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

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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.

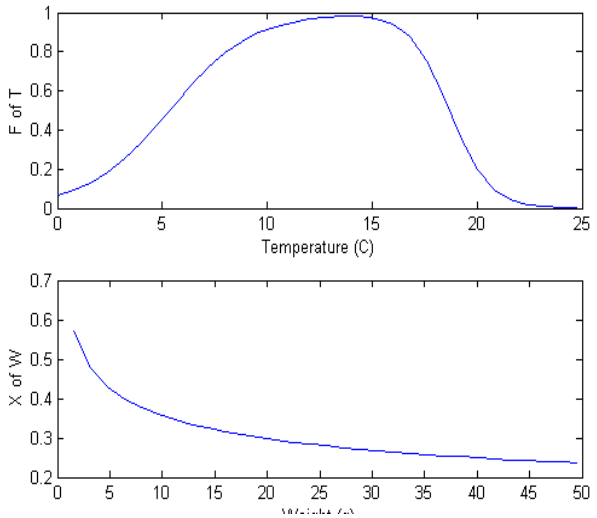

Fig. 2.1.1 Relationship between consumption and temperature from equation 2.1.4 (upper panel) and consumption and weight from equation 2.1.3 (lower panel).

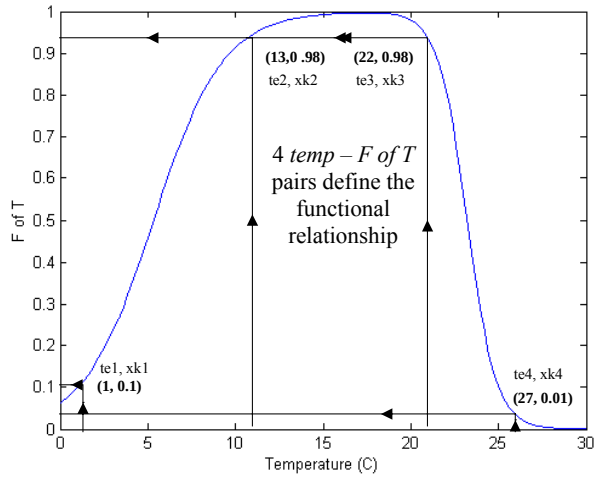

Fig. 2.1.2 Example of the Thornton and Lessem (1978) temperature adjustment curve for a theoretical set of parameters.

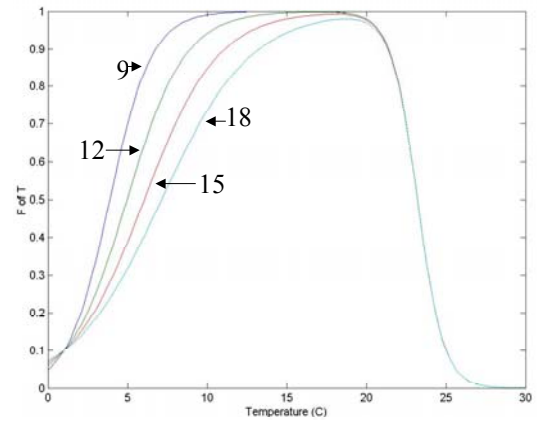

Fig. 2.1.3 Example of the Thornton and Lessem (1978) temperature adjustment curve from Figure 2.1.2 as a result of changing te2 from 9, 12, 15, 18.

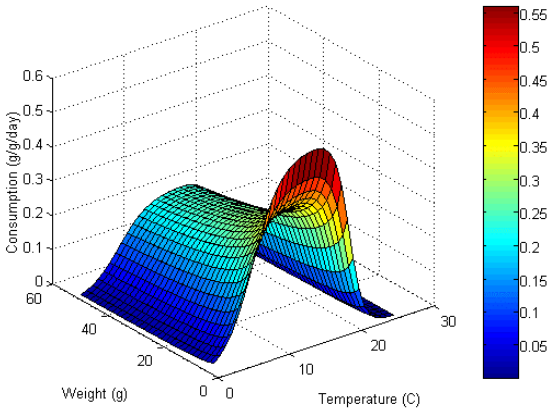

Fig. 2.1.4 Plot of the consumption, temperature and weight relationships from equation 2.1.2.

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.

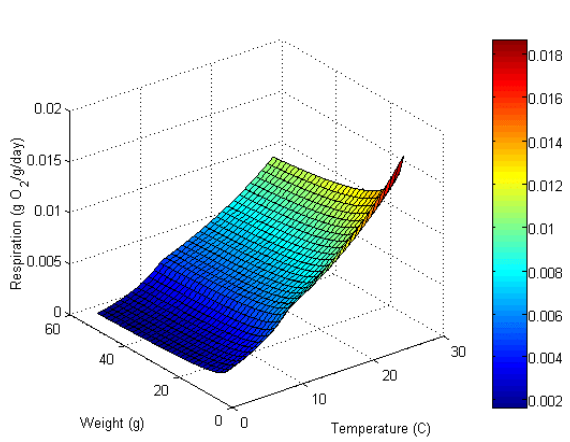

Fig. 2.1.5 Relationship between standard respiration, weight and temperature from equation 2.1.5.

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.

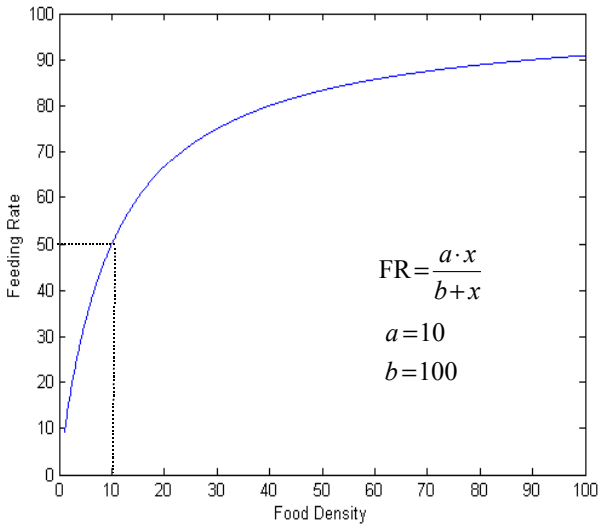

Fig. 2.1.6 Type II functional response describing the theoretical relationship between available food density and feeding rate when there is just one prey type.

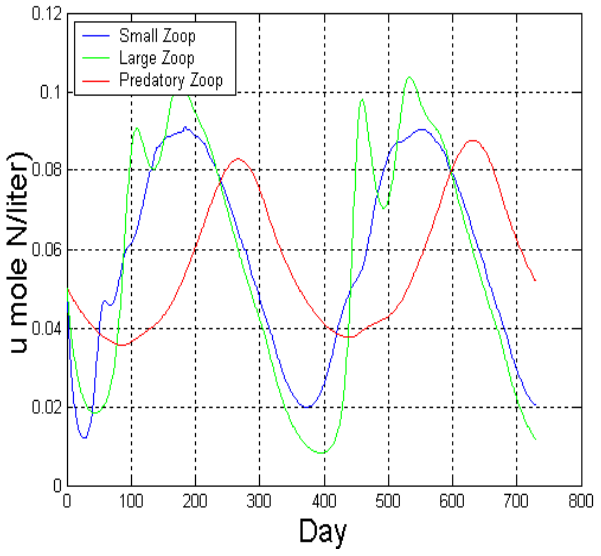

Fig. 2.1.7 NEMURO model output showing time-dependent dynamics of small, large and predatory zooplankton.

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

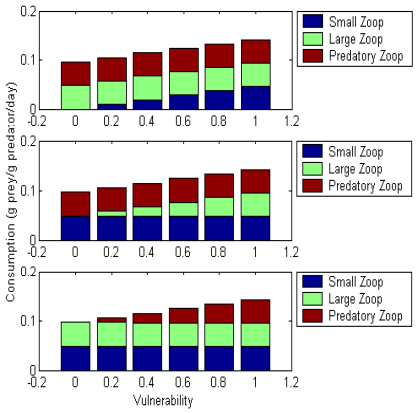

Fig. 2.1.8 An example of the mutispecies functional response formulation (equations 2.1.13 and 2.1.14) for three prey groups, varying the vulnerability of the target prey group one at a time.

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

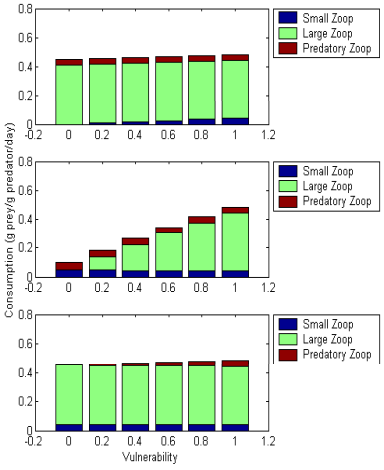

Fig. 2.1.9 An example of the multispecies functional response formulation (equations 2.1.13 and 2.1.14) for three prey groups, varying the vulnerability of the target prey group one at a time, and changing the half saturation constant for prey group 2 (K_2) from 100.0 to 10.0.

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

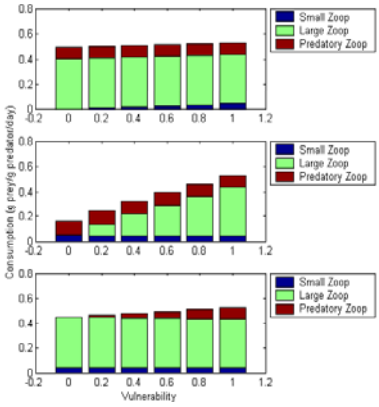

Fig.2.1.10 An example of the multispecies functional response formulation (equations 2.1.13 and 2.1.14) for three prey groups, varying the vulnerability of the target prey group one at a time, changing the half saturation constant for prey group 2 (K_2) from 100.0 to 10.0, and changing the density of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

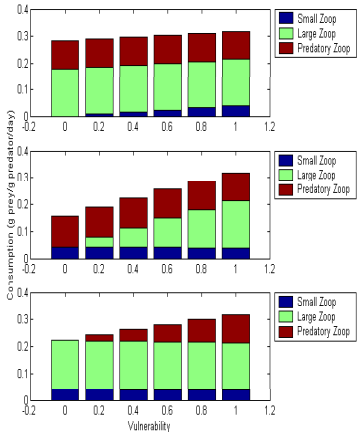

Fig. 2.1.11 An example of the multispecies functional response formulation (equations 2.1.13 and 2.1.14) for three prey groups, varying the vulnerability of the target prey group one at a time using the parameters in the herring model.

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.

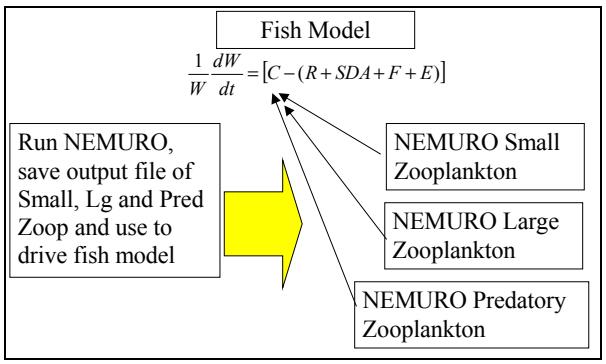

Fig. 2.1.12 Example of a static linkage between NEMURO and the bioenergetics fish model.

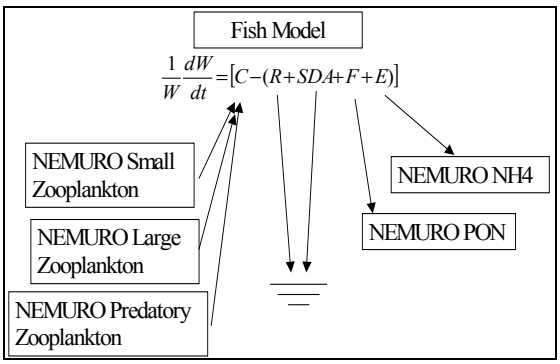

Fig. 2.1.13 Example of a dynamic linkage between NEMURO and the bioenergetics fish model..

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.