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Growth of Baltic Sea young-of-the-year herring *Clupea harengus* is resource limited

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ABSTRACT: We have determined the *in situ* food consumption rate of young-of-the-year (YOY, length 25 to 94 mm) Baltic Sea herring. This consumption increased with increasing food availability, which suggests that the growth rate of young Baltic herring is food limited. This has been described previously for larval stages, but not for metamorphosed fish. The daily food consumption rate of YOY herring decreased from about 8 to 15% of body weight for small fish in the summer to 0.6 to 2% for larger juveniles in late autumn.

KEY WORDS: Baltic Sea · Juveniles · Herring · Food consumption · Zooplankton

Herring *Clupea harengus* L. is a dominant predator on crustacean zooplankton in the Baltic Sea (e.g. Hansson et al. 1990, Rudstam et al. 1992, Arrhenius & Hansson 1993). It is possible that the effects of this predation indirectly influence other trophic levels (cf. experiences from lakes; Carpenter et al. 1985, Carpenter & Kitchell 1993). To evaluate the predation pressure exerted by herring on its prey (Hansson et al. 1990, Rudstam et al. 1992, 1994), food consumption has been estimated from a bioenergetics model, based on physiological assumptions and field data on fish growth, habitat temperature, and diet. These analyses have shown that, of the total zooplankton consumption by the Baltic herring population, young-of-the-year (YOY) fish consume 38 to 76%, making them the dominant zooplanktivorous age group (Arrhenius & Hansson 1993, Arrhenius 1997). Although these results indicate intensive predation on zooplankton, there are few studies that present a quantitative relationship between food availability and zooplanktivory in the

Baltic Sea (Rudstam et al. 1992, Thiel 1996). The objective of this study was to test if such a relationship exists.

Materials and methods. Using small charges of explosives (15 to 120 g of Primex 17 mm, Nitro Nobel AB), herring were sampled at approximately 2 h intervals during ten 24 h periods between July and November 1992 and 1993 (data from 1992 are from Arrhenius & Hansson 1994a,b). The explosives were detonated below the fish at varying depths (see Table 1) and explosion gases carried the fish to the surface where they were collected. The depth of the fish was found either empirically, from detonations on different depths, or from an echo sounder. Samples of about 10 fish per length class were taken within 10 min after a detonation. In 1992, the fish were immediately preserved in 70% ethanol; in 1993 they were deep-frozen (–18°C). All sampling was done in coastal areas of the northern Baltic proper (around 58° N, 17° E).

In the laboratory, the total length of each fish was measured to the nearest mm and the wet weight (WWT) was determined to the nearest mg. Weight data were corrected for effects of preservation (WWT = $0.02 + (1.05 \times \text{ethanol-weight [g]})$, $r^2 = 0.99$, $n = 40$ and WWT = $0.08 + (1.02 \times \text{deep-frozen-weight [g]})$, $r^2 = 0.99$, $n = 200$). Fish dry weight (DWT) was estimated as DWT = $-0.022 + (0.22 \text{ WWT [g]})$, $r^2 = 0.99$, $n = 300$. Stomachs were removed and stored in 70% ethanol for at least 1 mo to stabilise the biomass (Karjalainen 1992). Each stomach was cut open, rinsed with ethanol and food particles collected on a glass fibre filter (Whatman GF/F in 1992 and GF/D in 1993). DWT of stomach content was determined to the nearest µg (Sartorius micro M3P) after drying to stable weight at 60°C.

We assumed that the zooplankton prey used by the fish were found in the depth interval between the sur-

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face and the depth where the fish were caught. This water layer was sampled using a 90 μm WP-2 zooplankton net, which was towed vertically at a speed of 0.5 m s^{-1} . One daytime sample was taken on each sampling date, and immediately after collection it was preserved in a 4% buffered formaldehyde solution. Time constraints prevented us from taking more than

1 zooplankton sample per sampling date, but an earlier study in this area has shown that the horizontal distribution of zooplankton is relatively even (coefficient of variation among replicates $\sim 30\%$; Johansson et al. 1993). Before counting under an inverted microscope, the zooplankton samples were subsampled (Kott 1953) and at least 500 specimens from each sam-

Table 1. Fish length (in 5 mm intervals), dry weight, evacuation rates and daily food ration of young-of-the-year (YOY) herring in 1992 and 1993. The temperature intervals given are for 0 to 10 m in July/August and 0 to 30 m in September/October, corresponding to depth occupied by the YOY at these sampling occasions. The assumed feeding period was between sunrise and sunset. The number of fish analysed is not equal to the number of fish killed at different sampling dates and depths

Date	Depth (m)	Fish length interval (mm)	n	Fish dry weight (g)		Evacuation rate, ER (h^{-1})	Daily food ration (% of body weight, DWT)	Temp. ($^{\circ}\text{C}$) Mean	Feeding period (h)
				Mean	SD				
1992		25–29	95	0.0060	0.0020	0.35	11	17.4	
Jul 16–17	3	30–34	110	0.013	0.0038	0.39	15	17.4	
		35–39	83	0.031	0.0060	0.38	15	17.4	
									18.0
Aug 5–6	10	30–34	138	0.013	0.0035	0.29	12	17.4	
		35–39	129	0.028	0.0051	0.38	9.9	17.4	
		40–44	112	0.052	0.010	0.32	11	17.4	
	10	30–34	60	0.017	0.0046	0.24	7.1	16.5	
		35–39	89	0.034	0.0058	0.26	11	16.5	
		40–44	104	0.061	0.011	0.23	8.5	16.5	17.0
Aug 26–27	15	45–49	110	0.095	0.015	0.21	7.1	16.5	
		50–54	87	0.14	0.016	0.27	9.6	16.5	
		45–49	82	0.099	0.015	0.29	12	15.0	
	15	50–54	125	0.14	0.015	0.33	9.5	15.0	15.5
		55–59	130	0.20	0.023	0.21	8.3	15.0	
		60–64	108	0.27	0.028	0.26	7.9	15.0	
Sep 17–18	20	60–64	54	0.25	0.024	0.20	4.8	13.2	
		65–69	62	0.30	0.026	0.19	3.5	13.2	12.5
		70–74	55	0.38	0.036	0.28	4.8	13.2	
Oct 27–28	35	70–74	39	0.37	0.080	0.16	1.4	8.7	
		75–79	50	0.51	0.090	0.20	2.2	8.7	9.0
		80–84	63	0.64	0.11	0.23	1.8	8.7	
1993		25–29	174	0.0070	0.15	0.34	8.2	15.9	
Jul 15–16	10	30–34	187	0.018	0.012	0.37	7.7	15.9	
		35–39	168	0.030	0.0071	0.39	8.5	15.9	18.0
		40–44	162	0.059	0.010	0.37	6.1	15.9	
		45–49	97	0.091	0.014	0.34	9.8	15.9	
		30–34	101	0.015	0.013	0.28	7.4	15.4	
Aug 2–3	10	35–39	117	0.035	0.0079	0.39	8.3	15.4	
		40–44	96	0.049	0.011	0.33	9.5	15.4	17.0
		45–49	68	0.098	0.015	0.36	9.1	15.4	
		50–54	87	0.092	0.019	0.33	9.6	15.4	
		55–59	101	0.23	0.029	0.22	7.2	13.9	
Aug 24–25	10	60–64	130	0.29	0.036	0.24	7.0	13.9	15.5
		65–69	111	0.36	0.040	0.25	7.5	13.9	
		60–64	27	0.20	0.033	0.26	7.8	9.7	
Oct 6–7	10	65–69	43	0.37	0.042	0.32	6.1	9.7	
		70–74	62	0.45	0.067	0.27	5.1	9.7	11.5
		75–79	75	0.47	0.087	0.27	5.4	9.7	
		80–84	54	0.49	0.078	0.21	3.0	9.7	
		75–79	93	0.56	0.097	0.23	1.3	5.8	
Nov 2–3	30	80–84	127	0.73	0.11	0.25	1.1	5.8	9.0
		85–89	118	0.79	0.12	0.21	0.92	5.8	
		90–94	45	0.74	0.19	0.22	0.58	5.8	
Total no. of fish:			4128						

ple were identified to the lowest possible taxonomic level. Biomass was estimated from species and stage-specific values on individual WWT (Hernroth 1985, further details in Hansson et al. 1990), of which 13% was assumed to be DWT (Mullin 1969). YOY herring consume zooplankton roughly in proportion to their relative abundances (Arrhenius 1996) and we assumed that the food available to YOY herring was in direct proportion to the biomass in the zooplankton samples.

The stomach content of YOY herring showed a clear diel variation, indicating that they are eating only during daylight hours (sunrise to sunset; Arrhenius & Hansson 1994a). From these data, consumption rate ($Cons$, $g\ g^{-1}\ time\ interval^{-1}$) was estimated by the method of Elliott & Persson (1978):

$$Cons = \frac{(S_t - S_0 e^{-ER \times t}) ER \times t}{1 - e^{-ER \times t}} \quad (1)$$

where S_0 and S_t are specific stomach contents (expressed as the stomach content divided by the body mass, both in $g\ DWT$) at the beginning and end of a t (hours long) period (generally ~ 2 h). ER is the gastric evacuation rate, estimated from the decline in stomach content during the non-feeding period (assuming an exponential evacuation rate; Elliott & Persson 1978). We calculated the ER between approximately 1 h after sunset and 1 h before sunrise. Calculations were done separately for each sampling date and for 5 mm wide size classes of fish. More details are found in Arrhenius & Hansson (1994a,b).

Growth of a fish may be limited not only by food, but also by temperature if food is unlimited (cf. Kitchell et al. 1977). However, for Baltic Sea zooplanktivores, such as herring, temperature and food availability are correlated. Generally, the zooplankton population peaks in the summer when the water temperature is high and population is minimal in winter when the temperature also reaches its lowest values (Johansson 1992). To evaluate which of these factors was most limiting, zooplankton abundance or temperature, both were correlated with the hourly food consumption during the feeding (= daylight) period. However, since the weight-specific consumption rate (WSC) varied with size, we also included fish size in the analysis. This was done by using dummy variables as described by Chatterjee & Price (1991, p. 95 to 106). The regression equation fitted to the data became:

$$WSC = k_0 + k_1 \times zoopl + k_2 \times temp + \sum_{i=3}^{16} k_i \times dummy_i \quad (2)$$

where $zoopl$, $temp$ and $dummy_3$ - $dummy_{16}$ refer to the zooplankton biomass, temperature and the dummy variables for the 14 size classes of fish.

Results and discussion. Zooplankton samples were dominated by copepods (Fig. 1), mainly *Eurytemora affinis hirundoides*, *Temora longicornis* and *Acartia* spp. The cladocerans *Bosmina longispina maritima*, *Pleopsis polyphemoides* and rotifers each constituted only 1 to 15% of the biomass. The proportions of different zooplankton taxa were almost the same both years and the seasonal pattern followed earlier observations from the same area (Johansson 1992).

A total of 4128 YOY herring, ranging from 25 to 94 mm in length and 0.006 to 0.79 g DWT, were analysed. The estimated daily food consumption of YOY herring was 8 to 15% of the body weight for small fish in the

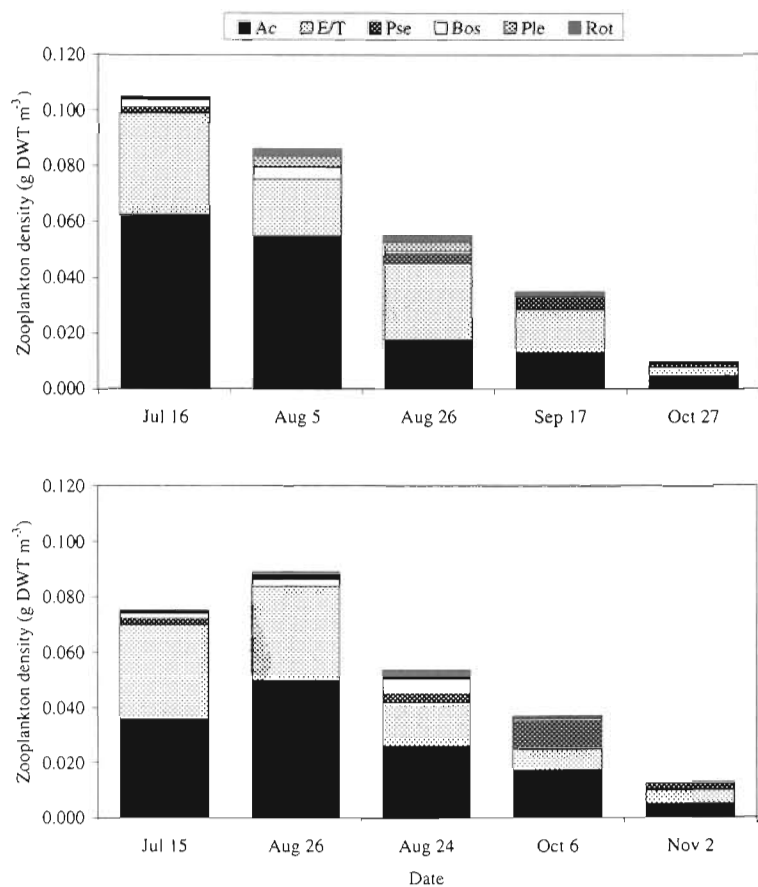


Fig. 1. Biomasses of rotifers, cladocerans and copepods for 1992 and 1993. Dominating species within each group are shown separately. Ac: *Acartia* spp., E/T: *Eurytemora affinis hirundoides*/*Temora longicornis*, Pse: *Pseudocalanus minutus elongatus*, Bos: *Bosmina longispina maritima*, Ple: *Pleopsis polyphemoides*, Rot: Rotatoria. *E. affinis hirundoides* and *T. longicornis* are merged in this graph, as they are difficult to separate in stomach contents from fish

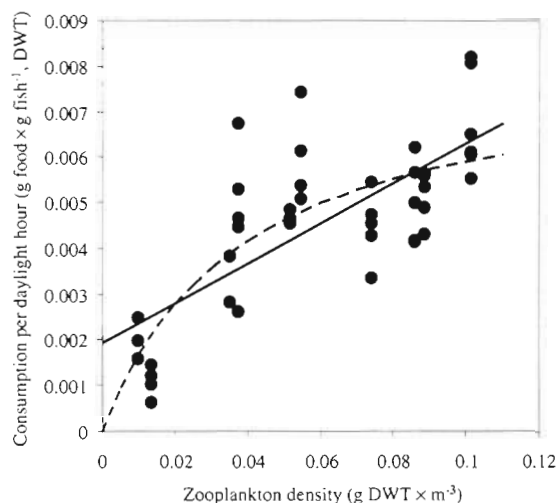


Fig. 2. Specific food consumption per hour (g DWT) of YOY Baltic herring plotted against the zooplankton density (●). The lines fitted to the data show a linear fit (—) ($WSC = 1.9 \times 10^{-3} + 4.4 \times 10^{-2} \times \text{zoopl}$) and a functional response Type II curve (-----) ($WSC = \frac{0.21 \times \text{zoopl}}{1 + 26 \times \text{zoopl}}$)

summer and 0.6 to 2% for larger juveniles in late autumn (Table 1). These consumption rates are similar to those observed in other field studies on YOY herring (Checkley 1984, Franek 1988) and are also consistent with the bioenergetics and growth rate of young herring (Arrhenius 1998).

In the regression analyses with food consumption as a function of temperature, zooplankton abundances and fish size (Eq. 2), the only statistically significant coefficient was that for the zooplankton biomass ($k_1 = 4.5 \times 10^{-2}$, $t = 2.11$, $p < 0.05$). Corresponding values for temperature were $k_2 = -4.1 \times 10^{-5}$, $t = -0.222$ and $p > 0.8$. When using only the zooplankton biomass as the independent variable, the regression became highly significant ($k_1 = 4.4 \times 10^{-2}$, $t = 7.07$, $p < 0.001$, $r^2 = 0.55$). If a functional response Type II curve (Holling 1959) was fitted to the data, a slight increase in the correlation coefficient was obtained ($r^2 = 0.63$, Fig. 2)

An implication of our results is that the food availability influences the growth of young Baltic herring (food consumption rate increases with increasing prey density). This has been described before for larval stages (i.e. Kjørboe et al. 1988, Fortier & Gagné 1990, the list is not supposed to be complete) but not for metamorphosed fish. This may influence recruitment either directly through starvation mortality or indirectly by influencing growth rate and hence the vulnerability to predation (Houde & Schekter 1981). To support this theory, Parmanne & Sjöblom (1988) have shown a positive correlation between Baltic herring recruitment and zooplankton abundance.

Our result, that at least YOY herring are resource limited, is of relevance not only from a basic science perspective. It has often been suggested that eutrophication of the Baltic has favoured herring (e.g. reviews by Hansson 1985, Hansson & Rudstam 1990, Thunro 1997). Prerequisites for this are that the production of crustacean zooplankton has increased in response to an increased primary production, and that herring are food limited and can respond to this increased production. Our results presented here, and recently published articles that describe growth and condition (fateness) changes in herring due to changes in the food supply (Raid & Lankov 1995, Flinkman et al. 1998), indicate that herring is food limited and likely to respond to changes at lower trophic levels.

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