# Getting fat in a hurry

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Background The Norwegian spring-spawning (NSS) herring lives in a seasonal environment where food is abundant during a short period of the year. During that period NSS herring store energy for the rest of the year, including reproduction next spring. We describe changes in body mass during the feeding migration. We also use a bioenergetics model to estimate the consumption required to fuel weight gain and migration costs, and we relate this to the life cycle and production of *Calanus finmarchicus*, the main prey of NSS herring.
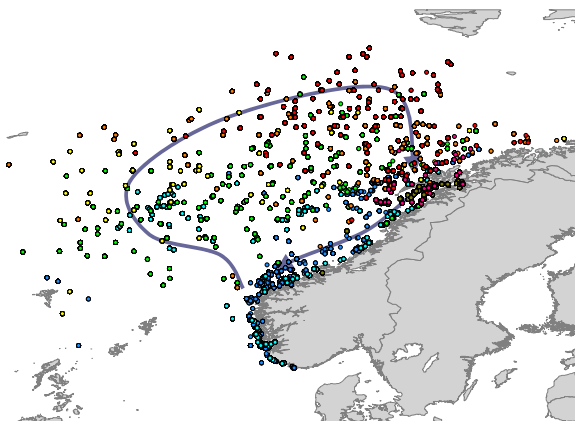
The migration of NSS herring. Feeding migration in the Norwegian Sea (Misund et al.) and spawning migration along the coast. Monthly distribution of catches (1990-2003), with colours as in the body mass figure. 54085 individuals were included in the study.
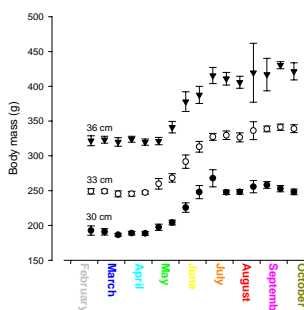
Body mass of some length groups of NSS herring (mean of means 1990-2003, and SE).

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.

The extremes. Herring may vary substantially in body mass for similar body lengths. Fish fed in captivity. Photo: A. Slotte.

Consumption

Total energy consumption during the feeding migration (15 March - 15 September) is 1.3×10^{17} J (Box), based on a population biomass of 6×10^6 tonnes. Assuming that 60% of the diet consists of *C. finmarchicus* (Dommasnes et al.) and assuming equal energy density of all prey (3500 J/g wet weight), the NSS herring population consumes 22×10^6 tonnes wet weight of *C. finmarchicus*. In comparison, total production of *C. finmarchicus* in the Nordic Seas (Norwegian, Icelandic and Greenland Sea) is about 75×10^6 tonnes (Aksnes & Blindheim).

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 longer individuals (Nøttestad et al.).

Equations, parameters and input of bioenergetics model

| Description	Equations	Parameters
Bioenergetics	$C = R + F + U + S + G$	
Respiration	$R = R(W) \times f(T) \times A(V)$	
Resting metabolism	$R(W) = RA \times W^{RB}$	RA = 0.0033, RB = -0.227
Temp. dependent respiration	$f(T) = e^{(RQ \times T)}$	RQ = 0.0548
Activity	$A(V) = e^{(RTO \times V)}$	RTO = 0.03, V = SC x BL
Egestion	$F = FA \times C$	FA = 0.16
Excretion	$U = UA(FA \times C)$	UA = 0.10
Specific Dynamic Action	$S = SDA(C-F)$	SDA = 0.175

Equations and parameters from Hanson et al.

W = body mass, T = temperature, V = swimming speed, SC = swimming speed coefficient, BL = body length, C = consumption, G = growth.

T = 5˚C, SC = 1, BL is 28-38 cm. Linear regression between ln(body mass) and ln(body length) is used to assign body mass to individuals of given body length. Interpolation between biweekly averages is used to get daily resolution. Average body length distribution (1990-2000) is used. Data on seasonally varying energy density (ED) of herring is included (Slotte).

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 length groups. With higher swimming speed, this sensitivity increased, and consumption was higher if the population was dominated by larger individuals such as in 1992.
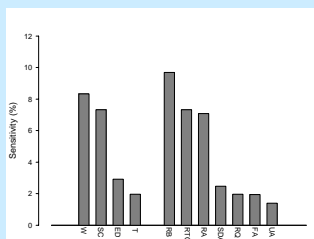
Sensitivity of consumption estimate to a 10% increase in parameters. Field based parameters to the left, laboratory based parameters to the right. See table for parameters.
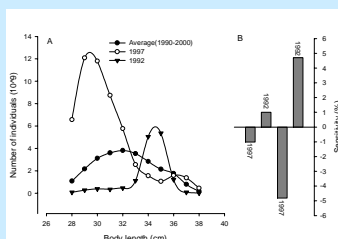
A) Body length distributions of the NSS herring population. B) Sensitivity of weight specific consumption estimates to body length distribution, as deviations from the consumption of the average body length distribution. For the two bars to the left swimming speed is 1 BL/s, and to the right, 2 BL/s.

Conclusions

• NSS herring gains weight quickly, particularly in June.

• Swimming speed is difficult to estimate, and estimates of consumption are sensitive to this parameter.

• As much as 50 % of the production of *C. finmarchicus* may be consumed by herring.

• The interactions between the two species are probably of major importance in shaping their behaviour and life histories.

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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 5.9×10^{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* (Dommasnes, 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 1.3×10^{17} J (based on the average population biomass of 5.9×10^6 tonnes). Assuming that 60% of the diet of NSS herring consists of *C. finmarchicus* (see Methods), the NSS herring population consumes 22×10^6 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 75×10^6 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

| Description	Equations	Parameters
Bioenergetics	$C = R + F + U + S + G$	
Respiration	$R = R(W) \times f(T) \times A(V)$	
Resting metabolism	$R(W) = RA \times W^{RB}$	$RA = 0.0033$, $RB = -0.227$
Temp. dependent respiration	$f(T) = e^{(RQ \times T)}$	$RQ = 0.0548$
Activity	$A(V) = e^{(RTO \times V)}$	$RTO = 0.03$, $V = SC \times BL$
Egestion	$F = FA \times C$	$FA = 0.16$
Excretion	$U = UA(FA \times C)$	$UA = 0.10$
Specific Dynamic Action	$S = SDA(C-F)$	$SDA = 0.175$

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.
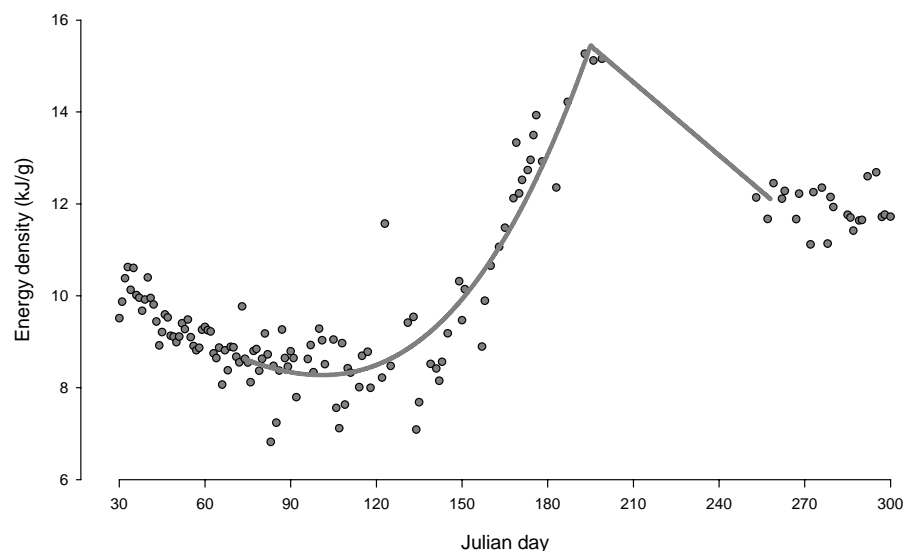
Figure 1 Energy density of NSS herring, adapted from Slotte (1999). A cubic and a linear curve is fitted to the data and used as input to the model.
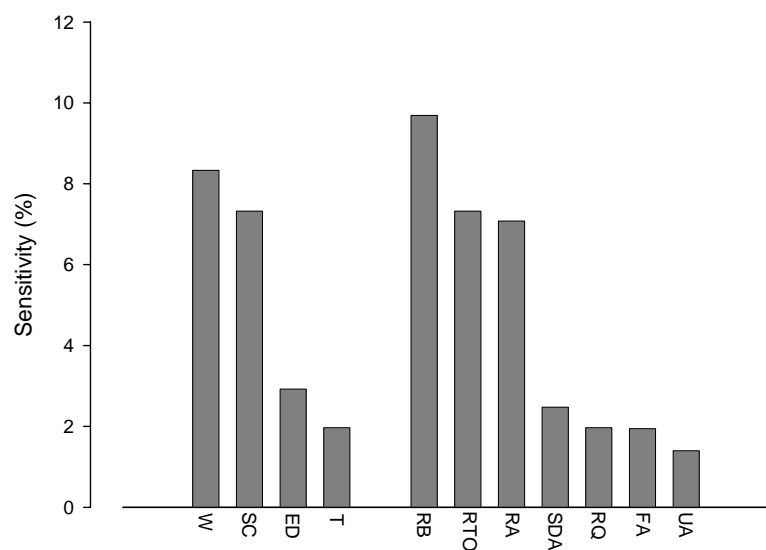
Figure 2 The sensitivity of consumption estimates to a 10% alteration of single model parameters. Field based parameters to the left, laboratory based parameters to the right. See table 1 for description of parameters.
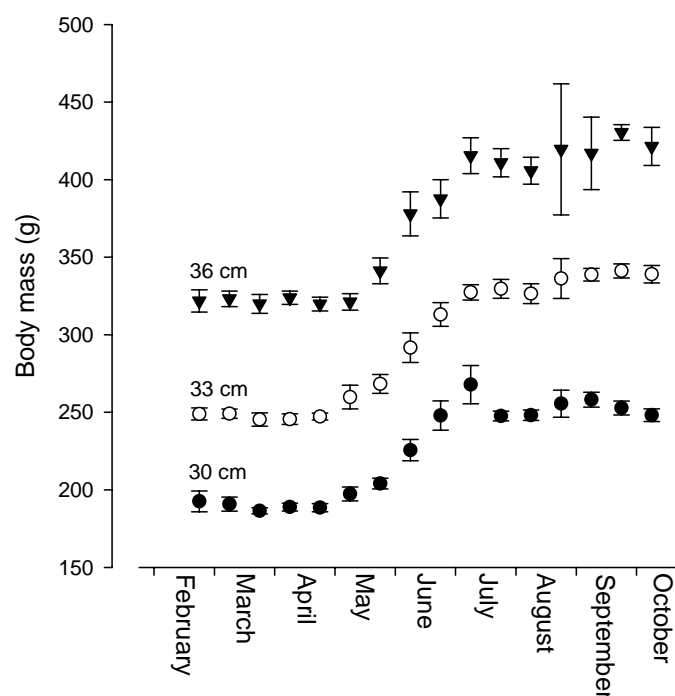
Figure 3 Body mass of some length groups of NSS herring during the feeding migration (mean of means 1990 – 2003 and SE).

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