Getting fat in a hurry

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Bioenergetics and sensitivity

The consumption required to fuel energy costs during the feeding season was estimated with a bioenergetics model (table). Growth was estimated from body mass changes. Swimming speed was set to 1 BL/s to account for longer migration by larger individuals (Nøttestad et al.).

Equations, parameters and input of bioenergetics model

<table>
<thead>
<tr>
<th>Description</th>
<th>Equation</th>
<th>Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Respiration</td>
<td>R = R0 (T - T0)</td>
<td>T, T0</td>
</tr>
<tr>
<td>Metabolism</td>
<td>M = M0 (1 + SC × T)</td>
<td>SC, T</td>
</tr>
<tr>
<td>Temperature</td>
<td>T(x) = T0 + (T1 - T0) × e^(-x/10)</td>
<td>T0, T1, x</td>
</tr>
<tr>
<td>Time, independent exponential</td>
<td>T = T0 × e^(-λx)</td>
<td>T0, λ, x</td>
</tr>
<tr>
<td>Activity</td>
<td>A = A0 (1 + SC × T)</td>
<td>SC, T</td>
</tr>
<tr>
<td>Sensitivity</td>
<td>S = S0 (1 + SC × T)</td>
<td>SC, T</td>
</tr>
<tr>
<td>Sensitivity</td>
<td>E = E0 (1 + SC × T)</td>
<td>SC, T</td>
</tr>
<tr>
<td>Sensitivity</td>
<td>H = H0 (1 + SC × T)</td>
<td>SC, T</td>
</tr>
</tbody>
</table>

A change in one model parameter always resulted in a smaller change in output. Of the field-based parameters, swimming speed is difficult to estimate, and after body mass, consumption estimates are most sensitive to this parameter.

With a swimming speed of 1 BL/s the model was not sensitive to how biomass was distributed in space, and the sensitivity increased, and consumption was higher if the population was dominated by larger individuals such as in 1992.

Seasonal body mass change

The NSS herring spawn at the coast of western Norway in February - March. After spawning it feeds in the Norwegian Sea, with a marked and rapid weight gain from the end of May to the beginning of July, while in the western part of the ocean. At that time, and in that area, the energy rich copepodite stages of C. finmarchicus dominate the diet (Dalpadado et al.). Towards the end of the summer, C. finmarchicus enters diapause at large depths and is unavailable for NSS herring.

References


Getting fat in a hurry: food consumption during the feeding migration of NSS herring

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Background

The Norwegian spring-spawning (NSS) herring Clupea harengus inhabits a seasonal environment where food is abundant only during a short period of the year. During that period NSS herring store energy for metabolic requirements for the rest of the year and for reproduction next spring (Dalpadado, et al. 2000, Slotte 1999). Here, we describe changes in body mass during the feeding migration. We also apply a bioenergetics model to estimate the consumption required to account for the observed body mass increase. Then we relate this consumption to the life cycle and production of Calanus finmarchicus, the main prey of NSS herring (Dalpadado, et al. 2000). In this extended abstract we give a detailed description of the methods and a short summary of results and conclusions.

Methods

Data and body mass estimates

The data on body mass of NSS herring are from annual surveys carried out between 1990 and 2003. Body mass changes are estimated for the feeding period; March-September. The NSS herring fast for the rest of the year, and the body mass changes for this period have been reported previously (Slotte 1999). For length group intervals of 1 cm, average body mass was calculated for the first and last period of each month (biweekly periods). We included individuals with body lengths 28-38 cm;
corresponding to the migrating fraction of the population in the Norwegian Sea, also roughly equivalent to the mature part of the population (Engelhard and Heino 2004).

To eliminate confounding effects related to small sample sizes, we omitted catches represented by less than 50 individuals. Within each year and length group at least five individuals were required, and only fish that had completed spawning, based on inspection of gonads, were included. Totally, 54085 individuals were included in the study of body mass changes. Length growth during the feeding migration was not accounted for. The body mass and consumption estimates are therefore conservative as some individuals necessarily grow in length during the feeding season.

**Bioenergetics model**

Energy consumption was estimated with a bioenergetics model where energy consumed equals energy accounted for by respiration, waste, specific dynamic action, and growth (Hanson, et al. 1997). Respiration is dependent on fish body mass, water temperature and activity. In the present model growth is synonymous with body mass increase. We estimated consumption from the functions given in table 1, and assumed that maximum consumption rate did not limit consumption during any day.

The model was parameterized as by Rudstam (1998, see also Arrhenius and Hansson 1993), who applied the results from bioenergetics studies on alewife *Alosa pseudoharengus* (Stewart and Binkowski 1986) on the Baltic herring population. Our approach deviates in the following three aspects. 1) The swimming speed used by Rudstam (1988) is too low to account for the feeding migration of NSS herring. The typical migration distance for large individuals estimated from Misund (1998) is about 2500 km, and to cover this distance in six months the minimum swimming speed must be 16 cm/s. We let swimming speed be a fixed proportion of body length (1 BL/s), because large individuals migrate longer (Misund, et al. 1998, Nøttestad, et al. 1999). This is a conservative representation because frequent turning and depth changes should be expected during the feeding migration (Misund, et al. 1998). 2) The energy density of NSS herring is higher than for the Baltic population (Rudstam 1988). We estimated daily energy density (Fig. 1) based on data from Slotte (1999). Energy density is needed to convert specific rates from g prey/g predator to joule/g predator. 3) Water temperature in the feeding area vary both spatially and temporally, but we
used a constant water temperature of 5°C (Dale, et al. 1999, Misund, et al. 1998). The bioenergetics equations and parameters are given in Table 1.

Consumption was calculated from 15 March – 15 September for each length group. For each biweekly period, length was converted to body mass based on the linear relationship between ln (yearly biweekly body mass averages) and ln (body length). Body mass was interpolated linearly between each biweekly mean, and we ran the model with time increments of one day. Total consumption was estimated based on the length distribution in the population before spawning and we assumed no mortality during the feeding season. Data on length distributions were available for 1990 – 2000, and the model was run with the average distribution for these years. This average population had a biomass of 5.9 x 10^6 tonnes at the start of the model (15 March).

We investigated the sensitivity of the consumption estimates to changes in parameter values. Alterations of single model parameters always resulted in smaller relative changes in output (Fig. 2), and among the field based parameters the consumption estimate is most sensitive to body mass and swimming speed.

The consumption of NSS herring was compared with the production of *C. finmarchicus*. About 62% of the diet (wet weight) of NSS herring is copepods, mainly *C. finmarchicus* (Domm asnes, et al. 2004). We assumed that this also holds by energy, although compared to other copepods *C. finmarchicus* has a high energy content (Laurence 1976). Hence, we assumed that *C. finmarchicus* account for 60% of the energy needs of NSS herring. An energy density of 3500 J/g wet weight for *C. finmarchicus* (Comita, et al. 1966, Laurence 1976) was used to convert consumption from joule to *C. finmarchicus* biomass. To establish this energy density, we assumed that dry weight = 0.13 x wet weight (Mullin 1969).

**Results and discussion**

*Seasonal body mass change*

The NSS herring spawn at the coast of western Norway in February – March. After spawning it feeds in the Norwegian Sea, and we observed a marked and rapid weight gain from the end of May to the beginning of July (Fig. 3). At that time NSS herring feed in the western part of the ocean (Misund, et al. 1998), and the energy rich copepodite stages of *C. finmarchicus* dominate the diet (Dalpadado, et al. 2000).
Towards the end of the summer, *C. finmarchicus* enters diapause at large depths and is unavailable for NSS herring.

**Consumption**

With the bioenergetics model, the total energy consumption during the feeding migration (15 March – 15 September) was estimated to $1.3 \times 10^{17}$ J (based on the average population biomass of $5.9 \times 10^6$ tonnes). Assuming that 60% of the diet of NSS herring consists of *C. finmarchicus* (see Methods), the NSS herring population consumes $22 \times 10^6$ tonnes wet weight of *C. finmarchicus*. Our consumption estimate is comparable to recent results by Dommasnes et al. (2004). They used consumption/biomass ratios from the literature and arrived at similar consumption estimates. In comparison, total production of *C. finmarchicus* in the Nordic Seas (Norwegian, Icelandic and Greenland Sea) is about $75 \times 10^6$ tonnes (Aksnes and Blindheim 1996).

**Conclusions**

NSS herring gain weight quickly, particularly in June, and based on available consumption estimates (Aksnes and Blindheim 1996) a large proportion of the production of *C. finmarchicus* in the Norwegian Sea may be consumed by NSS herring. As stated above, *C. finmarchicus* is also the most important prey for NSS herring (Dalpadado, et al. 2000, Dommasnes, et al. 2004). Consequently, the interactions between the two species are probably of major importance in shaping their behaviour and life histories.
Table 1  Equations, parameters and input of bioenergetics model

<table>
<thead>
<tr>
<th>Description</th>
<th>Equations</th>
<th>Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bioenergetics</td>
<td>C = R + F + U + S + G</td>
<td></td>
</tr>
<tr>
<td>Respiration</td>
<td>R = R(W) × f(T) × A(V)</td>
<td>RA = 0.0033, RB = -0.227</td>
</tr>
<tr>
<td>Resting metabolism</td>
<td>R(W) = RA × W^RB</td>
<td></td>
</tr>
<tr>
<td>Temp. dependent respiration</td>
<td>f(T) = e^{(RQ × T)}</td>
<td>RQ = 0.0548</td>
</tr>
<tr>
<td>Activity</td>
<td>A(V) = e^{(RTO × V)}</td>
<td>RTO = 0.03, V = SC x BL</td>
</tr>
<tr>
<td>Egestion</td>
<td>F = FA × C</td>
<td>FA = 0.16</td>
</tr>
<tr>
<td>Excretion</td>
<td>U = UA(FA × C)</td>
<td>UA = 0.10</td>
</tr>
<tr>
<td>Specific Dynamic Action</td>
<td>S = SDA(C - F)</td>
<td>SDA = 0.175</td>
</tr>
</tbody>
</table>

Equations and parameters from Hanson et al. (1997) and Rudstam (1988).

W = body mass (g), T = temperature (˚C), V = swimming speed (cm/s), SC = swimming speed coefficient, BL = body length (cm), C = consumption, G = growth. Specific rates are in joule/g herring per day after herring body mass is corrected for energy density. T = 5˚C, SC = 1, BL is 28-38 cm.

Figure 1  Energy density of NSS herring, adapted from Slotte (1999). A cubic and a linear curve is fitted to the data and used as input to the model.
Figure 2  The sensitivity of consumption estimates to a 10% alteration of single model parameters. Field based parameters to the left, laboratory based parameters to the right. See table 1 for description of parameters.

Figure 3  Body mass of some length groups of NSS herring during the feeding migration (mean of means 1990 – 2003 and SE).
References


