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Exploring the dynamics of herring consumption in the Baltic: Applications of an energetic model of fish growth

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Abstract

A bioenergetic model was parameterized for herring *(Clupea harengus)* using information available in the literature. In this model, all components of the energy budget are functions of temperature and fish weight. The model is used to simulate herring growth and consumption in a coastal area of the northern Baltic proper. Simulated seasonal growth curves restrained to fit one weight per age class are similar to observed growth curves, indicating the importance of temperature in determining herring growth rates in the Baltic. Calculated food consumption and conversion efficiencies are compared with other published estimates.

Introduction

Planktivorous fish affect abundance and species compositon of their zooplankton prey (HRBACECK et al. 1961, BROOKS and DODSON 1965) and, may therefore also affect such ecosystem processes as nutrient cycling and primary production (HENRIKSSON et al. 1980, CARPENTER et al. 1985). Such "cascading trophic interactions" could be important in the Baltic Sea and need to be assessed if we are to understand ecosystem processes, including responses to increased nutrient loadings (eutrophication).

However, predation rates are far from constant in time and space. As a first step, we need reasonable estimates of the seasonal changes in predation rates from major Baltic fish species. Bioenergetic models have been used since WINBERG (1956) to estimate fish growth and fish consumption. KITCHELL el al. (1977) developed a model of fish growth for yellow perch *(Perca flavescens)* and walleye *(Stizostedion vitreum)* that has subsequently been adapted for many fish species, including a clupeoid (alewife, *Alosa pseudoharengus*, STEWART and BINKOWSKI 1986). This approach is especially useful for calculating food consumption from measurements of fish growth (RICE and COCHRAN 1984). The use of these models has led to predictions of the responses of the Lake Michigan ecosystem to perturbations of the fish populations that has subsequently been supported by field observation (KITCHELL and CROWDER 1986).

In this paper I present a bioenergetic model for herring *(Clupea harengus)* structured after KITCHELL et al. (1977) and STEWART and BINKOWSKI (1986) and parameterized using information available in the literature. The choice of parameter values are briefly discussed. The model is used to simulate seasonal growth and consumption patterns of herring from age 0 to 8. These simulated patterns are compared with other published estimates of growth, conversion efficiency, and food consumption by Baltic herring.

The Model

The structure of the bioenergetic model used in this paper is indentical to the one presented by STEWART and BINKOWSKI (1986) for alewife *Alosa pseudohaerangus),* a euryhaline clupeoid common to Lake Michigan. The model is a mass balance equation where growth equals consumption minus losses through metabolism, egestion and excretion. For a full explanation of rationale and equations, including an extensive sensitivity analysis, consult KITCHELL et al.(1977), STEWART and BINKOWSKI (1986) and BARTELL et al. (1986). The parameter choices presented here for herring are based on experiments using herring and similar fish species reported in the literature. A model for fish growth based on the von Bertalanffy growth equations was applied to herring by URSIN (1979), but that approach is less useful for investigating seasonal growth patterns. To facilitate cross-references with previous work, I will keep the notation indentical to the one used by STEWART and BINKOWSKI (1986). Computer programs with documentation are available (HEWETT and JOHNSON 1987). The model is parameterized for metamorphosed herring and probably perform poorly for the larval stages. A model for larval herring is available (KERR and DICKIE 1985).

Metabolism

Metabolism is modeled as a function of fish weight, temperature, and swimming speed:

(1) $R = \alpha \cdot W^{\beta} \cdot \exp(\rho\ T) \cdot \exp(v\ U)$

where R is respiration in g/g day, W is wet weight in g, T is temperature in °C, and U is swimming speed in cm/s. α, β, ρ and v are constants.

The weight dependence coefficient (β) has been estimated to − 0.227 for Atlantic herring (DESILVA and BALBONTIN 1974) and to −0.022 for Baltic herring at 10°C (CHEKUNOVA 1979). I chose the former value because it is closer to estimates for other clupeids (−0.18 to −0.28, Atlantic menhaden, *Brevoortia tyrannus* HETTLER 1976; −0.215, alewife, STEWART and BINKOWSKI 1986) and it is also closer to values reported by WINBERG (1956) for non-salmonid fishes. The temperature dependence coefficient is chosen to 0.0548 after BURBRIDGE (1974) (experiments on blueback herring, *Alosa aestivalis)* and STEWART and BINKOWSKI (1986) (experiments on alewife). The intercept (α) is taken from STEWART and BINKOWSKI (alewife) as 0.0033 (in g O_2/g day for input into the model). This intercept is changed during the course of a simulation to give respiration in units of g food consumed/g fish weight and day by accounting for changes in fish diet and fish energy density.

To account for metabolism due to swimming activity, the function for metabolism is multiplied by exp (vU) where U is swimming speed (cm/s) and v is the coefficient relating swimming speed to metabolism. v has been estimated to 0.03 for aholehole, *Kuhlia sandvicensis,* a moderatly sized euryhaline fish with similar body shape as herring (MUIR and NIIMI 1972). Swimming speed is assumed to be a power function of body weight (WARE 1978, STEWART et al. 1983) and exponential function of temperature (STEWART et al. 1983). Data on volitional swimming speed of herring is rare. PITCHER et al. (1985) report a volitional swimming speed of 30 cm/s for 21 cm long herring and GIBSON and EZZI (1985) report swimming speeds of 16 to 24 cm/s when feeding and 16–40 cm/s when not feeding for 16 cm long herring. There is no information on the effect of temperature on swimming speed for herring. For alewife (COLBY 1973) and chub mackerel, *Scomber japonicus* (SCHAEFER 1986), swimming speed decreased with decreasing temperature below 9°C. Here, I follow WARE'S (1978) suggestion that swimming speed is proportional to fish weight to the 0.13 power (based on calculations of optimal cruising and foraging speeds) and STEWART and BINKOWSKI'S (1986) model for temperature dependence of swimming speed (based on COLBY 1973). The equations are modified to fit the swimming speeds observed for herring.

(2) $U = 3.9\ W^{0.13} \exp(0.149\ T)\ T$ for $T < 9°C$ and
$U = 15\ W^{0.13}$ for $T > 9°C$

Metabolism calculated from equations 1 and 2 corresponds resonably well with the results of ANEER (1979) and CHEKUNOVA (1979) on Baltic herring. ANEER found an oxygen consumption at 11°C of 5.8 mg O_2/g/day for a 27.4g herring and of 4.8 mg O_2/g/day for a 40.8 g herring. Using my equations I obtain 5.7 mg O_2/g/day for a 27.4 g fish and 5.4 mg O_2/g/day for a 40.8 g fish at 11°C. Respiration calculated from the equations given by CHEKUNOVA (1979) gives an oxygen consumption of 4.6 – 4.9 mg O_2/g/day for fish from 9 to 104 g at 10–11°C. The Q_{10} for metabolism including swimming speed is 2.3 for a 15 g herring between 5 and 15°C. URSIN (1979) assumed a Q_{10} of 2 in his model for herring growth.

Consumption

Maximum daily consumption is modeled as:

(3) $Cmax = a\ W^b\ F(T)$

where F(T) is a dome-shaped function of temperature (T) (THORNTON and LESSEM 1978). This function was used by STEWART and BINKOWSKI (1986) for alewife. Maximum daily ration has een measured for juvenile herring by DESILVA and BALBONTIN (1974) at two temperatures (6.5°C and 14.5°C). The fish were fed to satiation twice daily. I will use their value (−0.256) for the weight specific exponent (b). STEWART and BINKOWSKI (1986) used −0.3 for alewife.

Maximum daily ration increases with temperature to a maximum around the preferred temperature and decreases at higher temperatures for most investigated fish species (see STEWART and BINKOWSKI 1986). I will assume this to be true also for herring. Unfortunately, we do not know the preferred temperature of herring. Our field data indicate that young herring occur above the thermocline in 16°C water when available and older herring in cooler water (approximately 12°C). HAIST and STOCKER (1986), using a regression analysis of size of Pacific herring and temperature, found a maximum herring weight at age 2 at a temperature of 12°C and speculate that this may be close to the temperature of optimum growth for herring. The temperature of optimum growth is generally close to or a few degrees below the preferred temperature (JOBLING 1981). As a first approximation, I will use 16°C for age 0 and 1 herring and 14° for age 2 and older herring as the temperature of maximum consumption.

The mean ad lib ration reported by DESILVA and BALBONTIN (1974) were 5 % of body weight at 6.5°C and 11 % at 11°C for young herring fed to satiation twice daily. I fitted the constants in the temperature dependence function to give the shape suggested by these rations, but increased the maximum ration to 3 times the mean ration. The maximum daily ration reported by DESILVA and BALBONTIN (1974) was 17–20 % on some days and alewife fed up to 7 times a day had even higher maximum rations (STEWART and BINKOWSKI 1986). Also, consumption calculations are very insensitive to this parameter (BARTELL et al. 1986).

Specific dynamic action, Egestion and Excretion

These functions are modeled as in STEWART and BINKOWSKI'S (1986) alewife model as I have not found any specific herring values. Consumption and growth calculations are relatively insensitive to these parameters (BARTELS et al. 1986). The equations are:

(3) $SDA = 0.175\ (C-F)$

(4) $F = 0.16\ C$

(5) $E = 0.10\ (C-F)$

where SDA is specific dynamic action, F is egestion, E is excretion and C is consumption, all in g/g/day. C–F then represent assimilated food. All model parameters are summarized in Table 1.

Table 1

Summary of parameter values used in the herring model

Symbol	Parameter description	Value
Consumption, Cmax		
a	Intercept: Cmax (at $(\theta + \theta_3)/2$	0.642
b	Coefficient: Cmax versus weight	–0.256
θ_1	Temperature for K1 (in °C)	1[a], 1[b]
θ_2	Temperature for K2 (in °C)	15[a], 13[b]
θ_3	Temperature for K3 (in °C)	17[a], 15[b]
θ_4	Temperature for K4 (in °C)	25[a], 23[b]
K1	Proportion of Cmax at θ_1	0.10
K2, K3	Proportion of Cmax at θ_2 and θ_3	0.98
K4	Proportion of Cmax at θ_4	0.01
Metabolism, R		
α	Intecept: R	0.0033
β	Coefficient: R versus weight	–0.227
ρ	Coefficient: R versus temperature	0.0548
v	Coefficient: R versus swimmingspeed	0.03
SDA	Coefficient: specific dynamic action	0.175
Swimming speed, U		
ω	Intercept: U (< 9°C) (in cm/s)	3.9
ω	Intercept: U (> 9°C) (in cm/s)	15
δ	Coefficient: U versus weight	0.13
Φ	Coefficient: U versus temperature (<9°C)	0.149
Φ	Coefficient: U versus temperature (>9°C)	0
Egestion and Excretion, F and E		
f	Proportion of consumed food egested	0.16
ε	Proportion of assimilated food excreted	0.10

a) values for age 0 and 1 herring

b) values for age 2 and older herring

Site specific parameters

To calculate consumption from this model, we need the temperatures the fish occupies, and energy density of the fish and of its prey. The model fits a proportionality constant (P) of the maximum ration that the fish would consume given observed growth. From this value, we calculate total food consumption by an individual fish or by a popoulation if we know the number of fish present.

Temperature – Water temperature profiles were measured weekly, biweekly or monthly depending on season by a monitoring program at the Askö Laboratory. The temperatures used here are inferred from fish distributions in vertical gill nets set at night and acoustic data collected day and night. These data were collected in the Askö area, northern Baltic proper, from early July to the end of October, 1985 (RUDSTAM and HANSSON, unpubl.). Diel vertical migrations were not large from early July through October. Diel vertical migrations of herring are more pronounced in spring and early summer (OJAVEER 1981). Since water column temperatures are more homogeneous during that time, this will not give serious errors.

Fish weight and energy density – ANEER (1975), presents data on fish weights at age and energy density of herring collected in 1970 – 1972 in our area. The energy density decreased from January to June, increased from July to September and was reasonably constant from September to the end of the year. Energy density ranged from 5120 to 5940 J/g wet weight (mean of 5533 J/g ww, SD = 216, N=22). This pattern was fairly consistent over the two years.

Diet and prey energy density – The diet of herring is assumed to be 100 % copepods in the present simulations. I use an energy density of 2580 J/g wet weight taken from LAURENCE'S (1976) mean value for seven marine and estuarine copepods and converted to wet weights assuming dry weights are 13 % of wet weights (MULLIN 1969).

Results and discussion

An example of simulated growth of herring from age 0 to 8 is shown in Fig. 1. This simulation is forced through a weight at the end of each year (from ANEER 1975) and assumes that the fish feed at a constant proportion of its maximum daily food intake throughout the year as long as temperatures are above 1°C. Below 1°C, the fish is forced to consume enough food to maintain its weigth. This will be further discussed below. Fish age 3 and older are assumed to spawn in the beginning of June with a resulting weight loss of 15 % (ANEER, unpubl.).

The seasonal growth pattern of fish age 0 to 2 are presented in more detail in Fig. 2 and is compared with herring sizes from our area reported by ANEER (1975) for 1970–72, NELLBRING (1976) for 1975, BERGSTRÖM (1979) for 1978 and RUDSTAM and HANSSON (unpubl.) for 1985. The simulated growth pattern is reasonably close to observations, indicating the importance of temperature in influencing herring growth rates in the Baltic Sea. However, food intake is also governed by hormonal changes during spawning. POPIEL (1951) showed a seasonal development of herring consumption rates for spring spawning herring which is similar to my simulations, but autumn spawning herring had a very different seasonal food consumption pattern with low food intake during spawning time in late summer and autumn. ILES (1980) even suggested that the consumption rate of North Sea herring is decoupled from temperature. Thus, the success of this model for Baltic herring may be coincidental and due to the current dominance of the spring spawning group (ANEER 1985).

ANEER (1975) did not show large changes in herring weights during the winter. The consumption rates necessary to prevent excessive weight loss with this model during the winter are, however, rather high (Table 2). Herring, especially younger individuals, may feed during the winter (POPIEL 1951, ZALACHOWSKI et al. 1976, ANEER et al. 1979, YADCHENKO 1982), but these feeding rates are generally low. ANEER did his study in 1970–72 which were mild winters with no ice cover in the Askö area. This may have

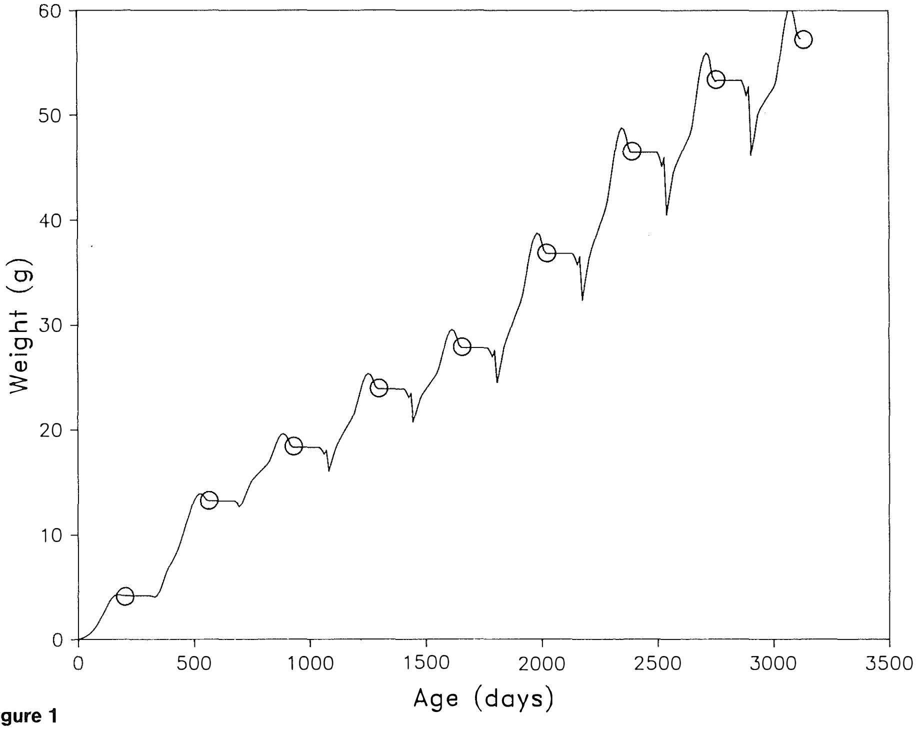

Figure 1

Simulated growth of Baltic herring from age 0 to 8. The vertical drop in fish weight of age 3 and older fish represents weight loss due to spawning. The fish is forced to grow through one weight per age class marked in the figure. During the winter (temperatures below 1°C) the herring is assumed to consume enough food to maintain its body weight (see text).

allowed higher feeding rates of herring during the winter (better light conditions). Lower winter consumptions would result if the energy density cycle is more pronounced than indicated by ANEER'S (1975) values. MIKICINSKA (1952) reported a decrease in energy content of Baltic herring from 6056 J/g wet weight in the autumn to 3310 J/g wet weight after spawning in the spring. Similar extreme energy density cycles have been observed for alewife in Lake Michigan (FLATH and DIANA 1985). Also, URSIN (1979) showed a large decrease in North Sea herring weights during the winter. Thus, it is possible that larger energy and weight losses occur during normal winters. Alternatively, herring may have a lower metabolic rates at low temperatures than assumed in the model, even though this rate is modeled as only 1.2 times the standard metabolic rate. ILES (1980) considered overwintering North Sea herring to be anabolically inert. In the Baltic, older herring has been observed to over-winter in large aggregations were individual fish move very little and do not feed (ANEER et al. 1979). Both herring physiology at low temperatures and changes in energy density over the winter warrants further study.

Daily consumption rates calculated from this model (Table 2) range from 9.2 % per day for age 1 herring during the summer to 1.2 % per day for older herring during the winter (excluding larval stages). These values are higher than some published estimates for Baltic Sea herring. ZALACHOWSKI et al. (1976), using analysis of stomach contents, obtained daily consumption rates between 0.2 and 2.5 % depending on season for 10–15 cm long Baltic herring. Their food intake, though, was calculated using a linear evacuation

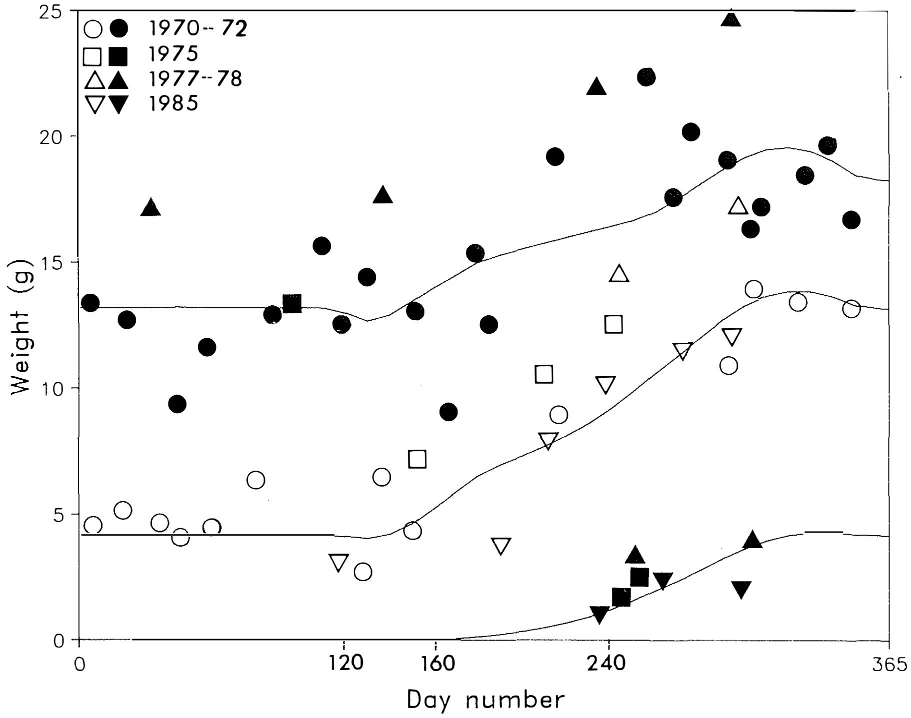

Figure 2

Simulated growth of herring up to age 3 (broken line) compared with weight at age from our area reported by ANEER (1975) for 1970-72, NELLBRING (1976) for 1975, BERGSTRÖM (1979) for 1977-78 and RUDSTAM and HANSSON (unpubl.) for 1985. Herring growth is forced to go through a weight at age at the end of the year. Weights of age 1 herring are marked with open symbols.

rate and ELLIOTT and PERSSON (1978) has shown that this may underestimate daily food intake with a factor 4 compared with calculation using an exponential evacuation rate. ANEER (1980) also estimated comparatively low mean daily food intake over a year for age 1 to 9 Baltic herring (1.5 % of body weight) using an energy budget. The differences between ANEER'S and my estimates are partly due to differences in energy density of the prey (ANEER used mixed prey with an energy density of 3800 J/g wet weight) and partly due to differences in the energy budgets used (ANEER used monthly time steps, an average temperature of the water column from 0–40m, and did not include any cost for standard dynamic action). He obtained energy conversion efficiencies of 27.3 % for age 1 herring declining to 2.7 % for age 9 in the Askö area, that is approximately twice as high as my values (Table 2). CHEKUNOVA (1979) obtained annual average daily food rations more similar to mine (2.6 – 2.8 % by weight for age 2 to 7). DESILVA and BALBONTIN (1974) reported conversion efficiencies of 7 to 10 % (on a weight basis) for young herring. Levels of metabolism can be assumed to be comparatively high and therefore, conversion efficiencies comparatively low for actively swimming pelagic fish like the herring (DESILVA and BALBONTIN 1974, CHEKUNOVA 1979, SOOFIANI and HAWKINS 1985).

Lower conversion efficiencies has implications for estimates of food consumption by herring in the Baltic. ELMGREN (1984) used efficiencies for age 1 to 9 based on ANEER

Table 2
Simulated consumption and conversion efficiencies of different herring age groups. The year has been divided in four seasons defined by the day numbers given. The seasons are not of equal lengths.

Age class	Weight gain (g)	Consumption Winter (1-120)	Spring (121-160)	Summer (161-240)	Fall (241-365)	Year	Conversion efficiency (%) (g/g)	(J/J)
Total consumption: (g wet weight)								
0	4.2			7.5	25.0	32.5	12.9	29.7
1	9.0	9.9	10.5	53.8	62.3	136.5	6.6	15.2
2	5.1	24.1	20.3	73.4	75.1	193.0	2.6	6.0
3	5.6	31.1	26.4	90.8	95.6	243.9	2.3	5.3
4	3.9	38.2	31.7	105.4	107.1	282.4	1.4	3.2
5	9.0	43.1	38.4	131.9	138.6	351.9	2.6	6.0
6	9.7	53.5	48.1	162.9	168.3	432.7	2.2	5.1
7	6.7	64.0	56.4	185.8	186.1	492.3	1.4	3.2
8	4.0	71.2	61.6	199.7	196.2	528.7	1.3	3.0
Average daily consumption: (% of body weight)								
0				26.1	4.4	13.7		
1		2.0	6.7	9.2	4.1	4.7		
2		1.6	4.4	5.9	3.2	3.4		
3–8		1.5–1.2	4.9–3.5	6.0–4.9	3.2–2.7	3.3–2.7		

(1980) to estimate total food intake by herring and sprat in the Baltic Sea and found these fish to consume 25 % of the yearly zooplankton production. The proportion attributable to older herring would approximately double using the model presented here.

A bioenergetic model is a synthesis that provides both a tool for explorations into the seasonal dynamics of herring growth and consumption and an assesment of available information on herring physiology. BARTELL et al. (1986) used Monte Carlo simulations to investigate the effect of errors in model parameters on model output. Consumption calculated from fish growth was most sensitive to errors in parameters governing the temperature dependence of respiration and swimming speed and to the weight dependence of respiration. None of these parameters can be said to be sufficiently well known for herring. Further research on these aspects of herring physiology is clearly warranted given the importance of herring both for fisheries and for the ecology of the Baltic Sea.

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