

ICES Statuary meeting 1993



C.M. 1993/L:23, Ref:J

IN SITU FOOD CONSUMPTION BY YOUNG BALTIC SEA HERRING (*CLUPEA HARENGUS*) - A TEST OF A BIOENERGETICS MODEL

by

Fredrik Arrhenius & Sture Hansson

Department of Systems Ecology, S-106 91 Stockholm, SWEDEN

ABSTRACT

The food of juvenile herring was dominated by zooplankton, mainly copepods (*Acartia* spp. and *Eurytemora affinis*) and cladocerans (*Bosmina longispina maritima* and *Pleopsis polyphemoides*) in the summer. The food consumption decreased with body sizes and temperature from 20 % of body weight d^{-1} in the summer to 4 % d^{-1} by the end of October for young-of-the-year. There was a diurnal variation in stomach fullness, with one maxima in the morning and one in the evening. Model simulation of the food consumption demonstrate that a bioenergetics model based on data mainly from adult fish, was valid also for young-of-the-year herring.

1. Introduction

In fish biology, bioenergetics models have been developed, with which food consumption is estimated from growth data (Hewett & Johnson, 1992). Generally these models are based on a more or less general bioenergetics assumptions and for each species specific parameters. Most bioenergetics model are based on parameters derived from studies of adult fish, while few models are built from data for juvenile fish. We don't know the error behind these figures, but for yellow perch (*Perca flavescens*) parameters of respiration and consumption for adult fish have been shown to be in appropriate for young-of-the-year (YOY) fish (Post, 1990).

For bioenergetics model, a common short-coming is that they never have been tested against realistic consumption data. Hansen et al. (1993) pointed out, that for more complete studies on bioenergetics of fish, information for larval and juvenile under field condition are badly needed. It has been suggested that of larvae and juvenile fish can have a major impact on zooplankton production and community structure (Hansson, et al. 1990, Rudstam, et al. 1992, Arrhenius & Hansson, 1993) and therefore it is important to investigate the validation on field estimates vs. model predictions.

The objectives of this study were to measure the food consumption and diel patterns of feeding activity of juvenile herring (*Clupea harengus* L.) and compare that with estimates given by the bioenergetics model for herring (Rudstam, 1988).

2. Methods and material

2.1 Fish sampling

Using small charges of explosives (15-120 g of Primex 17 mm, Nitro Nobel AB), herring were sampled in the northern Baltic proper (Figure 1) during five 24-h periods between July - October 1992. Collections were made at approximately 2 h intervals during each 24-h

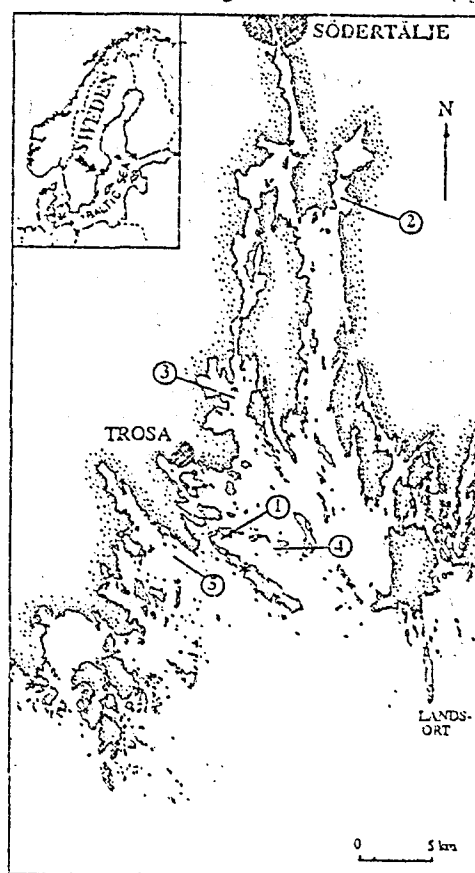


Figure 1. The study area with the sampling stations for collections of YOY herring and zooplankton.

experiment. A minimum sample of 10 fish per length class was taken within 10 minutes every 2h. On the first sampling two stations with different depth, were used in the same area, as small larvae were in shallower water than large larvae (c.f. Urho & Hildén, 1990). Capture fish were immediately preserved in 70 % ethanol.

2.2 Diel feeding patterns and daily rations

In the laboratory, the total length of each fish, i. e. length from the tip of the snout to the end of the tail fin, was measured to the nearest 1 mm and the wet weight was measured to the nearest 1 mg. The dry weight of the stomach contents were determined drying oven at 60 °C for 3 days. Water temperature was measured at each 24-h sampling.

Diel feeding patterns were evaluated by determining at 2-h intervals, to the nearest 0.001 mg the mean stomach content in dry weight. From these data, daily rations were estimated by the method by Elliott & Persson (1978). Evacuation rates were calculated from the decline in intestinal tract content in dry weight as proportion of body mass during nonfeeding periods assuming an exponential evacuation rate (Persson, 1986). The assumption was that the herring don't feed during darkness but only evacuate the gut content. We calculate the evacuation rate between approximately one hour after sunset and one hour before sunrise. For two of the sampling dates (August 5-6, September 16-17), sampling intervals were shorter than 24-h, due to hard weather condition, therefore the data have been extrapolated (Figure 3 c & e).

2.3 Feeding

When possible, 10 fish were taken at random from each sample and length interval. Individual stomach were analysed using a stereo microscope and an inverted microscope. Each prey was determined to the lowest possible taxonomic level. If a stomach contained a large number of prey, a subsample of 200 items was analysed. The contents of a stomach was expressed as the percentages of different taxa, calculated from the number of identified items. From these percentages, means were calculated to represent diet of fish at different stations and dates. In order to characterise the feeding of herring, the electivity were calculated (Chesson, 1983).

2.4 Zooplankton

From each sampling occasion, a zooplankton sample taken with a WP-2 have been analysed. We assumed that the mesozooplankton used by the fish was found in the uppermost 10 (Station 1-3 in Figure 1) and 30 m (Station 4 & 5 in Figure 1), respectively. The plankton net were towed vertically from the depth to the surface at a speed of 0.5 m/s. Samples was filtered through 90 μ m nets and

preserved in 4 % formalin. Before counting under an inverted microscope, the zooplankton samples were subsampled (Kott, 1953) and at least 500 specimen from each sample were determined to lowest taxonomic level. Biomass were estimated from values on individual wet weights (Henroth, 1985), of which 5 % was assumed to be carbon (Mullin, 1969). The samples were counted, plankton was identified according to development stage (adult, copepodite and nauplii) and sex.

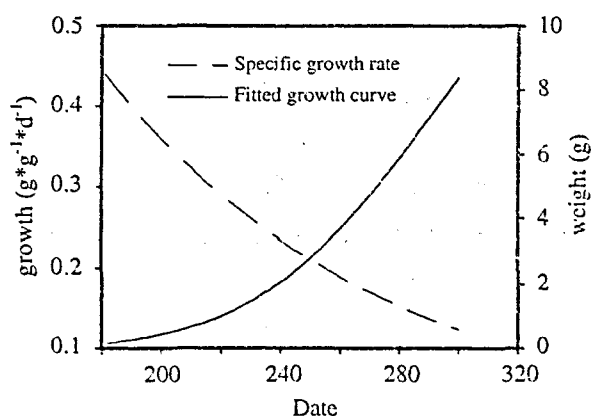


Figure 2. Fitted growth curve, and calculated specific growth rate for young-of-the-year herring in the northern Baltic Sea from Arrhenius & Hansson (1993).

2.5 Bioenergetics model

A bioenergetics model of individual Baltic herring has been developed by Rudstam (1988), using software developed by Hewett & Johnson (1992). The parameters used in the model were derived from a variety of sources but in all cases were from adult fish.

We compared the model predictions of daily consumption with the field estimates from gut evacuation rated and fullness. The input parameters for juvenile herring used in the bioenergetics model, were taken from ICES-area 28-29 in Arrhenius & Hansson (1993). The growth rate were derived from growth in length and length-weight relationship in the model (Figure 2). Temperature regime were taken from this study.

Table 1. Estimated fish length (in 5 mm intervals), wet weight, daily food ration and evacuation rate of juvenile herring in 1992. Temperature was taken every date between 0-10 m in July-August and 0-30 m in September-October. The number of fish analysed (1885) is not equal to the number of fish killed at different sampling dates and depths.

Date	Depth	Length intervall (mm)	Fish			Evacuation rate		Daily food ration	Temperature range
			n	length (mm)	SD	wet weight (g)	SD	h ⁻¹	% of body weight
<hr/>									
July 16-17									
	3 m	25-29	95	27.3	1.3	0.040	0.012	0.708	21.24
		30-34	110	31.9	1.4	0.089	0.025	0.811	13.49
		35-39	83	37.1	1.3	0.198	0.044	0.511	15.92
	10 m	30-34	138	32.1	1.3	0.085	0.023	0.770	16.19
		35-39	129	36.7	1.4	0.181	0.038	0.688	21.75
		40-44	112	41.5	1.3	0.329	0.061	0.473	15.15
August 5-6									
	10 m	30-34	60	32.6	1.4	0.106	0.030	0.664	11.06
		35-39	89	37.2	1.3	0.215	0.045	0.556	13.50
		40-44	104	42.1	1.3	0.386	0.067	0.425	9.70
		45-49	110	47.0	1.5	0.588	0.087	0.446	9.24
		50-55	87	52.1	1.3	0.855	0.087	0.525	15.60
August 26-27									
	15 m	45-49	82	47.6	1.3	0.611	0.084	0.812	25.98
		50-54	125	52.3	1.3	0.857	0.081	0.755	18.91
		55-59	130	57.0	1.3	1.160	0.117	0.552	16.45
		60-64	108	61.8	1.4	1.488	0.132	0.684	16.43
September 17-18									
	20 m	60-64	54	62.2	1.3	1.354	0.117	0.315	7.59
		65-69	62	67.0	1.4	1.638	0.122	0.549	5.27
		70-74	55	71.5	1.3	1.986	0.151	0.220	8.20
October 27-28									
	35 m	70-74	39	72.0	1.4	1.911	0.336	0.800	5.21
		75-79	50	76.9	1.5	2.491	0.350	0.604	8.02
		80-84	63	81.9	1.4	2.999	0.387	0.670	6.40
<hr/>									
Σ			1885						

3 Results

3.1 Fish sampling

Herring (*Clupea harengus*) were caught at all depths in each station, but showing a diel cycle with generally closer to the surface during night than during day. The depth of catches varied between 0-35 m, depending on the season and water temperature (Table 1).

3.2 Diel feeding patterns and daily rations

The stomach content varied with time of day for each diel series (Figure 3 a-f). The content of the stomachs was lowest during nighttime, indicating that herring fed

little or not at all during darkness. There was a tendency towards two maxima each day, one in the morning and one in the evening, and the times for these maxima varied depending on the time for sunset and sunrise.

Estimates of gastric evacuation rate (Table 1) and daily rations were highest during July-August, dropping in the autumn. For small juveniles, in the summer daily food consumption was about 20 % of the body weight while for larger juveniles in late fall daily consumption was about 4 %.

3.3 Feeding

Crustacean zooplankton dominated the stomach content of juvenile herring, and the copepods were clearly domi-

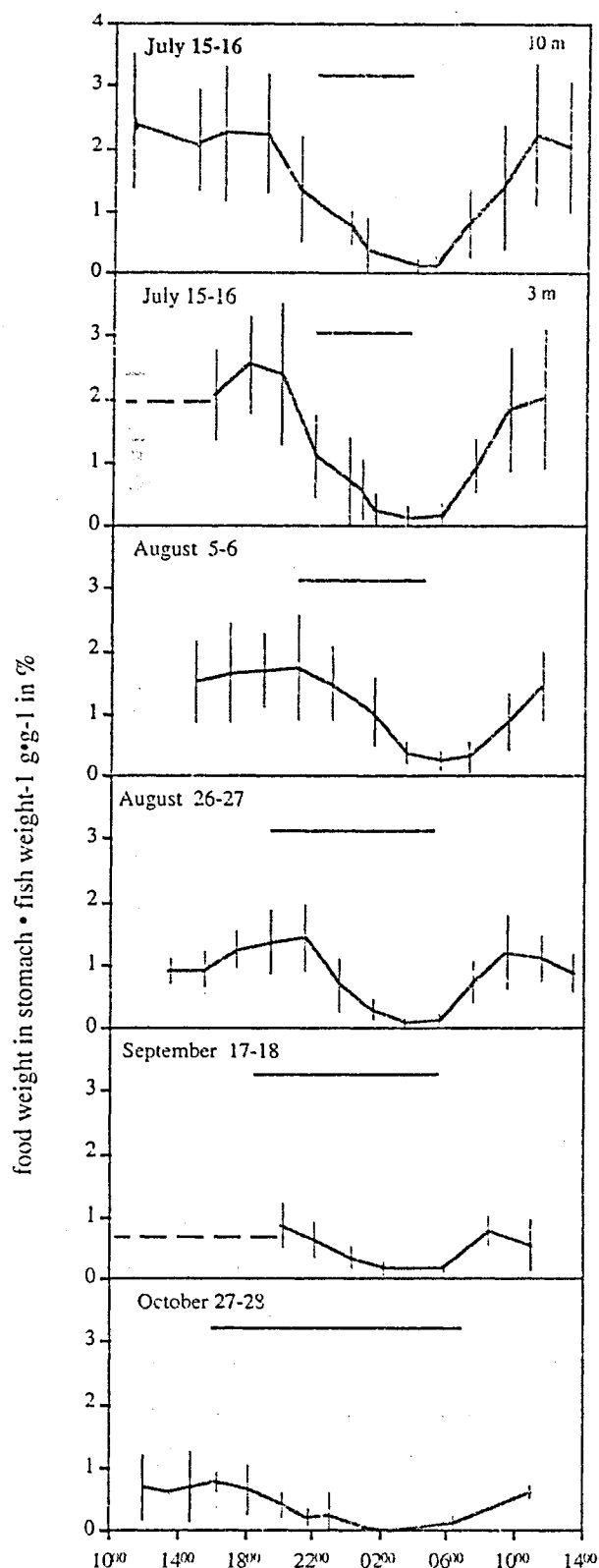


Figure 3 a-f. The diel cycle of food content in herring stomach for each sampling and sites. Each point represent the average stomach content at each sampling time. The period between sunset and sunrise is also marked (—). Dates with shorter sampling intervals, the data have been extrapolated (— —).

nating (Table 2). Among copepods, *Acartia* spp. (*Acartia bifilosa*, Giesbrecht, and/or *A. longiremis* (Liljeborg)) and *Eurytemora affinis hirundoides* (Nordquist) were dominated. Copepod nauplii were relatively common in the stomachs. Copepods were also the dominant prey items in the herring stomachs in August-October (Table 2). Other copepods were only in small numbers in the stomachs. In July and early August respectively, the cladocerans *Bosmina longispina maritima*, P.E. Müller, and *Pleopsis polyphemoides*, Leuckart, was consumed. Rotifers were rare and tintinnids were absent.

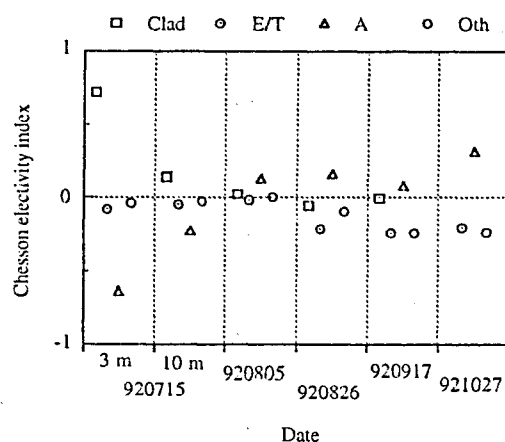


Figure 4. Electivity indices (Chesson, 1983) for juvenile herring between July and the end of October for 4 prey groups: Cladocerans (Clad), copepodites and adults of *Eurytemora* / *Temora* (E), *Acartia* (A) and other copepods (Oth, primarily *Pseudocalanus*).

Juvenile herring, selected cladocerans over copepods and *Acartia* over other copepod species (Figure 4). Cladocerans were not selected except at the shallow station in July sample. These pattern was not as clear and differ during sampling dates.

3.4 Zooplankton

In terms of abundance, zooplankton was dominated by copepods in July and in autumn and rotifers in August (Figure 5 & 6). Among copepods, *Eurytemora* and *Acartia* dominated. Together they constitute at least half

Table 2. Estimated proportions of zooplankton in herring stomachs (% by volume) and proportions of identified zooplankton taxa (% by numbers). Proportion were calculated as the average of proportions in individual fish. Length of fish, number of stomachs analyzed (N), number of empty stomachs (E) and the total number of identified prey items are also given. Prop.: proportion; zoopl.: zooplankton; id.: identified; ad&cop.: adult and copepodites; Bal.: *Balanus*; E/T: *Eurytemora/Temora*; A: *Acartia*; Unid.: unidentified; Bos.: *Bosmina*; Ple.: *Pleopsis*; Ker.: *Keratella*

Date	Stn	Time	Fish length interval (mm)	N	E	Prop. Zoopl. (%)	No. of identified prey	Naupl. Cop.	Bal.	Copepoda (ad & cop.)				Cladocera			Other zoopl	Egg
										E/T	A	Other	Unid.	Bos.	Ple.	Ker.		
July 16-17																		
3 m	18.00	25-29	10	0	100	978	1.8	0	0.1	1.1	0	0	95.5	0.2	0.7	0	0.5	
		30-34	10	0	100	989	1.2	0.4	0.1	1.4	0	0.4	95.2	0.1	0.4	0	0.8	
		35-39	10	0	100	999	4.2	0.0	0.1	0.9	0	0.7	92.2	0.7	0.3	0.4	0.5	
10 m	19.00	30-34	6	0	100	421	11.4	0.7	2.1	48.0	0.2	1.7	26.6	0.5	8.6	0.2	0	
	19.00	35-39	10	0	100	955	10.7	0.1	1.8	51.7	0.7	2.4	23.5	0.3	7.7	0.3	0.8	
	19.00	40-44	10	0	100	957	5.7	0.3	3.4	55.9	0.7	1.1	20.3	0.1	11.7	0.6	0.2	
August 5-6																		
10 m	20.30	30-34	4	0	100	356	14.8	3.8	0.5	13.0	0.8	2.5	59.2	1.8	0.8	0	2.8	
	20.30	35-39	3	0	100	280	10.7	3.0	1.3	17.3	0	2.3	60.6	1.3	1.1	0.4	2.0	
	20.30	40-44	10	0	100	941	11.3	1.6	3.1	11.7	1.2	1.0	64.9	1.9	2.1	0.4	0.8	
	20.30	45-49	10	0	100	957	4.7	3.1	1.9	16.2	1.2	2.8	66.9	0.9	1.1	0.5	0.7	
	20.30	50-55	10	0	100	963	1.8	2.7	5.0	19.2	0.6	0	65.8	3.6	0.6	0.2	0.5	
August 26-27																		
15 m	19.15	45-49	4	0	100	393	20.6	2.0	19.6	48.3	1.3	1.8	0	5.1	0.5	0.3	0.5	
	19.15	50-54	10	0	100	998	14.6	3.1	13.4	53.3	1.1	0.6	0	10.5	1.4	1.0	1.0	
	19.15	55-59	10	0	100	963	13.1	1.5	32.6	39.6	0.9	0.2	0	4.8	1.9	0.8	4.6	
	19.15	60-64	10	0	100	898	4.6	1.1	35.5	52.7	1.2	0	0	1.0	1.4	0.3	2.2	
September 17-18																		
20 m	20.15	60-64	9	0	100	890	6.2	0	8.4	84.1	0	0	0	0	1.3	0	0	
	20.15	65-69	10	0	100	927	11.3	0	3.2	83.3	0	0	0	0	0.3	0	1.9	
	20.15	70-74	10	0	100	998	10.1	0	3.8	81.6	0	0	0	0	2.7	0	1.8	
October 27-28																		
35 m	18.15	70-74	2	0	100	200	12.5	0	7.0	90.5	0	0	0	0	0	0	0	
	18.15	75-79	4	0	100	400	6.5	0	10.2	82.0	1.0	0.3	0	0	0	0	0	
	18.15	80-84	5	0	100	500	8.6	0	11.6	79.4	0.4	0	0	0	0	0	0	
Σ				167														

of the biomass. Other common copepods were *Temora longicornis* (P. Müller) and *Pseudocalanus minutes longatus*. Among cladocerans, *Bosmina* and *Pleopsis* constitutes 95-100 % of the numbers and *Keratella* spp. and *Synchaeta* spp. were dominated among rotifers. In spite of high numbers, tintinnids generally represented <1% of the biomass.

3.5 Bioenergetics model

The results were analysed with linear regression analysis (SYSTAT, 1992), using data from field estimates as the independent variable and data from model predictions as the dependent variable. There were no significantly differences between the model and field estimates of food consumption (Figure 7).

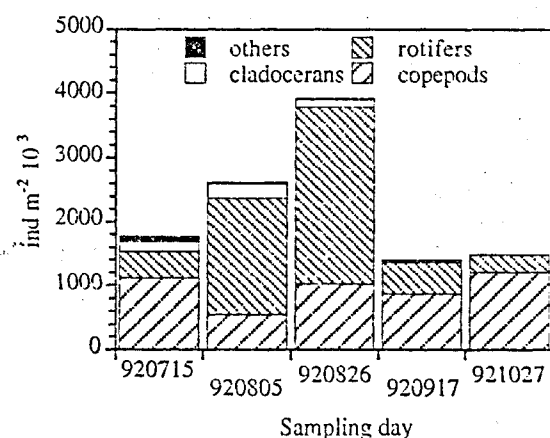


Figure 5. The total abundance of zooplankton on the different sampling stations. The three first was sampled between 0-10 m (station 1-3 in Figure 1) and the last two was sampled 0-30 m (station 4-5 in Figure 1).

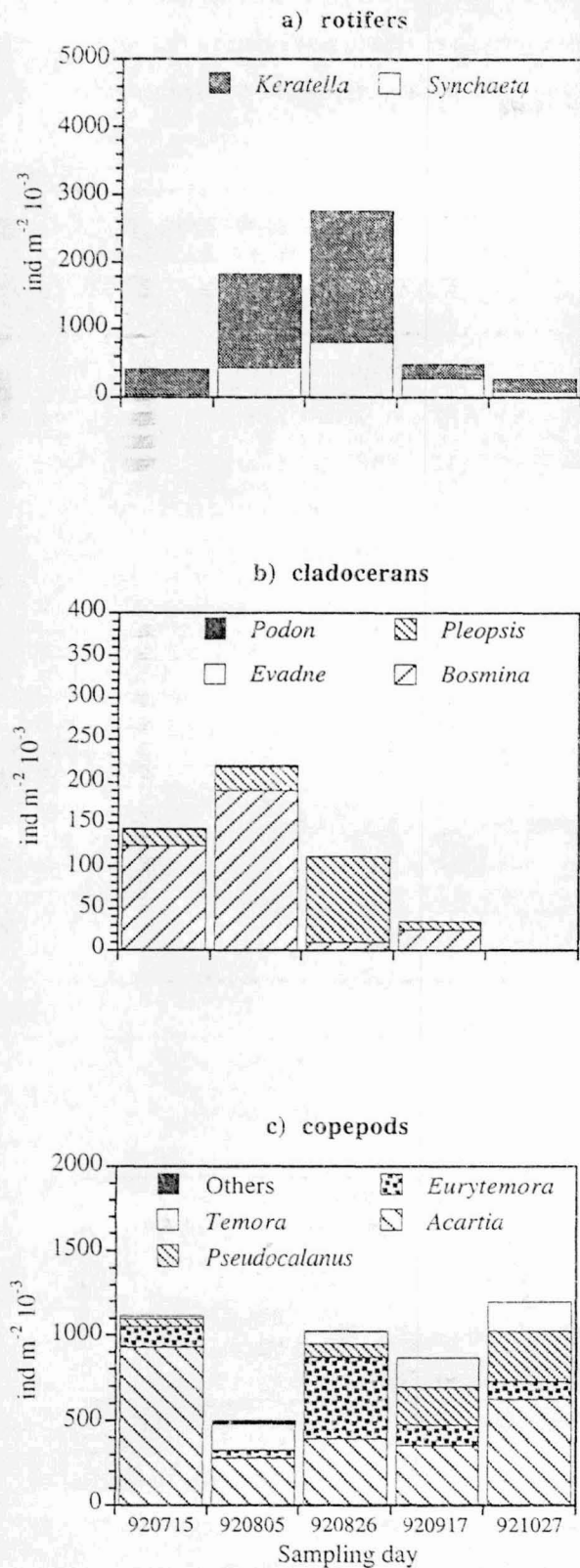


Figure 6. The abundance of total rotifers (a), cladocerans (b) and copepods (c). The dominating species within each group are shown separately.

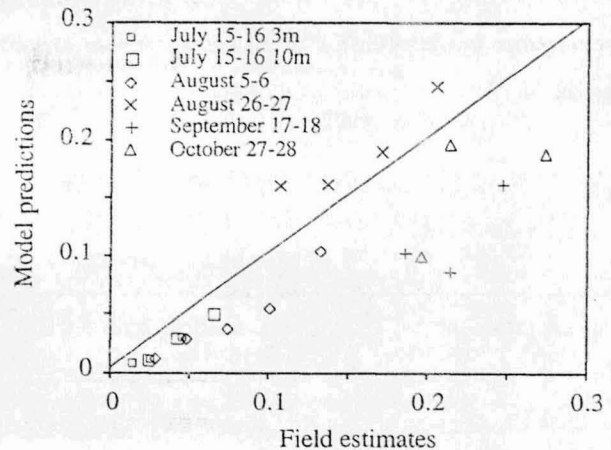


Figure 7. The food consumption predicted by the model against the field data. The black line is the 1:1 relation. The slope and the intercept do not differ significantly from 1 ($n=21$, $r^2=0.61$, slope=0.74, SE=0.14, $p=0.07$).

4. Discussion

Juvenile herring (*Clupea harengus*) foraged predominantly on zooplankton. There was a shift from cladocerans in early life stage to copepods in older stages on juveniles. Herring preferred cladoceran over copepods in shallower waters in the summer. There have been shown in this area that cladocerans are selected over copepods and the seasonal changes in proportions of copepods and cladocerans consumed reflect the seasonal changes in zooplankton composition (Johansson, 1992, Rudstam et al., 1992). The preferred species of cladocerans and copepods were according to other studies on juvenile herring in the northern Baltic Sea (Hudd, 1982, Parmanne & Sjöblom, 1984, Raid, 1985, Rudstam et al., 1992).

There was a difference between shallow water and deep stations in the food content and in fish length. Fish closer to the shore had more cladoceran than copepods in their stomachs and were also shorter in average length. Herring larvae seem to be retained in the nearshore zone during the larval period to experience a temperature regime similar to optimum for growth and to avoid predation (Urho & Hildén, 1990).

There were a diurnal dynamics of stomach fullness with a tendency that herring consume more in the evening than in the morning, which has also been shown by Raid (1985). The gastric evacuation rate were high in the summer and lower in the autumn except the October serie. The evacuation rate are mainly governed by the water temperature (Elliott & Persson, 1978) and more or less unaffected of fish size, food size and the frequency of feeding (Elliott, 1972, De Silva & Balbontin, 1974). The high values in October maybe due to difficulty to calculate the evacuation rate, because of low temperature and growth rate of herring.

The food consumption decreases from 20 % of body weight d^{-1} in the summer to 4 % d^{-1} by the end of October for juveniles. Similar specific consumption rates have been reported elsewhere by field estimates of daily rations (De Silva & Balbontin, 1974, Franek, 1988, Rudstam et al., 1992).

Despite that the bioenergetics model for herring is based on data from adult fish, it does not predict consumption rates that differ significantly from those we estimated for YOY fish. This is contrary to studies on yellow perch (*Perca flavescens*) that measure invalid parameters for larvae and juvenile with modeling with adult parameters (Post, 1990). Still, the in situ estimates are based on the variation in stomach content between few individuals whereas variation in the model predictions are based on the variability in body size of larger numbers of individuals. Since growth is cumulative and the daily growth data used in the model is integrated over time, but the model can't predict day to day variability in consumption, but it can accurately predict cumulative consumption. Therefore we need further investigation to get more information on larval and juvenile on field measurement of key parameters for the bioenergetics model. We also need to investigate the maximum consumption (functional responses, e. g. Murdoch, 1973; Abrams, 1987) in the field to redefine the maximum consumption function in the model.

This study show that the main diet for juvenile herring is zooplankton and consumption decrease with

temperature. It also indicate that the available bioenergetics model for adult herring, can be used to estimate the food consumption for juvenile herring.

Acknowledgements: Sture Nellbring, Markus Nikula and Joakim Westberg helped in the field. Financial support was provided by the Swedish Environmental Protection Agency, Swedish Natural Science Research Council, Hierta-Retzius foundation, Alice & Lars Siléns fund, Stockholm Centre for Marine Research and Nitro Nobel AB.

5. Literature cited

- Abrams, P. (1987). The functional response of adaptive consumers of two resources. *Theor. Popul. Biol.* 32: 262-288.
- Arrhenius, F., Hansson, S. (1993). Food consumption of larval, young and adult herring and sprat in the Baltic Sea. *Mar. Ecol. Prog. Ser.* 96:125-137.
- Chesson, J. (1983). The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64: 1297-1304.
- De Silva, S. S., Balbontin, F. (1974). Laboratory studies on food intake, growth and food conversion of young herring, *Clupea harengus* (L.). *J. Fish Biol.* 56: 645-658.
- Elliott, J. M. (1972). Rates of gastric evacuation in brown trout, *Salmo trutta* L.. *Freshw. Biol.* 5: 287-303.
- Elliott, J. M., Persson, L. (1978). The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* 47: 977-991.
- Franek, D. (1988). 0+ smelt (*Osmerus eperlanus* L.) and herring (*Clupea harengus* L.) in the food chain of the Barter Bodden. *ICES 1988 BAL/No. 13.*
- Hansen, M. J., Boisclair, D., Brandt, S. B., Hewatt, S. W., Kitchell, J. F., Lucas, M. C., Ney, J. J. (1993) Applications of bioenergetics models to fish ecology and management: Where do we go from here? *Trans. Am. Fish. Soc.* In press.
- Hansson, S., Larsson, U., Johansson, S. (1990). Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. *J. Plankton Res.* 12(5): 1099-1116.
- Hay, D. E. (1981). Effects of capture and fixation on gut contents and body size of Pacific herring. *Rapp. Cons. Int. Explor. Mer.* 178: 395-400.
- Hernroth, L. (1985). Recommendations on methods for marine biological studies in the Baltic Sea. Meso-zooplankton biomass assessment. *Baltic Marine Biologists, Publications no. 10*, pp. 1-32.
- Hewett, S. W., Johnson, J. L. (1992). Fish bioenergetics model 2. An upgrade of a generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea

Grant Technical Report No. WIS-SG-92-250.
2nd edition. p. 1-79.

- Hudd, R. (1982). Feeding of Baltic herring larvae (*Clupea harengus* L.) in the Gulf of Finland. Finnish Fish. Res. 4: 27-34.
- Johansson, S. (1992). Regulating factors for coastal zooplankton community structure in the northern Baltic proper. PhD thesis. Inst. Zool., Stockholm univ.
- Kott, P. (1953). Modified whirling apparatuses for the subsampling of plankton. Aust. J. Mar. Freshwater Res., 4: 387-393.
- Mullin, M. M. (1969). Production of zooplankton in the ocean: the present status and problems. Oceanogr. Mar. Biol. Rev., 7: 293-310.
- Murdoch, W. W. (1973). The functional response of predators. J. Appl. Ecol. 10: 335-342.
- Parmanne, R., Sjöblom, V. (1984). The abundance of spring spawning Baltic herring larvae in the Seas around Finland in 1982 and 1983 and the correlation between the zooplankton abundance and the herring year class strength. ICES C.M. 1984/J:18.
- Persson, L. (1986). Patterns of food evacuation in fishes: a critical review. Env. Biol. Fish. 16(1-3): 51-58.
- Post, J. R. (1990). Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): In situ estimates and bioenergetics models. Can. J. Fish. Aquat. Sci. 47: 554-560.
- Raid, T. (1985). The reproduction areas and ecology of Baltic herring in the early stages of development found in the Soviet zone of the Gulf of Finland. Finnish Fish. Res. 6: 20-34.
- Rudstam, L. G. (1988). Exploring the dynamics of herring consumption in the Baltic: Applications of an energetic model of fish growth. Kieler Meeresforsch., Sonderh. 6: 312-322.
- Rudstam, L. G., Hansson, S., Johansson, S., Larsson, U. (1992). Dynamics of planktivory in a coastal area of the northern Baltic Sea. Mar. Ecol. Progr. Ser. 80(2-3): 159-173.
- SYSTAT. (1992). SYSTAT: Statistics, Version 5.2 Ed. Evanston, I. L.: SYSTAT Inc: 724 pp.
- Urho, L., Hildén, M. (1990). Distribution patterns of Baltic herring larvae, *Clupea harengus*, L., in the coastal waters off Helsinki, Finland. J. Plankton Res. 12(1): 41-54.