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Otolith microstructure characteristics in White Sea spring-spawning herring (*Clupea pallasi marisalbi* Berg) larvae

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Otolith microstructure characteristics were studied in White Sea spring-spawning herring (*Clupea pallasi marisalbi* Berg) in the laboratory and in nature. Slow daily growth rate (~0.15 mm d^{-1}), small increment width (~0.8 μm), and irregular increment deposition were observed in the experimental group of larvae raised at lower temperatures (2.8 and 9.1°C before and after hatching, respectively), low plankton density and unnatural photoperiod. By contrast, a fast daily growth rate (~0.31 mm d^{-1}), wider increments (~4.1 μm) and daily increment deposition were found in the group of larvae cultivated at higher temperatures (11.0 and 12.3°C before and after hatching, respectively), high plankton density and with continuous light. Back-calculation showed that in the field, larvae hatched mainly between 1 June and 7 June, and the average daily growth rate was 0.51 mm d^{-1}.

Key words: herring, larvae, otolith, growth rate.

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Introduction

The main commercial stock of the White Sea, the spring-spawning *Egor'evskaya* herring of a the Kandalaksha Bay (*Clupea pallasi marisalbi* Berg), is characterized by unique reproductive biology. Spawning occurs mainly under the ice, from the end of April to the beginning of May, at −0.2–0.3°C, the period of egg development lasts over a month, and free embryos and larvae begin to develop in June during the polar day (Altukhov *et al.*, 1958; Tambovtsev, 1962). These features of early ontogeny are reflected in the otolith microstructure.

Daily increments on the otoliths were registered in early ontogeny of many fish species and used for the estimation of age, growth rates and the timing of ontogenetic events (Panella, 1971; Jones, 1986; Moksness and Fossum, 1991; Moksness, 1992a; Hare and Cowen, 1994). The information stored on the otoliths does not change with time and in herring can be read even in adult specimens (Zhang and Moksness, 1993). On the otoliths of Atlantic herring (*Clupea harengus*) and Pacific herring (*Clupea pallasi*), daily increments were registered in outdoor mesocosms with environmental conditions similar to natural ones (Gjøsæter and Øiestad, 1981; Moksness and Wespestad, 1989; Campana and Moksness, 1991; Moksness, 1992a; Moksness *et al.*, 1995). Based on the daily pattern of otolith growth, back-calculation of hatching date, and growth rate was applied to field-caught larvae and juveniles of Atlantic herring (Moksness, 1992a, b; Moksness and Fossum, 1992; Stenevik *et al.*, 1996). In White Sea herring, regarded as a Pacific subspecies (Berg, 1934; Svetovidov, 1952; Altukhov

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et al., 1958), otolith microstructure has not been studied before.

Otolith microstructure can be also used for stock identification. In particular, the young of spring and autumn-spawned Atlantic herring can be distinguished on the basis of otolith patterns (Moksness and Fossum, 1991). At the same time, the relationships between Atlantic and Pacific herring have not been understood well. As was found recently, some populations of Atlantic herring in Norwegian waters, e.g. herring from Rossfjord and Balsfjord, are characterized by a smaller number of vertebrae and intertidal spawning behaviour, and, in this respect, are very particularly similar to Pacific herring and to White Sea herring (Hognestad, 1994; Jørstad *et al.*, 1994). Young Norwegian spring-spawning herring (*C. harengus*) and White Sea herring (*C. pallasi*) can occur together in the Barents Sea and adjacent waters, causing a problem for the identification of fish of different origins. Therefore, comparison of the otolith microstructure in the White Sea herring and in other stocks of Atlantic and Pacific herring are important for developing methods for distinguishing stocks of Norwegian and Russian origin and for understanding herring evolution in Pacific and Atlantic Oceans.

The aims of this study are: (i) to observe growth patterns of sagitta in the White Sea spring-spawning herring, and to determine whether otolith increments form daily; (ii) to calculate age, hatching date, and growth rate of the herring in the field; (iii) to assess the possibility of distinguishing stocks of Pacific herring (in particular, White Sea herring) and Atlantic herring, based on otolith microstructure.

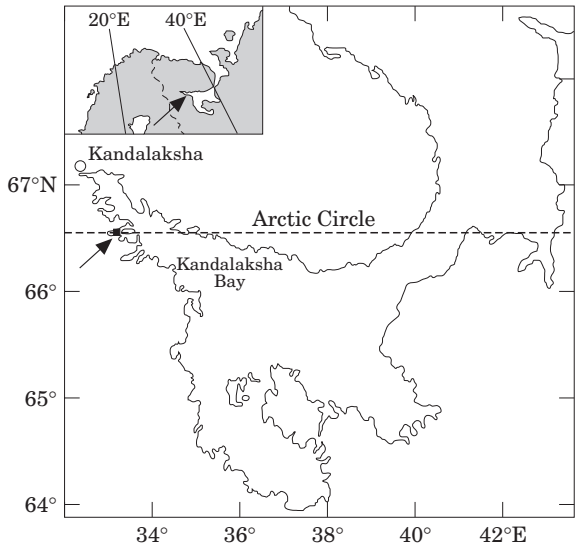

Figure 1. Sampling location (arrows).

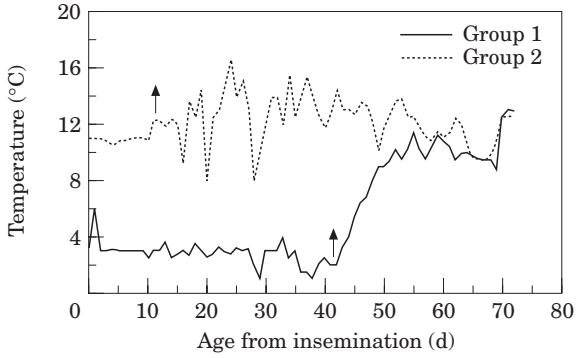

Figure 2. Regimes of temperature during egg and larvae cultivation in two groups of the White Sea herring. Arrows show the dates of mass hatching.

Material and methods

Laboratory experiments

The experiments were carried out at the White Sea Biological Station of Moscow State University (WBS MSU) in spring and summer 1996. The Station is situated in the south-western part of Kandalaksha Bay at the latitude of the Arctic Circle (66°34′N; 33°08′E) (Fig. 1).

To study development of the larvae and their otoliths, ripe spawners of herring were collected in Palkina Creek, near Kandalaksha, on 27 April. Average total length (TL) of fish was 21.7 cm (limits 19–24 cm), and average age (determined by scales) was 6 years (limits 4–8 years) (n=17). The gonads were removed, placed in plastic bags, and transported to the WBS MSU within 6 h. Then the eggs were artificially inseminated. Two egg and larva groups were used in the study.

Group 1

The eggs from eight females, attached to nets and to glass plates, were incubated in the aquarium with a closed system of water circulation at a constant temperature (3.0°C) until 7 May. This temperature represents the lower temperature limit for normal hatching of herring embryos (Pavlov and Shadrin, 1998). Then the eggs were transferred to a tank of approximately 1 m^3 capacity and installed in a room with regulated temperature. Continuous weak light (two lamps, 60 W each) was used during the incubation. Average temperature from egg insemination to mass hatching was 2.8°C (SD 0.8) (Fig. 2). Mass hatching was observed on 7 June, at age 43 d from insemination. After hatching, the larvae were reared in the same tank for 30 d. The average temperature was 9.1°C (SD 2.6). Two lamps (100 W each) were installed above the tank, and an artificial light cycle (18L:6D) was used. The larvae were fed dry pellets (produced for tropical marine fish) and natural zooplankton for one week from hatching, and only natural zooplankton subsequently. Plankton density was

Table 1. Dates of sampling and standard length of larvae collected in the field.

Date of sampling	Standard length (mm)				N
	Average	s.d.	Min.	Max.	
9–11 June	7.2	0.6	6.2	8.2	10
2–4 July	15.9	1.8	13.9	17.5	3
13 July	22.7	2.3	17.8	27.2	82

comparatively low, due to the large volume of the tank. Mortality of larvae by age 30 d reached about 95% from their initial number at hatching, probably caused by starvation and activity of small hydroid medusas, which occasionally were placed into the tank together with the plankton. Larvae (30 samples for each analysis) were fixed in 96% ethanol at age 1 d from mass hatching, in the beginning of exogenous feeding (age 5 d), at the stage of the total resorption of the yolk sac (age 9 d), and then at age 20 and 30 d.

Group 2

The eggs from three females were attached to nets installed in an aquarium (100 l) with a closed system of water circulation. A stable water temperature (11.0°C) and natural photoperiod (with light from a window) were used during incubation. Mass hatching was observed on 8 May, at age 11 d from insemination. The larvae were transferred into a small aquarium (40 l) with low water level (10 cm), and at age 30 d from hatching, to a larger aquarium (150 l) with water level 20–30 cm. The temperature for 62 d from hatching was 12.3°C (SD 1.7), with maximum fluctuations from 8 to 16.6°C (Fig. 2). The natural light cycle (with the light from a window) and additional continuous light from a lamp (100 W) were used during rearing of young. Larvae were fed dry pellets and natural zooplankton on the third day from hatching, and only zooplankton after a week from hatching. Due to the small volume of the aquarium, plankton density was much higher than in group 1. Mortality of eggs was low, and mortality of larvae and juveniles by age 62 d from hatching was approximately 80% of the total number of larvae at hatching. At hatching a part of larvae (n=38) was fixed in 96% ethanol and their standard length was measured. In these larvae the otoliths were not removed. On 9 July, at age 62 d from hatching, 30 juveniles were anaesthetized and fixed in 96% ethanol. In addition, 17 specimens were fixed at earlier stages of development at age from 20–53 d.

Field samples

Herring larvae were sampled near the WBS MSU in 1997. The dates of sampling and standard length of larvae are given in Table 1. The larvae <18 mm SL were collected with a conical net, 80 cm diameter, towed horizontally behind the boat at the water surface. The larger larvae were sampled on 13 July in a bay near the shore at the depth of 0.5–2 m. Herring schools were registered visually and the fish were sampled by two conical hand-nets, 50 cm diameter, which were synchronously and quickly moved towards each other from the small boat. After catching, the larvae were preserved in 96% ethanol. The larvae (n=82) collected on 13 July were used for the back-calculation analysis. The relationship between the standard length and sagitta radius was established based on the data for all specimens sampled in the field.

Otolith analysis

The otoliths were removed and mounted on glass slides with clear nail polish for subsequent light microscopy. Some of the otoliths from group 1 were lost during the preparation. The total number of otoliths used for the analysis was as follows: group 1 143+135 (sagitta+lapillus); group 2, 47 (sagitta); field, 95 (sagitta). The standard length of the preserved larvae and juveniles was measured under the binocular microscope before removing otoliths. To observe the degree of shrinkage, the same larvae were measured before fixing and a week later. The SL values were 9.3 (SD 0.5) mm and 8.8 (SD 0.6) mm (n=50) respectively. Thus, the correction for shrinkage due to preservation in 96% ethanol was 5.4%. This value is similar to that (4%) given by Moksness and Fossum (1992), when 80% ethanol was used for the preservation of specimens. Standard length (SL) of preserved larvae and juveniles was used in this study, and no correction for shrinkage was made.

Otoliths of most group 2 herring juveniles were polished with fine grit paper to expose growth rings. The magnification used for the analysis of the otoliths from group 1 was ×1000. At this magnification, many additional rings (probably a result of interference) were observed on the larger otoliths from group 2 and from the field group. Therefore, the magnification ×400 was applied to read the otoliths of the latter two groups. In all groups of larvae, maximum distance from the sagitta centre to the hatch check (hatch check radius) and maximum distance from the sagitta centre to the sagitta

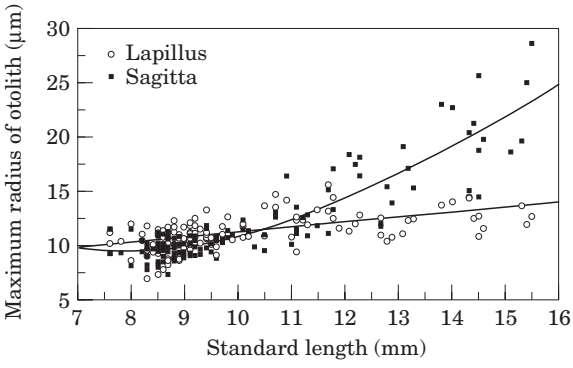

Figure 3. Relationship between lapillus and sagitta radii and standard length in the White Sea herring larvae (group 1). Lapillus: $y=6.5191+0.45367x$; $r^2=0.32$. Sagitta: $y=36.094-7.4331x+0.60692x^2-0.011661x^3$; $r^2=0.81$.

edge (sagitta radius) were measured, and the increment number was counted. In addition, maximum lapillus radius was measured in group 1. A detailed description of the otolith analyzing system and computer software used in this study are given by Andersen and Moksness (1988).

Statistical tests were performed using Student's t-test and procedures described by Zar (1974).

Results

Relative growth of lapillus and sagitta

The difference between the sizes of lapillus and sagitta was not significant up to approximately 11.5 mm SL (Fig. 3). The relationships between lapillus radius and SL, and sagitta radius and SL, can be described by linear and polynomial equations, respectively. Due to the very slow growth rate of the lapillus, this otolith was not used for the subsequent analysis.

Growth of larvae and formation of sagitta increments in the experimental groups

Initial growth rate of larvae was much higher in group 2 than in group 1 (Fig. 4a). At age 20 d from hatching, average standard length of larvae was 13.6 and 11.4 mm respectively. During subsequent development to age 30 d growth rate in the two groups was approximately at the same level. Average daily growth rate was 0.31 mm d^{-1} in group 2 and 0.15 mm d^{-1} in group 1.

In group 1, the increment formation was not daily (Fig. 4b). The average number of increments in larvae at age 30 d from hatching was only 9.5. However, in group 2 the increment deposition rate (gradient) was not significantly different from one increment per day ($p=0.98$). Due to observed difference between the actual age and increment number in group 2, to calculate the age of larvae in the field group, 13 was added to the number of increments.

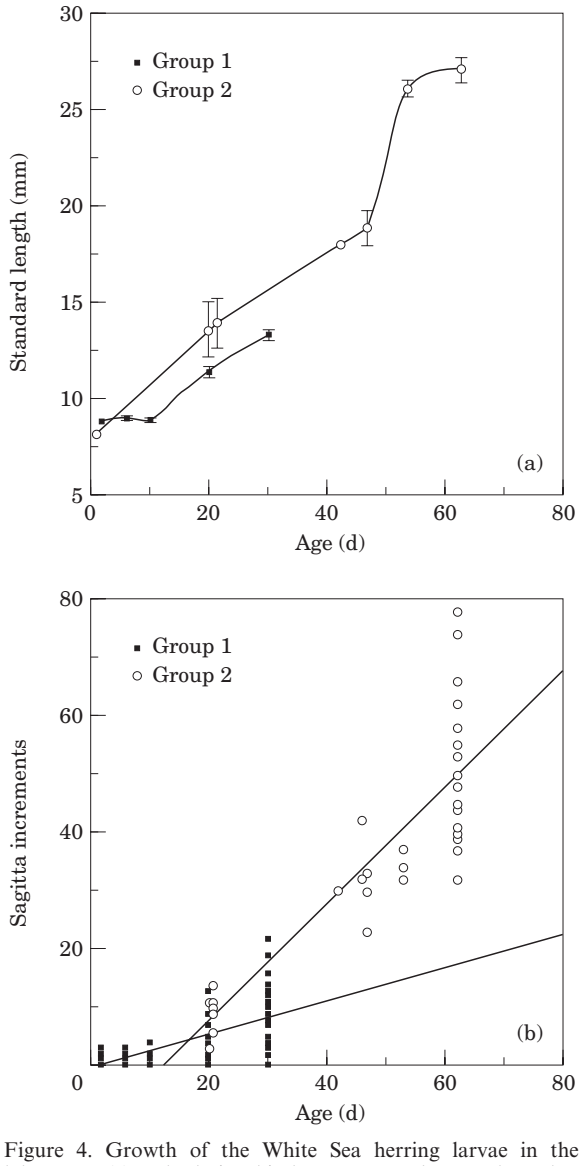

Figure 4. Growth of the White Sea herring larvae in the laboratory (a) and relationship between actual age and number of sagitta increments (b) in groups 1 and 2. Error bars (a) are the standard errors. Each point (b) may represent more than one value. Group 1: $y=-0.57458+0.27987x$; $r^2=0.43$. Group 2: $y=-12.839+1.0029x$; $r^2=0.74$.

Radius of hatch check

The frequency distributions of the hatch check radius in the two experimental groups and in the field group collected on 13 July overlapped (Fig. 5). The largest difference was observed between groups 1 and 2, with the mean values 9.4 (SD 1.1) μm and 11.7 (SD 1.8) μm.

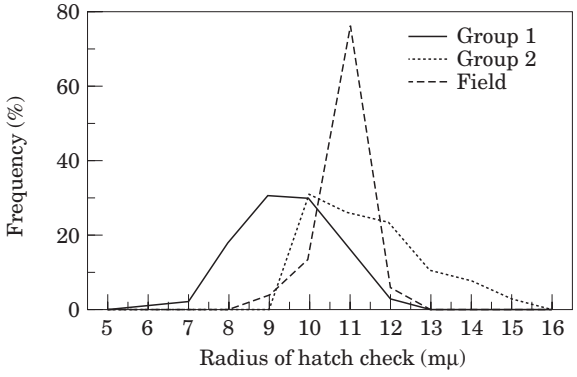

Figure 5. Frequency distribution of the hatch check radius in the White Sea herring larvae from the experimental groups and field group collected on 13 July.

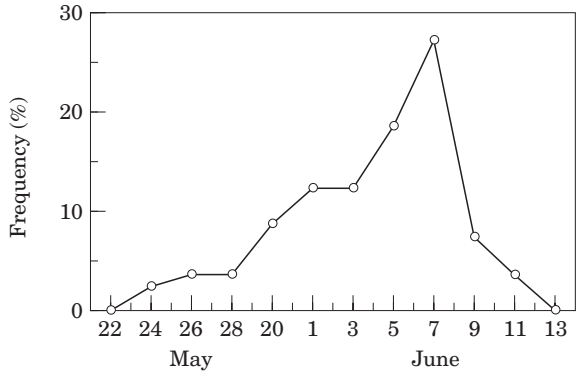

Figure 7. Estimated frequency distribution of the hatching dates in the field group of the White Sea herring larvae collected on 13 July.

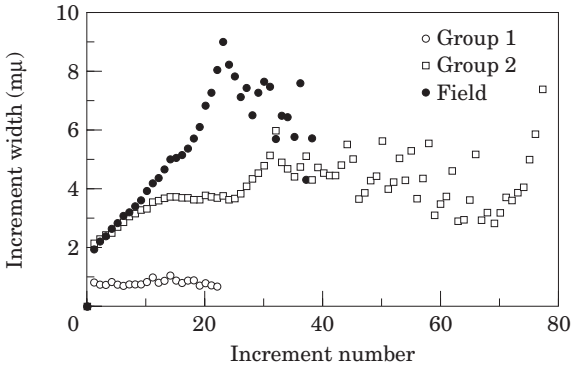

Figure 6. Increment width in the White Sea herring larvae from the experimental groups and field group collected on 13 July.

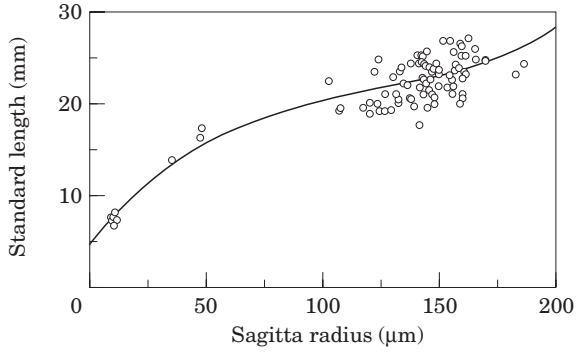

Figure 8. Relationship between standard length and sagitta radius in the White Sea herring larvae collected in the field. Each point may represent more than one value. $y=4.3072+0.32453x-0.0022776x^2+0.0000062898x^3$; $r^2=0.84$.

The hatch check radius in the field group was lower than that in group 2, with mean 10.9 μm (SD 0.5). The differences between the average hatch check radii in the three groups of larvae were significant ($p<0.001$).

Increment width

Average increment width in group 1 remained at a very low level during development of larvae, with an average 0.8 μm (SD 0.2) (Fig. 6). In group 2, the average increment width increased from hatching to age 46 d (increment number: 13) and then stabilized at a comparatively high level: 4.4 μm (SD 0.9). In the field group, the increment width increased abruptly to age 36 d, reaching the maximum value 9.1 μm, and then decreased up to 4.3–5.7 μm by age 51 d.

Hatching date and growth rate in the field

The histogram of hatching dates back-calculated for the field group collected on 13 July showed a broad distribution with a mode on 7 June (Fig. 7). According to the histogram, the majority of larvae from this group (70.4%) hatched between 1 June and 7 June.

Based on the data of Table 1, the actual average daily growth rate of larvae in the field was 0.47 mm d^{-1}. To back-calculate daily growth rate of larvae, a relationship between SL and sagitta radius was established for the larvae collected in the field (Fig. 8). This relationship is described well by the polynomial equation. The back-calculated linear growth and daily growth rate are shown in Fig. 9. The average daily growth rate reached maximum (0.7 mm d^{-1}) at age from 14 to 28 days and then decreased to approximately 0.4 mm d^{-1} at age from 29 to 51 days.

Discussion

Different patterns of growth were observed in this study for lapillus and sagitta in the larvae of the White Sea herring. By 11–12 mm SL of larvae (approximately 10 d after the total resorption of the yolk sac in group 1), the growth rate of the sagitta increased abruptly, but the

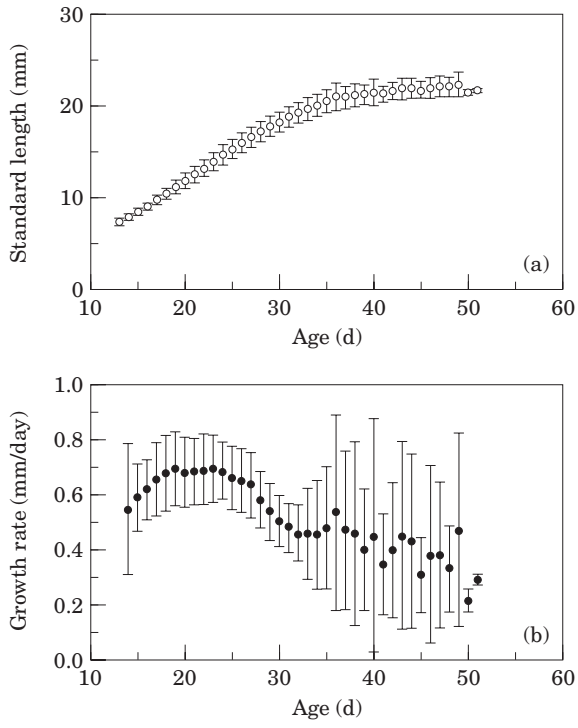

Figure 9. Estimated linear growth (a) and daily growth rate (b) in the field group of the White Sea herring larvae collected on 13 July.

growth rate of the lapillus remained at a low level. However, according to Bolz and Burns (1996), in Atlantic herring, an initially very slow growth rate of lapilli substantially increased at approximately 2.5 months of age.

The results of this study support the major influence of the environment on the deposition of increments on otoliths. The growth rate was very slow and the periodicity of increment formation was not regular and not daily in the group of larvae reared at lower temperature and at a low prey density. An unnatural photoperiod for the White Sea herring larvae, with 6 h darkness, probably had an additional negative effect on the growth rate. On the contrary, fast growth rate and daily deposition of increments were observed in the group reared at a comparatively high temperature and high zooplankton density.

The results of this study support the previous investigations of the growth of herring larvae. As it is known (Blaxter and Hunter, 1982), the growth rate of herring depends mainly on temperature and food abundance. In laboratory experiments, increments did not form daily, as a result of poor conditions and slow growth rate (Lough *et al.*, 1982). Geffen (1982) demonstrated an interaction between growth rate and increment deposition rate. Daily periodicity of increment deposition was observed only in the case of a fast growth rate (0.42 mm d^{-1}). Daily increment appearance in Atlantic and Pacific herring was also registered in mesocosms with environmental conditions similar to those in the natural habitats (Gjøsaeter and Øiestad, 1981; Moksness and Wespestad, 1989; Campana and Moksness, 1991; Moksness, 1992a). Other observations conducted on Atlantic herring (Campana *et al.*, 1987) and on a viviparous fish *Micrometrus minimus* (Schultz, 1990) showed that in the case of slow growth rate, actual increment deposition might be daily, but the resolution of light microscope was too low to determine narrow increments (less than 1 µm wide). The increments of such width were registered in group 1, and therefore, the resolution hypothesis can explain a low rate of increment formation.

The average increment width registered in the White Sea herring from age 30 d in group 2 and in the field (4.3 µm and 6.9 µm, respectively) was higher than that observed in Atlantic herring. In particular, the average increment width of Norwegian spring-spawning herring larvae raised in the mesocosm, at age >30 d, was approximately 3.0 µm (Moksness, 1992a). In the field, the average increment width in the herring larvae from the same stock older than 30 d was about 2.7 µm (Moksness and Fossum, 1992) and 2.2 µm (Stenevik *et al.*, 1996). Average increment width reached 3.4 µm in the herring of the North Sea to the east of the Dogger Bank at age >40 d (Moksness, 1992b).

The average daily growth rate in Norwegian spring-spawning herring larvae in a mesocosm (0.27 mm d^{-1} up to age 65 d) (Moksness, 1992a) was lower than that for group 2 in this study (0.31 mm d^{-1}). The average estimated daily growth rate of Norwegian spring-spawning herring and North Sea herring in the field (0.24–0.38 mm d^{-1} up to age 60 d) (Moksness, 1992b; Moksness and Fossum, 1992) was lower than that in the White Sea herring, both estimated (0.51 mm d^{-1}) and calculated based on the length of the field-caught samples (0.47 mm d^{-1}). Comparatively low average daily growth rate (0.23–0.36 mm d^{-1} up to age 60 d) was registered from 1976 to 1994 in Atlantic herring in the Gulf of Maine-Georges Bank region (Bolz and Burns, 1996). At the same time, average daily growth rate of Pacific herring cultivated in a mesocosm to age 62 d was 0.66 mm d^{-1} (Wespestad and Moksness, 1989; Moksness and Wespestad, 1989). According to the estimate of Moksness and Wespestad (1989), average daily growth rate of Pacific herring larvae in Bristol Bay, Alaska, can be even higher, reaching 0.74 mm d^{-1}.

Thus, the analysis of literature and our data showed that both in artificial conditions and in nature, increment width was larger and growth rate was higher in Pacific herring (*C. pallasi*) than in Atlantic herring (*C. harengus*). The difference may be caused by the higher temperature and better feeding conditions during

development of the former species, as well as by its higher growth potential.

The difference between the increment number and actual age of the White Sea herring larvae, raised at a temperature similar to the natural one, was 13 d. Thus, the first increment formed approximately 10 d after resorption of the yolk sac. The observed difference between estimated and actual age was higher than that reported for Pacific herring (8 d at 8°C) (Moksness and Wespestad, 1989) and Atlantic herring (10 d at 7–8°C) (Moksness, 1992a). However, based on the literature data for Atlantic herring of Gulf of Maine-Georges Bank region, a correction factor of 19 was added to the number of increments to estimate age of larvae in days in this area (Bolz and Burns, 1996).

According to our data, the radius of the hatch check in herring larvae from group 1, obtained from the eggs incubated at a lower temperature, was significantly lower than that in group 2. However, the standard length of larvae at hatching was significantly ($p<0.0001$) higher in group 1 than in group 2, with means 8.73 (SD, 0.28) and 8.06 (SD, 0.35) mm ($n=38$), respectively. The difference in sagitta size can be associated with the different stages at hatching (at higher temperature herring could hatch at a more advanced stage of development), or with different growth patterns of sagittae. In general, the values of the hatch check radius in White Sea herring were similar to those registered in the stocks of Atlantic herring (Moksness, 1992b).

According to Kuznetsov (1960), egg deposition of the spring-spawning herring of the Kandalaksha Bay occurred at the end of April or at the beginning of May, and the period of egg development lasted for 45–50 days as the temperature rose from −0.2–0.3°C to 10–12°C. However, according to the data reported by Soin (1963) for the same herring stock, the duration of this period was 33–35 d as the temperature rose from −0.8°–−0.2° to 9–13°C. We collected the larvae with the remnants of the yolk sacs from 9 to 11 June at water temperature of 10.0°C. An experimental study (Pavlov and Shadrin, 1998) showed that mass hatching of these larvae may occur 3–6 d earlier. Therefore, the back-calculated hatching dates (1–7 June) apparently reflect the real situation in nature.

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