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TEMPERATURE AND GROWTH RATE EFFECT ON THE OTOLITH SIZE • FISH SIZE RELATIONSHIP ESTIMATED FOR BALTIC HERRING FROM THE VISTULA LAGOON

By

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ABSTRACT

Daily growth increments in otoliths were used to estimate the age of larval and juvenile spring-spawned herring (*Clupea harengus* L.) collected between April and June 1999 in the Polish part of the Vistula Lagoon (Baltic Sea). The.. hatching and spawning time were back-calculated from otoliths and the results were related to temperature conditions. Two cohorts of herring larvae were distinguished. The growth of 12-38 mm (SL) herring was linear and the rate was 0.56 mm d^{-1} for the first cohort and 0.68 mm d^{-1} for the second one. There was positive relationship between herring growth rate and mean water temperature for larvae and juveniles larger than 24 mm. Smaller larvae grew at the same rate despite evident differences in temperature experienced by the first and second cohorts. Differences in growth rates between cohorts were not related to feeding conditions, which were very favourable during the analysed period (April-May). The relationship between otolith size (perimeter, length, width, area) and fish size (SL) was calculated based on the assumption of proportionality between the otolith and somatic growth of a given specimen. It was found that faster growing larvae which experienced higher temperatures deposited larger otoliths. The analysis of marginal increment widths and the water temperature of the deposition suggest the possible role of temperature fluctuations on the otolith size-fish size relationship. In spring-spawned Baltic herring larvae and juveniles relatively high water temperatures in Vistula Lagoon may have a different effect on somatic and otolith growth, i.e. otolith growth was more pronounced than somatic growth.

INTRODUCTION

Otolith analysis, including daily growth increment investigations, provides a very powerful tool in the study of early life history of fishes and in the study of successful recruitment mechanism (Fossum *et* al., 2000). Counting daily increments allows for age estimation (Campana and Nielson, 1985), growth rate calculation (e.g. Jones, 1986; Quinonez-Velazqez, 1998; Rilling and Houde, 1999), back-calculation of birthdate (e.g. Jones, 1985; Thorrold and Williams, 1989; Stenevic *et al.,* 1996; Anderson and Dalley, 2000) and habitat shift investigation (Linkowski, 1996; Wilson and McCornick 1997: Fisher, 1999; Shafer, 2000). All these possibilities have appeared since Panella's (Panella. 197 1) discovery of daily structures in the otoliths. Additionally, reconstruction of individual growth histories can be performed by examining increment widths (Volk *et* al., 1984; Thorrold and Williams, 1989; Gallego, 1996; Sirois et al., 1998; Wang and Tzeng, 1999). However, these methods assume that there is a significant relationship between otolith and somatic growth, so the changes in increment width represent differences in growth and condition, on a daily level, among larvae collected from different environmental conditions (Campana and Nielson, 1985). On the other hand, it has already been reported that slow-growing fish tend to have larger otoliths than fast-growing ones of the same length (Templemen and Squires, 1956; Marshall and Parker, 1982; Reznick *et al.,* 1989; Secor and Dean, 1989, 1992; Secor *et* al., 1989; Wright *et* al., 1990; Francis *et* al., 1993; Schirripa and Goodyear, 1997). Additionally, under some circumstances, otolith growth may be related more to metabolic rate than to somatic growth (Mosegaard *et al.*, 1988; Hoff and Fuiman 1993). The problem of age, growth rate and the ontogeny effect on the otolith size-fish size relationship has also been presented and discussed by Hare and Cowen (1995). It may be concluded that more work is still required to more deeply understand the ability of daily increments to record the growth history of larval and juvenile fish.

Since the daily periodicity in increment formation has already been validated for herring (Moksness and Wespestad, 1989; Campana and Moksness, 199 1; Moksness, 1992b), including those from the Vistula Lagoon (Fey, in preparation) and many other species (Neilson and Geen, 1982; Volk *et* al., 1984; Jones, 1986; Radtke and Hourigan, 1990; Radtke and Fey, 1996; Vigiola. 1997), it was assumed in this paper that the rate of increment formation is one per day and starts

at the onset of the first feeding after yolk-sac absorption (Lough et *al.*, 1982, 1985; McGurk, 1984; Moksness et al., 1987; Moksness, 1992b; Arhenius and Hansson, 1996).

The main goal of this research was to provide information on the effect of environmental variables (zooplankton and temperature) on mature herring spawning time and hatch-day distribution of larvae. The growth rate of early life stages of spring-spawning herring in the Vistula Lagoon as well as the relationship between otolith growth, somatic growth and temperature were investigated.

METHODS

Herring larvae and juveniles were collected from the Vistula Lagoon, Poland during the April to June 1999 period (Fig. 1). The area of the Polish part of the Lagoon is 838 km', the salinity is low (0.7-2.8 ‰) and the depth does not exceed 5 m (2.4 m on average). A Neuston net with a 2 m^2 opening and 0.5 mm mesh size was used for sampling the 1.5 m surface layer at 15 stations. Each tow took 2-12 min, after which the collected material was preserved in 10 % formalin buffered with sodium borate to pH 8-9. Herring larvae and juveniles were sorted out during the following few days and were transferred to 95 % ethanol. Each fish was measured to the nearest 0.1 mm SL. The lengths were not corrected for shrinkage. A sub-sample of the larvae available from each sampling day was randomly selected for otolith analysis (2 10 specimens). After the sagittae were dissected an&mounted on microscope slides in eukit, most of them were ground and polished prior to examination. The daily increments were counted twice, on different occasions, at 400x and 1000x magnification by one reader using a transmitted-light microscope (Olympus BH-2) and an image analysis system (Optimas 6.2, BioScan, USA). Since the first increment is deposited in herring otoliths after yolk-sac absorption at the onset of the first feeding (Lough *et* al., 1982; McGurk, 1984; Moksness et al., 1987; Moksness, 1992b; Arhenius and Hansson, 1996), the age was calculated as the number of increments plus 10d. Widths of 3 marginal increments were measured as well as a few otoiith dimensions: length, width, perimeter and area.

The hatching dates were back-calculated and two cohorts were distinguished. In order to avoid data overlapping in future analysis (growth rate, otolith size-fish size relationship, marginal increments analysis), 14 individuals hatched on day 120- 122 were excluded. The spawning

season was back calculated from the hatch dates using the equation presented by Herra (1986) in his experimental work on Baltic herring embryo development:

$$Y = 39.49e^{-0.167x},$$

where: Y = time from fertilization to hatching (days);

x = mean incubation temperature (°C).

Zooplankton samples were collected from five stations during each cruise using a submersible pump which provided 40 l of water from the whole water column for filtration through 40 µm gauze. Temperature data were collected with an electronic temperature recorder (Seamon mini, Hugrun Inc.) placed at a depth of 1.5 m which measured the temperature every six hours. The mean water temperature from hatching to collection time was calculated for each specimen and related to the growth rate estimated as:

$$GR = (SL_{catch} - SL_{hatch})\ Age^{-1}$$

It was assumed that the size at hatching was 7.0 mm (Blaxter and Hempel, 1963; Ojaveer, 1981; Herr-a, 1986; Arrhenius and Hannson, 1996). The growth rate was also estimated for each cohort from the regression describing length at age data. The differences in slopes was tested by covariance analysis (ANCOVA).

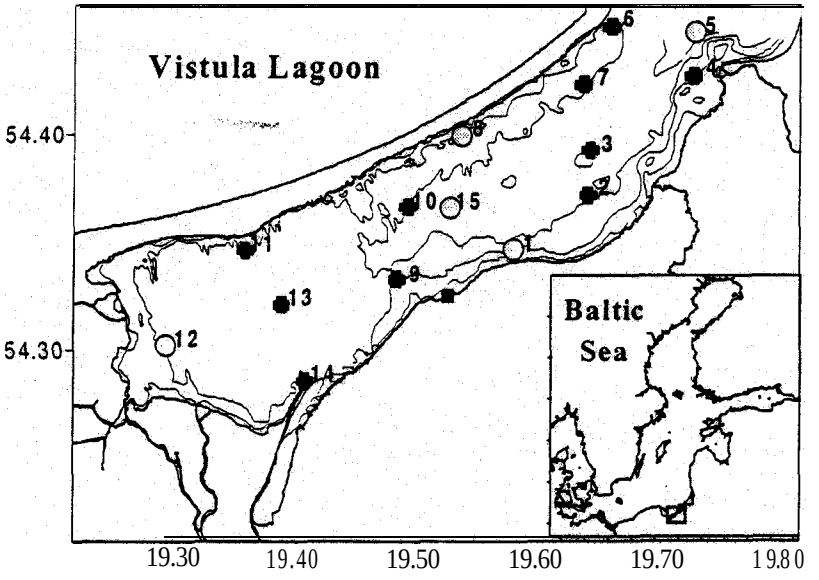

Fig. 1. Study area showing 15 stations where larval and juvenile herring were collected. Circles indicate 5 tations where zooplankton was analysed.

RESULTS

Length frequency data is presented in Fig. 2. Three cohorts were identified. however. the third one was represented by a very low number of larvae (14) and was not included in the otolith analysis. Due to herring emigration from the lagoon, only 16 juveniles were collected on 2 l-22 June. The otoliths of these juveniles were not used in the analysis because of difficulties in evaluating which cohort the specimens originated from. When analyzing the length frequency distribution for the first herring cohort collected on 8-9 June, the abrupt disappearance of juveniles larger than 35 mm was noted and was probably due to emigration from the lagoon. Hatching took place between April 12 and May 23 as back calculated from the otoliths (Fig. 3a). During this time, the temperature ranged from 7.6°C to 13°C. The spawning time, back-calculated from hatching

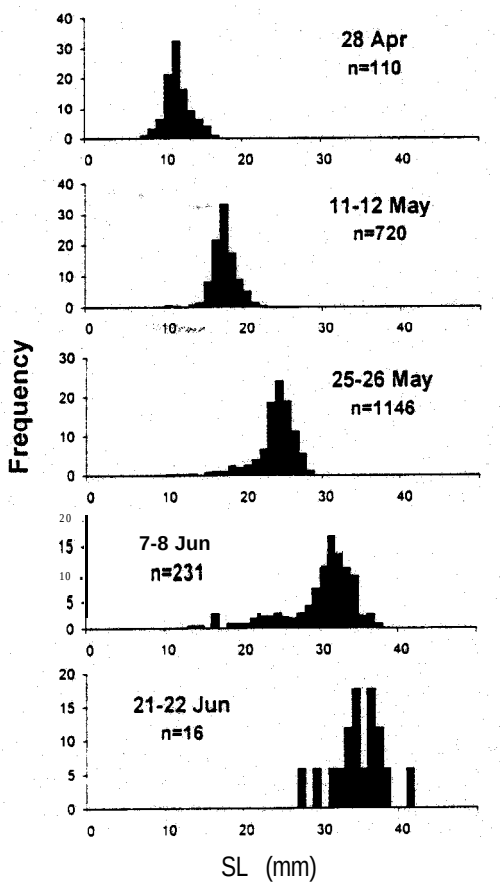

Fig.2. Length frequency distribution for larval and juvenile herring from the Vistula Lagoon, Baltic Sea.

data, started on 29 March at 6.1°C, and was completed on 18 May, a few days after the temperature reached 13°C (Fig. 3b). Spawning intensity seemed to be determined by temperature fluctuations.

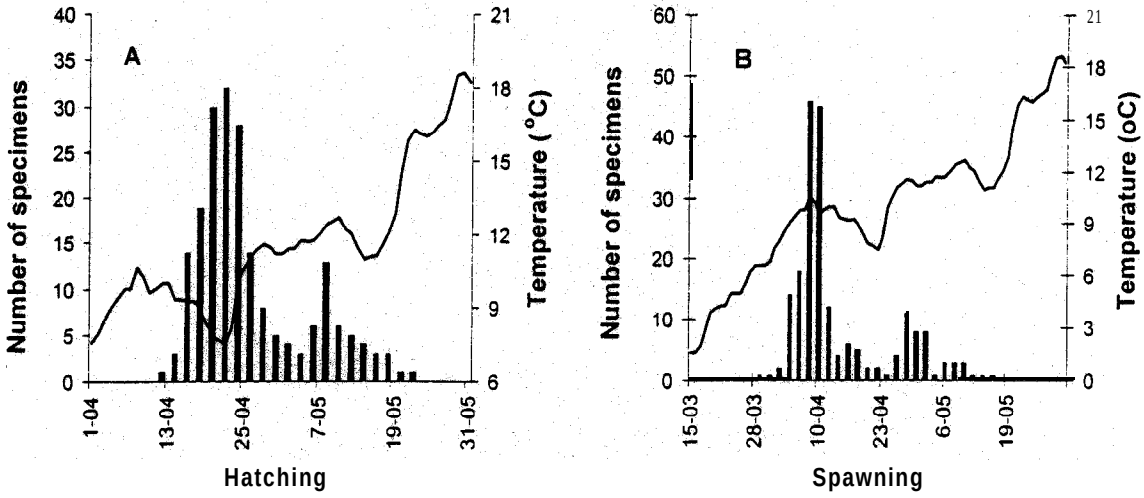

Fig. 3. Hatching and spawning time back-calculated from otoliths of young herring summarized by two day intervals and presented together with temperature data.

The growth rate of herring larvae and juveniles, estimated from the length at age data, differ significantly between cohorts (ANCOVA, $F = 13.35$, $P < 0.001$)(Fig. 4). The average growth rates for cohorts one and two were 0.56 and 0.68 mm d^{-1}, respectively. The growth rate in the first cohort seems to slow down at the age of 40-45 d and the size of 28-30 mm (Fig. 4). In order to identify what the growth differences between the cohorts were related to, feeding conditions from hatching to the time the last otolith sample was collected (8 June) were compared (Fig. 5). It was evident that the availability of both small zooplankton (rotifers, copepod naupli) at the first feeding, as well as larger zooplankton (copepods) during the subsequent weeks was very good throughout this time period. Thus, up to 8 June, both cohorts grew under favorable feeding conditions. From 8 June up to the first week of July, the abundance of naupli and larger stages of copepods was much lower (<30 prey L^{-1}), however, the abundance of rotifers was still quite high.

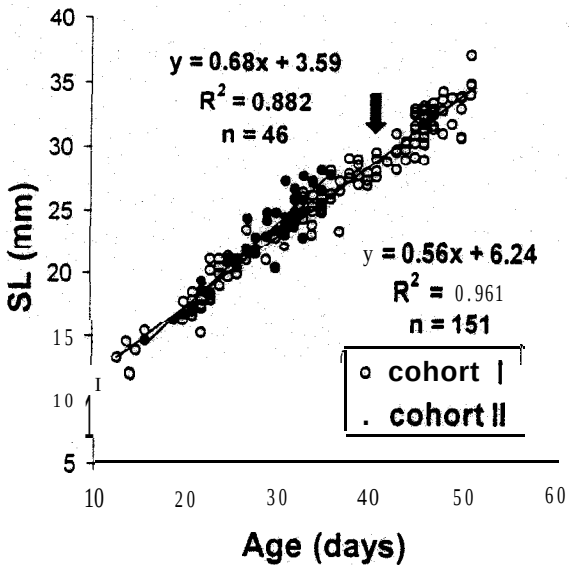

Fig. 4. Length at age data for two main cohorts of herring collected in the Vistula Lagoon in 1999. Period of growth decrease in the second cohort is marked with a black arrow.

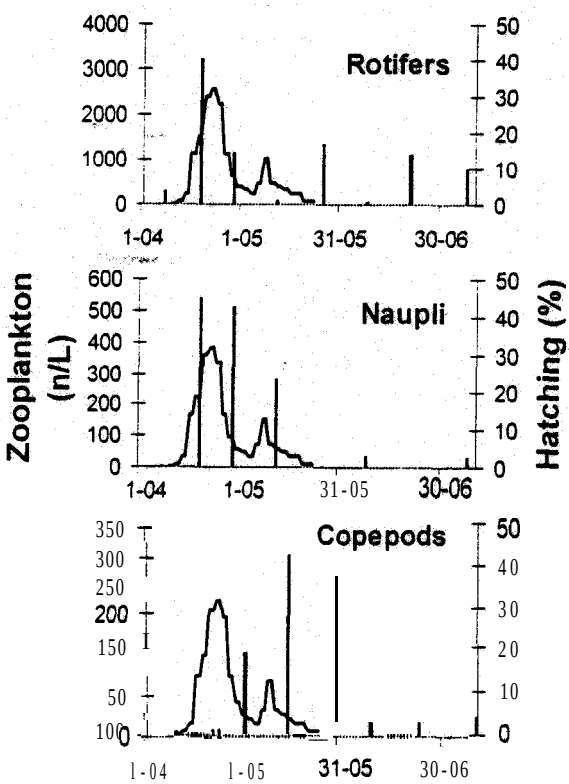

Fig. 5. Feeding conditions (bars) at hatching and subsequent growth of herring larvae.

The relationship between growth rate and the average temperature a given specimen experienced from the moment of hatching is presented in Fig. 6. When the analysis included only larvae <24 mm SL, the growth rate was the same for cohort one and two (-0.52 mm d^{-1}) despite significant differences in temperature. For larvae 24-28 mm SL, a size range represented by specimens from both cohorts, there was a significant positive relationship between temperature and growth rate. The rate at which temperature increased during the life of a given larva was also calculated. For individuals <24 mm it was 0.20°C d^{-1} for the first cohort and 0.29°C d^{-1} for the second one. In the case of larger larvae and juveniles (24 - 28 mm) it was 0.23 and 0.25°C d^{-1} for cohort one and two, respectively.

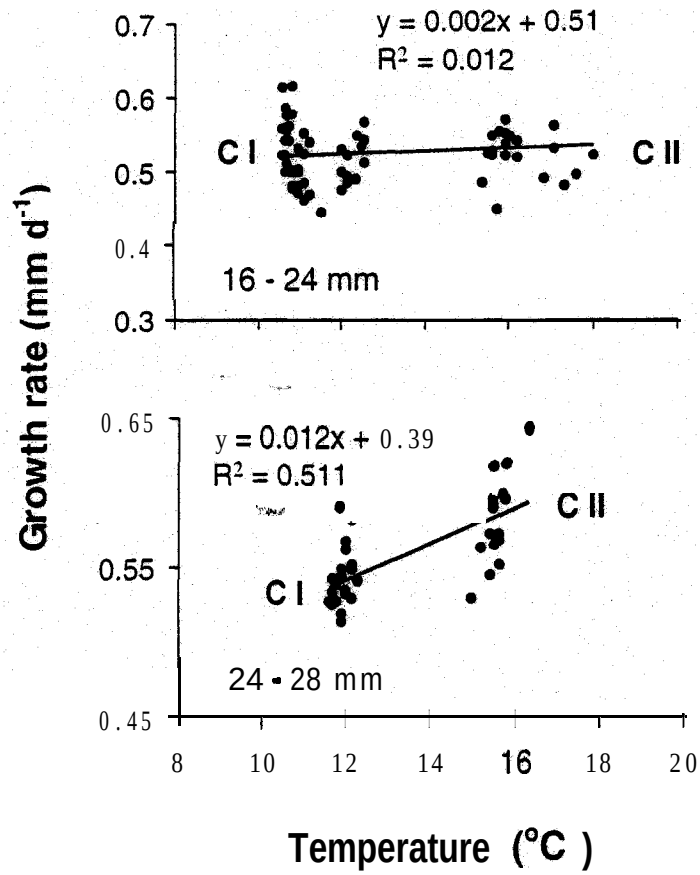

Fig. 6. Effect of temperature on larval and juvenile herring growth rate, presented separately for individuals of different size. CI: cohort one; CII: cohort two.

The relationship between otolith size (length, width, area and perimeter) and fish length and age for cohort one and two is presented in Fig. 7. It is obvious that larvae from cohort two had larger otoliths, at the same length and age, than larvae from cohort one. When analyzing the otolith size-fish size relationship and age for cohort two, discontinuity occurs at a length of 28-30 mm and age of 40 d.

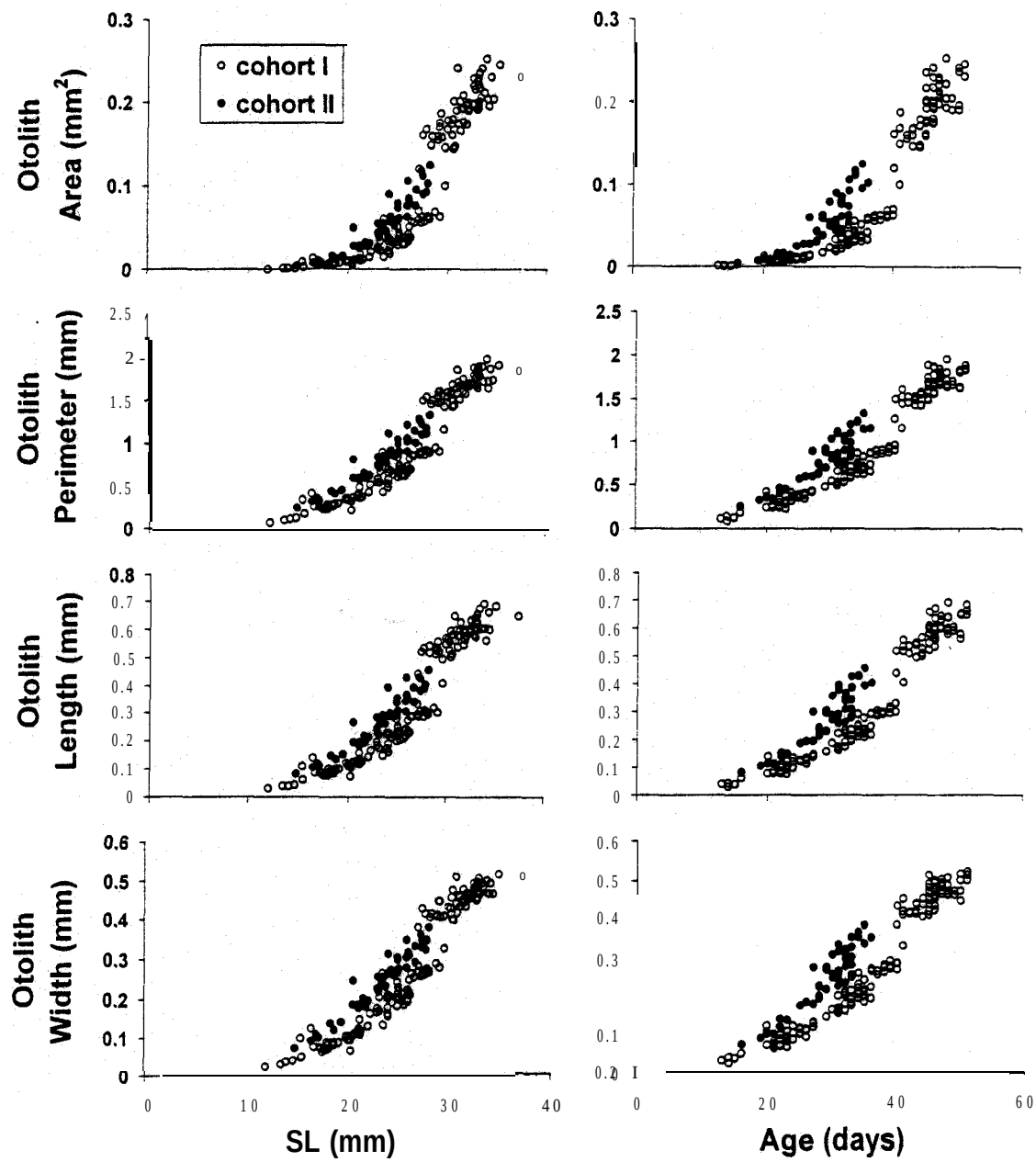

Fig. 7. Otolith size plotted against size and age of two young herring cohorts.

Substantial differences in the width of daily increments deposited in the otoliths of larvae and juveniles of a given length and age was observed between cohorts (Fig. 8). Wider increments were formed by the second, faster growing cohort. Since there were no differences in growth rate between cohorts when analyzing larvae <24 mm SL (Fig. 6), there must have been another explanation for the wider increment formation by smaller larvae from cohort two. In Fig. 9 the data were separated according to the time of sample collection. As one can see, the width of marginal increments was very well related to the temperature at the time the increment was laid down.

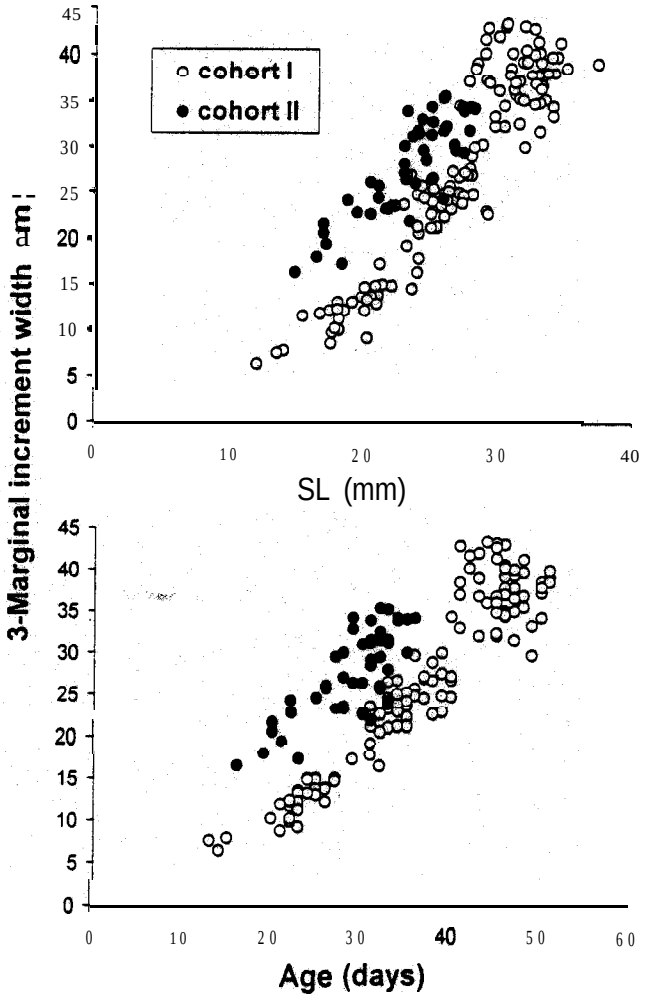

Fig. 8. Changes in the width of marginal increments with size and age of herring larvae and juveniles originating from two cohorts.

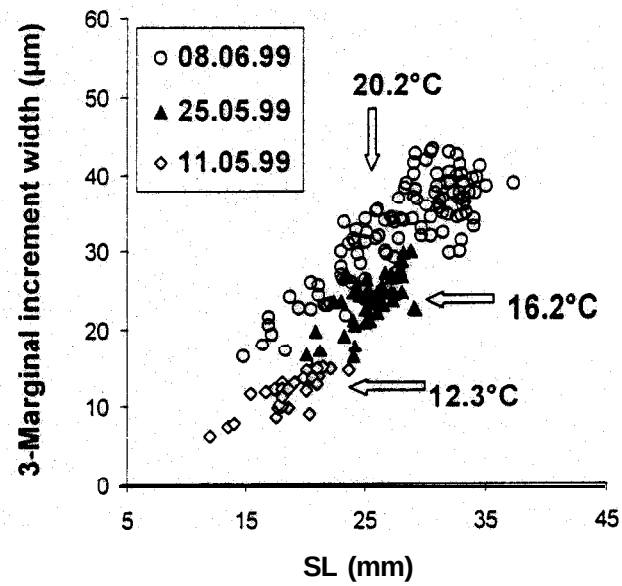

Fig. 9. Effect of temperature on the width of daily increments deposited during three days before sample collection in May - June. Average temperature for three days before collection is indicated.

DISCUSSION

Herring larvae and juveniles spend up to 4 months in the Vistula Lagoon. after which they emigrate from the lagoon to the open waters of the Baltic Sea (Krasovskaya, 1998). In 1999, the emigration started at the beginning of June and by the end of June very few juveniles were still present in the Polish part of the lagoon. This emigration occurred after the metamorphosis at 35 mm SL, but it also seemed to be related to a drastic decrease in zooplankton abundance. In previous years (1997-1998)(Fey, in preparation) all of these events, zooplankton abundance decrease, herring metamorphosis and emigration to open waters, also occurred at the same time. Thus, it may be difficult to distinguished which of the two factors, low food supply or metamorphosis, is of more importance in connection with emigration from the lagoon.

Three cohorts were identified and the hatching and spawning time was back-calculated from otoliths for the two principal ones. The third cohort was represented only by several larvae and was not included in the analysis. According to the Mach-Mismatch theory (Cushing, 1975), it

is hypothesized that fish populations in temperature waters spawn in relation to seasonal plankton blooms. This theory was modified by Sinclair and Trembley (1984) assuming that the spawning timing of a herring population is a function of the time necessary to complete the larval phase and still metamorphose within the seasonal envelope. A similar idea concerning cod and the importance of metamorphosis in spawning time regulations is presented by Thorisson (1992). The results presented here confirm both theories since spawning in the Vistula Lagoon in 1999 occurred at such a time so that both the first feeding and the metamorphosis took place exactly at the peak times of zooplankton abundance. More data from different years are required to further analyze this problem, however, because of very fast herring development and quick emigration from the Vistula Lagoon it may be difficult to distinguish which of these factors. first feeding or metamorphosis, is of more importance when spawning time initiation is concerned. In any case. the starting point for mature herring to spawn seems to be the increase of temperature above 5-6°C. Spawning was completed seven weeks later at 13°C. These results are consistent with other studies concerning Baltic herring spawning season (Oulasvirta et *al.,* 1985; Herra, 1986) which report that the temperature at spawning ranges from 5°C to 15°C.

The growth rate calculated for the first and second cohort was 0.56 and 0.68 mm d^{-1}, respectively. These are very high values when compared to Norwegian herring (0.24-0.41 mm d^{-1}) (Moksness and Fossum, 1992); (0. 18-0.26 mm d“) (Stenevik et *al.,* 1996); North Sea herring (0.20-0.38 mm d^{-1}) (Moksness, 1992a) and also Baltic herring (0.37 mm d^{-1}) (Arhenius and Hansson, 1996). A similar growth rate (0.57 mm d^{-1}) to those from the Vistula Lagoon was reported for juvenile (>40 mm) Baltic herring by Arhenius and Hansson (1996).

Still, there is a question concerning the differences in growth rates between the two cohorts identified. The two most important variables affecting growth rate are temperature (Elliot, 1982; Radtke and Fey, 1996; Larson and Berglund, 1998; Edsall, 1999) and feeding conditions (Neilson and Geen, 1995; Tzeng and Yu, 1992). Zooplankton abundance in 1999 was very high until the first week of June when the last otolith samples were analysed (up to: 3000 prey L^{-1} - rotifers; 500 prey L^{-1} - copepod naupli; 300 prey L^{-1} - copepods). Thus, food supply should not be the cause of growth rate differences between cohorts. However, later in June and at the beginning of July the availability of prey fell significantly (copepod naupli: <50 prey L^{-1}; copepods: <30 prey L^{-1}) and this might have caused considerable mortality among the second cohort larvae, unless they switched to rotifers or emigrated from the lagoon earlier. Werner and

Blaxter (1980) reported that for 4 to 12-wk-old Clyde herring fed with Artemia naupli survival was reduced at 30 naupli L^{-1} and growth rate decreased at 30 and 100 naupli L^{-1}.

Temperature has been found to affect larval growth rate, but only those larger than 24 mm SL. The smaller ones grew at the same rate despite significantly higher temperatures (~16°C) experienced by the second cohort larvae in comparison to the first cohort (~ I 1°C). These results may be surprising since temperature is known to have positive effect on growth rate (Elliot, 1982; Radtke & Fey, 1996; Edsall, 1999). Even if it is true only for the optimum window (Larson & Berglund, 1998; Edsall, 1999), 16°C should not be stressful for Baltic herring. Rather, the problem may be related to differences in the rate at which the temperature increased. which was 0.20°C d^{-1} and 0.29°C d^{-1} for the "small" larvae from the first and second cohort. respectively. It is also possible that the "small" larvae had already reached the maximum growth rate (0.56 mm d^{-1}) in the lower temperature.

It is frequently assumed that higher growth rate positively affects the survival of larvae (Crecco and Sadovy, 1985) which, in turn, affects potential recruitment success. In the case of the Vistula Lagoon, hatching in the first part of the 1999 spawning season was less advantageous due to the slower growth rate, but provided a greater chance of going through metamorphosis and emigrating from the lagoon before the decrease in zooplankton abundance occurred. Since the decrease in zooplankton abundance seems to be a typical phenomenon in the Vistula Lagoon in June - July (Linkowski *et al.*, in preparation), it may be concluded that cohorts hatching later, even if potentially they grow faster, may not metamorphose before the low food period and thus experience significantly higher mortality.

Slower growing larvae from the first cohort had smaller otoliths, at the same length and age, than the faster growing second cohort larvae. These results are not consistent with other authors' information on uncoupling, which indicates that relatively larger otolith formation is seen in slower growing individuals (Templemen and Squires, 1956; Marshall and Parker, 1982; Mosegaard et al., 1988; Reznick *et* al., 1989; Secor and Dean, 1989, 1992; Secor et al., 1989; Molony et al., 1990; Wright et al., 1990; Francis et al., 1993). In the present study, larger otolith formation by larvae from the second cohort was the result of much wider increment deposition (20-100%). At first sight, it might be stated that the second cohort has wider increments as a result of a higher growth rate, especially since it is commonly known that there is a positive relationship between somatic and otolith growth (Taubert and Coble, 1977; Wilson and Larkin,

1982; Volk *et al.*, 1984). However, there were no differences in growth rate for specimens <24 mm between cohorts, but still there were significant differences in increment widths (80-100%). Finally, it has been concluded that wider increment deposition in the otoliths of smaller larvae from the second cohort, in comparison to the first cohort, was caused by temperature differences at the time of sample collection (cohort I: 12.3- 16.2°C; cohort II: 20.2°C). Thus, the present field study confirms the results of experimental work by Hoff and Fuiman (1993) who reported that larvae kept at higher temperatures had larger and heavier otoliths than those kept at lower temperatures. Similar results were obtained by Mosegaard *et* al. (1988) during experimental research which show that the otolith growth rate continued to increase with increasing temperature despite somatic growth rate reduction.

When analysing the fish size-otolith size relationship, a very abrupt discontinuity was observed at the length of 28-30 mm. It seems reasonable to suspect that this was the result of metamorphosis, at which growth in length decreases for a short period of time, but the number of increments, very wide ones (>10 urn), continue to increase with age. The tendency for a growth decrease during metamorphosis has already been described for Baltic herring (Arrhenius and Hansson, 1996) and also other clupeoids (Houde, 1987). If this were the case, it can be concluded that the metamorphosis in the Vistula Lagoon spring-spawned herring larvae, as the result of a high growth rate, occurs very early (40-45 d) in comparison to other herring populations (SO-100 d)(Arrhenius and Hansson, 1996).

It can be concluded, that daily increment width analysis may be a very useful tool in growth rate and condition back-calculation as long as the somatic and otolith growth are coupled. Unfortunately, it may be hard to detect whether the relationship no longer exists or what may happen during sudden temperature variations. Still, it should be possible to use marginal increment width analysis to evaluate growth differences among larvae collected in various conditions (e.g. feeding), but at the same temperature.

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