}$ 0.0548, $a_{A=}$ 15.0,
b_A = 0.13, c_A=0.0 and d_R=0.03

In the final set of simulations, the Arrhenius (1998) equations 3.5 and 3.6 were modified after Klumb *et al.* (in press) to use the parameters.

if age=0 then
$a_{R=}$ 0.00528, b_R = -0.007, $c_{R=}$ 0.0548, $a_{A=}$ 1.0,
b_A = 0.0, c_A=0.0 and d_R=0.0.

In all simulations, equations for age 1 and older Pacific herring were the same as described in Arrhenius (1998).

The coefficients of SDA, egestion, and excretion in equations 2.1.6, 2.1.11, and 2.1.12 were made age dependent with the parameters given in Table 3.1.

Formulation for energy density

The energy density of clupeids varies seasonally. Instead of using constant conversion factors, as in equation 2.1.1, we incorporated a simple energy cycle based on data in Paul *et al.* (1998) for age-2 and greater herring. Paul *et al.* (1998) found energy density peaked at 9800 J/g wet wt. (range 9400 - 10200) in fall (October 1), and in spring (March 1) dropped to 5750 J/g wet wt. (range 5200 - 6300). For age-0 and age-1 herring we assumed a constant energy density of 4460 J/g wet wt. (Foy and Paul 1999). Age-0 herring do exhibit a seasonal energy cycle from 5000 J/g wet wt. in November to 3900 J/g wet wt. in March, and could be included in future modifications of the model.

The following code was used to implement a straight-line approximation to a sinusoid that described seasonal changes in energy density. The period between March 1 and October 1 consisted of 214 days. The period prior to March 1 and the period after October 1, together summed to 151 days.

Table 3.1 Summary of final parameter values used in the herring bioenergetics model.

Symbol	Parameter description		Value		
Consumption, C_{MAX}					
a_C	Intercept for C_{MAX} at		0.642		
b_C	coefficient for C_{MAX} versus weight	-0.256			
te1	Temperature for xk1 (in ºC)		8.0[a]	8.0[b]	8.0[c]
te2	Temperature for xk2 (in ºC)		10.897[a]	10.897[b]	10.483[c]
te3	Temperature for xk3 (in ºC)		11.310[a]	11.310[b]	10.897[c]
te4	Temperature for xk4 (in ºC)		12.552[a]	12.966[b]	12.552[c]
xk1	Proportion of C_{MAX} at te1	0.10			
xk2	Proportion of C_{MAX} at te2	0.98			
xk3	Proportion of C_{MAX} at te3	0.98			
xk4	Proportion of C_{MAX} at te4	0.01			
Metabolism, R					
a_R	Intercept for R		0.00528[a]	0.0033[bc]	
b_R	Coefficient for R versus weight		-0.007[a]	-0.227[bc]	
c_R	Coefficient for R versus temperature		0.083[a]	0.0548[bc]	
d_R	Coefficient for R versus swimming speed	0.0[a]	0.03[bc]		
S	Coefficient for Specific Dynamic Action	0.125[a]	0.175[b]	0.175[c]	
Swimming Speed, U					
a_A	Intercept U (< 9.655 ºC) (in cm/s)	3.9[bc]			
a_A	Intercept U (≥9.655 ºC) (in cm/s)	15.0[bc]			
b_A	Coefficient U versus weight		0.13[bc]		
c_A	Coefficient U versus temperature (<9.655 ºC)		0.149[bc]		
c_A	Coefficient U versus temperature (≥9.655 ºC)	0.0[bc]			
Egestion and Excretion, F and E					
a_F	Proportion of consumed food egested		0.125[a]	0.16[bc]	
a_E	Proportion of consumed food excreted		0.078[a]	0.10[bc]	
Multispecies Functional Response					
V_{11}	Vulnerability of prey group 1 to predator 1	1.0			
V_{12}	Vulnerability of prey group 2 to predator 1	1.0			
V_{13}	Vulnerability of prey group 3 to predator 1	1.0			
K_{11}	Half saturation constant for prey group 1 to predator 1 (g wet weight/m^3)		750.0		
K_{12}	Half saturation constant for prey group 2 to predator 1 (g wet weight/m^3)		75.0		
K_{13}	Half saturation constant for prey group 3 to predator 1 (g wet weight/m^3)		750.0		

a - values for age-0 herring, b - values for age-1 herring, c - values for age-2 and older herring

```
if(iage.ge.2)then
      enMar1=5750.
      jdMar1=60
      enOct1=9800.
      jdOct1=274
if(jjday.lt.60)then
      delen=(enMar1-enOct1)/151
      en=enOct1+(90+jjday)*delen
end if
if(jjday.ge.60.and.jjday.lt.274)then
      delen=(enOct1-enMar1)/(jdOct1-jdMar1)
      en=enMar1+(jjday-jdMar1)*delen
end if
if(jjday.ge.274)then
      delen=(enMar1-enOct1)/151
      en=enOct1+(jjday-jdOct1)*delen
end if
else
      en=4460.
end if
```

Figure 3.9 shows the straight line approximation to seasonal energy density. Forcing prey fields are given in Figure 2.1.7.

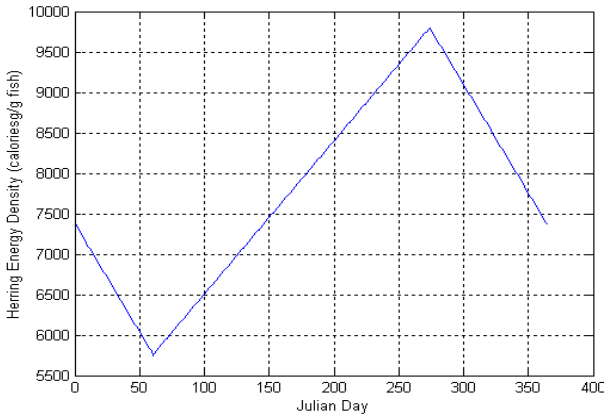

Fig. 3.9 Straight line approximation to a seasonal energy density curve.

Simulation results and final modifications to the herring model

The base model included YOY processes, included no multi-species functional response and provided a comparison of observed and predicted size-at-age, and included no spawning (observed data were taken after feeding but before spawning). Figures 3.10 to 3.12 show the fit of observed size (weight)-at-age compared to size-at -age predicted by the herring bioenergetics model by adjusting the "p" parameter of equation 2.1.2.

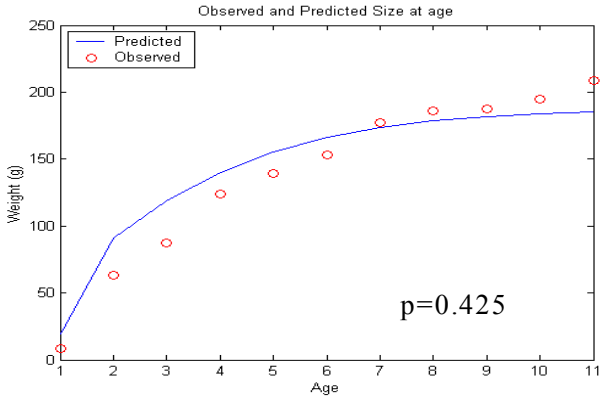

Fig. 3.10 Observed size-at-age of the 1973 herring year-class and size-at-age predicted from the herring bioenergetics model using p=0.425.

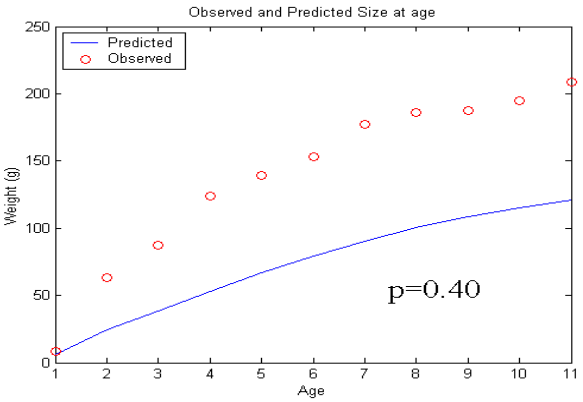

Fig. 3.11 Observed size-at-age of the 1973 herring year-class and size-at-age predicted from the herring bioenergetics model using p=0.40.

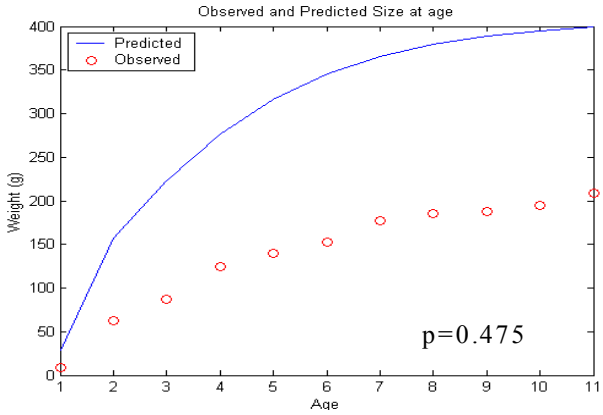

Fig. 3.12 Observed size-at-age of the 1973 herring year-class and size-at-age predicted from the herring bioenergetics model using p=0.475.

Observed herring size-at-age data were taken from the Straight of Georgia herring data using the 1973 age class, seen as age-1 in 1973 and present in the fishery until age 12 in 1984. As can be seen from these figures the model predictions of size-at-age were extremely sensitive to changing this parameter, the best fit being when p=0.425. A long-term simulation with these parameters is shown in Figure 3.13.

The base case was modified to include YOY improvements, age specific rates, multispecies functional response, location specific temperature description and change of temperature curve parameters, re-adjustment of p and k's to temperature change, and seasonal and age dependent energy density for fish.

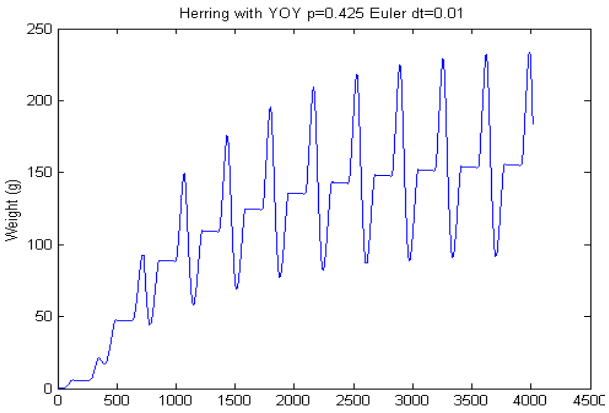

Fig. 3.13 Example of a long-term simulation of herring growth using tuned model parameters.

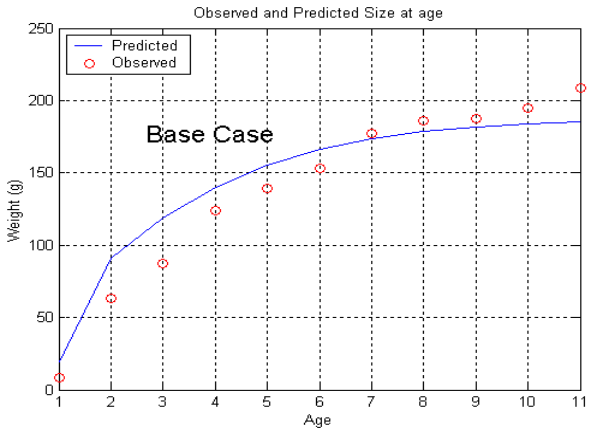

Fig. 3.14 Comparison of observed and predicted size-at-age, base case.

Figure 3.14 shows the base case. Figure 3.15 shows the base curve plotted against a run where the SDA, E and F equations were made age dependent. Age dependent parameters are given in Table 3.1. Also plotted in Figure 3.15 are model predictions when modifying the respiration equation to more accurately reflect the metabolic requirements of an age-0 herring (R) (Klumb *et al.* In review). The final curve in Figure 3.15 (All) demonstrates model output when all of these features were activated.

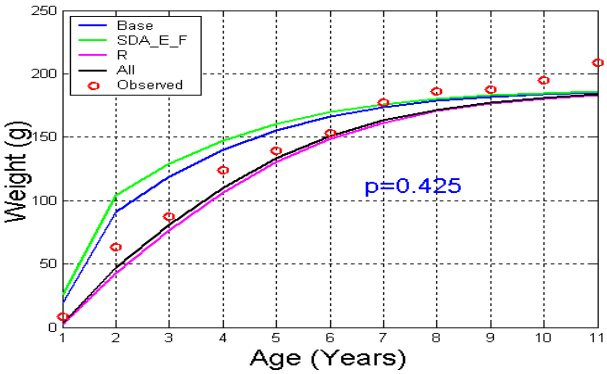

Fig. 3.15 YOY sensitivity. Observed and predicted size-at-age due to implementing age specific formulation for Specific Dynamic Action, egestion, excretion, respiration one at a time. The "all" line represents the run where all processes are age dependent and compared to the base run.

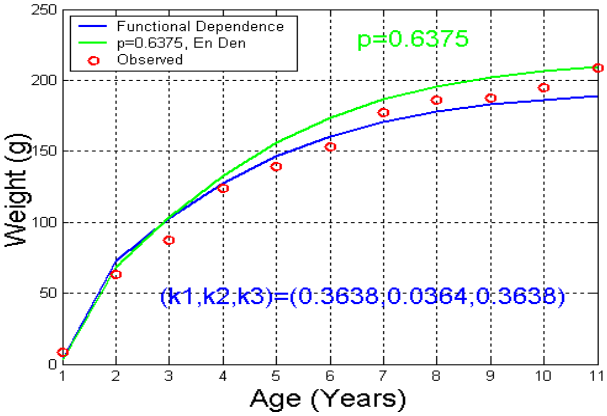

Fig. 3.16 Simulation run incorporating new temperature dependent values (seasonal range 8-14ºC) and the seasonal herring energy density algorithm. Comparisons are made of observed size-at-age between adjusting little "p" in equation 2.1.2 and using the multispecies functional dependence function (equations 2.1.13 and 2.1.14) with the k values as described above.

Finally, Figure 3.16 demonstrates results of the customized herring model for a p value of 0.6375, and for a run where the multispecies functional response to three prey types was activated using the parameters (k1, k2 and k3) shown in Figure 3.16, as well as the seasonal energy density algoritm. Note that to implement the multispecies functional response feature the line "con=0.75*gcmax" in the FORTRAN code needs to be commented out.

Trends in size-at-age: some ideas for hypothesis testing

Douglas Hay has data for size-at-age of Pacific herring over several decades. Over the last 20 years, the mean size-at-age has decreased at several locations for fish aged greater than 3 years. However, the mean size-at-age for ages 1–3 years did not show a significant decrease which may result from difficulties in sampling small fish (*i.e.* gear selectivity). In agreement to the observed size-at-age data, measurements from scale annuli collected over the same period from larger herring also showed no consistent decrease in growth for fish during the first 3 years of life. This decrease in size-at-age first appears when herring can begin to eat euphausiids in addition to copepods (age 3+). Generally, when euphausiids are abundant, the predation on herring by other piscivores that also eat euphausiids is reduced. Given this double benefit of more available food and less predation, the growth of herring should be highly sensitive to euphausiid production. The predatory zooplankton (ZP) compartment in the NEMURO model was designed to represent euphausiids.

Thus the coupled NEMURO-herring bioenergetics model could be used to examine the effects of temperature and other physical forcings (*e.g.*, Pacific Decadal Oscillation) on the production of euphausiids and thereby on the size-at-age of herring.

4.0 Saury group report and model results

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The members of "team saury" were D. Huang, C. Hong, Y. I. Zuenko, T. Katukawa, T. Azumaya, S. Chiba, M. Fujii, M. J. Kishi, K. Tadokoro, M. B. Kashiwai, Y. Yamanaka, T. Okunishi, A. Tsuda, D. Mukai, M. Inada, T. Aiki and S. Ito.

According to the life history of Pacific saury, S. Ito proposed to have saury bioenergetics model coupled with the ecosystem model composed of a three- ocean-box model which corresponds to Kuroshio, Oyashio, and the mixed water region. But the three-box model is a little complicated to start with. As a first step we started from a coupled saury bioenergetics-ecosystem model with one box, and adapted the same type of governing equations for bioenergetics model as the ones for Pacific herring.

Model parameters are discussed for applying the model to Pacific saury. Here we report the discussion summary and model results.

Life history stages

Pacific saury are spawned in the Kuroshio and the mixed water region from autumn to spring. The larvae are advected to the Kuroshio extension region and juveniles migrate to the Oyashio region

through the mixed water region. After sufficient feeding in the Oyashio region, they migrate back to the spawning region. The swimming activity, feeding habitat and metabolism are different according to the life history stages. Odate (1977) and Kosaka (2000) divided the Pacific saury life history stages according to knob length (KL) (Table 4.1).

Table 4.1 Life stages of Pacific saury after Odate (1977).

Stage	Knob length
larvae	< 2.5 cm
juvenile	2.5 - 5.9 cm
earlier young	6.0 - 9.9 cm
later young	10.0 - 14.9 cm
small	15.0 - 19.9 cm
adult	> 20.0 cm

About the earlier stage growth, Watanabe and Kuji (1991) reared the saury larvae from hatching and they showed that it takes 60 days to grow to 79 mm KL. Watanabe *et al.* (1988) analyzed the growth rate of Pacific saury and they showed that it takes about 100 days to grow to 100 mm KL. According to their result, it takes about 180 days to become adult saury. Suyama *et al.* (1996) showed lower growth rate and it takes about 200 days to become an adult. For simplicity, only three life stages are assumed in the saury bioenergetics model (Table 4.2).

Table 4.2 Life stages of Pacific saury in the saruy bioenergetics model.

Stage	Age
larvae and juvenile	< 60 days
young and premature	60-180 days
adult	> 180 days

Maximum consumption rate C_{MAX}

Because adult Pacific saury are too difficult to rear in laboratories, there is no experimental estimation of consumption rate. Field data showed the average ration of the Pacific saury are 5.0 gww/day/individual for 20 cm, 7.2 gww/day/individual for 26 cm, and 10.2 gww/day/individual for 30 cm saury (Kurita and Sugisaki; in preparation). These data were estimated in the Oyashio region. Comparing this with observational data, we adapted 0.6 for a_c and -0.256 for b_c parameters. Figure 4.1 shows the C_{MAX} curve and observational value of ration per unit wet weight of the Pacific saury.

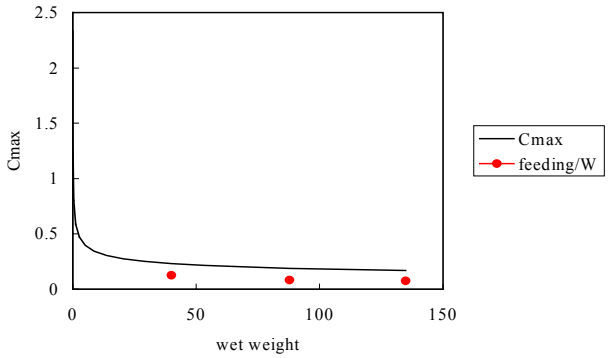

Fig. 4.1 C_{MAX} curve and observational value of ration per unit wet weight of the Pacific saury.

Temperature dependency for C_{MAX}

Oozeki (in preparation) analyzed the relationship between saury growth rate and environmental factors using the same field data reported in Watanabe *et al.* (1997). His result showed positive contributions from surface temperature and food density to growth rate. The SST range was between 16-22°C. Oozeki and Watanabe (2000) reared Pacific saury in the laboratory with different water temperatures and found a strong dependence of growth rate on temperature. The temperature range was between 12-24°C.

For adult saury we have no measures of growth rate at different temperatures. But the habitat temperature is between 16 and 20°C. We adapted the following values for the temperature dependency parameters for C_{MAX} of Pacific saury (Table 4.3). Figure 4.2 shows the temperature dependence function for each stage.

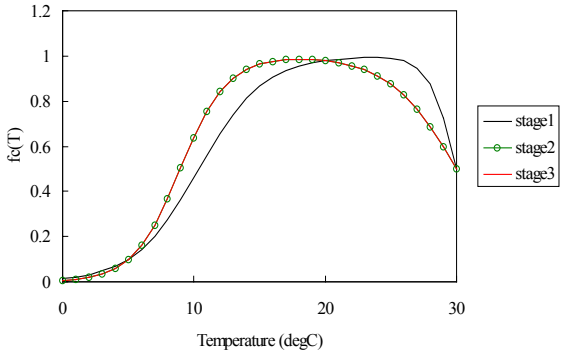

Fig. 4.2 Temperature dependence function of consumption rate of Pacific saury for each life stage.

Table 4.3 Temperature dependency parameters for C_{MAX}.

		Stage 1	Stage 2	Stage 3
te1	Temperature for xk1 (in ºC)	5	5	5
te2	Temperature for xk2 (in ºC)	20	16	16
te3	Temperature for xk3 (in ºC)	26	20	20
te4	Temperature for xk4 (in ºC)	30	30	30
xk1	Proportion of C_{MAX} at te1		0.10	
xk2	Proportion of C_{MAX} at te2		0.98	
xk3	Proportion of C_{MAX} at te3		0.98	
xk4	Proportion of C_{MAX} at te4		0.5	

Swimming speed

Although we do not have actual data on swimming speed of Pacific saury, other small pelagic fish swim at speeds of several times their body length per second. We assumed the normal swimming speed is two times of the knob length (nearly same as body length) per weight (Fig. 4.3).

$$U = 2.0\ KL$$

On the other hand, the wet weight (g)-knob length (cm) relation was proposed by Kosaka (2000) as:

larvae and juvenile
$\log W = -2.069 + 2.42439 \log L$
earlier young
$\log W = -2.483 + 3.06174 \log L$
later young
$\log W = -2.335 + 2.93760 \log L$
small
$\log W = -2.688 + 3.22526 \log L$
adult
$\log W = -2.685 + 3.21229 \log L$

Figure 4.4 shows the wet weight-knob length relation curves of Kosaka (2000). If we adapt the simple one curve for all stages, it becomes

$$W = (KL / 6.13)^3$$

and the curve will look like Figure 4.4. The broken line in Figure 4.3 shows the same curve.

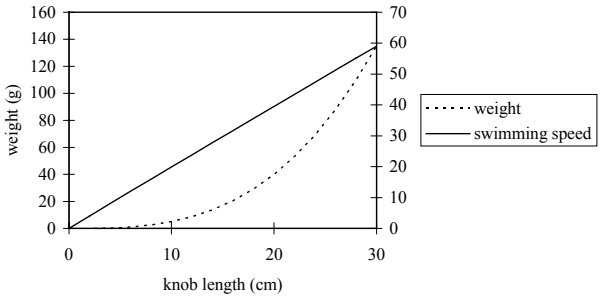

Fig. 4.3 Swimming speed (cm/s) and wet weight (g) as a function of body length (cm).

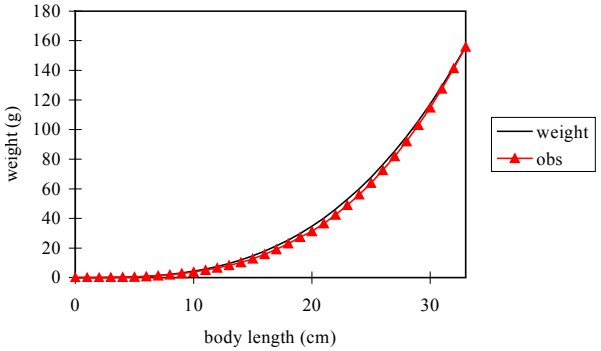

Fig. 4.4 Wet weight (g)-knob length (cm) relation curves of Kosaka (2000) (red) and fitting curve (black).

The last equation could be rewritten as

$$KL = 6.13\ W^{0.33}$$

and the swimming speed becomes

$$U = 12.3\ W^{0.33}$$

and we adapted 12.3 as a_A parameter when the temperature is higher than 12°C and 0.33 for b_A value. For temperatures less than 12°C we adapted 2.0 as a_A. The weight - swimming speed relation looks like Figure 4.5 when the temperature is higher than 12°C.

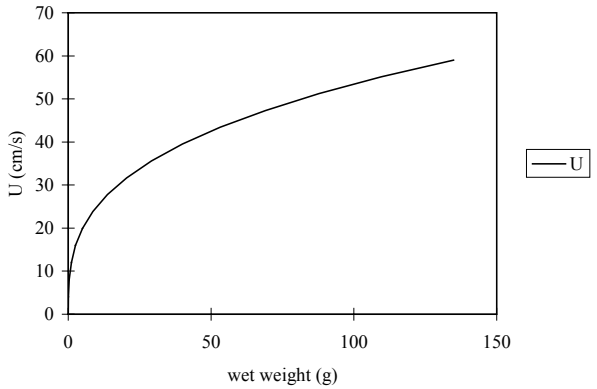

Fig. 4.5 Wet weight (g)-swimming speed (U-cm/s) relation curve for higher temperature.

The parameters we adapted for Pacific saury bioenergetics model are summarized on Table 4.4.

Table 4.4 Summary of parameter values used in the saury bioenergetics model.

Symbol	Parameter description	Value
Consumption, C_{MAX}		
a_C	Intercept for C_{MAX} at (te1+te3)/2	0.6
b_C	coefficient for C_{MAX} versus weight	-0.256
te1	Temperature for xk1 (in ºC)	5, 5, 5
te2	Temperature for xk2 (in ºC)	20, 16, 16
te3	Temperature for xk3 (in ºC)	26, 20, 20
te4	Temperature for xk4 (in ºC)	30, 30, 30
xk1	Proportion of C_{MAX} at te1	0.10
xk2	Proportion of C_{MAX} at te2	0.98
xk3	Proportion of C_{MAX} at te3	0.98
xk4	Proportion of C_{MAX} at te4	0.5
Metabolism, R		
a_R	Intercept for R	0.0033
b_R	Coefficient for R versus weight	-0.227
c_R	Coefficient for R versus temperature	0.0548
d_R	Coefficient for R versus swimming speed	0.03
S	Coefficient for Specific Dynamic Action	0.175
Swimming speed, U		
a_A	Intercept U (< 12 ºC) (in cm/s)	2.0
a_A	Intercept U (≥ 12 ºC) (in cm/s)	12.3
b_A	Coefficient U versus weight	0.33
c_A	Coefficient U versus temperature (< 12 ºC)	0.149
c_A	Coefficient U versus temperature (≥ 12 ºC)	0.0
Egestion and excretion, F and E		
a_F	Proportion of consumed food egested	0.16
a_E	Proportion of consumed food excreted	0.10
Multispecies functional response (by saury size groups)		

V_{11}	Vulnerability of prey group 1 to predator 1	1.0
V_{12}	Vulnerability of prey group 2 to predator 1	0.0
V_{13}	Vulnerability of prey group 3 to predator 1	0.0
K_{11}	Half saturation constant for prey group 1 to predator 1 (g wet weight/m^3)	100.0
K_{12}	Half saturation constant for prey group 2 to predator 1 (g wet weight/m^3)	100.0
K_{13}	Half saturation constant for prey group 3 to predator 1 (g wet weight/m^3)	100.0
V_{21}	Vulnerability of prey group 1 to predator 2	1.0
V_{22}	Vulnerability of prey group 2 to predator 2	1.0
V_{23}	Vulnerability of prey group 3 to predator 2	0.0
K_{21}	Half saturation constant for prey group 1 to predator 2 (g wet weight/m^3)	100.0
K_{22}	Half saturation constant for prey group 2 to predator 2 (g wet weight/m^3)	100.0
K_{23}	Half saturation constant for prey group 3 to predator 2 (g wet weight/m^3)	100.0
V_{31}	Vulnerability of prey group 1 to predator 3	0.0
V_{32}	Vulnerability of prey group 2 to predator 3	1.0
V_{33}	Vulnerability of prey group 3 to predator 3	1.0
K_{31}	Half saturation constant for prey group 1 to predator 3 (g wet weight/m^3)	100.0
K_{32}	Half saturation constant for prey group 2 to predator 3 (g wet weight/m^3)	100.0
K_{33}	Half saturation constant for prey group 3 to predator 3 (g wet weight/m^3)	100.0

start day is February 1st

stage 1	0-50mm	0-30days
stage 2	50-200mm	30-150days
stage 3	>200mm	150day-720days

Model result

The parameters which are revised for the Pacific saury were used to integrate the bioenergetics model coupled with the ecosystem model. Figure 4.6 shows the result of the integration, and shows that the weight of saury reached 120 g after one year. This seems reasonable for Pacific saury. The model shows a high growth rate around 13ºC water temperature. This corresponds to the habitat temperature in the Oyashio region during the feeding season.

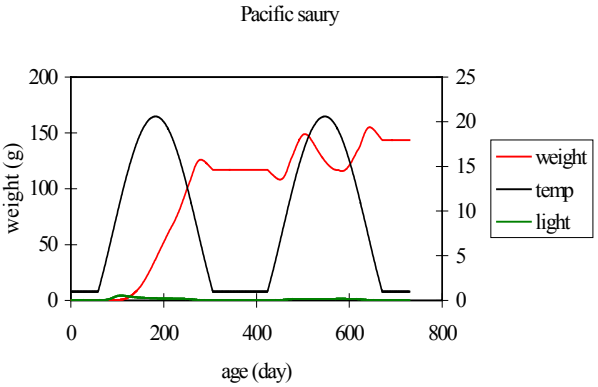

Fig. 4.6 Result of Pacific saury bioenergetics model. Light is in units of ly/min.

Figure 4.7 shows the interannual experiment of ecosystem-saury coupled model with realistic

forcing of A7 (Akkeshi line St 7 off Hokkaido, Japan). The model results show low growth rate in the third and fourth year cohort. The result strongly depends on water temperature.

Future work

This model is not perfect and needs improvements in several respects.

- The weight of the earliest stage is not reproduced well. We should re-parameterize values for this stage.
- More than half of the Pacific saury spawn in the first year and all of them spawn in the second year (Kurita and Sugisaki; in preparation). We should include the effect of spawning in this model.
- In this model only one ocean region is included. But the saury migrate from the subtropical to the subarctic region through the mixed water region, each with its own seasonal cycle of temperature and prey. We should include at least three ocean regions in the ecosystem-saury coupled model. We suggest Figure 4.8 as a prototype three ocean region model. This kind of model is very useful for the analysis of interannual variability of saury growth.

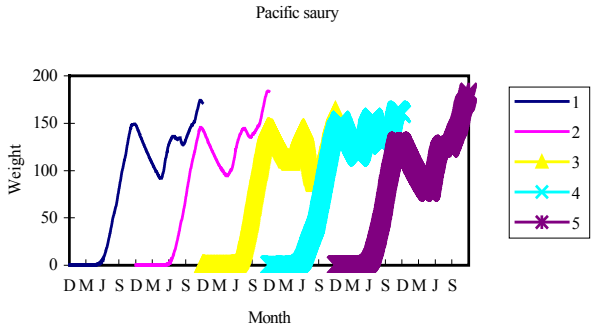

Fig. 4.7 Result of Pacific saury bioenergetics model with realistic forcing.

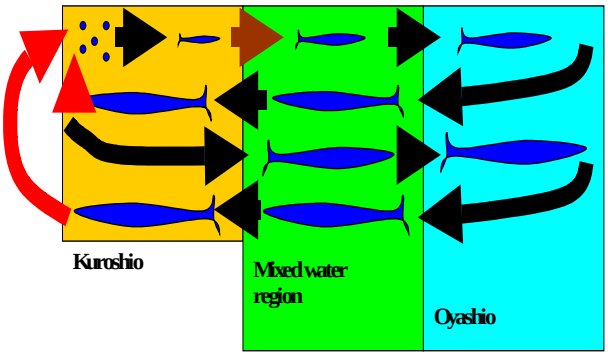

Fig. 4.8 Schematic picture of a three-ocean-box model. This model includes three ocean regions but only one saury bioenergetic model.

5.0 Model experiments and hypotheses

Several model experiments were discussed to test hypotheses regarding the effects of climate change. The details of the experiments and hypotheses are described below.

Space hypothesis

Geographic variation in fish growth: Differences in environmental conditions, and resulting differences in lower trophic conditions, can account for the differences in herring growth rates among selected sites in the North Pacific ecosystem. There exist long-term data sets on size-at-age of herring from many locations in the North Pacific. These data sets show that herring growth rates over the past decades have varied consistently among the different locations. Understanding the extent to which environmental conditions account for these temperature differences in herring growth is important for predicting climate change effects and for effective management of these fisheries in the future.

Key regions contributing to fish growth and biomass variations: Pacific saury are spawned in the subtropical and transition zone from autumn to spring, and migrate from the subtropical to the subarctic ocean through a transition zone. The environments of these three regions show different interannual variability, and it is very difficult to distinguish which location (or season) is most important to the interannual variability of fish growth and biomass. We will tune up the NPZ model coupled to the fish growth model with long-

term climate and weather records by comparing the model results of fish growth with interannual variability in observed size composition. To understand which region contributes most to the interannual variability in fish growth and biomass, sensitivity tests of this model will be very useful. Understanding key regions in fish growth and biomass variation is also important for predicting climate change effects and for effective management of these fisheries in the future.

Time hypothesis

Understanding regime shifts: Synchronous changes in herring growth rates across locations may be accounted for by basin-wide decadal-scale changes in environmental conditions. Preliminary examination of herring growth rates at several locations showed sudden shifts in growth rates occurring in the same years across all locations. We will combine the long-term datasets on herring growth, where possible, with regional and local long-term climate and weather records, and use the NPZ model coupled to the fish growth model to examine possible environmental regime changes.

Understanding how regime shifts cascade up the food web may be our best chance for using past conditions to infer future effects of climate change.

Change of dominant species: Changes in the dominant small pelagic fish species seems to coincide with basin-wide decadal-scale changes in environmental conditions. For example, the dominant species changed from sardine to saury across the regime shift in 1987.

Comparing different fish bioenergetics models with the same NPZ model is very useful to understand the climate change effects on ocean ecosystems through bottom-up processes.

Climate change hypothesis

Global climate change effects on energy pathways and fish production: Climate change may result in energy being diverted from the pelagic pathway and shunted through the microbial pathway, resulting in less food for pelagic fish and consequently slower fish growth rates. We will use the coupled NPZ and fish models, the long-term datasets, and defined climate change scenarios to predict how climate change might affect energy cycling, shift the dominance among different phytoplankton and zooplankton groups, and affect fish growth and production in the North Pacific ecosystem. Model simulations will be performed under present-day (baseline) environmental conditions, and for a suite of realistic climate change scenarios. Comparing these linkages and pathways under baseline and climate change scenarios for a variety of locations that have different environmental conditions (*e.g.*, shallow coastal versus deep blue water) will aid in the interpretation and generalization of our results.

6.0 Recommendations

Results of the model work accomplished at the workshop resulted in several recommendations. They are listed here in priority. A description of workplan scheduling is indicated after each item in parentheses and in italics:

1. Develop site-specific applications (*to be scheduled*);
2. Perform herring comparison between the Sea of Okhotsk and Vancouver Island (*to be scheduled*);
3. Incorporate data observations into NEMURO (*to be programmed*);
   a. Obtain physical parameters (radiation, cloud cover, wind stress);
   b. Obtain realistic time series of SST and photosynthetically active light;
   c. Obtain physical observed time series;
   d. Obtain observed zooplankton time series;
4. Execute a dynamics linkage in NEMURO.FISH (*to be scheduled*);

5. Revise physiological parameters (fish and LTL) (*to be scheduled*);
6. Public web distribution (PICES to support) (*to be scheduled*);
7. Meet in Qingdao with (1) and (2) finished (*to be scheduled*);
8. Consider explicit spatial (x, y, z) and temporal structure (*to be programmed*);
9. Dissemination of NEMURO.FISH results in GLOBEC newsletter and scientific publications (*to be scheduled*);
10. Develop a project home page (*to be scheduled*);
11. Incorporate age structure, reproduction and early life history into NEMURO.FISH (*to be programmed*).

The last recommendation was discussed at length because of a perceived need to provide a tool for the management of fisheries.

It was noted that fish biomass at any time can be represented as the product of fish weight (W) and fish numbers (N).

$$(6.1)\quad B_t = N_t \cdot W_t$$

The rate of change of fish biomass can be written as

$$(6.2)\quad \frac{dB}{dt} = N\frac{dW}{dt} + W\frac{dN}{dt}$$

where we know from the fish bioenergetics model that

$$(6.3)\quad \frac{dW}{dt} = C - (R + SDA + E + F)\cdot W$$

and from fish population dynamics we know that

$$(6.4)\quad \frac{dN}{dt} = e^{-(F+M)} \cdot N$$

where F is the instantaneous fishing mortality rate and M is the instantaneous natural mortality rate. Thus all of the components of equation 6.2 are known or can be estimated.

Also note that with this approach we can compare observed growth to von Bertalanffy growth, a growth model very commonly used in fisheries science.

The von Bertalanffy empirical growth model (von Bertalanffy 1938) is written

$$(6.5)\quad W(t) = W_\infty \cdot (1 - e^{-k\cdot(t-t_0)})^3$$

where W_∞ is the asymptotic weight, W is the weight at time t, k is the growth parameter with units t^{-1}, and t_0 is the theoretical age the fish would have zero weight had they always grown as described by (6.5).

The differential form of (6.5) is

$$(6.6)\quad \frac{dW}{dt} = 3k \cdot (W^{2/3} \cdot W_\infty^{1/3} - W)$$

We know that the change in weight formulation from the fish bioenergetics model (6.3) can be collapsed into a simpler form because most terms are dependent on consumption thus they are proportional to C and the C and R terms are weight dependent. So (6.3) can be simplified to

$$(6.7)\quad \frac{dW}{dt} = p3 \cdot C - p1 \cdot W^{p2}$$

Equating (6.7) and (6.6) we can calculate the rate of consumption required for von Bertalanffy growth, C*, as

$$(6.8)\quad C^* = \frac{1}{p3} \cdot \left[3k \cdot W^{2/3} \cdot W_\infty^{1/3} - 3k \cdot W + p1 \cdot W^{p2} \right]$$

So it seems the theoretical foundation of extending NEMURO.FISH to a population level model useful for fisheries management is possible with a few minor modifications.

7.0 Achievements and future steps

The achievements of the Workshop can be listed as follows:

1. Developed the prototype model, *NEMURO.FISH*. This was an extremely important step because it translates our science into something tangible and economically relevant to human populations that rely on fishes for food - obtaining food from the seas on a sustainable basis;
2. Assembled an international team of marine biologists, fisheries biologists, and physical oceanographers who collectively achieved a consensus on the structure and function of a PICES Climate Change and Carrying Capacity (CCCC) prototype lower trophic level (LTL) ecosystem model for the North Pacific Ocean that included pelagic fishes, and named it "*NEMURO.FISH*";
3. Developed a computer simulation model of fish bioenergetics and growth;
4. Coupled the fish model to the NEMURO lower trophic level model;
5. Adapted the fish bioenergetics model to Pacific herring (*Clupea harengus pallasi*) in the eastern North Pacific and Pacific saury (*Cololabis saira*) in the western North Pacific;
6. Made recommendations for future modeling activities.

The significance of these achievements will ultimately be evaluated by how well the CCCC Program effectively utilizes and embraces these models as a basis of future modeling activity.

8.0 Acknowledgements

This workshop was proposed and convened by PICES, more precisely the PICES/CCCC-IP/MODEL and REX Task Teams. On behalf of the workshop participants, the co-conveners would like to express sincere thanks for giving us a timely and valuable opportunity to participate in the development of a linked higher trophic level - lower trophic level marine ecosystem model common among component programs of the PICES GLOBEC Program. The Heiwa-Nakajima Foundation of Japan contributed the major part of financial support for this workshop. We note this valuable support, for without it, the workshop would not have been possible. Nemuro was selected as the venue due in large part to the invitation from the Nemuro Supporting Committee. The conveners express their very deep appreciation for the warm welcome and perfect support arranged and given by the Nemuro Supporting Committee, their staff, and the people of Nemuro.

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Appendix 2 Herring bioenergetic model FORTRAN code for the base case.

```
C ------------------------------------------------------------------------
C Bioenergetic herring model based on the paper of Rudstam (1988).
C Exploring the dynamics of herring consumption in the Baltic:
C Aplications of an energetic model of fish growth.
C Kieler Meeresforsch Sonderth 6:312-322.
C
C Originally coded as difference equation in FORTRAN by Kenny Rose 26 Dec 01
C
C Corrected and changed to differential equation with Euler and
C Runge Kutta numerical integration scheme
C
C                       01/03/02 Bernard A. Megrey
C
C Added observed and predicted size at age data
C                       01/12/02 Bernard A. Megrey
C
C Added YOY formulations per Arrhenius (1998)
C                       01/22/02 Bernard A. Megrey
C
C All relic code removed for general distribution at
C Nemuro 2002 workshop
C                       01/25/02 Bernard A. Megrey
C
C
C ------------------------------------------------------------------------
      program NemuroHerring

          include 'stuff.cmn'
          include 'state.cmn'
          include 'sizeaa.cmn'
          REAL NYEARS, NSTEPS, NSTEP

      OPEN(UNIT=11,FILE='nemuro.txt',STATUS='unknown')
      OPEN(UNIT=8,FILE='compareEuler.out',STATUS='unknown')
      OPEN(UNIT=9,FILE='sizeatage.out',STATUS='unknown')
C
C-----read in the 3 zoop groups from Nemuro output (7th, 9th and 11th columns)
C
      do 45 ii=1,731
      READ(11,999)id(ii),zop1(ii),zop2(ii),zop3(ii)
  999    FORMAT(1x,i3,1x,5(13x,1x),2(e13.6,1x,13x,1x),e13.6)
C
C-----   take the first year for now
C
      IF(ii.le.365)then
        zoop1(ii)=zop1(ii)
        zoop2(ii)=zop2(ii)
        zoop3(ii)=zop3(ii)
      endif
```

```
45    continue

C------convert Nemuro zoop in uM N/L to g ww/m3
C------  tt1 is conversion from uM N/liter to g ww/m3
C------  14 ug N/uM * 1.0e-6 g/ug * 1 g dw/0.07 g N dw
C------   * 1 g ww/0.2 g dw *
C------   1.e3 liters/m3
      do 55 i=1,365
        tt1=14.0*1.0e-6*(1.0/0.07)*(1.0/0.2)*1.0e3
        zoop1(i)=zoop1(i)*tt1
        zoop2(i)=zoop2(i)*tt1
        zoop3(i)=zoop3(i)*tt1

C----initial weight and age of newly metamphosed herring
             x(1)=0.2
        iage=0
        maxage=0
  55       continue
C
C --- number of state variables
C
      nstate=1
C
C - time initialization
C
        TZERO = 0.0
        NYEARS = 11.0
        NSTEPS = 100.0
        TEND = 365.0*NYEARS
        dt= 1/NSTEPS
        TPRINT = 1.0
        TEPS = 1.0E-05

C
C --- MAIN TIME LOOP
C
      NSTEP=0.0
      DO WHILE (time .LT. TEND)
        NSTEP=NSTEP+1.0
        time= TZERO + NSTEP*dt
        CALL EULER(x,xdot,nstate,dt,time)
C       CALL KUTTA(x,xdot,nstate,dt,time)
        iday=int(amod(time,365.0))+1
        iyr=int(time/365.)+1
C
C-----   update age every time iday 365 goes by and
C-----   after NSTEP have gone by
C-----   the NSTEPS test is to avoid incrementing iage
C-----   every dt
C
        IF(iday.eq.365 .and. amod(NSTEP,NSTEPS).eq.0) then
```

```
        iage=iage+1
            jpage(iage)=iage
        psizeaa(iage)=x(1)
        if(iage .gt. maxpage) maxpage=iage
       endif
C
C --- check for time to print
C
      IF(ABS(AMOD(time,TPRINT)) .LT. TEPS) THEN
      write(8,1001) time, x(1), wtemp, gcmax
1001   format(1x,4(f9.3,1x))
C      ENDIF
     ENDIF
     END DO
     kage=min(maxoage,maxpage)
C
C --- write predicted and observed size-at-age output
C
     do 73 i=1,kage
          write(9,1002) i, psizeaa(i), osizeaa(i)
73    continue
1002  format(1x,i4,2(1x,f9.3))

     close(8)
     close(9)
     STOP
     END
    SUBROUTINE DER(x,xdot,time)

C-------------------------------------------------------
C
C Herring bioenergetics differential equation process.
C Prey base are in units of micromoles N /m^3 and are
C converted
C via converson factors
C
C    programmed by BAM 01/05/02
C
C Added YOY formulations per Arrhenius (1998)
C                    01/22/02 Bernard A. Megrey
C
C-------------------------------------------------------

   include 'stuff.cmn'
   include 'state.cmn'

C          WRITE(*,*) 'IN DER', time


   iday=int(amod(time,365.0))+1
   iyr=int(time/365.)+1
```

```
C
C zero out xdot
C
          DO 15 i=1,nstate
          xdot(i)=0.0
  15 CONTINUE
C----  start age-0 on day 200
C----  jday is julian day (1,..., 400) but goes past 365
C----  iday is counter for day in model simulation
C----- jjday is julian day (i.e., jday reset for >365)
C----  I start on day 200; i you want different then change 200
C---   below and 165, which 365 minus the start day.
         jday=iday+200
         IF(jday.le.365)then
           jjday=jday
         else
           jjday=iday-165
         endif

C
C-----  generate daily temperatures for a year -- made up
C
       t1=float(jjday)
       t2=12.75-10.99*cos(0.0172*t1)-6.63*sin(0.0172*t1)
       wtemp=t2-5.0
       IF(wtemp.le.1.0)wtemp=1.0
C          write(*,*) "wtemp",wtemp
C50    continue

C
C Herring = x(1)
C

C
C----- set vulnerabilities and k values for 3 zoop groups
C
     vul(1)=1.0
     vul(2)=1.0
     vul(3)=1.0

     k(1)=100.0
     k(2)=10.0
     k(3)=100.0
C
C-----if using constant p rather than functional response, set p
C-----here
C      p=0.6


C-----  loop over years
C      do 100 iyr=1,9
```

```
C----    loop over days for each year
C       do 200 iday=1,365
C         write(*,*) 'iday jday jjday', iday,jday,jjday

C-----iiday is running value of days in simulation (1,...., 2000)
C          iiday=(iyr-1)*365+iday

         tt1=1.0/x(1)
         t1=0.0033*tt1**0.227
C         write(*,*) 't1 tt1', x(1), t1, tt1

c----***this is the new stuff from Arrhenius (1998) for YOY only***
c-----   The 5.258 puts resp is in units of g zoop/g fish/day
c----- [13560 joules/gram oxygen]/4.18 joules/cal = 3244 cal/gO2
c------[2580 joules/gram zoop]/4.18 joules/cal = 617 cal/g zoop
c------ 3244/617 = 5.258

         IF(iage.eq.0)then
           IF(wtemp.le.15.0)then
             v=5.76*EXP(0.0238*wtemp)*x(1)**0.386
           endif
           IF(wtemp.gt.15.0)then
             v=8.6*x(1)**0.386
           endif
           a=EXP((0.03-0.0*wtemp)*v)
           resp=t1*EXP(0.0548*wtemp)*a*5.258
         endif
c------***back to the old equations for respiration for age-1 and
C------older ***
         IF(iage.ge.1)then
           IF(wtemp.le.9.0)then
            u=3.9*x(1)**0.13*EXP(0.149*wtemp)
           else
            u=15.0*x(1)**0.13
           endif
           resp=t1*EXP(0.0548*wtemp)*EXP(0.03*u)*5.258
         endif
C         write(*,*) 'after new stuff'
C                   IF(wtemp.lt.9.0)then
C            u=3.9*x(1)**0.13* exp(0.149*wtemp)
C          else
C            u=15.0*x(1)**0.13
C          endif
c--   ---  13,560 joules/g O2  1 cal/4.18 joules  1 g ww/5533 cal
C        resp=t1*EXP(0.0548*wtemp)*EXP(0.03*u)*0.59

C
C-----     Thornton and Lessem (1978)temperature effect
c----**Arrhenius (1998) for age-0  changed te4 from 25 to 23 degrees***
         IF(iage.eq.0)then
           xk1=0.1
```

```
          xk2=0.98
          xk3=0.98
          xk4=0.01

          te1=1.0
          te2=15.0
          te3=17.0
          te4=23.0
        endif
C
        IF(iage.eq.1)then
          xk1=0.1
          xk2=0.98
          xk3=0.98
          xk4=0.01

          te1=1.0
          te2=15.0
          te3=17.0
          te4=25.0
        endif
        IF(iage.gt.1)then
          xk1=0.1
          xk2=0.98
          xk3=0.98
          xk4=0.01

          te1=1.0
          te2=13.0
          te3=15.0
          te4=23.0
        endif
C
C- non age dependent temperature effect on consumption
C           xk1=0.1
C           xk2=0.98
C           xk3=0.98
C           xk4=0.01
C           te1=1.0
C           te2=13.0
C           te3=15.0
C           te4=23.0

        tt5=(1.0/(te2-te1))
        t5=tt5 * alog(0.98*(1.0-xk1)/(0.02*xk1))
        t4=exp(t5*(wtemp-te1))

        tt7 = 1.0/(te4-te3)
        t7=tt7*alog(0.98*(1.0-xk4)/(0.02*xk4))
        t6=exp(t7*(te4-wtemp))
```

```
          gcta=(xk1*t4)/(1.0+xk1*(t4-1.0))
          gctb=xk4*t6/(1.0+xk4*(t6-1.0))
          gctemp=gcta * gctb
          gcmax=0.642*tt1**0.256*gctemp
C
C----- no tempeature effect
C           gcmax=0.642*tt1**0.256*1.0

C-----  either use fixed p or call functional response
C      con=p*gcmax
C      write(*,*) 'der time iday iyr jjday zoop123',time,iday,
C      iyr,
C      jjday, zoop1(jjday),zoop2(jjday), zoop3(jjday)
     cnum=zoop1(jjday)*vul(1)/k(1)+zoop2(jjday)*vul(2)/k(2)
    $      +zoop3(jjday)*vul(3)/k(3)
          c1=gcmax*zoop1(jjday)*vul(1)/k(1)
          c2=gcmax*zoop2(jjday)*vul(2)/k(2)
          c3=gcmax*zoop3(jjday)*vul(3)/k(3)
          con1=c1/(1.0+cnum)
          con2=c2/(1.0+cnum)
          con3=c3/(1.0+cnum)
          con=con1+con2+con3
C
C --- for comparison to Kenny's version
C
C           con=0.75*gcmax
C
C --- to tune to observed size at age data
          con=0.48*gcmax
C
C --- egestion
C
          f=0.16*con
C
C --- excretion
          e=0.1*(con-f)
C
C --- Specific Dynamic Action
C
c------   *******Arrhenius (1998)  changed SDA from 17.5% to 15% ****
          IF(iage.eq.0)sda=0.15*(con-f)
          IF(iage.ge.1)sda=0.175*(con-f)


c-----   J/g ww 1 cal=4.18 J
C                    con1=con*2580.0/5533.0
C          write(*,*) 'der',con1,resp,xdot(1)
C
C --- bioenergetics differential equation
C
         xdot(1)=(con-resp-f-e-sda)*x(1)*2580./5533.
```

```
        IF(wtemp.le.1.0)xdot(1)=0.0
              t1=float(jjday)
                    if(amod(t1,365.0).ge.152.0.and.amod(t1,365.0).le.156.0) then
        write(*,*) 'in spawn'
                     xdot(1)=(con-resp-f-e-sda-0.20)*x(1)*2580./5533.
        endif


c-----   update age every time day 365 goes by
c        IF(iday.eq.365) then
c                     iage=iage+1
c           jage(iage)=iage
c          psizeaa(iage)=x(1)
c           write(*,*)'iday, iyr, jjday, iage, maxage',iday, iyr,
c     $      jjday, iage, maxage
c          if(iage .gt. maxage) maxage=iagec
c             endif

C          WRITE(*,*) 'OUT OF DER'
      RETURN
      END
           SUBROUTINE EULER(x,xdot,nstate,dt,time)
C-------------------------------------------------------
C
C USE THE EULER METHOD TO SOLVE A SYSTEM OF NONLINEAR
C DIFFERENTIAL EQUATIONS. A SUBROUTINE DER IS NEEDED
C TO COMPUTE THE DERIVATIVS OF THE STATE VARIBALES
C
C X - STATE VARIABLE ARRAY
C XDOT - ARRAY OF DERIVATIVES OF STATE ARIABLES
C NSTATE - NUMBER OF STATE VARIABLES
C DT - TIME STEP
C TIME - CURRENT TIME
C
C-------------------------------------------------------
           include 'stuff.cmn'
           include 'state.cmn'


      INTEGER I

       CALL DER(x,xdot,time)

        DO 10 i=1, nstate
             x(i) =x(i) + dt * xdot(i)
  10  CONTINUE

      RETURN
      END
           SUBROUTINE KUTTA(x,xdot,nstate,dt,time)
```

```
C-------------------------------------------------------
C
C USE THE 4TH ORDER RUNGE KUTTA METHOD TO SOLVE A SYSTEM OF NONLINEAR
C DIFFERENTIAL EQUATIONS. A SUBROUTINE DER IS NEEDED
C TO COMPUTE THE DERIVATIVS OF THE STATE VARIBALES
C
C X - STATE VARIABLE ARRAY
C XDOT - ARRAY OF DERVATIVES OF STATE VARIABLES
C NSTATE - NUMBER OF STATE VARIABLES
C DT - TIME STEP
C TIME - CURRENT TIME
C
C programmed by Bernard A. Megrey 01/06/02
C
C
C-------------------------------------------------------
      include 'stuff.cmn'
            include 'state.cmn'

      INTEGER I
      REAL SUMDX(16), DTO2, XPLUS(16)
C           WRITE(*,*) 'IN KUTTA'

      DTO2 = dt/2.0

      CALL DER(x,xdot,time)

      DO 10 I=1, nstate
             XPLUS(I) = x(I) + DT02 * xdot(I)
             SUMDX(I)= xdot(I)
  10  CONTINUE

      CALL DER(XPLUS,xdot,time)

      DO 20 I=1, nstate
            XPLUS(I) = x(I) + DTO2 * xdot(I)
            SUMDX(I) = SUMDX(I) + 2.0 * xdot(I)
  20  CONTINUE

      CALL DER(XPLUS,xdot,time)

      DO 30 I=1, nstate
            XPLUS(I) = x(I) + dt * xdot(I)
            SUMDX(I) = SUMDX(I) + 2.0 * xdot(I)
   30 CONTINUE

      CALL DER(XPLUS,xdot,time)

      DO 40 I=1, nstate
            SUMDX(I) = SUMDX(I) + xdot(I)
            x(I) = x(I) + dt * SUMDX(I) / 6.0
```

```
   40 CONTINUE
C      WRITE(*,*) 'OUT OF KUTTA'
       RETURN
       END


C=======================================================
C
C Include file: state.cmn
C state variable declarations
C
C  BAM 1/02/02
C-------------------------------------------------------
       REAL*4 dt, time, x(1), xdot(1)
       INTEGER*4 nstate


C=======================================================
C
C Include file: stuff.cmn
C miscellaneous common block variables
C
C  BAM 1/2/02
C-------------------------------------------------------
       COMMON /ZOO/ zoop1(365), zoop2(365), zoop3(365)
       COMMON /ISV/ wtemp, con, gcmax,f, e ,sda, con1, resp
             COMMON /TIMER/ iday, jday, iyr, iage
             REAL*4 zoop1,zoop2,zoop3,k(3),vul(3)
       REAL*4 zop1(731),zop2(731),zop3(731)
             INTEGER*4 id(731)


C=======================================================
C
C Include file: sizeaa.cmn
C Size at age common block
C
C   BAM 1/06/02
C
C-------------------------------------------------------
       COMMON /SIZEAA/joage(25),jpage(25),psizeaa(25),osizeaa(25),
      $               maxoage,maxpage
C --- joage Observed age
C --- jpage Predicted age
C --- psizeaa Predicted size at age
C --- osizeaa Observed size at age

       INTEGER*4 joage, jpage, maxoage, maxpage
       REAL*4 psizeaa, osizeaa
       DATA maxoage /11/
       DATA joage /1,2,3,4,5,6,7,8,9,10,11,14*0/
```

```
C
C --- observed size at age Pacific herring  data (wt) from the C
C --- 1973 year class
C --- as supplied by Doug Hay
C
     DATA osizeaa /8.75,63.0,87.66,124.13,139.26,152.98,177.43,
    $              185.78,187.64,195.0,208.73,14*0.0/
```

Appendix 3 Fully customized herring subroutine. See Appendix 2 for main program and common block including files.

```
SUBROUTINE DER(x,xdot,time)

C-------------------------------------------------------
C
C Herring bioenergetics differential equation process.
C Prey base are in units of micromoles N /m^3 and are converted
C via converson factors
C
C    programmed by B.A. Megrey 01/05/02
C
C Added YOY formulations per Arrhenius 1998
C                    01/22/02 B.A. Megrey

C modifications and customizations by F.E.Werner and R.A.Klumb 1/26/02
C while at the Nemuro workshop
C
C-------------------------------------------------------

      include 'stuff.cmn'
      include 'state.cmn'

C
C- calculate date and year
C
      iday=int(amod(time,365.0))+1
           iyr=int(time/365.)+1
C
C zeroout xdot
C
           DO 15 i=1,nstate
           xdot(i)=0.0
   15 CONTINUE
c
c----  start age-0 on day 200
c----       jday is julian day (1,..., 400) but goes past 365
c----       iday is counter for day in model simulation
c----       jjday is julian day (i.e., jday reset for >365)
c----      I start on day 200; i you want different then change 200
c----       below and 165, which 365 minus the start day.
          jday=iday+200
          IF(jday.le.365)then
            jjday=jday
          else
            jjday=iday-165
          endif
C
C-----  generate daily temperatures for a year -- made up
C
```

```
      t1=float(jjday)                                  ! BaseCase T
      t2=12.75-10.99*cos(0.0172*t1)-6.63*sin(0.0172*t1)        ! BaseCase T
      wtemp=t2-5.0                                     ! BaseCase T
      IF(wtemp.le.1.0)wtemp=1.0                        ! BaseCase T
          pi=acos(-1.)
          wtemp=7.717+(5.6796*0.5*(1.-cos(2.*pi*(t1-30.)/365.)))
C
C--- Herring weight state variable = x(1)
C--- weight affect on respiration
C
          tt1=1.0/x(1)
          t1=0.0033*tt1**0.227
C
C --- *********this is the new stuff from Arrhenius (1998) for YOY only*********
C --- The 5.258 puts resp (g oxygen/fish) into units of g zoop/g fish/day
C --- [13560 joules/gram oxygen]/4.18 joules/cal = 3244 cal/gO2
C --- [2580 joules/gram zoop]/4.18 joules/cal = 617 cal/g zoop
C --- so respiration in grams/oxygen/g fish/day is multiplied
C --- by 3244/617 = 5.258
C --- to get food energy equivalents of a gram of oxygen respired
C
c          IF(iage.eq.0)then                                ! BASE
c            IF(wtemp.le.15.0)then                                ! BASE
c              v=5.76*EXP(0.0238*wtemp)*x(1)**0.386                       ! BASE
c            endif                                          ! BASE
c            IF(wtemp.gt.15.0)then                                ! BASE
c              v=8.6*x(1)**0.386                                  ! BASE
c            endif                                          ! BASE
c            a=EXP((0.03-0.0*wtemp)*v)                            ! BASE
c            resp=t1*EXP(0.0548*wtemp)*a*5.258                          ! BASE
c          endif                                            ! BASE
C
          IF(iage.eq.0)then                    !  R.A. Klumb (26 Jan 2002)
               t1=0.00528*tt1**0.007                !  R.A. Klumb (26 Jan 2002)
               resp=t1*EXP(0.083*wtemp)*5.258       !  R.A. Klumb (26 Jan 2002)
             end if                             !  R.A. Klumb (26 Jan 2002)
C
C --- *********back to the old equations for respiration for age-1 and
C --- older********
C
          IF(iage.ge.1)then
C Base            IF(wtemp.le.9.0)then
            IF(wtemp.le.9.655)then
             u=3.9*x(1)**0.13*EXP(0.149*wtemp)
            else
             u=15.0*x(1)**0.13
            endif
            resp=t1*EXP(0.0548*wtemp)*EXP(0.03*u)*5.258
          endif
C
C --- Thornton and Lessem temperature effect
```

```
C --- age dependent values
C --- *******Arrhenius (1998)for age-0  changed te4 from 25 to 23 degrees******
C
        IF(iage.eq.0)then
          xk1=0.1
          xk2=0.98
          xk3=0.98
          xk4=0.01

C Base          te1=1.0
C Base          te2=15.0
C Base          te3=17.0
C Base          te4=23.0

          te1=8.0
          te2=10.897
          te3=11.310
          te4=12.552
        endif
C
        IF(iage.eq.1)then
          xk1=0.1
          xk2=0.98
          xk3=0.98
          xk4=0.01

C Base          te1=1.0
C Base          te2=15.0
C Base          te3=17.0
C Base          te4=25.0

          te1=8.0
          te2=10.897
          te3=11.310
          te4=12.966
        endif

        IF(iage.gt.1)then
          xk1=0.1
          xk2=0.98
          xk3=0.98
          xk4=0.01

C Base          te1=1.0
C Base          te2=13.0
C Base          te3=15.0
C Base          te4=23.0

          te1=8.0
          te2=10.483
          te3=10.897
```

```
          te4=12.552
        endif

        tt5=(1.0/(te2-te1))
        t5=tt5 * alog(0.98*(1.0-xk1)/(0.02*xk1))
        t4=exp(t5*(wtemp-te1))

        tt7 = 1.0/(te4-te3)
        t7=tt7*alog(0.98*(1.0-xk4)/(0.02*xk4))
        t6=exp(t7*(te4-wtemp))

        gcta=(xk1*t4)/(1.0+xk1*(t4-1.0))
        gctb=xk4*t6/(1.0+xk4*(t6-1.0))
        gctemp=gcta * gctb
        gcmax=0.642*tt1**0.256*gctemp
C
C --- multispecies functional response
C --- usse either this or adjust little p
C
C----- set vulnerabilities and k values for 3 zoop groups
C
     vul(1)=1.0
     vul(2)=1.0
     vul(3)=1.0

     k(1)=0.3638
     k(2)=0.0364
     k(3)=0.3638

c      k(1)=2000.0
c      k(2)=200.0
c      k(3)=2000.0

     cnum=zoop1(jjday)*vul(1)/k(1)+zoop2(jjday)*vul(2)/k(2)
    $      +zoop3(jjday)*vul(3)/k(3)
        c1=gcmax*zoop1(jjday)*vul(1)/k(1)
        c2=gcmax*zoop2(jjday)*vul(2)/k(2)
        c3=gcmax*zoop3(jjday)*vul(3)/k(3)
        con1=c1/(1.0+cnum)
        con2=c2/(1.0+cnum)
        con3=c3/(1.0+cnum)
        con=con1+con2+con3
C
C-----if using constant p rather than functional response, set p here
C --- to tune to observed size at age data. If using functional response
C --- comment the next line out
C
       con=0.6375*gcmax
C
C --- egestion
C
```

```
        f=0.16*con                  ! Base Case
        IF(iage.eq.0)f=0.125*con          ! Age-dependent – R.A. Klumb (26 Jan 2002)
C
C --- excretion
        e=0.1*(con-f)               ! Base Case
        IF(iage.eq.0)e=0.078*con          ! Age-dependent – R.A. Klumb (26 Jan 2002)
C
C --- Specific Dynamic Action
C
c------  *******Arrhenius (1998) age dependent SDA from 17.5% to 15% ****
        IF(iage.eq.0)sda=0.15*(con-f)     ! Base Case
        IF(iage.eq.0)sda=0.125*(con-f)    ! Age-dependent – R.A. Klumb (26 Jan 2002)
        IF(iage.ge.1)sda=0.175*(con-f)
C
C --- use the ratio of calories/g of zoop (2580) to calories/g of fish (5533)
C
C --- bioenergetics differential equation - constant energy density for herring
C
C         xdot(1)=(con-resp-f-e-sda)*x(1)*2580./5533.      ! Base Case
C
C    include seasonal variation of energy density for .ge. 2 yr olds
C
        if(iage.ge.2)then
          enMar1=5750.
          jdMar1=60
          enOct1=9800.
          jdOct1=274
          if(jjday.lt.60)then
              delen=(enMar1-enOct1)/151
              en=enOct1+(90+jjday)*delen
            end if
            if(jjday.ge.60.and.jjday.lt.274)then
              delen=(enOct1-enMar1)/(jdOct1-jdMar1)
              en=enMar1+(jjday-jdMar1)*delen
            end if
            if(jjday.ge.274)then
              delen=(enMar1-enOct1)/151
              en=enOct1+(jjday-jdOct1)*delen
            end if
          else
            en=4460.
          end if
        xdot(1)=(con-resp-f-e-sda)*x(1)*2580./en

        IF(wtemp.le.1.0)xdot(1)=0.0
C
C --- Spawning section. Assume loose 20% of body weight/day
C            t1=float(jjday)
c                   if(amod(t1,365.0) .ge. 152.0 .and.
c    &            amod(t1,365.0) .le. 156.0) then
c                     xdot(1)=(con-resp-f-e-sda-0.20)*x(1)*2580./5533.
```

```
c       endif

        RETURN
        END
```

Appendix 4 NEMURO.FISH (NEMURO FORTRAN code supplied by Yasuhiro Yamanaka) with the herring bioenergetic model (base case) (supplied by Bernard Megrey and Ken Rose). The herring model is linked to NEMURO in a one-way static link.

```
!***********************************************************************
!    NEMURO model     Jun 13, 2002  written by Yasuhiro Yamanaka
!***********************************************************************
 program NEMURO.FISH
      implicit none
!     ..... Control for Time Ingration .....
      character(19)     :: Cstart = '0001/07/20 00:00:00'  ! Starting date
      character(19)     :: Cend   = '0011/07/21 00:00:00'  ! Ending date
      character(19)     :: Cstep  = '0000/00/00 01:00:00'  ! Time step
      character(19)     :: Cmon   = '0000/00/01 00:00:00'  ! Monitor Interval
      character(19)     :: CTime
      real(8)           :: dt, TTime, Tbefore, Season, Tmon
      integer           :: Iyr, Imon, Iday, Ihour, Imin, Isec
!     ..... scale conversion .....
      real(8),parameter :: d2s       = 86400.0d0    ! day ---> sec
      real(8),parameter :: mcr       = 1.0d-6       ! micro
!     ..... Prognostic Variables (with initial conditions) and Thier Source Term .....
      real(8)           :: TPS    =  0.1D-6, QPS    ! Small Phytoplankton [molN/l]
      real(8)           :: TPL    =  0.1D-6, QPL    ! Large Phytoplankton
      real(8)           :: TZS    =  0.1D-6, QZS    ! Small Zooplankton
      real(8)           :: TZL    =  0.1D-6, QZL    ! Large Zooplankton
      real(8)           :: TZP    =  0.1D-6, QZP    ! Pradatory Zooplankton
      real(8)           :: TNO3   =  5.0D-6, QNO3   ! Nitrate
      real(8)           :: TNH4   =  0.1D-6, QNH4   ! Ammmonium
      real(8)           :: TPON   =  0.1D-6, QPON   ! Particulate Organic Nitrogen
      real(8)           :: TDON   =  0.1D-6, QDON   ! dissolved Organic Nitrogen
      real(8)           :: TSiOH4 = 10.0D-6, QSiOH4 ! Silicate
      real(8)           :: TOpal  =  0.1D-7, QOpal  ! Particulate Opal
!     ..... Prognostic Variables (with initial conditions) and Thier Source Term .....
!      real(8)          :: THrr   =  0.2D0,  QHrrl  ! Particulate Opal
!     ..... Light Condition Parameters .....
      real(8),parameter :: alpha1   = 4.0D-2     ! Light Dissipation coefficient of sea water[/m]
      real(8),parameter :: alpha2   = 4.0D4      ! PS+PL Selfshading coefficientS+PL      [l/molN/m]
      real(8),parameter :: IoptS    = 0.15D0     ! PS Optimum Light Intensity  S          [ly/min]
      real(8),parameter :: IoptL    = 0.15D0     ! PL Optimum Light Intensity             [ly/min]
      integer,parameter :: LLN      = 10         ! Number of sublayer for calculating of Lfc
      real(8)           :: LfcS                  ! Light factor for PS
      real(8)           :: LfcL                  ! Light factor for PL
      real(8)           :: kappa, Lint, dLint, LfcUS, LfcUL, LfcDS, LfcDL
      integer           :: L
!     ..... biological Parameters .....
      real(8),parameter :: VmaxS    = 0.4D0/d2s  ! PS Maximum Photosynthetic rate @0degC   [/s]
      real(8),parameter :: KNO3S    = 1.0D-6     ! PS Half satuation constant for Nitrate  [molN/l]
      real(8),parameter :: KNH4S    = 0.1D-6     ! PS Half satuation constant for Ammonium [molN/l]
      real(8),parameter :: PusaiS   = 1.5D6      ! PS Ammonium Inhibition Coefficient      [l/molN]
      real(8),parameter :: KGppS    = 6.93D-2    ! PS Temp. Coeff. for Photosynthetic Rate [/degC]
      real(8),parameter :: MorPS0   = 5.85D4/d2s ! PS Mortality Rate @0degC               [/s]
```

```
real(8),parameter :: KMorPS   = 6.93D-2    ! PS Temp. Coeff. for Mortality          [/degC]
real(8),parameter :: ResPS0   = 0.03D0/d2s ! PS Respiration Rate at @0degC          [/s]
real(8),parameter :: KResPS   = 0.0519D0   ! PS Temp. Coeff. for Respiration       [/degC]
real(8),parameter :: GammaS   = 0.135D0    ! PS Ratio of Extracell. Excret. to Photo.[(nodim)]
real(8),parameter :: VmaxL    = 0.8D0/d2s  ! PL Maximum Photosynthetic rate @0degC  [/s]
real(8),parameter :: KNO3L    = 3.00D-6    ! PL Half satuation constant for Nitrate  [molN/l]
real(8),parameter :: KNH4L    = 0.30D-6    ! PL Half satuation constant for Ammonium [molN/l]
real(8),parameter :: KSiL     = 6.00D-6    ! PL Half satuation constant for Silicate [molSi/l]
real(8),parameter :: PusaiL   = 1.50D6     ! PL Ammonium Inhibition Coefficient      [l/molN]
real(8),parameter :: KGppL    = 6.93D-2    ! PL Temp. Coeff. for Photosynthetic Rate [/degC]
real(8),parameter :: MorPL0   = 2.90D4/d2s ! PL Mortality Rate @0degC              [/s]
real(8),parameter :: KMorPL   = 6.93D-2    ! PL Temp. Coeff. for Mortality          [/degC]
real(8),parameter :: ResPL0   = 0.03D0/d2s ! PL Respiration Rate at @0degC          [/s]
real(8),parameter :: KResPL   = 0.0519D0   ! PL Temp. Coeff. for Respiration       [/degC]
real(8),parameter :: GammaL   = 0.135D0    ! PL Ratio of Extracell. Excret. to Photo.[(nodim)]
real(8),parameter :: GRmaxS   = 0.40D0/d2s ! ZS Maximum Rate of Grazing PS @0degC   [/s]
real(8),parameter :: KGraS    = 6.93D-2    ! ZS Temp. Coeff. for Grazing           [/degC]
real(8),parameter :: LamS     = 1.40D6     ! ZS Ivlev constant                     [l/molN]
real(8),parameter :: PS2ZSstar= 0.043D-6   ! ZS Threshold Value for Grazing PS      [molN/l]
real(8),parameter :: AlphaZS  = 0.70D0     ! ZS Assimilation Efficiency            [(nodim)]
real(8),parameter :: BetaZS   = 0.30D0     ! ZS Growth Efficiency                  [(nodim)]
real(8),parameter :: MorZS0   = 5.85D4/d2s ! ZS Mortality Rate @0degC              [/s]
real(8),parameter :: KMorZS   = 0.0693D0   ! ZS Temp. Coeff. for Mortality         [/degC]
real(8),parameter :: GRmaxLps = 0.10D0/d2s ! ZL Maximum Rate of Grazing PS @0degC   [/s]
real(8),parameter :: GRmaxLpl = 0.40D0/d2s ! ZL Maximum Rate of Grazing PL @0degC   [/s]
real(8),parameter :: GRmaxLzs = 0.40D0/d2s ! ZL Maximum Rate of Grazing ZS @0degC   [/s]
real(8),parameter :: KGraL    = 6.93D-2    ! ZL Temp. Coeff. for Grazing           [/degC]
real(8),parameter :: LamL     = 1.4000D6   ! ZL Ivlev constant                     [l/molN]
real(8),parameter :: PS2ZLstar= 4.00D-8    ! ZL Threshold Value for Grazing PS      [molN/l]
real(8),parameter :: PL2ZLstar= 4.00D-8    ! ZL Threshold Value for Grazing PL      [molN/l]
real(8),parameter :: ZS2ZLstar= 4.00D-8    ! ZL Threshold Value for Grazing ZS      [molN/l]
real(8),parameter :: AlphaZL  = 0.70D0     ! ZL Assimilation Efficiency            [(nodim)]
real(8),parameter :: BetaZL   = 0.30D0     ! ZL Growth Efficiency                  [(nodim)]
real(8),parameter :: MorZL0   = 5.85D4/d2s ! ZL Mortality Rate @0degC              [/s]
real(8),parameter :: KMorZL   = 0.0693D0   ! ZL Temp. Coeff. for Mortality         [/degC]
real(8),parameter :: GRmaxPpl = 0.20D0/d2s ! ZP Maximum rate of grazing PL @0degC   [/s]
real(8),parameter :: GRmaxPzs = 0.20D0/d2s ! ZP Maximum rate of grazing ZS @0degC   [/s]
real(8),parameter :: GRmaxPzl = 0.20D0/d2s ! ZP Maximum rate of grazing ZL @0degC   [/s]
real(8),parameter :: KGraP    = 6.93D-2    ! ZP Temp. Coeff. for grazing           [/degC]
real(8),parameter :: LamP     = 1.4000D6   ! ZP Ivlev constant                     [l/molN]
real(8),parameter :: PL2ZPstar= 4.00D-8    ! ZP Threshold Value for Grazing PL      [molN/l]
real(8),parameter :: ZS2ZPstar= 4.00D-8    ! ZP Threshold Value for Grazing ZS      [molN/l]
real(8),parameter :: ZL2ZPstar= 4.00D-8    ! ZP Threshold Value for Grazing ZL      [molN/l]
real(8),parameter :: PusaiPL  = 4.605D6    ! ZP Preference Coeff. for PL           [l/molN]
real(8),parameter :: PusaiZS  = 3.010D6    ! ZP Preference Coeff. for ZS           [l/molN]
real(8),parameter :: AlphaZP  = 0.70D0     ! ZP Assimilation Efficiency            [(nodim)]
real(8),parameter :: BetaZP   = 0.30D0     ! ZP Growth Efficiency                  [(nodim)]
real(8),parameter :: MorZP0   = 5.85D4/d2s ! ZP Mortality Rate @0degC              [/s]
real(8),parameter :: KMorZP   = 0.0693D0   ! ZP Temp. Coeff. for Mortality         [/degC]
real(8),parameter :: Nit0     = 0.03D0/d2s ! NH4 Nitrification Rate @0degC         [/s]
real(8),parameter :: KNit     = 0.0693D0   ! NH4 Temp. coefficient for Nitrification [/degC]
```

```
    real(8),parameter :: VP2N0    = 0.10D0/d2s ! PON Decomp. Rate to Ammonium @0degC     [/s]
    real(8),parameter :: KP2N     = 6.93D-2    ! PON Temp. Coeff. for Decomp. to Ammon.  [/degC]
    real(8),parameter :: VP2D0    = 0.10D0/d2s ! PON Decomp. Rate to DON @0degC          [/s]
    real(8),parameter :: KP2D     = 6.93D-2    ! PON Temp. Coeff. for Decomp. to DON     [/degC]
    real(8),parameter :: VD2N0    = 0.20D0/d2s ! DON Decomp. Rate to Ammonium @0degC     [/s]
    real(8),parameter :: KD2N     = 6.93D-2    ! DON Temp. Coeff. for Decomp. to Ammon.  [/degC]
    real(8),parameter :: VO2S0    = 0.10D0/d2s ! Opal Decomp. Rate to Silicate @0degC    [/s]
    real(8),parameter :: KO2S     = 6.93D-2    ! Opal Temp. Coeff. for Decomp.to Silicate[/degC]
    real(8),parameter :: RSiN     = 2.0D0         !Si/N ratio                  [molSi/molN]
    real(8),parameter :: RCN      = 106.0D0/16.0D0 !C/N ratio                  [molC/molN]
!   ..... bottom boundary Condition .....
    real(8),parameter :: setVPON  = 40.0D0/d2s ! Settling velocity of PON              [m/s]
    real(8),parameter :: setVOpal = 40.0D0/d2s ! Settling velocity of Opal             [m/s]
    real(8),parameter :: TNO3d   =  25.0d-6    ! Nitrate Concentraion in the Deep Layer  [molN/l]
    real(8),parameter :: TSiOH4d =  35.0d-6    ! Silicate Concentraion in the Deep Layer [molSi/l]
!   ..... Paramters of ZL Vertical Migration .....
    character(19)     :: CZup ='0000/04/01 00:00:00' ! Date Coming up to the Euphotic Layer
    character(19)     :: CZdwn='0000/09/01 00:00:00' ! Date Returning to the Deep Layer
    real(8)           :: TZup, TZdwn, TZLd, SVRate=0.2D0
    integer           :: IyrU, ImonU, IdayU ,IhourU, IminU, IsecU
    integer           :: IyrD, ImonD, IdayD ,IhourD, IminD, IsecD
!
    real(8)           :: GppPSn,  GppNPSn, GppAPSn, RnewS, ResPSn,  MorPSn,  ExcPSn
    real(8)           :: GppPLn,  GppNPLn, GppAPLn, RnewL, ResPLn,  MorPLn,  ExcPLn
    real(8)           :: GppPLsi, GppSiPLsi,              ResPLsi, MorPLsi, ExcPLsi
    real(8)           :: GraPS2ZSn, GraPS2ZLn,  GraPL2ZLn, GraPL2ZLsi, GraZS2ZLn
    real(8)           :: GraPL2ZPn, GraPL2ZPsi, GraZS2ZPn, GraZL2ZPn
    real(8)           :: EgeZSn, MorZSn, ExcZSn, EgeZLn, EgeZLsi, MorZLn, ExcZLn
    real(8)           ::                    EgeZPn, EgeZPsi, MorZPn, ExcZPn
    real(8)           :: DecP2N, DecP2D, DecD2N, DecO2S, Nit
    real(8)           :: ExpPON, ExpOpal,ExcNO3, ExcSiOH4
    integer           :: lt=0 , nt
!
!   ..... Environmental Condition .....
    real(8)           :: Temp                    ! Temperature [degC]
    real(8)           :: Lint0                   ! Light Intencity at sea surface [ly/min]
    real(8)           :: MLD = 30.0d0            ! Mixed Layer Depth [m]
    real(8)           :: ExcTime = 1.0d0 / (100.0d0*d2s) ! Exch. Coeff. between Sur-Deep [/s]
!   ..... statement function & def. type of functions .....
    real(8)           :: cd2tt, nd2tt
    character(19)     :: tt2cd
    real(8)           :: Td, GraF, Mich, a, b, c
    Td  (a,b)   = a * exp(b*Temp)
    GraF(a,b,c) = MAX( 0.0D0, 1.0 - exp(a * (b - c)))
    Mich(a,b)   = b / ( a + b )
!
!   ***** Initial Setting *****
!   ..... for time control .....
    TTime = cd2tt(Cstart)                  ! Starting Date
    CTime = TT2CD(TTime)                   ! present time (charactor form)
    dt    = cd2tt(Cstep) - cd2tt('0000/00/00 00:00:00')  ! Time Step (real8 form)
```

```
      Tmon  = cd2tt(Cmon)  - cd2tt('0000/00/00 00:00:00')  ! Monitor Interval (real8 form)
      nt = NINT( ( cd2tt(Cend) - cd2tt(Cstart) ) / dt )    ! Total Time Steps
!     ..... for Vertical Migration ......
      TZup  = CD2TT( CZup  )
      TZdwn = CD2TT( CZdwn )
      call TT2ND(IyrU, ImonU, IdayU ,IhourU, IminU, IsecU ,TZup )
      call TT2ND(IyrD, ImonD, IdayD ,IhourD, IminD, IsecD ,TZdwn)
      TZLd = TZL  ! ZL living in the deep layer at the initial condition
      TZL  = 0.0
!     ..... File Open for monitoring output .....
      open( 10, file='Results.csv', form='FORMATTED' )
      write(10,'(A,13(",", A))') 'Time(day)', &
                 'NO3'   , 'NH4'     , 'PS'     , 'PL'      , &
                 'ZS'    , 'ZL'      , 'ZP'     , 'PON'     , &
                 'DON'   , 'SiOH4'   , 'Opal'   , 'TotalN'  , 'TotalSi'
      write(10,'(A,11(",", F8.4))') CTime, &
                 TNO3/mcr, TNH4  /mcr, TPS  /mcr, TPL /mcr, &
                 TZS /mcr, TZL   /mcr, TZP  /mcr, TPON/mcr, &
                 TDON/mcr, TSiOH4/mcr, TOpal/mcr
      open( 11, file='Forcing.csv', form='FORMATTED' )
      write(11,'(A,13(",", A))') 'Time(day)','Lint0', 'TMP', 'MLD', 'ExcTime'
      write(11,'(A,13(",", 1PE10.4))') CTime, Lint0, Temp, MLD, ExcTime*d2s
!
!     ****** Main Loop *****
      do lt = 1, nt
!       ..... time control (Season : 0 to 1, parcentage in a year).....
        Tbefore = TTime                          ! one step before present time
        TTime   = TTime + dt                       ! present time (real8 form)
        CTime = TT2CD(TTime)                           ! present time (charactor form)
        CALL TT2ND(Iyr, Imon, Iday ,Ihour, Imin, Isec ,TTime)
        Season = ( TTime                - ND2TT(Iyr  ,1,1,0,0,0) )/  &
                 ( ND2TT(Iyr+1,1,1,0,0,0) - ND2TT(Iyr  ,1,1,0,0,0) )
!
!       ..... Example of Boundray condition .....
        Lint0 = 0.1d0 * ( 1.0D0 + 0.3d0 * cos( 2.0d0*3.1415926536d0*(Season - 0.50D0) ) )
        Temp  =          6.0D0 + 4.0d0 * cos( 2.0d0*3.1415926536d0*(Season - 0.65D0) )
        if (Temp .lt. 4.0 ) then
          MLD = MLD + dt * (150.0d0 - MLD ) / ( 100.0d0 * d2s )
          ExcTime = ExcTime + dt * ( 1.0d0/( 40.0d0*d2s) - ExcTime ) / (100.0d0*d2s)
        else
          MLD = MLD + dt * ( 30.0d0 - MLD ) / (   5.0d0 * d2s )
          ExcTime = ExcTime + dt * ( 1.0d0/(100.0d0*d2s) - ExcTime ) / (  5.0d0*d2s)
        end if
!
!       ..... Light Factors (LfcS, LfcL).....
        Lint = Lint0
        LfcDS = Lint/IoptS * exp(1.0D0 - Lint/IoptS)
        LfcDL = Lint/IoptL * exp(1.0D0 - Lint/IoptL)
        LfcS  = 0.0D0
        LfcL  = 0.0D0
        Kappa = alpha1 + alpha2 * ( TPS + TPL )
```

```
      dLint = exp( -Kappa * (MLD/LLN) )
      do L = 1, LLN
        LfcUS  = LfcDS
        LfcUL  = LfcDL
        Lint   = Lint      * dLint
        LfcDS  = Lint/IoptS * exp( 1.0D0 - Lint/IoptS )
        LfcDL  = Lint/IoptL * exp( 1.0D0 - Lint/IoptL )
        LfcS   = LfcS + ( LfcUS + LfcDS ) * 0.5D0 / LLN
        LfcL   = LfcL + ( LfcUL + LfcDL ) * 0.5D0 / LLN
      end do
!     ..... Photosynthesis of PS .....
      GppNPSn   = Mich( KNO3S, TNO3 ) * exp( - PusaiS * TNH4 )
      GppAPSn   = Mich( KNH4S, TNH4 )
      GppPSn    = Td(VmaxS, KGppS) * LfcS * TPS * ( GppNPSn + GppAPSn )
      RnewS     = GppNPSn / ( GppNPSn + GppAPSn )
      ResPSn    = Td( ResPS0, KResPS ) * TPS
      MorPSn    = Td( MorPS0, KMorPS ) * TPS * TPS
      ExcPSn    = GammaS             * GppPSn
!     ..... Photosynthesis of PL .....
      GppNPLn   = Mich( KNO3L, TNO3   ) * exp( - PusaiL * TNH4 )
      GppAPLn   = Mich( KNH4L, TNH4   )
      GppSiPLsi = Mich( KSiL , TSiOH4 )
      GppPLn    = Td(VmaxL, KGppL) * LfcL * TPL * min( ( GppNPLn + GppAPLn ), GppSiPLsi )
      RnewL     = GppNPLn / ( GppNPLn + GppAPLn )
      ResPLn    = Td( ResPL0, KResPL ) * TPL
      MorPLn    = Td( MorPL0, KMorPL ) * TPL * TPL
      ExcPLn    = GammaL             * GppPLn
!     ..... Grazing PS, PL, ZS, ZL --> ZS, ZL, ZP .....
      GraPS2ZSn = Td(GRmaxS,  KGraS) *GraF(LamS,PS2ZSstar,TPS) *TZS
      GraPS2ZLn = Td(GRmaxLps,KGraL) *GraF(LamL,PS2ZLstar,TPS) *TZL
      GraPL2ZLn = Td(GRmaxLpl,KGraL) *GraF(LamL,PL2ZLstar,TPL) *TZL
      GraZS2ZLn = Td(GRmaxLzs,KGraL) *GraF(LamL,ZS2ZLstar,TZS) *TZL
      GraPL2ZPn =  Td(GRmaxPpl,KGraP) *GraF(LamP,PL2ZPstar,TPL) *TZP * exp( -PusaiPL *(TZL
       + TZS))
      GraZS2ZPn = Td(GRmaxPzs,KGraP) *GraF(LamP,ZS2ZPstar,TZS) *TZP * exp( -PusaiZS * TZL )
      GraZL2ZPn = Td(GRmaxPzl,KGraP) *GraF(LamP,ZL2ZPstar,TZL) *TZP
!     ..... Mortality, Excration, Egestion for Zooplanktons
!     ..... Commented out after Saito-san Meeting at 19 Jun, 2000 .....
!     BetaZS = 0.3 ** (  1.0 + Mich( TPL, TPS )  )
      ExcZSn = (AlphaZS-  BetaZS)   * GraPS2ZSn
      EgeZSn = (1.0    - AlphaZS)   * GraPS2ZSn
      MorZSn = Td( MorZS0, KMorZS ) * TZS * TZS
      ExcZLn = (AlphaZL-  BetaZL)   * (GraPS2ZLn+GraPL2ZLn+GraZS2ZLn)
      EgeZLn = (1.0    - AlphaZL)   * (GraPS2ZLn+GraPL2ZLn+GraZS2ZLn)
      MorZLn = Td( MorZL0, KMorZL ) * TZL * TZL
      ExcZPn = (AlphaZP-  BetaZP)   * (GraPL2ZPn+GraZS2ZPn+GraZL2ZPn)
      EgeZPn = (1.0    - AlphaZP)   * (GraPL2ZPn+GraZS2ZPn+GraZL2ZPn)
      MorZPn = Td( MorZP0, KMorZP ) * TZP * TZP
!     ..... Decomposition PON, DON, Opal ---> NH4, DON, SiOH4 .....
      DecP2N    = Td( VP2N0  , KP2N ) * TPON
      DecP2D    = Td( VP2D0  , KP2D ) * TPON
```

```
      DecD2N    = Td( VD2N0  , KD2N ) * TDON
      DecO2S    = Td( VO2S0  , KO2S ) * TOpal
      Nit       = Td( Nit0   , KNit ) * TNH4
!     ..... silica fluxes .....
      GppPLsi    = GppPLn    * RSiN
      ResPLsi    = ResPLn    * RSiN
      MorPLsi    = MorPLn    * RSiN
      ExcPLsi    = ExcPLn    * RSiN
      GraPL2ZLsi = GraPL2ZLn * RSiN
      GraPL2ZPsi = GraPL2ZPn * RSiN
      EgeZLsi    = GraPL2ZLsi
      EgeZPsi    = GraPL2ZPsi
!
!     ..... Tendency Terms for biological processes .....
      QNO3   = -( GppPSn - ResPSn ) * RnewS   &
             -( GppPLn - ResPLn ) * RnewL + Nit
      QNH4   = -( GppPSn - ResPSn ) * (1.0 - RnewS)   &
             -( GppPLn - ResPLn ) * (1.0 - RnewL)   &
             - Nit + DecP2N + DecD2N + ExcZSn + ExcZLn + ExcZPn
      QPS    = GppPSn - ResPSn - MorPSn - ExcPSn - GraPS2ZSn - GraPS2ZLn
      QPL    = GppPLn - ResPLn - MorPLn - ExcPLn - GraPL2ZLn - GraPL2ZPn
      QZS    = GraPS2ZSn - GraZS2ZLn - MorZSn - ExcZSn - EgeZSn - GraZS2ZPn
      QZL    = GraPL2ZLn + GraZS2ZLn - MorZLn - ExcZLn - EgeZLn + GraPS2ZLn - GraZL2ZPn
      QZP    = GraPL2ZPn + GraZS2ZPn - MorZPn - ExcZPn - EgeZPn + GraZL2ZPn
      QPON   = MorPSn  + MorPLn  + MorZSn  + MorZLn + MorZPn   &
           + EgeZPn  + EgeZSn  + EgeZLn  - DecP2N - DecP2D
      QDON   = ExcPSn  + ExcPLn  + DecP2D  - DecD2N
      QSiOH4 =-GppPLsi + ResPLsi + ExcPLsi + DecO2S
      QOpal  = MorPLsi + EgeZLsi + EgeZPsi - DecO2S
!
!     ..... Exchange Fluxes between the Surface and Deep Layers .....
      ExpPON   = setVPON  / MLD * TPON
      ExpOpal  = setVOpal / MLD * TOpal
      ExcNO3   = ExcTime * ( TNO3d   - TNO3   )
      ExcSiOH4 = ExcTime * ( TSiOH4d - TSiOH4 )
      QNO3   = QNO3   + ExcNO3
      QSiOH4 = QSiOH4 + ExcSiOH4
      QPON   = QPON   - ExpPON
      QOpal  = QOpal  - ExpOpal
!
!     ..... Time Integration with Forward Scheme .....
      TNO3   = TNO3   + dt * QNO3
      TNH4   = TNH4   + dt * QNH4
      TPS    = TPS    + dt * QPS
      TPL    = TPL    + dt * QPL
      TZS    = TZS    + dt * QZS
      TZL    = TZL    + dt * QZL
      TZP    = TZP    + dt * QZP
      TPON   = TPON   + dt * QPON
      TDON   = TDON   + dt * QDON
      TSiOH4 = TSiOH4 + dt * QSiOH4
```

```
      TOpal  = TOpal  + dt * QOpal
!
!     ..... Vertical Migration of ZL .....
      TZdwn = ND2TT(Iyr, ImonD, IdayD ,IhourD, IminD, IsecD )
      TZup  = ND2TT(Iyr, ImonU, IdayU ,IhourU, IminU, IsecU )
      if ( (Tbefore .lt. TZdwn).and.(TTime .ge. TZdwn) ) then
        TZLd = TZL
        TZL  = 0.0
        write(*,*) '*** Down ***', CTime
      end if
      if ( (Tbefore .lt. TZup).and.(TTime .ge. TZup) ) then
        TZL = SVRate * TZLd
        write(*,*) '***  UP  ***', CTime
      end if
!
      call Herring(TTime, Tbefore, TZS, TZL, TZP, Temp)
!
!     ..... Monitor .....
      if ( int(TTime/Tmon).ne. int(Tbefore/Tmon) ) then
!       write(*,'(A,13(",", F8.4))') CTime, Season
        write(10,'(A,11(",", F8.4))') CTime, &
              TNO3/mcr, TNH4  /mcr, TPS  /mcr, TPL /mcr, &
              TZS /mcr, TZL   /mcr, TZP  /mcr, TPON/mcr, &
              TDON/mcr, TSiOH4/mcr, TOpal/mcr
        write(11,'(A,13(",", 1PE10.4))') CTime, Lint0, Temp, MLD, ExcTime*d2s
      end if
    end do
!
    close(10); close(11)
!
    stop
    end
!*******************************************************************************
    Subroutine Herring(TTime, Tbefore, TZS, TZL, TZP, Temp)
!
    implicit none
    real(8)          :: TTime, Tbefore, TZS, TZL, TZP, Temp
    real(8),parameter :: d2s       = 86400.0d0    ! day ---> sec
    integer          :: Iyr, Imon, Iday, Ihour, Imin, Isec
    character(19)    :: CAge ='0000/07/19 00:00:00' ! Date of Aging ( JJday = 200 )
    character(19)    :: CTime
    real(8)          :: TAge
    integer          :: iage = 0
    integer, save    :: IyrA, ImonA, IdayA ,IhourA, IminA, IsecA
    integer          :: JJday
    real(8)          :: ZooP1, ZooP2, ZooP3, tt1
    real(8)          :: t1,t2,wtemp
    real(8)          :: x(1) =0.2d0, xdot(1)
    real(8)          :: cd2tt, nd2tt
    character(19)    :: tt2cd
    real(8)          :: vul(3), k(3)
```

```
      integer(4)        :: id(365)
      real(8)           :: zop1(365), zop2(365), zop3(365)
      real(8):: v, a, u, resp
     real(8) :: xk1,xk2,xk3,xk4,te1,te2,te3,te4,tt5,t5,t4,tt7,t7,t6, gcta,gctb,gctemp,gcmax
     real(8) :: cnum,c1,c2,c3,con1,con2,con3,con
     real(8) :: f,e, sda
!
      integer, save     :: First = 1
!
!    ==================
      if ( First .eq. 1 ) then; First = 0
        TAge  = CD2TT( CAge  )
        call TT2ND(IyrA, ImonA, IdayA ,IhourA, IminA, IsecA ,TAge )
        open( 20, file='Herring.csv', form='FORMATTED' )
!
!!!!        OPEN(UNIT=111,FILE='nemuro.txt',STATUS='unknown')
!!!!        -----read in the 3 zoop groups from Nemuro output last 3 columns
!!!!        do JJday=1,365
!!!!          READ(111,999)id(JJday),zop1(JJday),zop2(JJday),zop3(JJday)
!!!!  999      FORMAT(1x,i3,1x,3(e13.6,1x))
!!!!        end do
      end if
!    ==================
!
      CTime = TT2CD(TTime)                          ! present time (charactor form)
      CALL TT2ND(Iyr, Imon, Iday ,Ihour, Imin, Isec ,TTime)
      JJday = 1 + ( TTime - ND2TT(Iyr  ,1,1,0,0,0) ) / d2s
!
!------convert Nemuro zoop in uM N/L to g ww/m3
!------  tt1 is conversion from uM N/liter to g ww/m3
!------  14 ug N/uM * 1.0e-6 g/ug * 1 g dw/0.07 g N dw * 1 g ww/0.2 g dw *
!------       1.0e3 liters/m3
!
      tt1=14.0*1.0e-6*(1.0/0.07)*(1.0/0.2)*1.0e3
      zoop1 = TZS*tt1 *1.0d6
      zoop2 = TZL*tt1 *1.0d6
      zoop3 = TZP*tt1 *1.0d6
!!!!     zoop1 = zop1(JJday) * tt1
!!!!     zoop2 = zop2(JJday) * tt1
!!!!     zoop3 = zop3(JJday) * tt1
!
!     ..... Temperature Seting .....
!
      t1=float(jjday)
      t2=12.75-10.99*cos(0.0172*t1)-6.63*sin(0.0172*t1)
      wtemp=t2-5.0
      IF(wtemp.le.1.0)wtemp=1.0

!      write(*,*) TT2CD(cd2tt('0002/01/01 00:00:00')+200.0*86400.0)
!      stop
!     ..... Aging of Herring ......
```

```
      TAge = ND2TT(Iyr, ImonA, IdayA ,IhourA, IminA, IsecA )
      if ( (Tbefore .lt. TAge).and.(TTime .ge. TAge) ) then
           write(*,*) '*** Aging +1 of Herring ***', CTime
           iage = iage + 1
       end if
!
!--- Herring weight state variable = x(1)
!
!----- set vulnerabilities and k values for 3 zoop groups
!
      vul(1) =   1.0; vul(2) =  1.0; vul(3) =   1.0
      k  (1) = 0.3638; k  (2) = 0.0364; k  (3) = 0.3638
!
! --- weight affect on respiration
!
      tt1 = 1.0 / x(1)
      t1  = 0.0033 * tt1**0.227
! --- *********this is the new stuff from Ahhrenius for YOY only*********
! --- The 5.258 puts resp (g oxygen/fish) into units of g zoop/g fish/day
! --- [13560 joules/gram oxygen]/4.18 joules/cal = 3244 cal/gO2
! --- [2580 joules/gram zoop]/4.18 joules/cal = 617 cal/g zoop
! --- so respiration in grams/oxygen/g fish/day is multiplied by 3244/617 = 5.258
! --- to get food energy equivalents of a gram of oxygen respired
!
      IF (iage .eq. 0 )then
        IF(wtemp.le.15.0)then
          v = 5.76 * exp( 0.0238 * wtemp ) * x(1)**0.386
        else
          v = 8.6 * x(1)**0.386
        endif
        a=EXP((0.03-0.0*wtemp)*v)
        resp=t1*EXP(0.0548*wtemp)*a*5.258
! --- *********back to the old equations for respiration for age-1 and older********
      else   ! (iage .gt. 0)
        IF (wtemp.le.9.0)then
          u=3.9*x(1)**0.13*EXP(0.149*wtemp)
        else
          u=15.0*x(1)**0.13
        endif
          resp=t1*EXP(0.0548*wtemp)*EXP(0.03*u)*5.258
      endif
!C
!C --- Thornton and Lessem temperature effect
!C --- age dependent values
!C --- *******Arrhenius for age-0 he changed te4 from 25 to 23 degrees******
!C
      if ( iage .eq. 0 ) then
        xk1 = 0.1;  xk2 = 0.98;  xk3 = 0.98;  xk4 = 0.01
        te1 = 1.0;  te2 = 15.0;  te3 = 17.0;  te4 = 23.0
      else if ( iage .eq. 1 ) then
        xk1 = 0.1;  xk2 = 0.98;  xk3 = 0.98;  xk4 = 0.01
```

```
        te1 = 1.0;  te2 = 15.0;  te3 = 17.0;  te4 = 25.0
      else if( iage .gt. 1 ) then
        xk1 = 0.1;  xk2 = 0.98;  xk3 = 0.98;  xk4 = 0.01
        te1 = 1.0;  te2 = 13.0;  te3 = 15.0;  te4 = 23.0
      endif
!
      tt5 = ( 1.0 / ( te2 - te1 ) )
      t5  = tt5 * log( 0.98 * ( 1.0 - xk1 ) / ( 0.02 * xk1 ) )
      t4  = exp( t5 * ( wtemp - te1 ) )
!
      tt7 = 1.0 /( te4 - te3 )
      t7  = tt7 * log( 0.98 * ( 1.0 - xk4 ) / ( 0.02 * xk4 ) )
      t6  = exp( t7 * ( te4 - wtemp ) )
!
      gcta  = ( xk1 * t4 ) / ( 1.0 + xk1 * ( t4 - 1.0 ) )
      gctb  = xk4 * t6 / ( 1.0 + xk4 * ( t6 - 1.0 ) )
      gctemp= gcta * gctb
      gcmax = 0.642 * tt1**0.256 * gctemp
!
! --- multispecies functional response
! --- usse either this or adjust little p
!
      cnum=zoop1 * vul(1)/k(1) + zoop2*vul(2)/k(2) +zoop3 * vul(3)/k(3)
      c1=gcmax*zoop1*vul(1)/k(1)
      c2=gcmax*zoop2*vul(2)/k(2)
      c3=gcmax*zoop3*vul(3)/k(3)
      con1=c1/(1.0+cnum)
      con2=c2/(1.0+cnum)
      con3=c3/(1.0+cnum)
      con= con1+con2+con3
!
!-----if using constant p rather than functional response, set p here
! --- to tune to observed size at age data
!     con=0.425*gcmax
!
! --- egestion
!
          f=0.16*con
!
! --- excretion
          e=0.1*(con-f)
!
!
! --- Specific Dynamic Action
!
!c------   *******Arrhenius age dependent SDA from 17.5% to 15% ****
          IF ( iage .eq. 0 ) then
            sda=0.15*(con-f)
          else
            sda=0.175*(con-f)
          end if
```

```
!C
!C --- use the ratio of calories/g of zoop (2580) to calories/g of fish (5533)
!C
!C --- bioenergetics differential equation
!C
        xdot(1)=(con-resp-f-e-sda)*x(1)*2580./5533.
!
        IF(wtemp.le.1.0)xdot(1)=0.0
!C
!C --- Spawning section. Assume loose 20% of bosy weight/day
!C            t1=float(jjday)
!      if( mod(JJday,365) .ge. 152.0 .and. mod(JJday,365) .le. 156.0) then
!         xdot(1)=(con-resp-f-e-sda-0.20)*x(1)*2580./5533.
!         write(*,*) '### Spawning ###'
!      endif
!
!     if (iage .eq. 1 ) then
!      write(*,*) JJday, wtemp, x(1), xdot(1)
!      stop
!      end if
!      write(*,'(A,I4,3(1PE14.5))') Ctime, JJday, wtemp, x(1), xdot(1)
!
!     Time Integration
!
     x(1) = x(1) + 3600.0d0 /d2s * xdot(1)
!
!     ..... for Check .....
    if ( int(TTime/d2s) .ne. int(Tbefore/d2s) ) then
!!       write(*,'(A,I4,3(1PE14.5))') Ctime, JJday, wtemp, x(1), xdot(1)
!!        stop
!!      write(*,*) TZS, zop1(JJday), TZL,zop2(JJday), TZP,zop3(JJday)
!!      write(*,*) TZP*1.0d6, zop3(JJday)
       write(20,'(A,11(",", F12.4))') CTime, x(1), wtemp, gcmax
     end if
!
     return
!
     stop
     end
!*******************************************************************************
!* Utilities for Date Control  Writtien by Yasuhiro Yamanaka (galapen@ees.hokudai.ac.jp) *
!*******************************************************************************
!    exp. 1997/12/31 23:59:59 --> 6.223158719900000E+10
!    exp. 0000/01/01 00:00:00 --> 0.000000000000000E+00
!*******************************************************************************
     real(8) function CD2TT( Cdate )
!
     integer       :: Iyr, Imon, Iday , Ihour, Imin, Isec
     real(8)       :: ND2TT
     character(19) :: Cdate
!
```

```
    if ( len( Cdate ) .ne. 19 ) then
      write(*,*) '### Length of date is no good ###'
      stop
    end if
    read (Cdate( 1: 4),*)  Iyr
    read (Cdate( 6: 7),*)  Imon
    read (Cdate( 9:10),*)  Iday
    read (Cdate(12:13),*)  Ihour
    read (Cdate(15:16),*)  Imin
    read (Cdate(18:19),*)  Isec
!
    CD2TT = ND2TT(Iyr, Imon, Iday , Ihour, Imin, Isec)
!
    return
    end function
!**********************************************************************
!    exp. 6.223158719900000E+10 --> 1997/12/31 23:59:59
!**********************************************************************
    character(19) function TT2CD(tt)
!
    integer :: Iyr, Imon, Iday , Ihour, Imin, Isec
    real(8) :: tt
!
    call TT2ND( Iyr, Imon, Iday, Ihour, Imin, Isec , tt )
!
    write(TT2CD,'(I4.4,5(A,I2.2))') Iyr, '/', Imon, '/', Iday, &
                        ' ', Ihour, ':', Imin, ':', Isec
!
    return
    end function
!**********************************************************************
!    exp. 1997,12,31,23,59,59 --> 6.223158719900000E+10
!**********************************************************************
    real(8) function ND2TT(Iyr, Imon, Iday, Ihour, Imin, Isec)
!
    integer   :: IM2D(12,0:1) = &
      reshape( (/ 0,31,59,90,120,151,181,212,243,273,304,334,  &
                  0,31,60,91,121,152,182,213,244,274,305,335  /), (/12,2/) )
    integer   :: Iyr, Imon, Iday, Ihour, Imin, Isec
    integer   :: Iy4, Iy1, Ileap, Im, Itt
!
!
    Iy4 = 1461 * ( Iyr / 4 )
    Iy1 = 365 * mod( Iyr, 4 )
!
    if ( mod( Iyr, 4 ) .ne. 0 ) then
      Ileap = 0
    else
      Ileap = 1
    end if
    Im = IM2D( Imon, Ileap)
```

```
!
    Itt = Iy4 + Iy1 + Im + Iday - Ileap
!
    ND2TT = Ihour * 3600 + Imin * 60 + Isec
    ND2TT = ND2TT + Itt * 86400.0D0
!
    return
    end function
!**********************************************************************
!    exp. 6.223158719900000E+10 --> 1997,12,31,23,59,59
!**********************************************************************
    subroutine TT2ND(                                &
            Iyr   , Imon  , Iday   , Ihour, Imin, Isec,   & !O & I
            tt    )
!
    integer :: Iyr, Imon, Iday , Ihour, Imin, Isec
    integer :: Itt, Iy, Iy4, Iyd, Iy1, Ileap, Imd, Im, Its
    integer   :: IM2D(12,0:1) = &
      reshape( (/ 0,31,59,90,120,151,181,212,243,273,304,334,  &
                  0,31,60,91,121,152,182,213,244,274,305,335  /), (/12,2/) )
    integer :: IY2D(4) = (/0,366,731,1096/)
    real(8) :: tt, tt0, ND2TT
!
!
!    ..... ITT [day] .....
    Itt = 1 + tt / 86400.0D0
!
    Iy4   = (Itt-1) / 1461
    Iyd   = Itt - Iy4 * 1461
    do IY = 1, 4
      if ( IY2D(Iy) + 1 .le. Iyd ) then
        Iy1 = Iy
      end if
    end do
!
    Iyr   = Iy4 * 4 + Iy1 - 1
    if ( mod(Iyr,4) .ne. 0 ) then
      Ileap = 0
    else
      Ileap = 1
    end if
    IMD = IYD - IY2D(IY1)
!
    do IM = 1, 12
      if ( IM2D(IM,ILEAP)+1 .le. IMD ) then
        IMON = IM
      end if
    end do
    IDAY = IMD - IM2D(IMON,ILEAP)
!
    TT0 = ND2TT(IYR, IMON, IDAY ,0,0,0)
```

```
      ITS = nint(  TT - TT0 )
      Ihour = ITS / 3600
      Imin  = ( ITS - Ihour * 3600 ) / 60
      Isec  = ITS - Ihour * 3600 - Imin * 60
!
      return
      end subroutine
!
```

Appendix 5 NEMURO.FISH (NEMURO FORTRAN code supplied by Yasuhiro Yamanaka) with the saury bioenergetic model (base case) (supplied by Bernard Megrey and Ken Rose and modified by "team saury"). The saury model is linked to NEMURO in a one-way static link.

```
!*******************************************************************************
!    NEMURO model     Jun 13, 2002  written by Yasuhiro Yamanaka
!                          modified by Masahiko Fujii
!                                Shin-ichi Ito
!*******************************************************************************
      program NEMURO
      implicit none
!     ..... Control for Time Ingration .....
      character(19)     :: Cstart = '0001/02/01 00:00:00'  ! Starting date
      character(19)     :: Cend   = '0003/02/01 00:00:00'  ! Ending date
      character(19)     :: Cstep  = '0000/00/00 01:00:00'  ! Time step
      character(19)     :: Cmon   = '0000/00/01 00:00:00'  ! Monitor Interval
      character(19)     :: CTime
      real(8)           :: dt, TTime, Tbefore, Season, Tmon
      integer           :: Iyr, Imon, Iday, Ihour, Imin, Isec
!     ..... scale conversion .....
      real(8),parameter :: d2s       = 86400.0d0    ! day ---> sec
      real(8),parameter :: mcr       = 1.0d-6       ! micro
!     ..... Prognostic Variables (with initial conditions) and Thier Source Term .....
      real(8)           :: TPS    =  0.1D-6, QPS    ! Small Phytoplankton [molN/l]
      real(8)           :: TPL    =  0.1D-6, QPL    ! Large Phytoplankton
      real(8)           :: TZS    =  0.1D-6, QZS    ! Small Zooplankton
      real(8)           :: TZL    =  0.1D-6, QZL    ! Large Zooplankton
      real(8)           :: TZP    =  0.1D-6, QZP    ! Pradatory Zooplankton
      real(8)           :: TNO3   =  5.0D-6, QNO3   ! Nitrate
      real(8)           :: TNH4   =  0.1D-6, QNH4   ! Ammmonium
      real(8)           :: TPON   =  0.1D-6, QPON   ! Particulate Organic Nitrogen
      real(8)           :: TDON   =  0.1D-6, QDON   ! dissolved Organic Nitrogen
      real(8)           :: TSiOH4 = 10.0D-6, QSiOH4 ! Silicate
      real(8)           :: TOpal  =  0.1D-7, QOpal  ! Particulate Opal
!     ..... Prognostic Variables (with initial conditions) and Thier Source Term .....
!      real(8)          :: THrr   =  0.2D0,  QHrrl  ! Particulate Opal
!     ..... Light Condition Parameters .....
      real(8),parameter :: alpha1   = 4.0D-2     ! Light Dissipation coefficient of sea water[/m]
      real(8),parameter :: alpha2   = 4.0D4      ! PS+PL Selfshading coefficientS+PL      [l/molN/m]
      real(8),parameter :: IoptS    = 0.15D0     ! PS Optimum Light Intensity  S          [ly/min]
      real(8),parameter :: IoptL    = 0.15D0     ! PL Optimum Light Intensity             [ly/min]
      integer,parameter :: LLN      = 10         ! Number of sublayer for calculating of Lfc
      real(8)           :: LfcS                  ! Light factor for PS
      real(8)           :: LfcL                  ! Light factor for PL
      real(8)           :: kappa, Lint, dLint, LfcUS, LfcUL, LfcDS, LfcDL
      integer           :: L
!     ..... biological Parameters .....
      real(8),parameter :: VmaxS    = 0.4D0/d2s  ! PS Maximum Photosynthetic rate @0degC   [/s]
      real(8),parameter :: KNO3S    = 1.0D-6     ! PS Half satuation constant for Nitrate  [molN/l]
      real(8),parameter :: KNH4S    = 0.1D-6     ! PS Half satuation constant for Ammonium [molN/l]
```

```
real(8),parameter :: PusaiS   = 1.5D6      ! PS Ammonium Inhibition Coefficient      [l/molN]
real(8),parameter :: KGppS    = 6.93D-2    ! PS Temp. Coeff. for Photosynthetic Rate [/degC]
real(8),parameter :: MorPS0   = 5.85D4/d2s ! PS Mortality Rate @0degC                [/s]
real(8),parameter :: KMorPS   = 6.93D-2    ! PS Temp. Coeff. for Mortality           [/degC]
real(8),parameter :: ResPS0   = 0.03D0/d2s ! PS Respiration Rate at @0degC           [/s]
real(8),parameter :: KResPS   = 0.0519D0   ! PS Temp. Coeff. for Respiration         [/degC]
real(8),parameter :: GammaS   = 0.135D0    ! PS Ratio of Extracell. Excret. to Photo.[(nodim)]
real(8),parameter :: VmaxL    = 0.8D0/d2s  ! PL Maximum Photosynthetic rate @0degC   [/s]
real(8),parameter :: KNO3L    = 3.00D-6    ! PL Half satuation constant for Nitrate  [molN/l]
real(8),parameter :: KNH4L    = 0.30D-6    ! PL Half satuation constant for Ammonium [molN/l]
real(8),parameter :: KSiL     = 6.00D-6    ! PL Half satuation constant for Silicate [molSi/l]
real(8),parameter :: PusaiL   = 1.50D6     ! PL Ammonium Inhibition Coefficient      [l/molN]
real(8),parameter :: KGppL    = 6.93D-2    ! PL Temp. Coeff. for Photosynthetic Rate [/degC]
real(8),parameter :: MorPL0   = 2.90D4/d2s ! PL Mortality Rate @0degC                [/s]
real(8),parameter :: KMorPL   = 6.93D-2    ! PL Temp. Coeff. for Mortality           [/degC]
real(8),parameter :: ResPL0   = 0.03D0/d2s ! PL Respiration Rate at @0degC           [/s]
real(8),parameter :: KResPL   = 0.0519D0   ! PL Temp. Coeff. for Respiration         [/degC]
real(8),parameter :: GammaL   = 0.135D0    ! PL Ratio of Extracell. Excret. to Photo.[(nodim)]
real(8),parameter :: GRmaxS   = 0.40D0/d2s ! ZS Maximum Rate of Grazing PS @0degC    [/s]
real(8),parameter :: KGraS    = 6.93D-2    ! ZS Temp. Coeff. for Grazing             [/degC]
real(8),parameter :: LamS     = 1.40D6     ! ZS Ivlev constant                       [l/molN]
real(8),parameter :: PS2ZSstar= 0.043D-6   ! ZS Threshold Value for Grazing PS       [molN/l]
real(8),parameter :: AlphaZS  = 0.70D0     ! ZS Assimilation Efficiency              [(nodim)]
real(8),parameter :: BetaZS   = 0.30D0     ! ZS Growth Efficiency                    [(nodim)]
real(8),parameter :: MorZS0   = 5.85D4/d2s ! ZS Mortality Rate @0degC                [/s]
real(8),parameter :: KMorZS   = 0.0693D0   ! ZS Temp. Coeff. for Mortality           [/degC]
real(8),parameter :: GRmaxLps = 0.10D0/d2s ! ZL Maximum Rate of Grazing PS @0degC    [/s]
real(8),parameter :: GRmaxLpl = 0.40D0/d2s ! ZL Maximum Rate of Grazing PL @0degC    [/s]
real(8),parameter :: GRmaxLzs = 0.40D0/d2s ! ZL Maximum Rate of Grazing ZS @0degC    [/s]
real(8),parameter :: KGraL    = 6.93D-2    ! ZL Temp. Coeff. for Grazing             [/degC]
real(8),parameter :: LamL     = 1.4000D6   ! ZL Ivlev constant                       [l/molN]
real(8),parameter :: PS2ZLstar= 4.00D-8    ! ZL Threshold Value for Grazing PS       [molN/l]
real(8),parameter :: PL2ZLstar= 4.00D-8    ! ZL Threshold Value for Grazing PL       [molN/l]
real(8),parameter :: ZS2ZLstar= 4.00D-8    ! ZL Threshold Value for Grazing ZS       [molN/l]
real(8),parameter :: AlphaZL  = 0.70D0     ! ZL Assimilation Efficiency              [(nodim)]
real(8),parameter :: BetaZL   = 0.30D0     ! ZL Growth Efficiency                    [(nodim)]
real(8),parameter :: MorZL0   = 5.85D4/d2s ! ZL Mortality Rate @0degC                [/s]
real(8),parameter :: KMorZL   = 0.0693D0   ! ZL Temp. Coeff. for Mortality           [/degC]
real(8),parameter :: GRmaxPpl = 0.20D0/d2s ! ZP Maximum rate of grazing PL @0degC    [/s]
real(8),parameter :: GRmaxPzs = 0.20D0/d2s ! ZP Maximum rate of grazing ZS @0degC    [/s]
real(8),parameter :: GRmaxPzl = 0.20D0/d2s ! ZP Maximum rate of grazing ZL @0degC    [/s]
real(8),parameter :: KGraP    = 6.93D-2    ! ZP Temp. Coeff. for grazing             [/degC]
real(8),parameter :: LamP     = 1.4000D6   ! ZP Ivlev constant                       [l/molN]
real(8),parameter :: PL2ZPstar= 4.00D-8    ! ZP Threshold Value for Grazing PL       [molN/l]
real(8),parameter :: ZS2ZPstar= 4.00D-8    ! ZP Threshold Value for Grazing ZS       [molN/l]
real(8),parameter :: ZL2ZPstar= 4.00D-8    ! ZP Threshold Value for Grazing ZL       [molN/l]
real(8),parameter :: PusaiPL  = 4.605D6    ! ZP Preference Coeff. for PL             [l/molN]
real(8),parameter :: PusaiZS  = 3.010D6    ! ZP Preference Coeff. for ZS             [l/molN]
real(8),parameter :: AlphaZP  = 0.70D0     ! ZP Assimilation Efficiency              [(nodim)]
real(8),parameter :: BetaZP   = 0.30D0     ! ZP Growth Efficiency                    [(nodim)]
real(8),parameter :: MorZP0   = 5.85D4/d2s ! ZP Mortality Rate @0degC                [/s]
```

```
    real(8),parameter :: KMorZP   = 0.0693D0   ! ZP Temp. Coeff. for Mortality          [/degC]
    real(8),parameter :: Nit0     = 0.03D0/d2s ! NH4 Nitrification Rate @0degC          [/s]
    real(8),parameter :: KNit     = 0.0693D0   ! NH4 Temp. coefficient for Nitrification [/degC]
    real(8),parameter :: VP2N0    = 0.10D0/d2s ! PON Decomp. Rate to Ammonium @0degC    [/s]
    real(8),parameter :: KP2N     = 6.93D-2    ! PON Temp. Coeff. for Decomp. to Ammon.  [/degC]
    real(8),parameter :: VP2D0    = 0.10D0/d2s ! PON Decomp. Rate to DON @0degC         [/s]
    real(8),parameter :: KP2D     = 6.93D-2    ! PON Temp. Coeff. for Decomp. to DON     [/degC]
    real(8),parameter :: VD2N0    = 0.20D0/d2s ! DON Decomp. Rate to Ammonium @0degC    [/s]
    real(8),parameter :: KD2N     = 6.93D-2    ! DON Temp. Coeff. for Decomp. to Ammon.  [/degC]
    real(8),parameter :: VO2S0    = 0.10D0/d2s ! Opal Decomp. Rate to Silicate @0degC   [/s]
    real(8),parameter :: KO2S     = 6.93D-2    ! Opal Temp. Coeff. for Decomp.to Silicate[/degC]
    real(8),parameter :: RSiN     = 2.0D0      !Si/N ratio                  [molSi/molN]
    real(8),parameter :: RCN      = 106.0D0/16.0D0 !C/N ratio               [molC/molN]
!   ..... bottom boundary Condition .....
    real(8),parameter :: setVPON  = 40.0D0/d2s ! Settling velocity of PON           [m/s]
    real(8),parameter :: setVOpal = 40.0D0/d2s ! Settling velocity of Opal          [m/s]
    real(8),parameter :: TNO3d   =  25.0d-6    ! Nitrate Concentraion in the Deep Layer  [molN/l]
    real(8),parameter :: TSiOH4d =  35.0d-6    ! Silicate Concentraion in the Deep Layer [molSi/l]
!   ..... Paramters of ZL Vertical Migration .....
    character(19)     :: CZup ='0000/04/01 00:00:00' ! Date Coming up to the Euphotic Layer
    character(19)     :: CZdwn='0000/09/01 00:00:00' ! Date Returning to the Deep Layer
    real(8)           :: TZup, TZdwn, TZLd, SVRate=0.2D0
    integer           :: IyrU, ImonU, IdayU ,IhourU, IminU, IsecU
    integer           :: IyrD, ImonD, IdayD ,IhourD, IminD, IsecD
!
    real(8)           :: GppPSn,  GppNPSn, GppAPSn, RnewS, ResPSn,  MorPSn,  ExcPSn
    real(8)           :: GppPLn,  GppNPLn, GppAPLn, RnewL, ResPLn,  MorPLn,  ExcPLn
    real(8)           :: GppPLsi, GppSiPLsi,          ResPLsi, MorPLsi, ExcPLsi
    real(8)           :: GraPS2ZSn, GraPS2ZLn,  GraPL2ZLn, GraPL2ZLsi, GraZS2ZLn
    real(8)           :: GraPL2ZPn, GraPL2ZPsi, GraZS2ZPn, GraZL2ZPn
    real(8)           :: EgeZSn, MorZSn, ExcZSn, EgeZLn, EgeZLsi, MorZLn, ExcZLn
    real(8)           ::                 EgeZPn, EgeZPsi, MorZPn, ExcZPn
    real(8)           :: DecP2N, DecP2D, DecD2N, DecO2S, Nit
    real(8)           :: ExpPON, ExpOpal,ExcNO3, ExcSiOH4
    integer           :: lt=0 , nt
!
!   ..... Environmental Condition .....
    real(8)           :: Temp                  ! Temperature [degC]
    real(8)           :: Lint0                 ! Light Intencity at sea surface [ly/min]
    real(8)           :: MLD = 30.0d0          ! Mixed Layer Depth [m]
    real(8)           :: ExcTime = 1.0d0 / (100.0d0*d2s) ! Exch. Coeff. between Sur-Deep [/s]
!   ..... statement function & def. type of functions .....
    real(8)           :: cd2tt, nd2tt
    character(19)     :: tt2cd
    real(8)           :: Td, GraF, Mich, a, b, c
    Td  (a,b)   = a * exp(b*Temp)
    GraF(a,b,c) = MAX( 0.0D0, 1.0 - exp(a * (b - c)))
    Mich(a,b)   = b / ( a + b )
!
!   ***** Initial Setting *****
!   ..... for time control .....
```

```
      TTime = cd2tt(Cstart)                          ! Starting Date
      CTime = TT2CD(TTime)                           ! present time (charactor form)
      dt    = cd2tt(Cstep) - cd2tt('0000/00/00 00:00:00')  ! Time Step (real8 form)
      Tmon  = cd2tt(Cmon)  - cd2tt('0000/00/00 00:00:00')  ! Monitor Interval (real8 form)
      nt = NINT( ( cd2tt(Cend) - cd2tt(Cstart) ) / dt )    ! Total Time Steps
!     ..... for Vertical Migration ......
      TZup  = CD2TT( CZup  )
      TZdwn = CD2TT( CZdwn )
      call TT2ND(IyrU, ImonU, IdayU ,IhourU, IminU, IsecU ,TZup )
      call TT2ND(IyrD, ImonD, IdayD ,IhourD, IminD, IsecD ,TZdwn)
      TZLd = TZL  ! ZL living in the deep layer at the initial condition
      TZL  = 0.0
!     ..... File Open for monitoring output .....
      open( 10, file='Results.csv', form='FORMATTED' )
      write(10,'(A,13(",", A))') 'Time(day)', &
                 'NO3'   , 'NH4'     , 'PS'     , 'PL'      , &
                 'ZS'    , 'ZL'      , 'ZP'     , 'PON'     , &
                 'DON'   , 'SiOH4'   , 'Opal'   , 'TotalN'  , 'TotalSi'
      write(10,'(A,11(",", F8.4))') CTime, &
                 TNO3/mcr, TNH4  /mcr, TPS  /mcr, TPL /mcr, &
                 TZS /mcr, TZL   /mcr, TZP  /mcr, TPON/mcr, &
                 TDON/mcr, TSiOH4/mcr, TOpal/mcr
      open( 11, file='Forcing.csv', form='FORMATTED' )
      write(11,'(A,13(",", A))') 'Time(day)','Lint0', 'TMP', 'MLD', 'ExcTime'
      write(11,'(A,13(",", 1PE10.4))') CTime, Lint0, Temp, MLD, ExcTime*d2s
!
!     ****** Main Loop *****
      do lt = 1, nt
!       ..... time control (Season : 0 to 1, parcentage in a year).....
        Tbefore = TTime                              ! one step before present time
        TTime   = TTime + dt                         ! present time (real8 form)
        CTime = TT2CD(TTime)                         ! present time (charactor form)
        CALL TT2ND(Iyr, Imon, Iday ,Ihour, Imin, Isec ,TTime)
        Season = ( TTime                - ND2TT(Iyr  ,1,1,0,0,0) )/  &
                 ( ND2TT(Iyr+1,1,1,0,0,0) - ND2TT(Iyr  ,1,1,0,0,0) )
!
!       ..... Example of Boundray condition .....
        Lint0 = 0.1d0 * ( 1.0D0 + 0.3d0 * cos( 2.0d0*3.1415926536d0*(Season - 0.50D0) ) )
        Temp  =          6.0D0 + 4.0d0 * cos( 2.0d0*3.1415926536d0*(Season - 0.65D0) )
        if (Temp .lt. 4.0 ) then
          MLD = MLD + dt * (150.0d0 - MLD ) / ( 100.0d0 * d2s )
          ExcTime = ExcTime + dt * ( 1.0d0/( 40.0d0*d2s) - ExcTime ) / (100.0d0*d2s)
        else
          MLD = MLD + dt * ( 30.0d0 - MLD ) / (   5.0d0 * d2s )
          ExcTime = ExcTime + dt * ( 1.0d0/(100.0d0*d2s) - ExcTime ) / (  5.0d0*d2s)
        end if
!
!       ..... Light Factors (LfcS, LfcL).....
        Lint = Lint0
        LfcDS = Lint/IoptS * exp(1.0D0 - Lint/IoptS)
        LfcDL = Lint/IoptL * exp(1.0D0 - Lint/IoptL)
```

```
      LfcS  = 0.0D0
      LfcL  = 0.0D0
      Kappa = alpha1 + alpha2 * ( TPS + TPL )
      dLint = exp( -Kappa * (MLD/LLN) )
      do L = 1, LLN
        LfcUS  = LfcDS
        LfcUL  = LfcDL
        Lint   = Lint      * dLint
        LfcDS  = Lint/IoptS * exp( 1.0D0 - Lint/IoptS )
        LfcDL  = Lint/IoptL * exp( 1.0D0 - Lint/IoptL )
        LfcS   = LfcS + ( LfcUS + LfcDS ) * 0.5D0 / LLN
        LfcL   = LfcL + ( LfcUL + LfcDL ) * 0.5D0 / LLN
      end do
!     ..... Photosynthesis of PS .....
      GppNPSn   = Mich( KNO3S, TNO3 ) * exp( - PusaiS * TNH4 )
      GppAPSn   = Mich( KNH4S, TNH4 )
      GppPSn    = Td(VmaxS, KGppS) * LfcS * TPS * ( GppNPSn + GppAPSn )
      RnewS     = GppNPSn / ( GppNPSn + GppAPSn )

      ResPSn    = Td( ResPS0, KResPS ) * TPS
      MorPSn    = Td( MorPS0, KMorPS ) * TPS * TPS
      ExcPSn    = GammaS             * GppPSn
!     ..... Photosynthesis of PL .....
      GppNPLn   = Mich( KNO3L, TNO3   ) * exp( - PusaiL * TNH4 )
      GppAPLn   = Mich( KNH4L, TNH4   )
      GppSiPLsi = Mich( KSiL , TSiOH4 )
      GppPLn    = Td(VmaxL, KGppL) * LfcL * TPL * min( ( GppNPLn + GppAPLn ), GppSiPLsi )
      RnewL     = GppNPLn / ( GppNPLn + GppAPLn )
      ResPLn    = Td( ResPL0, KResPL ) * TPL
      MorPLn    = Td( MorPL0, KMorPL ) * TPL * TPL
      ExcPLn    = GammaL             * GppPLn
!     ..... Grazing PS, PL, ZS, ZL --> ZS, ZL, ZP .....
      GraPS2ZSn = Td(GRmaxS,  KGraS) *GraF(LamS,PS2ZSstar,TPS) *TZS
      GraPS2ZLn = Td(GRmaxLps,KGraL) *GraF(LamL,PS2ZLstar,TPS) *TZL
      GraPL2ZLn = Td(GRmaxLpl,KGraL) *GraF(LamL,PL2ZLstar,TPL) *TZL
      GraZS2ZLn = Td(GRmaxLzs,KGraL) *GraF(LamL,ZS2ZLstar,TZS) *TZL
      GraPL2ZPn = Td(GRmaxPpl,KGraP) *GraF(LamP,PL2ZPstar,TPL) *TZP * exp( -PusaiPL *(TZL
     + TZS))
      GraZS2ZPn = Td(GRmaxPzs,KGraP) *GraF(LamP,ZS2ZPstar,TZS) *TZP * exp( -PusaiZS * TZL )
      GraZL2ZPn = Td(GRmaxPzl,KGraP) *GraF(LamP,ZL2ZPstar,TZL) *TZP
!     ..... Mortality, Excration, Egestion for Zooplanktons
!     ..... Commented out after Saito-san Meeting at 19 Jun, 2000 .....
!     BetaZS = 0.3 ** (  1.0 + Mich( TPL, TPS )  )
      ExcZSn = (AlphaZS-  BetaZS)   * GraPS2ZSn
      EgeZSn = (1.0    - AlphaZS)   * GraPS2ZSn
      MorZSn = Td( MorZS0, KMorZS ) * TZS * TZS
      ExcZLn = (AlphaZL-  BetaZL)   * (GraPS2ZLn+GraPL2ZLn+GraZS2ZLn)
      EgeZLn = (1.0    - AlphaZL)   * (GraPS2ZLn+GraPL2ZLn+GraZS2ZLn)
      MorZLn = Td( MorZL0, KMorZL ) * TZL * TZL
      ExcZPn = (AlphaZP-  BetaZP)   * (GraPL2ZPn+GraZS2ZPn+GraZL2ZPn)
      EgeZPn = (1.0    - AlphaZP)   * (GraPL2ZPn+GraZS2ZPn+GraZL2ZPn)
```

```
      MorZPn = Td( MorZP0, KMorZP ) * TZP * TZP
!     ..... Decomposition PON, DON, Opal ---> NH4, DON, SiOH4 .....
      DecP2N    = Td( VP2N0  , KP2N ) * TPON
      DecP2D    = Td( VP2D0  , KP2D ) * TPON
      DecD2N    = Td( VD2N0  , KD2N ) * TDON
      DecO2S    = Td( VO2S0  , KO2S ) * TOpal
      Nit       = Td( Nit0   , KNit ) * TNH4
!     ..... silica fluxes .....
      GppPLsi    = GppPLn    * RSiN
      ResPLsi    = ResPLn    * RSiN
      MorPLsi    = MorPLn    * RSiN
      ExcPLsi    = ExcPLn    * RSiN
      GraPL2ZLsi = GraPL2ZLn * RSiN
      GraPL2ZPsi = GraPL2ZPn * RSiN
      EgeZLsi    = GraPL2ZLsi
      EgeZPsi    = GraPL2ZPsi
!
!     ..... Tendency Terms for biological processes .....
      QNO3   = -( GppPSn - ResPSn ) * RnewS   &
             -( GppPLn - ResPLn ) * RnewL + Nit
      QNH4   = -( GppPSn - ResPSn ) * (1.0 - RnewS)   &
             -( GppPLn - ResPLn ) * (1.0 - RnewL)   &
             - Nit + DecP2N + DecD2N + ExcZSn + ExcZLn + ExcZPn
      QPS    = GppPSn - ResPSn - MorPSn - ExcPSn - GraPS2ZSn - GraPS2ZLn
      QPL    = GppPLn - ResPLn - MorPLn - ExcPLn - GraPL2ZLn - GraPL2ZPn
      QZS    = GraPS2ZSn - GraZS2ZLn - MorZSn - ExcZSn - EgeZSn - GraZS2ZPn
      QZL    = GraPL2ZLn + GraZS2ZLn - MorZLn - ExcZLn - EgeZLn + GraPS2ZLn - GraZL2ZPn
      QZP    = GraPL2ZPn + GraZS2ZPn - MorZPn - ExcZPn - EgeZPn + GraZL2ZPn
      QPON   = MorPSn  + MorPLn  + MorZSn  + MorZLn + MorZPn   &
           + EgeZPn  + EgeZSn  + EgeZLn  - DecP2N - DecP2D
      QDON   = ExcPSn  + ExcPLn  + DecP2D  - DecD2N
      QSiOH4 =-GppPLsi + ResPLsi + ExcPLsi + DecO2S
      QOpal  = MorPLsi + EgeZLsi + EgeZPsi - DecO2S
!
!     ..... Exchange Fluxes between the Surface and Deep Layers .....
      ExpPON   = setVPON  / MLD * TPON
      ExpOpal  = setVOpal / MLD * TOpal
      ExcNO3   = ExcTime * ( TNO3d   - TNO3   )
      ExcSiOH4 = ExcTime * ( TSiOH4d - TSiOH4 )
      QNO3   = QNO3   + ExcNO3
      QSiOH4 = QSiOH4 + ExcSiOH4
      QPON   = QPON   - ExpPON
      QOpal  = QOpal  - ExpOpal
!
!     ..... Time Integration with Forward Scheme .....
      TNO3   = TNO3   + dt * QNO3
      TNH4   = TNH4   + dt * QNH4
      TPS    = TPS    + dt * QPS
      TPL    = TPL    + dt * QPL
      TZS    = TZS    + dt * QZS
      TZL    = TZL    + dt * QZL
```

```
      TZP    = TZP    + dt * QZP
      TPON   = TPON   + dt * QPON
      TDON   = TDON   + dt * QDON
      TSiOH4 = TSiOH4 + dt * QSiOH4
      TOpal  = TOpal  + dt * QOpal
!
!     ..... Vertical Migration of ZL .....
      TZdwn = ND2TT(Iyr, ImonD, IdayD ,IhourD, IminD, IsecD )
      TZup  = ND2TT(Iyr, ImonU, IdayU ,IhourU, IminU, IsecU )
      if ( (Tbefore .lt. TZdwn).and.(TTime .ge. TZdwn) ) then
        TZLd = TZL
        TZL  = 0.0
        write(*,*) '*** Down ***', CTime
      end if
      if ( (Tbefore .lt. TZup).and.(TTime .ge. TZup) ) then
        TZL = SVRate * TZLd
        write(*,*) '***  UP  ***', CTime
      end if
!
      call Saury(TTime, Tbefore, TZS, TZL, TZP, Temp)
!
!     ..... Monitor .....
      if ( int(TTime/Tmon).ne. int(Tbefore/Tmon) ) then
!       write(*,'(A,13(",", F8.4))') CTime, Season
        write(10,'(A,11(",", F8.4))') CTime, &
              TNO3/mcr, TNH4  /mcr, TPS  /mcr, TPL /mcr, &
              TZS /mcr, TZL   /mcr, TZP  /mcr, TPON/mcr, &
              TDON/mcr, TSiOH4/mcr, TOpal/mcr
        write(11,'(A,13(",", 1PE10.4))') CTime, Lint0, Temp, MLD, ExcTime*d2s
      end if
    end do
!
    close(10); close(11)
!
    stop
    end
!*******************************************************************************
    Subroutine Saury(TTime, Tbefore, TZS, TZL, TZP, Temp)
!
    implicit none
    real(8)          :: TTime, Tbefore, TZS, TZL, TZP, Temp
    real(8),parameter :: d2s       = 86400.0d0    ! day ---> sec
    integer          :: Iyr, Imon, Iday, Ihour, Imin, Isec
    character(19)    :: CAge ='0000/03/01 00:00:00' ! Date of Aging ( JJday = 200 )
    character(19)    :: CTime
    character(19)    :: CAge2 ='0000/07/01 00:00:00' ! Date of Aging ( JJday = 200 )
    character(19)    :: CTime2
    real(8)          :: TAge
    real(8)          :: TAge2
    integer          :: iage = 0
    integer, save    :: IyrA, ImonA, IdayA ,IhourA, IminA, IsecA
```

```
      integer, save     :: IyrB, ImonB, IdayB ,IhourB, IminB, IsecB
      integer           :: JJday
      real(8)           :: ZooP1, ZooP2, ZooP3, tt1
      real(8)           :: t1,t2,wtemp
      real(8)           :: x(1) =0.2d0, xdot(1)
      real(8)           :: cd2tt, nd2tt
      character(19)     :: tt2cd
      real(8)           :: vul(3), k(3)
      integer(4)        :: id(365)
      real(8)           :: zop1(365), zop2(365), zop3(365)
      real(8):: v, a, u, resp
     real(8) :: xk1,xk2,xk3,xk4,te1,te2,te3,te4,tt5,t5,t4,tt7,t7,t6, gcta,gctb,gctemp,gcmax
     real(8) :: cnum,c1,c2,c3,con1,con2,con3,con
     real(8) :: f,e, sda
     real(8) :: phalf
!
      integer, save     :: First = 1
!
      PHalf=0.100

!     ==================
      if ( First .eq. 1 ) then; First = 0
        TAge  = CD2TT( CAge  )
        call TT2ND(IyrA, ImonA, IdayA ,IhourA, IminA, IsecA ,TAge )
        TAge2  = CD2TT( CAge2  )
        call TT2ND(IyrB, ImonB, IdayB ,IhourB, IminB, IsecB ,TAge2 )
        open( 20, file='saury.csv', form='FORMATTED' )

!
!!!!        OPEN(UNIT=111,FILE='nemuro.txt',STATUS='unknown')
!!!!        -----read in the 3 zoop groups from Nemuro output last 3 columns
!!!!        do JJday=1,365
!!!!          READ(111,999)id(JJday),zop1(JJday),zop2(JJday),zop3(JJday)
!!!!  999      FORMAT(1x,i3,1x,3(e13.6,1x))
!!!!        end do
      end if
!     ==================

!
      CTime = TT2CD(TTime)                          ! present time (charactor form)
      CALL TT2ND(Iyr, Imon, Iday ,Ihour, Imin, Isec ,TTime)
      JJday = 1 + ( TTime - ND2TT(Iyr  ,1,1,0,0,0) ) / d2s
!
!------convert Nemuro zoop in uM N/L to g ww/m3
!------  tt1 is conversion from uM N/liter to g ww/m3
!------  14 ug N/uM * 1.0e-6 g/ug * 1 g dw/0.07 g N dw * 1 g ww/0.2 g dw
!------       1.0e3 liters/m3
!
      tt1=14.0*1.0e-6*(1.0/0.07)*(1.0/0.2)*1.0e3
      zoop1 = TZS*tt1 *1.0d6
      zoop2 = TZL*tt1 *1.0d6
```

```
      zoop3 = TZP*tt1 *1.0d6
!!!!     zoop1 = zop1(JJday) * tt1
!!!!     zoop2 = zop2(JJday) * tt1
!!!!     zoop3 = zop3(JJday) * tt1
!
!     ..... Temperature Seting .....
!
      t1=float(jjday)
      t2=12.75-10.99*cos(0.0172*t1)-6.63*sin(0.0172*t1)
      wtemp=t2-5.0
      IF(wtemp.le.1.0)wtemp=1.0

!      write(*,*) TT2CD(cd2tt('0002/01/01 00:00:00')+200.0*86400.0)
!      stop
!     ..... Aging of saury ......
      TAge = ND2TT(Iyr, ImonA, IdayA ,IhourA, IminA, IsecA )
      if ( (Tbefore .lt. TAge).and.(TTime .ge. TAge) .and. (iage.eq.0)) then
           write(*,*) '*** Aging +1 of saury ***', CTime
           iage = iage + 1
      end if
      TAge2 = ND2TT(Iyr, ImonB, IdayB ,IhourB, IminB, IsecB )
      if ( (Tbefore .lt. TAge2).and.(TTime .ge. TAge2) .and. (iage.eq.1) ) then
           write(*,*) '*** Aging +1 of saury ***', CTime
           iage = iage + 1
      end if
!
!--- saury weight state variable = x(1)
!
!----- set vulnerabilities and k values for 3 zoop groups
!
      if ( iage .eq. 0 ) then
        vul(1) =   1.0; vul(2) =  0.0; vul(3) =   0.0
        k  (1) = phalf; k  (2) = phalf; k  (3) = phalf
      else if ( iage .eq. 1 ) then
        vul(1) =   1.0; vul(2) =  1.0; vul(3) =   0.0
        k  (1) = phalf; k  (2) = phalf; k  (3) = phalf
      else
        vul(1) =   0.0; vul(2) =  1.0; vul(3) =   1.0
        k  (1) = phalf; k  (2) = phalf; k  (3) = phalf
      endif
!
! --- weight affect on respiration
!
      tt1 = 1.0 / x(1)
      t1  = 0.0033 * tt1**0.227
! --- *********this is the new stuff from Ahhrenius for YOY only*********
! --- The 5.258 puts resp (g oxygen/fish) into units of g zoop/g fish/day
! --- [13560 joules/gram oxygen]/4.18 joules/cal = 3244 cal/gO2
! --- [2580 joules/gram zoop]/4.18 joules/cal = 617 cal/g zoop
! --- so respiration in grams/oxygen/g fish/day is multiplied by 3244/617 = 5.258
! --- to get food energy equivalents of a gram of oxygen respired
```

```
!
!ccc      IF (iage .eq. 0 )then
!ccc        IF(wtemp.le.15.0)then
!ccc          v = 5.76 * exp( 0.0238 * wtemp ) * x(1)**0.386
!ccc        else
!ccc          v = 8.6 * x(1)**0.386
!ccc        endif
!ccc        a=EXP((0.03-0.0*wtemp)*v)
!ccc        resp=t1*EXP(0.0548*wtemp)*a*5.258
! --- *********back to the old equations for respiration for age-1 and older********
!ccc      else   ! (iage .gt. 0)
!c         IF (wtemp.le.9.0)then
        IF (wtemp.le.12.0)then
!C           u=3.9*x(1)**0.13*EXP(0.149*wtemp)
          u=2.0*x(1)**0.33*EXP(0.149*wtemp)
        else
!c           u=15.0*x(1)**0.13
          u=11.7*x(1)**0.33
        endif
          resp=t1*EXP(0.0548*wtemp)*EXP(0.03*u)*5.258
!ccc      endif
!C
!C --- Thornton and Lessem temperature effect
!C --- age dependent values
!C --- *******Arrhenius for age-0 he changed te4 from 25 to 23 degrees******
!C
     if ( iage .eq. 0 ) then
!c         xk1 = 0.1;  xk2 = 0.98;  xk3 = 0.98;  xk4 = 0.01
!c         te1 = 1.0;  te2 = 15.0;  te3 = 17.0;  te4 = 23.0
        xk1 = 0.1;  xk2 = 0.98;  xk3 = 0.98;  xk4 = 0.5
        te1 = 5.0;  te2 = 20.0;  te3 = 26.0;  te4 = 30.0
     else if ( iage .eq. 1 ) then
!c         xk1 = 0.1;  xk2 = 0.98;  xk3 = 0.98;  xk4 = 0.01
!c         te1 = 1.0;  te2 = 15.0;  te3 = 17.0;  te4 = 25.0
        xk1 = 0.1;  xk2 = 0.98;  xk3 = 0.98;  xk4 = 0.5
        te1 = 5.0;  te2 = 16.0;  te3 = 20.0;  te4 = 30.0
     else if( iage .gt. 1 ) then
!c         xk1 = 0.1;  xk2 = 0.98;  xk3 = 0.98;  xk4 = 0.01
!c         te1 = 1.0;  te2 = 13.0;  te3 = 15.0;  te4 = 23.0
        xk1 = 0.1;  xk2 = 0.98;  xk3 = 0.98;  xk4 = 0.5
        te1 = 5.0;  te2 = 16.0;  te3 = 20.0;  te4 = 30.0
     endif
!
     tt5 = ( 1.0 / ( te2 - te1 ) )
     t5  = tt5 * log( xk2 * ( 1.0 - xk1 ) / ( (1.0-xk2) * xk1 ) )
     t4  = exp( t5 * ( wtemp - te1 ) )
!
     tt7 = 1.0 /( te4 - te3 )
     t7  = tt7 * log( xk3 * ( 1.0 - xk4 ) / ( (1.0-xk3) * xk4 ) )
     t6  = exp( t7 * ( te4 - wtemp ) )
!
```

```
      gcta  = ( xk1 * t4 ) / ( 1.0 + xk1 * ( t4 - 1.0 ) )
      gctb  = xk4 * t6 / ( 1.0 + xk4 * ( t6 - 1.0 ) )
      gctemp= gcta * gctb
!c      gcmax = 0.642 * tt1**0.256 * gctemp
      gcmax = 0.6 * tt1**0.256 * gctemp
!
! --- multispecies functional response
! --- usse either this or adjust little p
!
      cnum=zoop1 * vul(1)/k(1) + zoop2*vul(2)/k(2) +zoop3 * vul(3)/k(3)
      c1=gcmax*zoop1*vul(1)/k(1)
      c2=gcmax*zoop2*vul(2)/k(2)
      c3=gcmax*zoop3*vul(3)/k(3)
      con1=c1/(1.0+cnum)
      con2=c2/(1.0+cnum)
      con3=c3/(1.0+cnum)
      con= con1+con2+con3
!
!-----if using constant p rather than functional response, set p here
! --- to tune to observed size at age data
!     con=0.425*gcmax
!
! --- egestion
!
          f=0.16*con
!
! --- excretion
          e=0.1*(con-f)
!
!
! --- Specific Dynamic Action
!
!c------   *******Arrhenius age dependent SDA from 17.5% to 15% ****
          IF ( iage .eq. 0 ) then
            sda=0.15*(con-f)
          else
            sda=0.175*(con-f)
          end if
!C
!C --- use the ratio of calories/g of zoop (2580) to calories/g of fish (5533)
!C
!C --- bioenergetics differential equation
!C
         xdot(1)=(con-resp-f-e-sda)*x(1)*2580./5533.
!
         IF(wtemp.le.1.0)xdot(1)=0.0
!C
!C --- Spawning section. Assume loose 20% of bosy weight/day
!C             t1=float(jjday)
!      if( mod(JJday,365) .ge. 152.0 .and. mod(JJday,365) .le. 156.0) then
!         xdot(1)=(con-resp-f-e-sda-0.20)*x(1)*2580./5533.
```

```
!         write(*,*) '### Spawning ###'
!      endif
!
!     if (iage .eq. 1 ) then
!      write(*,*) JJday, wtemp, x(1), xdot(1)
!      stop
!      end if
!      write(*,'(A,I4,3(1PE14.5))') Ctime, JJday, wtemp, x(1), xdot(1)
!
!     Time Integration
!
      x(1) = x(1) + 3600.0d0 /d2s * xdot(1)
!
!     ..... for Check .....
     if ( int(TTime/d2s) .ne. int(Tbefore/d2s) ) then
!!        write(*,'(A,I4,3(1PE14.5))') Ctime, JJday, wtemp, x(1), xdot(1)
!!         stop
!!      write(*,*) TZS, zop1(JJday), TZL,zop2(JJday), TZP,zop3(JJday)
!!      write(*,*) TZP*1.0d6, zop3(JJday)
        write(20,'(A,11(",", F12.4))') CTime, x(1), wtemp, gcmax
      end if
!
      return
!
      stop
      end
!*************************************************************************************
!* Utilities for Date Control  Writtien by Yasuhiro Yamanaka (galapen@ees.hokudai.ac.jp) *
!*************************************************************************************
!     exp. 1997/12/31 23:59:59 --> 6.223158719900000E+10
!     exp. 0000/01/01 00:00:00 --> 0.000000000000000E+00
!*************************************************************************************
      real(8) function CD2TT( Cdate )
!
      integer       :: Iyr, Imon, Iday , Ihour, Imin, Isec
      real(8)       :: ND2TT
      character(19) :: Cdate
!
      if ( len( Cdate ) .ne. 19 ) then
        write(*,*) '### Length of date is no good ###'
        stop
      end if
      read (Cdate( 1: 4),*)  Iyr
      read (Cdate( 6: 7),*)  Imon
      read (Cdate( 9:10),*)  Iday
      read (Cdate(12:13),*)  Ihour
      read (Cdate(15:16),*)  Imin
      read (Cdate(18:19),*)  Isec
!
      CD2TT = ND2TT(Iyr, Imon, Iday , Ihour, Imin, Isec)
!
```

```
    return
    end function
!**********************************************************************
!    exp. 6.223158719900000E+10 --> 1997/12/31 23:59:59
!**********************************************************************
    character(19) function TT2CD(tt)
!
    integer :: Iyr, Imon, Iday , Ihour, Imin, Isec
    real(8) :: tt
!
    call TT2ND( Iyr, Imon, Iday, Ihour, Imin, Isec , tt )
!
    write(TT2CD,'(I4.4,5(A,I2.2))') Iyr, '/', Imon, '/', Iday, &
                        ' ', Ihour, ':', Imin, ':', Isec
!
    return
    end function
!**********************************************************************
!    exp. 1997,12,31,23,59,59 --> 6.223158719900000E+10
!**********************************************************************
    real(8) function ND2TT(Iyr, Imon, Iday, Ihour, Imin, Isec)
!
    integer   :: IM2D(12,0:1) = &
      reshape( (/ 0,31,59,90,120,151,181,212,243,273,304,334,  &
                  0,31,60,91,121,152,182,213,244,274,305,335  /), (/12,2/) )
    integer   :: Iyr, Imon, Iday, Ihour, Imin, Isec
    integer   :: Iy4, Iy1, Ileap, Im, Itt
!
!
    Iy4 = 1461 * ( Iyr / 4 )
    Iy1 = 365 * mod( Iyr, 4 )
!
    if ( mod( Iyr, 4 ) .ne. 0 ) then
      Ileap = 0
    else
      Ileap = 1
    end if
    Im = IM2D( Imon, Ileap)
!
    Itt = Iy4 + Iy1 + Im + Iday - Ileap
!
    ND2TT = Ihour * 3600 + Imin * 60 + Isec
    ND2TT = ND2TT + Itt * 86400.0D0
!
    return
    end function
!**********************************************************************
!    exp. 6.223158719900000E+10 --> 1997,12,31,23,59,59
!**********************************************************************
    subroutine TT2ND(                                &
            Iyr   , Imon  , Iday   , Ihour, Imin, Isec,   & !O & I
```

```
            tt    )
!
    integer :: Iyr, Imon, Iday , Ihour, Imin, Isec
    integer :: Itt, Iy, Iy4, Iyd, Iy1, Ileap, Imd, Im, Its
    integer   :: IM2D(12,0:1) = &
      reshape( (/ 0,31,59,90,120,151,181,212,243,273,304,334,  &
                  0,31,60,91,121,152,182,213,244,274,305,335  /), (/12,2/) )
    integer :: IY2D(4) = (/0,366,731,1096/)
    real(8) :: tt, tt0, ND2TT
!
!
!   ..... ITT [day] .....
    Itt = 1 + tt / 86400.0D0
!
    Iy4   = (Itt-1) / 1461
    Iyd   = Itt - Iy4 * 1461
    do IY = 1, 4
      if ( IY2D(Iy) + 1 .le. Iyd ) then
        Iy1 = Iy
      end if
    end do
!
    Iyr   = Iy4 * 4 + Iy1 - 1
    if ( mod(Iyr,4) .ne. 0 ) then
      Ileap = 0
    else
      Ileap = 1
    end if
    IMD = IYD - IY2D(IY1)
!
    do IM = 1, 12
      if ( IM2D(IM,ILEAP)+1 .le. IMD ) then
        IMON = IM
      end if
    end do
    IDAY = IMD - IM2D(IMON,ILEAP)
!
    TT0 = ND2TT(IYR, IMON, IDAY ,0,0,0)
    ITS = nint(  TT - TT0 )
    Ihour = ITS / 3600
    Imin  = ( ITS - Ihour * 3600 ) / 60
    Isec  = ITS - Ihour * 3600 - Imin * 60
!
    return
    end subroutine
!
```