

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

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

### 3.0 Herring group report and model results

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

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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

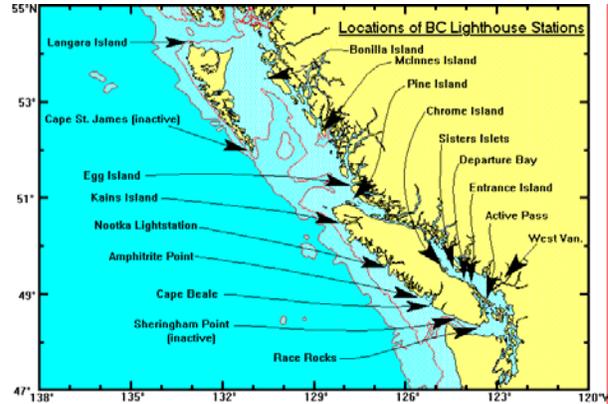
for consumption and cutoff temperature values, where swimming speed changes in the Rudstam model to describe the actual temperatures inhabited by Pacific herring, 2) accounting for known differences in larval and juvenile fish physiology (age-0) compared to adults, and 3) incorporating known seasonal 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:

$$(3.1) \quad TA = \frac{(TB - TB_{min}) \cdot (TA_{max} - TA_{min})}{(TB_{max} - TB_{min})} + TA_{min}$$

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

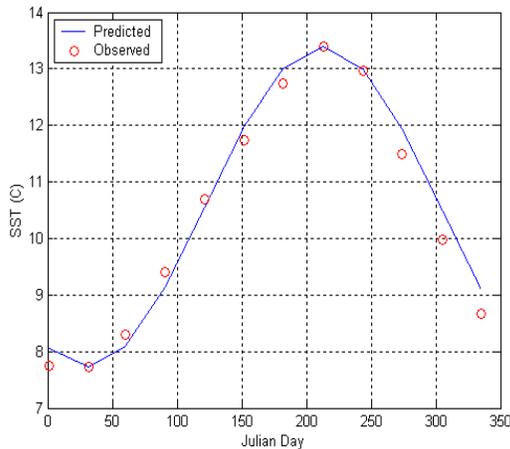
Temperatures in the respiration model, where activity changed needed to be re-computed for age-0 and age-1 herring:

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

$$(3.2) \quad T = 7.717 + \left( 5.6796 \cdot 0.5 \cdot \left( 1 - \cos \left( \frac{2 \cdot \pi \cdot (JDAY - 30)}{365} \right) \right) \right)$$

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

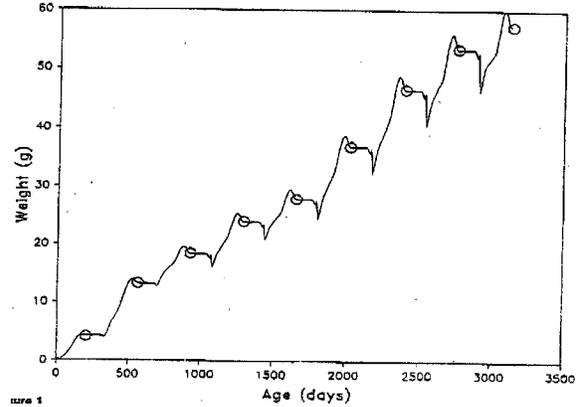


**Fig. 3.2** Observed and predicted mean SST at Amphitrite Lighthouse.

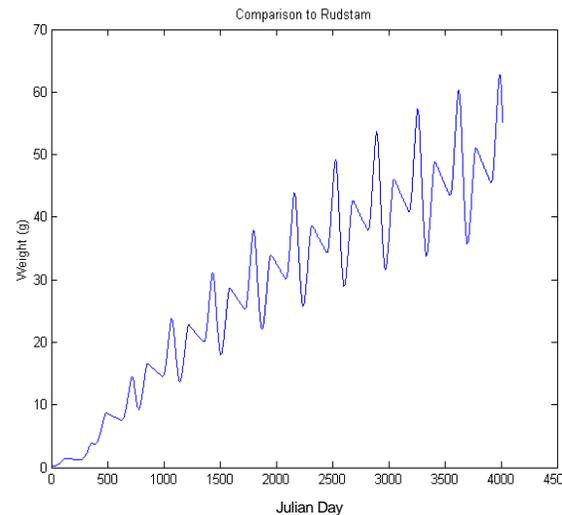
### Validation to Pacific herring

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

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

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

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

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

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

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  $T \leq 10.897$  °C then

$$a_R = 0.0033, b_R = -0.227, c_R = 0.0548, \\ a_A = 5.76, b_A = 0.386, c_A = 0.238 \text{ and } d_R = 0.03$$

if age=0 and  $T > 10.897$  °C then

$$a_R = 0.0033, b_R = -0.227, c_R = 0.0548, a_A = 8.6, \\ b_A = 0.386, c_A = 0.0 \text{ and } d_R = 0.03$$

if age $\geq$ 1 and  $T \leq 9.655$  °C then

$$a_R = 0.0033, b_R = -0.227, c_R = 0.0548, a_A = 3.9, \\ b_A = 0.13, c_A = 0.149 \text{ and } d_R = 0.03$$

if age $\geq$ 1 and  $T > 9.655$  °C then

$$a_R = 0.0033, b_R = -0.227, c_R = 0.0548, a_A = 15.0, \\ b_A = 0.13, c_A = 0.0 \text{ and } d_R = 0.03$$

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

$$a_R = 0.00528, b_R = -0.007, c_R = 0.0548, a_A = 1.0, \\ b_A = 0.0, c_A = 0.0 \text{ and } d_R = 0.0.$$

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
<b>Consumption, <math>C_{MAX}</math></b>		
$a_C$	Intercept for $C_{MAX}$ at	0.642
$b_C$	coefficient for $C_{MAX}$ versus weight	-0.256
$te_1$	Temperature for $xk_1$ (in °C)	8.0 <sup>a</sup> 8.0 <sup>b</sup> 8.0 <sup>c</sup>
$te_2$	Temperature for $xk_2$ (in °C)	10.897 <sup>a</sup> 10.897 <sup>b</sup> 10.483 <sup>c</sup>
$te_3$	Temperature for $xk_3$ (in °C)	11.310 <sup>a</sup> 11.310 <sup>b</sup> 10.897 <sup>c</sup>
$te_4$	Temperature for $xk_4$ (in °C)	12.552 <sup>a</sup> 12.966 <sup>b</sup> 12.552 <sup>c</sup>
$xk_1$	Proportion of $C_{MAX}$ at $te_1$	0.10
$xk_2$	Proportion of $C_{MAX}$ at $te_2$	0.98
$xk_3$	Proportion of $C_{MAX}$ at $te_3$	0.98
$xk_4$	Proportion of $C_{MAX}$ at $te_4$	0.01
<b>Metabolism, R</b>		
$a_R$	Intercept for R	0.00528 <sup>a</sup> 0.0033 <sup>bc</sup>
$b_R$	Coefficient for R versus weight	-0.007 <sup>a</sup> -0.227 <sup>bc</sup>
$c_R$	Coefficient for R versus temperature	0.083 <sup>a</sup> 0.0548 <sup>bc</sup>
$d_R$	Coefficient for R versus swimming speed	0.0 <sup>a</sup> 0.03 <sup>bc</sup>
S	Coefficient for Specific Dynamic Action	0.125 <sup>a</sup> 0.175 <sup>b</sup> 0.175 <sup>c</sup>
<b>Swimming Speed, U</b>		
$a_A$	Intercept U (< 9.655 °C) (in cm/s)	3.9 <sup>bc</sup>
$a_A$	Intercept U ( $\geq$ 9.655 °C) (in cm/s)	15.0 <sup>bc</sup>
$b_A$	Coefficient U versus weight	0.13 <sup>bc</sup>
$c_A$	Coefficient U versus temperature (<9.655 °C)	0.149 <sup>bc</sup>
$c_A$	Coefficient U versus temperature ( $\geq$ 9.655 °C)	0.0 <sup>bc</sup>
<b>Egestion and Excretion, F and E</b>		
$a_F$	Proportion of consumed food egested	0.125 <sup>a</sup> 0.16 <sup>bc</sup>
$a_E$	Proportion of consumed food excreted	0.078 <sup>a</sup> 0.10 <sup>bc</sup>
<b>Multispecies Functional Response</b>		
$V_{11}$	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 <sup>3</sup> )	750.0
$K_{12}$	Half saturation constant for prey group 2 to predator 1 (g wet weight/m <sup>3</sup> )	75.0
$K_{13}$	Half saturation constant for prey group 3 to predator 1 (g wet weight/m <sup>3</sup> )	750.0

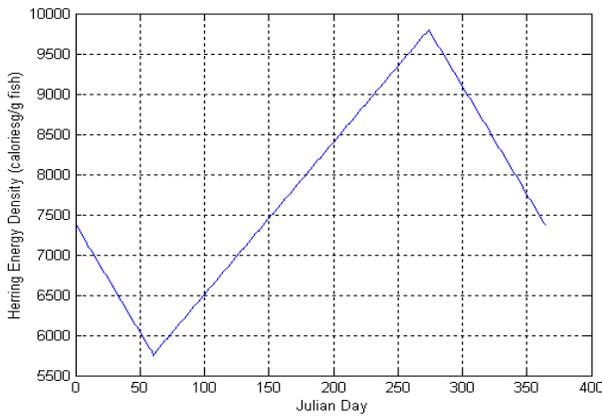
a - values for age-0 herring, b - values for age-1 herring, c - values for age-2 and older herring

```

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.

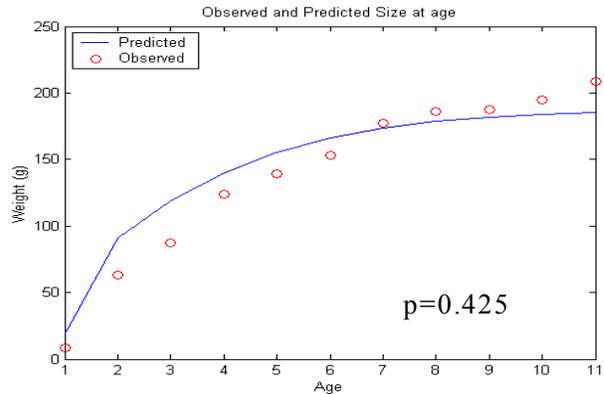


**Fig. 3.9** Straight line approximation to a seasonal energy density curve.

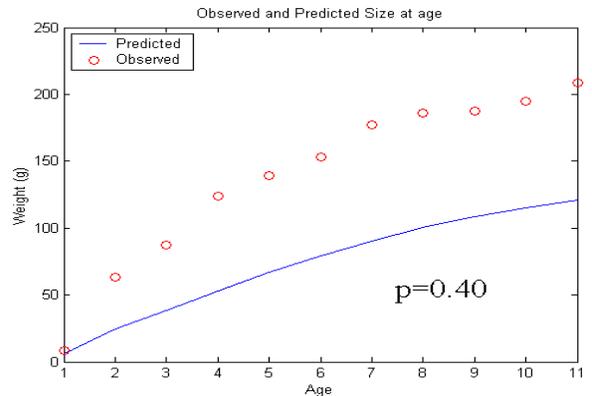
**Simulation results and final modifications to the herring model**

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-

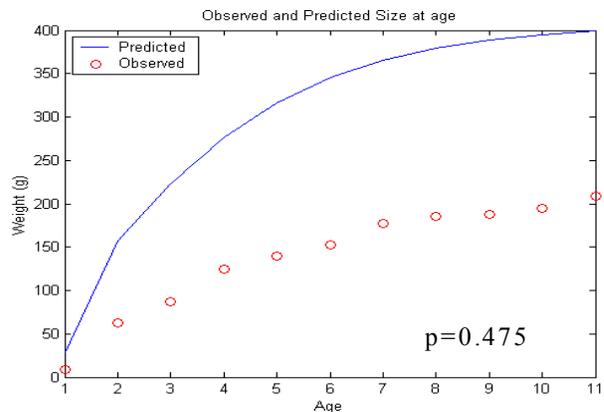
-age predicted by the herring bioenergetics model by adjusting the “p” parameter of equation 2.1.2.



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



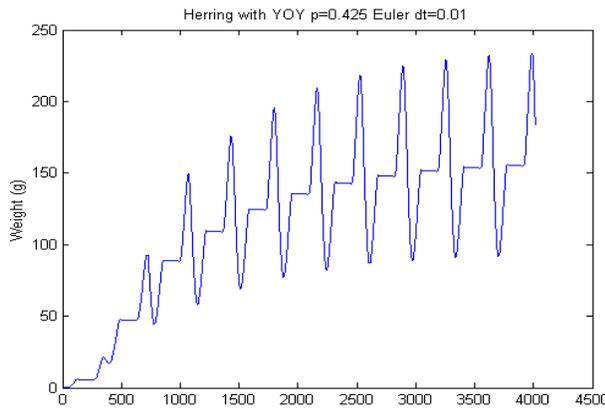
**Fig. 3.11** Observed size-at-age of the 1973 herring year-class and size-at-age predicted from the herring bioenergetics model using  $p=0.40$ .



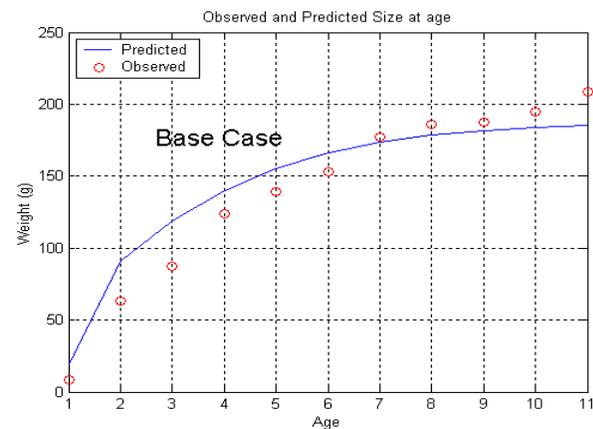
**Fig. 3.12** Observed size-at-age of the 1973 herring year-class and size-at-age predicted from the herring bioenergetics model using  $p=0.475$ .

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.

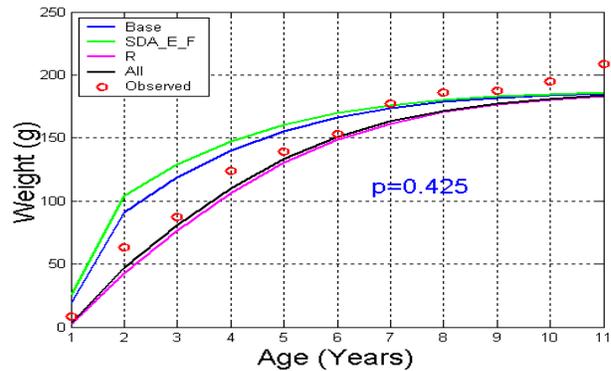


**Fig. 3.13** Example of a long-term simulation of herring growth using tuned model parameters.

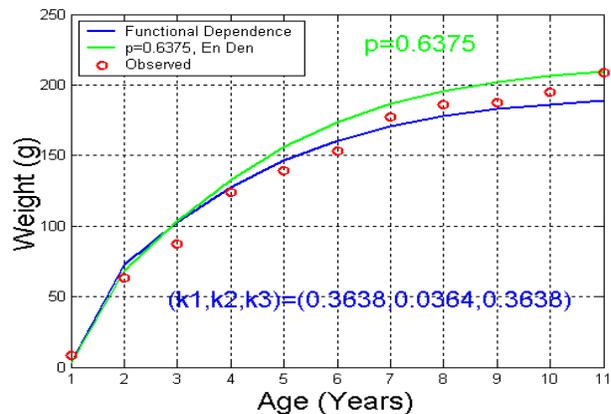


**Fig. 3.14** Comparison of observed and predicted size-at-age, base case.

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 8-14°C) 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 algorithm. 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