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GROWTH AND SEASONAL CHANGES IN ENERGY CONTENT OF YOUNG BALTIC SEA HERRING (*CLUPEA HARENGUS* L.)

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Abstract

Growth rates, hatch-date distributions and seasonal changes in energy densities of young-of-the-year (YOY) herring (*Clupea harengus*), the major Baltic Sea zooplanktivore, were studied in a coastal area. Otoliths (sagittae) showed daily patterns in microstructure, which we used to age the fish. The first increment (the hatch check) was formed at the end of the yolk sac stage. The averaged growth rate was estimated to 0.37 mm d^{-1} and 0.58 mm d^{-1} for larval and metamorphosed YOY 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 a warm spring and favourable survival conditions in 1993. Our data indicate the highest survival of YOY spawned from end of April to the middle of May. Young herring undergo seasonal and yearly fluctuations in body composition. There was an increase in energy density from 2200 to 2800 J g^{-1} WWT and 2900 to 4800 J g^{-1} WWT for larval and metamorphosed YOY respectively, with rather constant energy densities during the metamorphosis.

Introduction.

Herring, *Clupea harengus*, is one of the dominating 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 have been used to address a variety of ecological and fishery related questions (e.g. Helminen *et al.*, 1990; Wildhaber and Crowder, 1990; Hartman and Magraf 1992; Brandt *et al.*, 1992; He *et al.*, 1993; Hansson *et al.*, 1995). However, many bioenergetics models lack parameters for young stages, as has been stresses in a review 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 of our conclusions in that paper was the young-of-the-year (YOY) herring is the dominating age-class with regard to the consumption of zooplankton. We also found that the knowledge about some of the basic biology of YOY herring is surprisingly poor - this was particularly true for the fish after metamorphosis. Daily growth rates of YOY and their energy densities and mortality rates had to be extrapolated from 2 yr. old fish with several required assumptions (Arrhenius and Hansson, 1993). In this paper, we present data on energy densities of herring from 30 d old larvae to adult age. We also present daily growth rate data from hatching to an age of about half a year and hatch-date distributions, as determined by back-calculating from otolith microstructure.

Material 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) 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 (unpubl.).

Hatching experiment

Three times (Table 1), adult spawning herring were collected (around 59°30' N, 19°E) and artificial fertilization performed in the laboratory. Eggs were incubated at 12°C and 6.2‰ salinity in hatching boxes (22 L) supplied with air, using methods described by Munk & Rosenthal (1983). The photoperiod was kept at approximately 10 hours day :14 hours night.

Newly hatched larvae were collected every morning and transferred to a 100-L aquarium of 14°C. Larvae were sampled every day except on the first and third sampling period. After the larvae had reach the post yolk-stage, they were fed *ad lib.* on rotifers and copepod nauplii. 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 by drying 10 specimen at 60°C until constant weight was attained.

Otolith growth and microstructure

The largest otoliths, the sagittae, were removed under polarized light and mounted on glass with thermoplastic cement (Buehler). Otoliths from fish over 20 mm had to be ground, to exposure 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 read in a light microscope 400-1000X (Leitz DM RBE) using phase-contrast light. The analysis system consisted of a CCD videocamera attached to the light microscope and connected to a monitor, a multiscan digitizer board and a microcomputer. Otoliths images were analyzed with a image analysis software (Q500 MC Qwin, v 1.0, Leica). Daily growth increments in the otoliths were markedly improved by the use of ammonium picrate ($C_6H_6N_4O_7$) with glycerine ($C_3H_8O_3$) between glass and cover slip (c.f. Malmberg 1970), and further enhanced by the 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.

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 analyzer (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 analyzed 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 have 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 fertilized herring eggs hatched in 8 days (±1.3, SD) in 13°C (about 2500 degree-hours) and hatching success varied between 20% and 90% (Table 1). The percentage viable hatch varied mostly due to infection of *Saprolegia* sp.. Mass mortality was observed after about 15 days after hatching.

The standard length of newly hatch larvae was 7.2 mm and DWT 95 µg (about 830 µg WWT) (Table 1). There was no significant difference in length and weight between the three fertilization batches (ANOVA, $p<0.001$, $n=60$). The larvae decreased in weight during the endogenous feeding and increase in weight when the yolk-sac was consumed and the larvae started exogenous feeding (Fig. 1). The first larvae without yolk-sac was observed after 6 days and 80% of the larvae had it adsorbed after 14 days. After 8 days. 50 % of the larvae had absorbed their yolk-sac, and first larvae with food particle in the stomach were seen after 6 days.

Otolith microstructure

A total of 34 sagittae were investigated from newly hatch herring larvae. The first discontinuous zone correspond to the first feeding check (Campana, 1992) and the first larvae with an otolith ring appeared after 6 days and the average after 8 days (±1.7). The mean radius of the first feeding check was 10.6±4.3 µm.

When estimating the age of wild caught fish by adding 12 days to the number of daily checks in the otoliths. We used 12 days instead of 8, as the hatching experiments were made at temperatures higher than the *in situ* 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 to 187 (Table 2). 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 for the five different sampling periods (Fig. 2a-e). A period of slow growth occurred between days 80-100 after hatching (Fig 2a-b). Larvae, <80 days, showed a linear relationship between age and length and an average growth rate of 0.37 mm d^{-1} between age an length (Fig. 2a). For metamorphosed fish (>40 mm), the growth rate was 0.58 mm d^{-1} (Fig. 2c).

To determine the overall growth rate during the YOY period, a fourth order polynomial relationship between standard length and the age was fitted (Fig. 3a). Growth can also be expected to 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. We used surface temperature from a from a monitoring station in the area (U. Larsson unpubl.), 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 versus the number of degree-days that the fish had experienced (Fig. 3b).

Hatching date distribution

The distribution of back-calculated hatching dates were compared among the five sampling periods in July-November 1993 (Fig. 4a-e). As seen from the graphs, the sampled fish appear to come more or less from the same spawning periods (medians 23 April-16 May), although there was a considerable span in hatching dates within each and the samples (from March to June in the first sampling period).

Energy densities

A total of 396 larvae, metamorphosed YOY and subadults (range 20-180 mm in length) herring were analyzed for energy densities in fish flesh. Water content was about 90%

during early larval stage and 80% in metamorphosed fish (Fig. 5). Carbon content varied between 44-54% of body weight and increasing logarithmic with body weight for juvenile fish (0-5 g WWT). Nitrogen accounted for 10-14% of body weight and where linearly decreasing with body weight for juvenile fish. The relationship between carbon and nitrogen showed a relative constancy in relation to WWT for juveniles.

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

Discussion

Otolith microstructure

By otolith microstructure, the averaged growth rate was estimated to 0.37 mm d^{-1} and 0.58 mm d^{-1} for larvae and metamorphosed YOY herring. These observed growth patterns are in the range of earlier observations from the Baltic (Table 3). However, none of the these studies used otolith in estimating growth rates for young herring. In the North Sea, growth rate of YOY herring appears to be slower, both according to field studies and in laboratory experiments. Pacific herring, *Clupea pallasi*, has a similar range in larval and juvenile growth as the Baltic herring (Table 3).

Generally, most studies on the growth of YOY herring include only the larval stage and very few estimates include both larvae and metamorphosed fish. Several different models (i.e. linear and curvilinear) have been used when back-calculating the growth rates, and the method used often depends on the study period and the life stages of the fish (Ricker, 1979; Campana and Jones, 1992). Many of the earlier investigations were based on length frequency data, while nowadays otoliths microstructures are commonly used to back-calculate the growth rates. Otolith microstructure is a more valuable, but also more time consuming tool for estimating age of young fish.

When using microstructures in otoliths to estimate daily growth rates, some important basic information is needed. First, the age at the first increment formation must be known. In our investigation, this occurred on average at day 8 and coincidence with the end of yolk-sac stage. Values from other studies on herring range between 5 to 17 days for the Baltic (Herra, 1986; Kiørboe and Munk, 1986a), Atlantic herring (Gamble *et al.*, 1981; Geffen, 1982; Moksness *et al.*, 1987; Messieh *et al.*, 1987; Moksness, 1992b) and Pacific herring (Lough *et al.*, 1982; McGurk, 1984a; 1987; Moksness and Wespestad, 1989). The yolk-sac stage and subsequent adjustment period to active feeding are temperature-dependent (Radtke, 1989), although differences in the duration of yolk sac stages at the same temperature have between reported (5.5-14 days, Blaxter and Hempel, 1963).

The second basic information needed when using otolith microstructures in growth studies, is on the relevance of increment counts. Experiments have verified the growth of young herring can be determined from patterns in the otoliths (Messiah *et al.*, 1987; Moksness and Wespestad, 1989; Moksness, 1992b). There is however, a possible underestimation of age in case the larvae initially have a low growth rate and therefore very narrow increments close to the hatch-check (Geffen, 1982; McGurk, 1984a; Moksness and Wespestad, 1989; Moksness, 1992b). The increment size increases with age of the herring larvae (Moksness, 1992b). Geffen (1982) reported that increments were daily only when the growth rate of larval Atlantic herring was >0.4 mm d^{-1}. A problem discussed by Campana *et al.* (1987) and Campana and Jones (1992) were the importance of resolution-limiting increment visibility for ageing the herring, therefore, we used ammoniumpicrate with glycerine to enhance the contrast when reading the otolith increments in the light microscope.

Growth rate curve including both larvae and juveniles

A growth curve model can seldom be used to describe all life stages in a species (Brett, 1979; Ricker, 1979; Blaxter and Hunter, 1982; Campana and Jones, 1992). However, by fitting a fourth order polynomial growth rate curve for both larvae and metamorphosed YOY herring we got a good fit to the data. Our investigations covers a fairly long period of time over which neither temperature nor food concentration can be expected to be constant (c. f. Munk *et al.*, 1986; Eckmann and Pusch, 1989; Houde, 1989). We tried to account for effects of temperature on the growth of fish, but this did not contribute to 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 YOY herring could have been derived by inducing information of availability of zooplankton prey, as Arrhenius and Hansson (unpubl.)

have found these fish to be food limited. However, as we have no data on food availability, we can not include this in our growth analysis.

There was a drastic decrease in growth rate during metamorphosis, which has also been shown for other clupeoids (Houde, 1987), and this period was followed by increased growth (c. f. Deegan and Thompson, 1987; Raynie and Shaw, 1994). During the period of slow growth, energy densities were rather constant. The decrease in growth in this period may be explained by drastic physiological and morphological changes occurring during this period, but also by ecological factors. The herring larvae (about 15-30 mm in length) are in shallow areas and move to the pelagic zone when they have reached a length over 30 mm (Urho and Hildén, 1990). Therefore, slow growth might be due to limited food abundance in the littoral zone, before they perception of active movements with the beginning of metamorphosis (Blaxter, 1986) and starts to develop schooling behaviour (Gallego and Heath, 1994). Following this period, growth increased and an possible explanation is that, as the young herring can move over large areas, they are able to patches of high zooplankton abundance.

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 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 (Hay, 1985; Ware and Tanasichuk, 1989; Rajasilta, 1992) and the spring surface water temperatures in 1993 were more than 2°C warmer than normal (U. Larsson per. comm.). This probably explains why we found hatching this year to occur as early as in March and mainly already in April - early May.

In our first field sample (19-22 July), we found a considerable proportion of fish hatched in June, but very few fish from these summer spawnings occurred in later samples (Fig. 4). This indicate that a relatively early hatching was advantageous for survival in 1993 (hatching medians ranged between 23 April and 16 May). We suggest that "environmental conditions" were more favourable, and hence survival rate 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, 1975), that the larval period of a fish should be timed to an abundance peak in their prey. Another relevant observation in this perspective, is that herring larvae hatched early in the season grew faster than larvae hatch later (Jones, 1985), and 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).

Energy density

From larvae until late YOY stages energy densities increased, except during the metamorphosis stage, when it stabilized. Generally for herring, the energy density varies over the year, with increases in late summer and autumn (the growth season) and decrease 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 (Ursin 1979; Hunter and Leong, 1981; Flath and Diana, 1985; Rand *et al.*, 1994), and also for other juvenile and inmature fish as for cod *Gadus morhua* (Eliasson and Vahl, 1982) and sole, *Pleuronectes asper* (Paul *et al.*, 1993).

There are only few energy values available for larval and juvenile clupeoids and they are not strictly comparable because of differences in assumptions and methodology. First feeding larvae of Pacific herring had value of 25.25 KJ g^{-1} DWT (Eldridge *et al.*, 1977) converted to 2525 J g^{-1} WWT (assuming 90% water content). Northern anchovy, *Engraulis mordax*, of had a constant energy density of 22.6 KJ g^{-1} DWT from larvae to metamorphoses (Theilacker, 1987), but assuming declining water content from 90% to 80%, results in an increase in energy density 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, YOY Baltic herring increased in energy density to 4800 J g^{-1} WWT in December.

Conclusions

1. Our estimates of growth rate, based on otolith microstructures, were in the range of earlier estimates from the Baltic. The overall growth for all young stages could be described with a fourth order polynomial relationship between length and age.
2. Estimated hatching date were distributed between March and June. This is earlier than normally assumed for the Baltic Sea and was probably caused by the warm spring in 1993. Our data indicate the highest survival of YOY spawned from end of April to the middle of May.
3. Young herring undergo seasonal and yearly fluctuations in body composition (C/N and energy content). There was an increase from 2200 to 2800 J g^{-1} WWT and 2900 to 4800 J g^{-1} WWT for larvae and metamorphosed YOY respectively, with a rather constant energy density during the metamorphosis.

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Table 1. Adult spawning herring used in hatching experiments in June-July 1994. Incubation temperature, salinity, no. of days to hatching and viable hatch for all three fertilization periods. The standard length (mm) and dry weight (µg) were also measured of the larvae sampled at hatching.

	Spawners						Incubation				Larvae				
	Female size			Male size											
Date	n	Median (mm)	Range	n	Median (mm)	Range	Temp •C mean	Salinity ‰	Hatch days	Total hatch %	n	Standard length (mm)	SD	Dry weight (µg)	SD
30-maj	4	175	171-179	14	179	163-204	12.5	6.2	9	20[*]	20	7.2	0.41	93	5.3
15-jun	15	193	172-252	29	184	168-251	13.4	6.2	8	90[+]	20	7.3	0.54	101	8.7
22-jun	9	183	170-251	23	194	181-245	14.1	6.2	7	60[+]	20	7.1	1.2	92	6.9
Total/average	28	184	170-252	66	186	163-251	13.3	6.2	8	57	60	7.2	0.72	95	7.0

[*] Infected by *Saprolegia* sp.

[+] To prevent infections by *Saprolegia*, eggs
in this experiment were treated with Myxazin
(Waterlife Research, Ltd) at the start of the experiment.

Table 2. 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 incremments			Daily length increments		Temperature
1993	Date		(mm)	SD	range	(g)	SD	range	mean	SD	range	mean	SD	°C
I	19-jul	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-jul	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-jul	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-jul	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	02-aug	23	50	10	33-68	0.47	0.48	0.11-1.8	98	14	65-123	0.43	0.058	15.4
	03-aug	15	42	8.2	33-56	0.40	0.36	0.12-1.0	86	15	61-110	0.40	0.051	15.2
	04-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
	05-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	06-okt	17	73	12	48-90	2.4	0.96	0.95-4.0	148	15	105-173	0.47	0.051	9.7
V	02-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		

Table 3. A review of laboratory and field-estimated daily growth rates (mm d-1) for YOY Baltic, Atlantic and Pacific herring. Fish lengths, fish age (study period) and temperature in each study are also summarized. The methodologies used are given as Condition and Technique (method used to determine age).

Species Area	Fish length (mm)	Study period (days)	Temperature (°C)	Daily growth rate (mm/day)	Methodolgy Condition	 Technique	References
Clupea harengus							
Baltic Sea							
Southern Baltic	7-20	-	-	0.25-0.55	Field	Length	Schnack, 1972
Archipelago	7-25	-	-	0.19-0.33	Field	Length	Aneer, 1979
Southern Baltic	8-12	7-21	8	0.30	Laboratory	Length	Kiørboe and Munk, 1986
Archipelago	6-18	-	-	0.23-0.64	Field	Length	Peltonen, 1990
Archipelago	17-90	29-183	5.8-17.9	0.38-0.58	Field	Otolith	This study
Atlantic/North Sea							
W. Scotland	13-17	20-38	7-8	0.17	Laboratory	Age	Checkley, 1984
Thames estuary	6.8-11	0-28	10-16	0.18	Field	Length	Henderson et al., 1984
"	11-22	28-50	10-16	0.43	Field	Length	"
North Sea	7-35	-	9.0-11.5	0.10-0.44	Laboratory/Mesocosm	Length	review by McGurk, 1984b
North Sea	5-38	-	5.6-17	0.05-0.43	Field	Length	"
Norwegian	-	5-12	-	0.13-0.27	Field	Length	Johannessen, 1986
Norwegian	-	12-20	-	0.20-0.28	Field	Length	"
Norwegian	-	20-50	-	0.32-0.69	Field	Length	"
Clyde + Downs	8-12	7-21	8	0.40	Laboratory	Length	Kiørboe and Munk, 1986
Limfjord	8-13	7-22	8	0.17	Laboratory	Length	"
Buchan	8-12	-	-	0.13-0.17	Field	Length	Munk et al., 1986
"	12-20	-	-	0.25-0.26	Field	Length	"
St Lawrence	7-40	0-80	10-12	0.29	Laboratory	Otolith	Campana et al., 1987
St Lawrence	14-36	0-150	-	0.05-0.38	Field	Otolith	Messieh et al., 1987
Clyde	7-19			0.13-0.24	Field	Length	Kiørboe et al., 1988
Shetland/Buchan	7-35	-	-	0.13-0.19	Field	Length	Munk and Christensen, 1990
"	35-150	-	-	0.26-0.39	Field	Length	"
Clyde	7-18	4-35	8.5	0.09-0.25	Laboratory	Age	Pedersen et al., 1990
North Sea	7-39	-	-	0.04-0.19	Field	Otolith	Munk et al., 1991
Shetland/Buchan	7-22	20-50	-	0.20-0.26	Field	Otolith	Moksness, 1992a
Dogger bank	7-28	20-60	-	0.29-0.37	Field	Otolith	"
Skagerrak	7-29	20-40	-	0.38	Field	Otolith	"
Norwegian	9-27	0-65	6.8-15	0.27	Mesocosm	Otolith	Moksness, 1992b
"	7-27	0-60	-	0.24-0.41	Field	Otolith	Moksness and Fossum, 1992
Clupea harengus pallasi							
Pacific							
-	7-35	-	8.5-12.1	0.09-0.31	Laboratory/Mesocosm	Length	review by McGurk, 1984b
-	7-17	-	4-13	0.21-0.32	Field	Length	"
British Columbia	7-28	0-60	6-10	0.36-0.41	Field	Otolith	McGurk, 1987
Bearing Sea	8-95	0-62	8	0.31-1.48	Mesocosm	Otolith	Moksness and Wespestad, 1989
Sotheast Alaska	9-47	-	4-17	0.30	Field	Length	McGurk et al., 1993

Figure legends

Figure 1. The average weight (µg DWT) of hatch herring larvae until 12 days after hatching, with standard deviations.

Figure 2a-e. Estimated age *vs.* standard length (mm) for young herring sampled during five different sampling periods in July-November 1993 (see Table 2). Linear regressions are included for the larval period (a) and for metamorphosed YOY fish (c).

Figure 3a-b. a) The standard length (mm) plotted against age for all wild caught herring. To determine the overall growth rate during the YOY period a fourth order polynomial relationship were fitted. b) Growth can also be expected to be influenced by the water temperature and we calculated the number of degree-days from estimated hatching dates to the day the fish were caught.

Figure 4a-e. Hatching date distributions (in percent) of herring, estimated from five sampling periods in 1993. Medians for each period are indicated with arrows.

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 YOY period (December 31) are indicated with arrows.

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 - larval fish 0.03-0.13 g was fitted with an regression line, and fish 0.13-0.20 g was considered in metamorphosis stage, b) metamorphosed YOY herring, 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. Diamond symbols in the age 2 part of the graph are from Aneer (1975) and represent energy densities in adult Baltic herring.

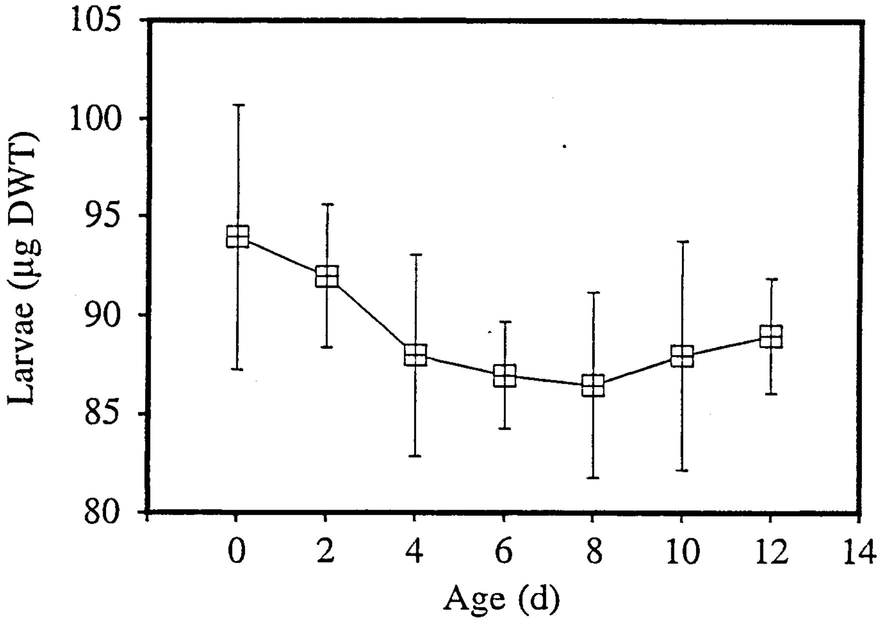

Figure 1.

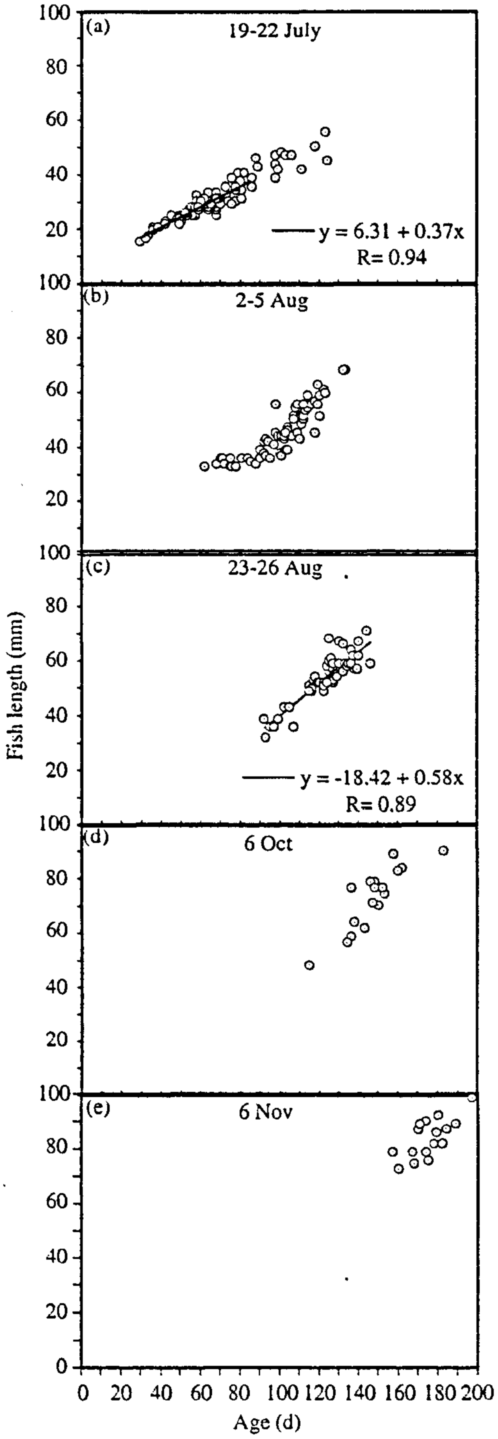
(a)
19-22 July
y = 6.31 + 0.37x
R= 0.94
(b)
2-5 Aug
(c)
23-26 Aug
y = -18.42 + 0.58x
R= 0.89
(d)
6 Oct
(e)
6 Nov
Fish length (mm)
Age (d)
0
20
40
60
80
100
120
140
160
180
200

Figure 2a-e.

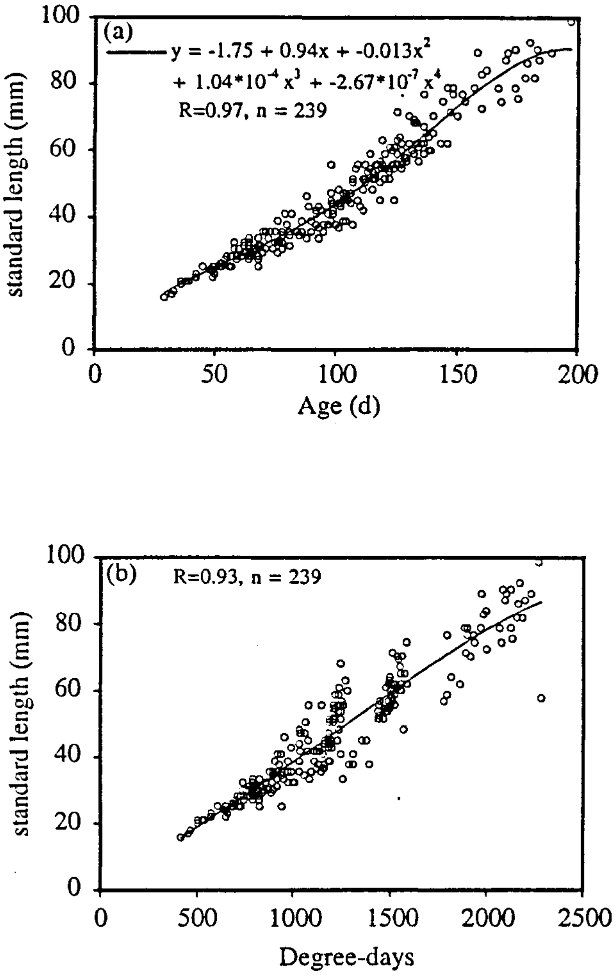
(a)
y = -1.75 + 0.94x + -0.013x^2 + 1.04*10^-4 x^3 + -2.67*10^-7 x^4
R=0.97, n = 239
standard length (mm)
0
20
40
60
80
100
0
50
100
150
200
Age (d)
(b)
R=0.93, n = 239
standard length (mm)
0
20
40
60
80
100
0
500
1000
1500
2000
2500
Degree-days

Figure 3a-b.

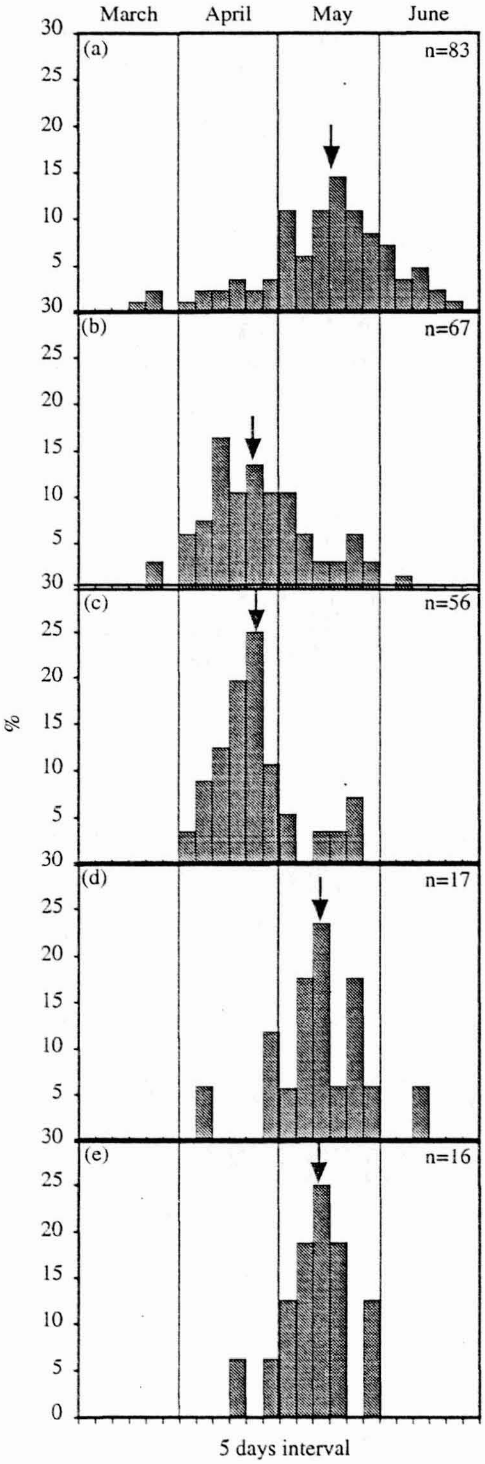
March
April
May
June
(a)
n=83
(b)
n=67
(c)
n=56
(d)
n=17
(e)
n=16
30
25
20
15
10
5
0
%
5 days interval

Figure 4a-e.

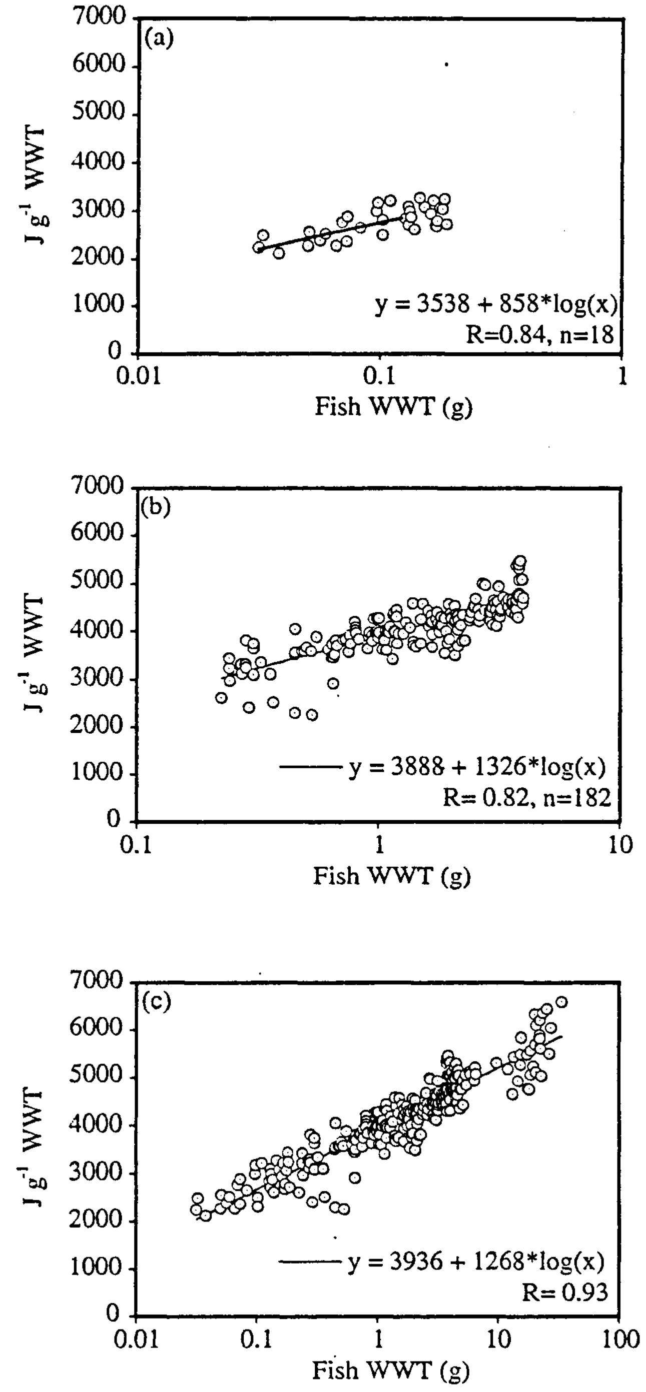
(a)
7000
6000
5000
4000
3000
2000
1000
0
J g^{-1} WWT
0.01
0.1
1
Fish WWT (g)
y = 3538 + 858*log(x)
R=0.84, n=18
(b)
7000
6000
5000
4000
3000
2000
1000
0
J g^{-1} WWT
0.1
1
10
Fish WWT (g)
y = 3888 + 1326*log(x)
R= 0.82, n=182
(c)
7000
6000
5000
4000
3000
2000
1000
0
J g^{-1} WWT
0.01
0.1
1
10
100
Fish WWT (g)
y = 3936 + 1268*log(x)
R= 0.93

Figure 6a-c.

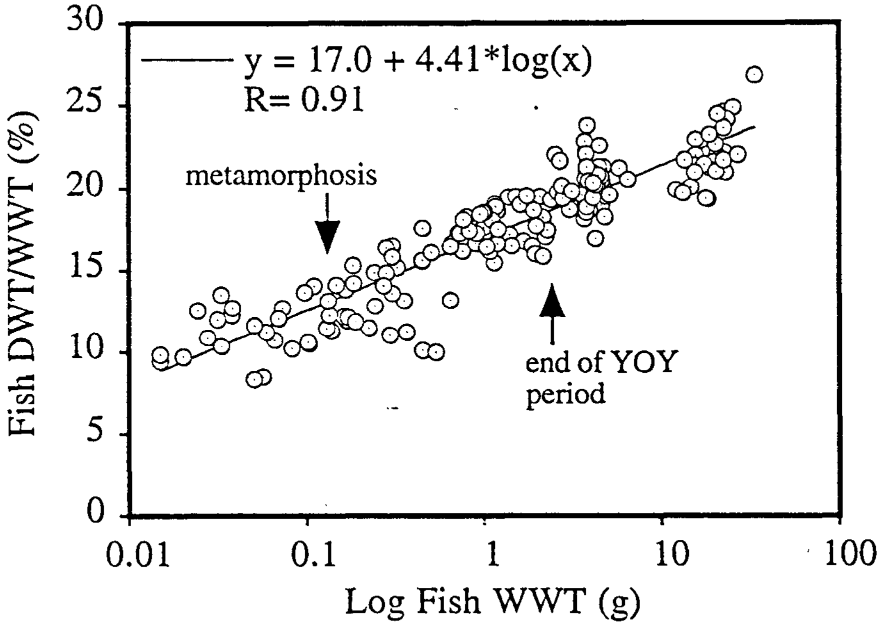

Figure 5.

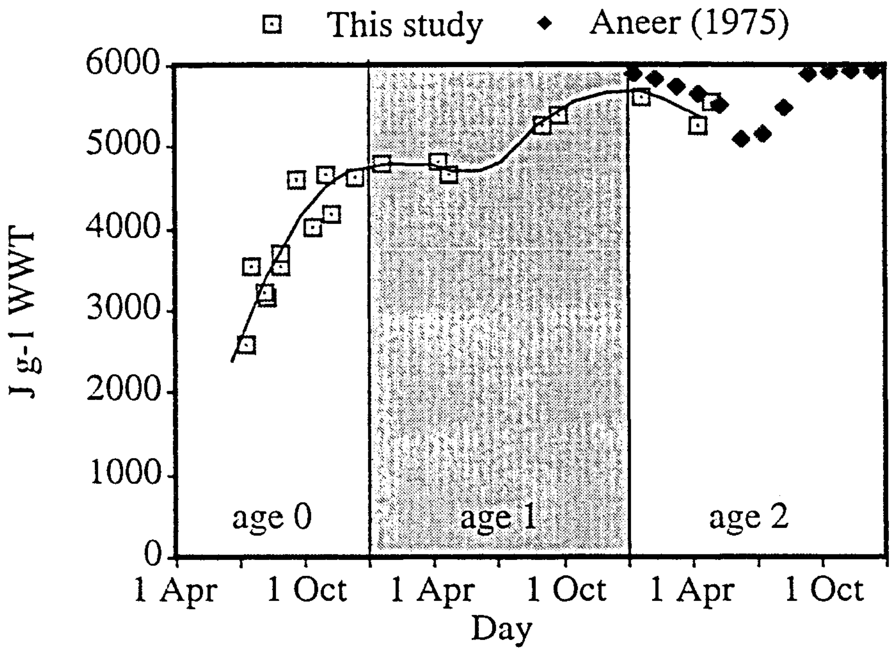

Figure 7.