Growth and seasonal changes in energy content of young Baltic Sea herring (*Clupea harengus* L.)

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Growth rates, hatch-date distributions and seasonal changes in energy content of larval and juvenile herring (*Clupea harengus*), the major Baltic Sea zooplanktivore, were studied in a coastal area. The first microstructure (ring) shown in the otoliths (sagittae) was formed at the end of the yolk-sac stage. The following rings occurred regularly and showed a pattern corresponding to daily growth rings, as described in the literature, and we used these rings to age the fish. The average growth rate was estimated at 0.37 mm d^{-1} and 0.58 mm d^{-1} for larval and metamorphosed herring, respectively. The overall growth for all young stages could be described with a fourth order polynomial relationship between length and age. Estimated hatching dates were distributed between March and June. This is earlier than normally assumed for the northern Baltic Sea and was probably caused by an early and warm spring in 1993. Our data indicate the highest survival for herring spawned from end of April to the middle of May. In terms of seasonal and yearly fluctuations in body composition, there was an increase in energy content from 2200 to 2800 J g^{-1} wet weight and 2900 to 4800 J g^{-1} wet weight for larval and metamorphosed herring, respectively, with nearly constant energy content during metamorphosis.

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Introduction

Herring, *Clupea harengus*, is a dominant predator on the crustacean zooplankton community in the Baltic Sea. To evaluate the predation pressure on its prey, food consumption estimates are needed. Direct measurements of food consumption by fish are, however, difficult to obtain and require considerable effort (Elliott and Persson, 1978). Therefore, bioenergetics models based on physiological assumptions and field data on fish growth, habitat temperature and diets have been developed (Kitchell *et al.*, 1977; Rice and Cochran, 1984; Ney, 1990; Hewett and Johnson, 1992). This approach has been used to address a variety of ecological and fishery-related questions (e.g. Hartman and Magraf, 1992; Brandt *et al.*, 1992; He *et al.*, 1993; Hansson *et al.*, 1996). However, many bioenergetics models lack parameters for young stages, as has been stressed by Hansen *et al.* (1993). When predictions from these bioenergetics models, based on parameters derived from adult fish, have been compared with observed consumptions by juveniles, considerable differences have been found (Post, 1990; Madon and Culver, 1993).

In a recent article, we combined a bioenergetics model and data on abundance, diet, and growth to estimate food consumption by Baltic Sea herring (Arrhenius and Hansson, 1993). One conclusion was that larvae and juvenile herring from the first year are the dominant age-class with regard to the consumption of zooplankton. We found, however, that data on these young fish are surprisingly poor, and rough assumptions had to be made regarding growth rates of larvae and juveniles, their energy content, and mortality rates. In this paper, we present data on energy content of herring from 30 d-old larvae to adults. We also present daily growth rate data from hatching to an age of about six months and hatch-date distributions, as determined by back-calculating from otolith microstructure.

Materials and methods

Field sampling

Fish were collected using small charges of explosives (15–120 g of Primex 17 mm, Nitro Nobel AB) in the Askö area (around 58°N, 17°E) during 1992–1993 and by a commercial trawler in the Nynäshamn area (around 58°N, 18°E) in 1994. A subsample of the fish was immediately preserved in 70% ethanol (1992) or deep-frozen (-18°C, 1993–1994). Water temperature was measured when sampling.

In the laboratory, the juvenile herring were measured to nearest mm (total length) and the wet weight (WWT) was measured to the nearest 1 mg. Length and weight data were corrected for effects of the ethanol and deep-freezing preservation, using empirical data from Arrhenius and Hansson (1995).

Hatching experiment

On three occasions, adult spawning herring were collected from around 59°30′N, 19°E and artificial fertilisation performed in the laboratory. Eggs were incubated at 13°C and 6.2‰ salinity in hatching boxes (22 l) supplied with air, using methods described by Munk and Rosenthal (1983). The photoperiod was kept at approximately 10 h day:14 h night.

Newly hatched larvae were collected every morning and transferred to a 100 l aquarium of 6.2‰ salt water at 13°C. Larvae were sampled every day except on the first and third sampling period. After the larvae had reached the end of the yolk-stage, they were fed *ad lib* on rotifers and copepod nauplii for 20 d. To prevent dissolving of otolith structures, the larvae were preserved in 95% ethanol (Butler, 1992). Correction for shrinkage of larvae due to alcohol preservation was 40% for dry weight and 4% for standard length (Moksness and Fossum, 1992). Larval dry weight (DWT) was determined to nearest 1 µg (Sartorius micro M3P) by drying ten specimens at 60°C until constant weight was attained.

Otolith growth and microstructure

The sagittae were removed under polarised light and mounted on glass with thermoplastic cement (Buehler). Otoliths from fish over 20 mm had to be ground to show the growth rings. The polishing procedure (Secor *et al.*, 1992) was done with fine grid paper (4 and 2 µm) and 0.3 µm alumina. The growth rings were examined using a phase-contrast light microscope 400-1000X (Leitz DM RBE). The analysis system consisted of a CCD video-camera attached to the light microscope and connected to a monitor, a multiscan digitiser board and a microcomputer. Otoliths images were analysed with image-analysis software (Q500 MC Qwin, v 1.0, Leica). Daily growth increments in the otoliths were improved markedly by the use of ammonium picrate ($C_6H_6N_4O_7$) with glycerine ($C_3H_8O_3$) between glass and cover slip (cf. Malmberg, 1970), and further enhanced using the image-analysis software. Most increment widths were greater than 1 µm and groups of narrowly spaced increments, having widths below the theoretical limits of resolution by microscope, were not evident. The otolith patterns and the increment widths were similar to those reported by Moksness and Fossum (1992), and shown to represent daily increments (Moksness and Wespestad, 1989; Moksness, 1992a).

Energy analysis

For the energy analyses, fish were freeze-dried and dry weights (DWT) were determined to the nearest 1 mg. Carbon (C) and nitrogen (N) contents were determined with a carbon/hydrogen/nitrogen analyser (Model 600-800-300, Leco Corporation) using EDTA (C: 41.1, H: 5.52, N: 9.59) as standard. Two replicates, each of about 2 mg, were analysed per sample. Calorimetric content was estimated from organic C, using the N-corrected formula of Salonen *et al.* (1976). The conversion factor from DWT to ash-free dry weight (AFDW) was 0.9 (Pascual and Yúfera, 1993). This method has been used in several other studies (Harris *et al.*, 1986; Minagawa *et al.*, 1993; Pascual and Yúfera, 1993; Yúfera *et al.*, 1993). Energy values are reported as Joules (J) g^{-1} (WWT).

Results

Hatching

The artificially fertilised herring eggs hatched in 8 d (s.d. ± 1.3) at 13°C (about 2500 degree-hours) and hatching success varied between 20% and 90%. The failure of a high viable hatch was caused by infection with *Saprolegia* sp.. Mass mortality was observed after about 15 d post-hatch if no food was offered.

The standard length of newly hatched larvae was 7.2 mm (s.d. ± 0.72) and DWT 95 µg (s.d. ± 7.0, about 830 µg WWT). There was no significant difference in length and weight between the three fertilisation batches (ANOVA, $p < 0.001$, $n = 60$). The larvae decreased in weight during the endogenous feeding and increased in weight when the yolk-sac was consumed and the larvae started exogenous feeding (Fig. 1). The first larvae without yolk-sacs were observed after 6 d. After 8 d, 50% of the larvae had absorbed their yolk-sac, and 80% of the larvae had absorbed the yolk after 14 d. The first larvae with food particles in the stomach were seen after 6 d.
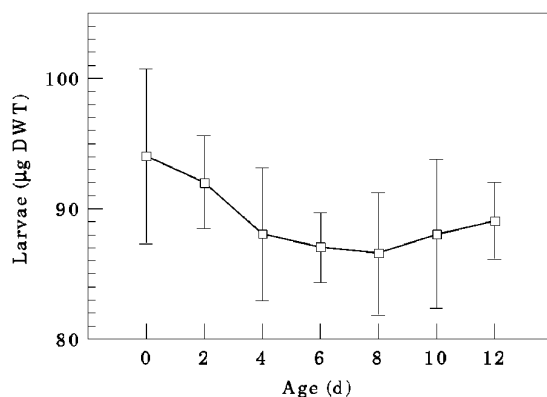
Figure 1. The average mean weight (µg DWT) of 10 herring larvae taken every second day, 0–12 d post-hatch. The larvae were fed. Error bars represent 1 standard deviation from the mean.

Otolith microstructure

A total of 34 sagittae were investigated from newly hatched larvae. The first otolith ring appeared on average in larvae from the 8th post-hatch day (the earliest 6 d post-hatch, s.d. ± 1.7 d). The mean radius of the first ring was 10.6 ± 4.3 µm and this check probably reflects the onset of exogenous feeding (Campana, 1992).

The age of wild-caught fish was estimated by adding 12 d to the number of daily checks in the otoliths. We used 12 d instead of 8, as the hatching experiments were made at temperatures higher than the sea temperature during the main hatching period in April (see discussion below, correction estimated from Herra (1986)).

A total of 231 wild-caught larvae and juveniles (16–99 mm in length), from five periods, were investigated for daily growth increments. The number of growth rings counted in the otoliths was between 19–187 (Table 1). A comparison between increment counts on the right and left sagittae showed no significant differences (Wilcoxon test, $p > 0.05$, n=42).

Growth rate

To determine the growth rate, the relationship between age and body size was plotted from the five different sampling periods (Fig. 2a–e). There was a tendency for growth to decline between 80–100 d post-hatch, i.e. at the time of metamorphosis (Fig. 2a–b). Larvae of <80 d post-hatch, showed a linear relationship between age and length and an average growth rate of 0.37 mm d^{-1} (Fig. 2a). For metamorphosed fish (>40 mm), the growth rate was 0.58 mm d^{-1} (Fig. 2c).

To determine the overall growth rate, a fourth order polynomial relationship between standard length and the age was fitted (Fig. 3a). Since growth may be influenced by the water temperature, and to determine if fish size was better described by temperature than by age

alone, another plot was made. Here, surface temperature from a monitoring station in the area (U. Larsson, unpubl.) was used to calculate the number of degree-days from the estimated hatching date of a fish to the day it was caught. Based on these data, fish size was plotted against the number of degree-days that the fish had experienced (Fig. 3b).

Hatching date distribution

The distribution of back-calculated hatching dates was compared between the five sampling periods in July–November 1993 (Fig. 4a–e). As seen from the graphs, the sampled fish appear to come from about the same spawning period (median range from 23 April to 16 May).

Energy content

A total of 396 larvae and juveniles (20–180 mm in length) were analysed for energy content of the flesh. Water content was about 90% during the early larval stage and 80% in metamorphosed fish (Figs 5). Carbon content varied between 44–54% of body weight and increased logarithmically with body weight for juvenile fish (0–5 g WWT). Nitrogen accounted for 10–14% of body weight and decreased linearly with body weight for juvenile fish. The ratio between carbon and nitrogen was relatively constant in relation to WWT for juveniles.

Energy ranged between 1800–6400 J g^{-1} WWT, depending on fish weight and season (Figs 6, 7). During the larval stage (0.003–0.13 g, about 20–40 mm in length) the energy content increased linearly from 2200 to 2800 J g^{-1} WWT, with a slight increase from 2800 to 2900 J g^{-1} WWT during metamorphosis (0.13–0.25 g WWT) (Fig. 6a). After metamorphosis, the energy content of fish between 0.25–3.5 g WWT increased linearly with fish size. At the end of the first season, values were about 4800 J g^{-1} WWT (Fig. 6b). Energy content remained near this level during winter, with a tendency for a decline in the spring both for fish age 1 and age 2, and then increased with fish size during the growing season of June–November (Fig. 7). Our data coincide well with the results for adult herring presented by Aneer (1975) (Fig. 7).

Discussion

Otolith microstructure

Using ageing by otolith microstructures, the average growth rate was estimated to be 0.37 mm d^{-1} and 0.58 mm d^{-1} for larvae and juvenile herring, respectively. These observed growth rates are in the range of earlier observations from the Baltic (Aneer, 1979;

Table 1. The number of wild caught fish analyzed for daily growth, their size, number of daily growth rings/checks in the otoliths, average daily length increments (mm) and the water temperature where the fish were caught.

| Sampling period		n	Average length			Average weight			Number of increments			Daily length increments		Temperature (°C)
1993	Date		(mm)	s.d.	Range	(g)	s.d.	Range	Mean	s.d.	Range	Mean	s.d.	
I	19 July	41	28	5.0	16–46	0.14	0.05	0.0021–0.46	49	13	19–78	0.42	0.048	17.5
	20 July	21	36	5.1	21–45	0.21	0.15	0.0086–0.43	65	13	25–82	0.41	0.042	17.6
	21 July	7	43	5.6	36–50	0.41	0.27	0.18–1.02	81	17	63–108	0.44	0.028	17.9
	22 July	14	42	5.7	35–56	0.47	0.48	0.18–1.1	87	15	66–114	0.40	0.043	17.6
II	2 Aug.	23	50	10	33–68	0.47	0.48	0.11–1.8	98	14	65–123	0.43	0.058	15.4
	3 Aug.	15	42	8.2	33–56	0.40	0.36	0.12–1.0	86	16	61–110	0.40	0.051	15.2
	4 Aug.	14	44	7.0	34–57	0.43	0.30	0.13–1.0	88	12	58–108	0.41	0.042	15.0
	5 Aug.	15	46	11	33–63	0.57	0.44	0.13–1.5	88	20	52–113	0.43	0.043	14.9
III	23 Aug.	16	54	8.8	34–62	0.99	0.47	0.14–1.3	110	14	82–126	0.42	0.039	12.5
	24 Aug.	15	57	3.6	53–64	1.2	0.25	0.88–1.7	114	4.9	105–122	0.43	0.024	12.4
	25 Aug.	12	59	5.8	51–70	1.4	0.45	0.78–2.2	120	8.7	105–130	0.43	0.026	12.9
	26 Aug.	13	57	14	38–75	1.4	0.63	0.20–2.2	112	18	85–136	0.43	0.073	12.2
IV	6 Oct.	17	73	12	48–90	2.4	0.96	0.95–4.0	148	15	105–173	0.47	0.051	9.7
V	2 Nov.	16	84	7.3	76–99	3.7	1.0	2.4–5.4	165	10	160–187	0.46	0.031	5.8
Σ		239										0.43		
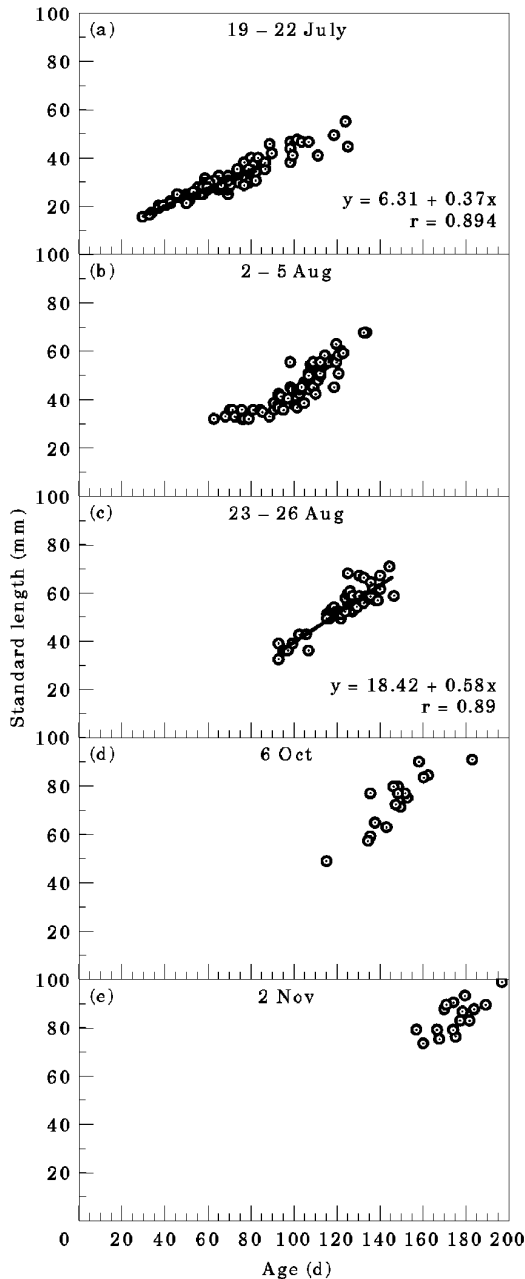
Figure 2a–e. The standard length (mm) of larvae and juvenile herring plotted against estimated age. Fish sampled during five different periods in July–November 1993 (see Table 1). Linear regressions are included for the larval period (a) and for metamorphosed fish (c).
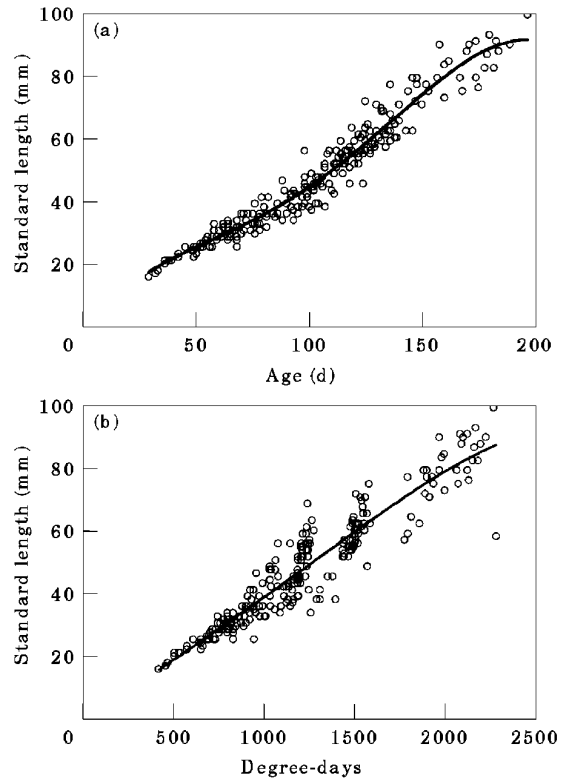

Figure 3. (a) The standard length (mm) of larval and juvenile herring plotted against estimated age (n=231). To describe the overall growth rate a fourth order polynomial relationship were fitted ($y = 11.75 + 0.94x - 0.013x^2 + 1.04 \times 10^{-4}x^3 - 2.67 \times 10^{-7}x^4$, r=0.97), (b) Growth can also be expected to be influenced by the water temperature and we calculate the number of degree-days from estimated hatching dates to the day the fish were caught ($y = -0.86 + 0.041x - 5.85 \times 10^{-6}x^2 - 6.35 \times 10^{-9}x^3 - 1.87 \times 10^{-12}x^4$, r=0.94).

Peltonen, 1990), none of which used otolith microstructures. In the North Sea, growth rate of juvenile herring appears to be slower, according to both field studies and laboratory experiments (Munk and Christensen, 1990; Munk *et al.*, 1991; Moksness 1992b). Pacific herring, *Clupea pallasi*, has a similar range in larval and juvenile growth as the Baltic herring (McGurk, 1987; Moksness and Wespestad, 1989; McGurk *et al.*, 1993).

When using otolith microstructure to estimate daily growth rates, some important basic information is needed. In particular, the age at first increment formation must be known. In our investigation, this occurred on average at 8 d post-hatch and coincided with the end of yolk-sac stage and the first exogenous feeding. Values from other studies on herring range between 5 to 17 d for the Baltic herring (Herra, 1986; Kiørboe and Munk, 1986), Atlantic herring (Geffen, 1982; Moksness, 1992a), and Pacific herring (McGurk, 1987; Moksness and Wespestad, 1989). The duration of the yolk-sac stage and subsequent adjustment period to active feeding is temperature-dependent (Radtke, 1989), although differences in the duration depending on egg size also have been reported (5.5–14 d, Blaxter and Hempel, 1963).

Further information is needed when using otolith microstructures in growth studies, namely the relevance of increment counts. Experiments have shown that the
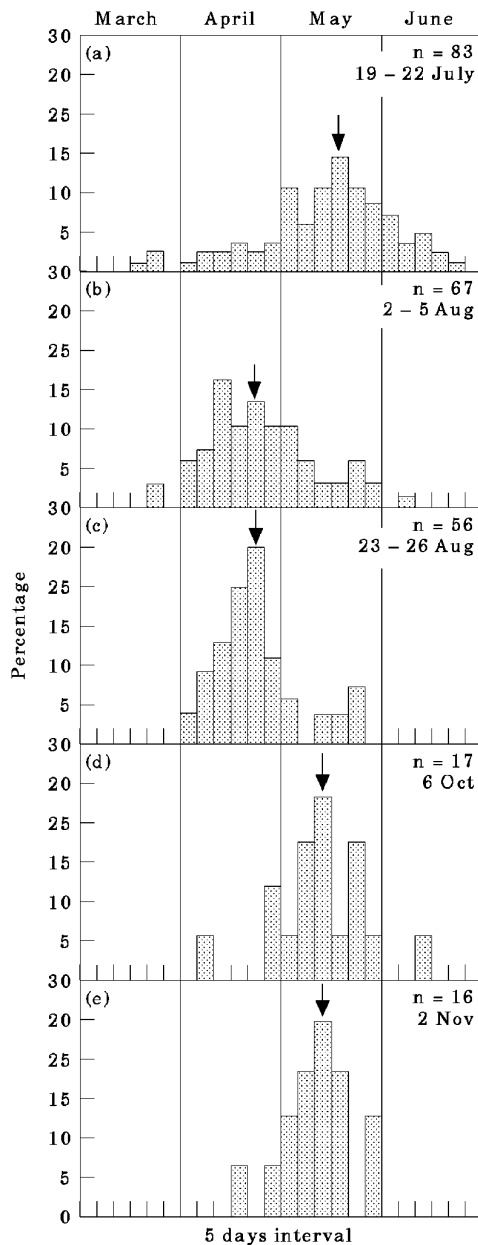
Figure 4a–e. Hatching date distributions (in per cent) of herring, as estimated from five different sampling periods (a–e, see Table 1) in 1993. The median for each period is indicated with an arrow.

Figure 5. The proportion of DWT to WWT of herring plotted against the fish weight (g WWT), from samples taken in 1992–1994 in the northern Baltic proper. Approximate sizes at metamorphosis and at the end of the first growth season (31 December) are indicated with arrows. $y = 17.0 + 4.41(\log x)$, $r = 0.91$, $n = 396$.

growth of young herring can be determined from patterns in the otoliths (Moksness and Wespestad, 1989; Moksness, 1992a). There is, however, a possible underestimation of age when the larvae initially have a low growth rate and therefore very narrow increments close to the hatch-check (Geffen, 1982; Moksness and Wespestad, 1989; Moksness, 1992a). The increment size increases with age of the herring larvae (Moksness,
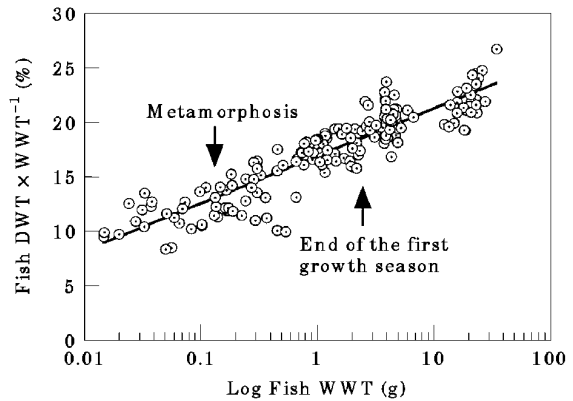
1992a). A problem discussed by Campana and Jones (1992) is the optical resolution in detecting increment checks. We increased this resolution significantly by enhancing the contrast with ammonium picrate and glycerine and, from these readings, we estimated growth rates between 0.28–0.65 mm d^{-1}. These values can be compared with a growth of 0.10 mm d^{-1} reported by Moksness *et al.* (1987) as the lowest detectable growth rate estimated from herring otoliths.

Growth rate curve including both larvae and juveniles

A growth curve model can seldom be used to describe all life stages in a species (Ricker, 1979; Campana and Jones, 1992). However, by fitting a fourth order polynomial curve for both larvae and metamorphosed herring we obtained a good fit to the data. Our investigations covered a fairly long period over which neither temperature nor food concentration could be expected to be constant (cf. Houde, 1989). We tried to account for effects of temperature on the growth of fish but this did not provide a better description of growth than did age alone (Fig. 3a, b). It is reasonable to assume that a better prediction of the growth of juvenile herring could have been derived by using information of availability of zooplankton prey because these fish appear to be food-limited (Arrhenius and Hansson, 1995). However, no such data are available.

There was a tendency for decreased growth during metamorphosis, which has also been shown for other clupeoids (Houde, 1987), and this period was followed by increased growth (cf. Deegan and Thompson, 1987; Raynie and Shaw, 1994). During the period of slow growth, energy content was fairly constant. The decrease
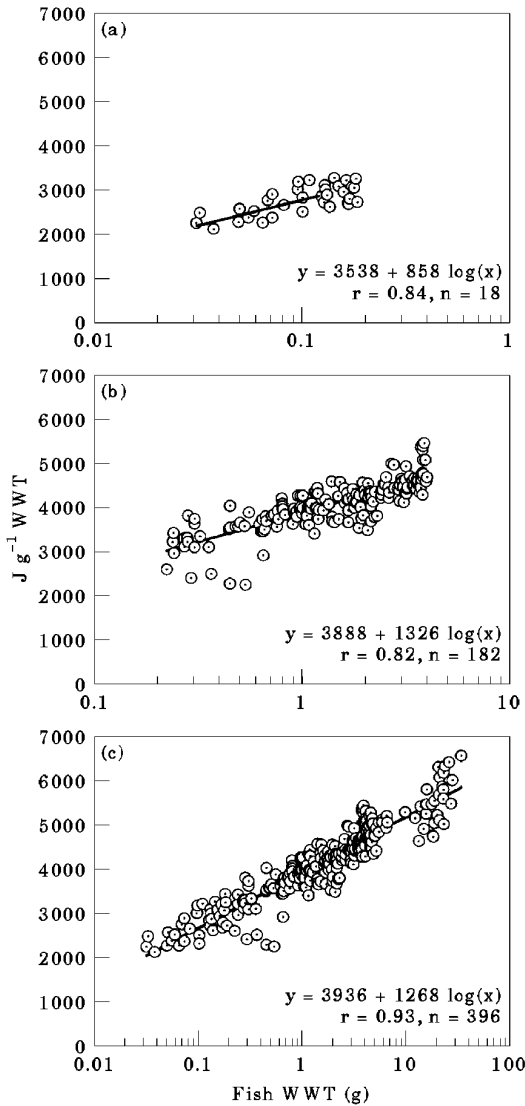
Figure 6a–c. Relationship between energy content (J g^{-1} WWT) and fish weight (g WWT) for young herring sampled 1992–1994. Data are presented in three graphs: (a) herring between 0.03 and 0.20 g – for larval fish (0.03–0.13 g) a regression line was fitted, while fish 0.13–0.20 g were considered to be in a stage of metamorphosis; (b) post-metamorphosed juvenile, 0.20–5.0 g; (c) for all sampled herring.

Figure 7. Relationship between average energy content (J g^{-1} WWT) and age in fish from 13 different samplings 1992–1994. The line was fitted by eye. Bullet symbols in the age 2 part of the graph are from Aneer (1975) and represent energy content in adult Baltic herring. ⊡=this study; ●=Aneer (1975).

Hatching distribution

Spawning of Baltic herring occurs when the water temperature is 5–15°C (Oulasvirta et al., 1985) and is normally most intense in early May at a temperature of 5–9°C, but occurs even in July–August (Aneer, 1979; Oulasvirta et al., 1985; Rajasilta, 1992). It has been shown that herring spawn early in warm springs (Ware and Tanasichuk, 1989; Rajasilta, 1992) and, in our study year (1993), the spring surface water temperatures were more than 2°C warmer than normal (U. Larsson, pers. comm.). This probably explains why we found hatching occurring as early as March, with a peak in April–early May.

In our first field sample (19–22 July 1993), we found a considerable proportion of hatched fish in June, but very few fish from this month occurred in later samples (Fig. 4). This indicates that a relatively early hatching was advantageous for survival in 1993 (hatching medians ranged between 23 April and 16 May, Fig. 4). We suggest that environmental conditions were more favourable, and hence survival rates higher, for these fish. Favourable environmental conditions include availability of suitable food organisms and relatively low predation pressure (Werner and Blaxter, 1980; Kiørboe et al., 1988; Fortier and Harris, 1989; Fortier and Gagné, 1990; McGurk et al., 1993). A proper concept in this respect is the "match-mismatch" theory (Cushing, 1990), that the larval period of a fish should be timed to an abundance peak in their prey. For yellow perch (Perca flavescens) it has been shown that faster growing members of a cohort have a higher survival rate in the first growing season (Post and Prankevicius, 1987).

in growth in this period may be explained by the drastic physiological and morphological changes occurring, and also by ecological factors. Herring larvae about 15–30 mm long live in shallow areas and move to the pelagic zone when they reach a length of over 30 mm (Urho and Hildén, 1990). Slow growth may therefore be caused by limited food abundance in the littoral zone before the start of schooling (Gallego and Heath, 1994).
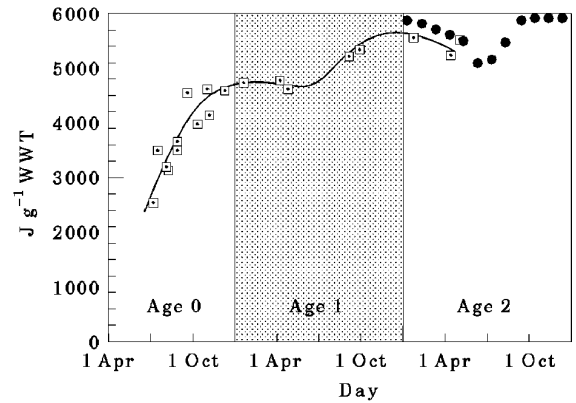
Energy content

From larvae until the late juvenile stages energy content increased, except during metamorphosis, when it stabilised. Generally for our herring, the energy content increased in late summer and autumn (the growth season) and decreased in the winter. For adult Baltic herring, the lowest values occur during the spring spawning period (Aneer, 1975). Strong seasonal cycles in energy storage are typical for clupeoids (Flath and Diana, 1985; Rand *et al.*, 1994) and for other juvenile and immature fish (cod *Gadus morhua* (Eliasson and Vahl, 1982) and sole, *Pleuronectes asper* (Paul *et al.*, 1993)).

There are few energy values available for larval and juvenile clupeoids and they are not strictly comparable because of differences in assumptions and methodology. Feeding larvae of Pacific herring had value of 25.25 kJ g^{-1} DWT (Eldridge *et al.*, 1977, assuming 90% water content). Northern anchovy, *Engraulis mordax*, had a constant energy content of 22.60 kJ g^{-1} DWT from larvae to metamorphosis (Theilacker, 1987) but, assuming a decline in water content from 90% to 80%, a recalculation indicates an increase in energy content from 2260 to 4520 J g^{-1} WWT (calculated in Hewett and Stewart, 1989). This can be compared with our values for Baltic herring, from 2200 to 2800 J g^{-1} WWT over the same period of life. After metamorphosis, juvenile Baltic herring increased in energy content to 4800 J g^{-1} WWT in December. Barrett *et al.* (1987) reported that herring between 3–7 cm had values between 4600–6000 J g^{-1} WWT. These values are higher than for herring from other parts of the North Sea (about 4000 J g^{-1} WWT, Hislop *et al.*, 1991).

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