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Daily growth rate and hatching-date distribution of Norwegian spring-spawning herring (*Clupea harengus* L.)

Erlend Moksness and Petter Fossum

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Hatching-date distribution and daily growth rate were back-calculated from otoliths of 2-month-old Norwegian spring-spawned herring larvae of the 1985 and 1989 year-classes. These hatching-date distributions were compared with the hatching-date distribution estimated directly from the larvae sampled on the spawning grounds. Herring hatched significantly earlier in 1985, with an average hatching-date of 27 March, compared to 2 April in 1989. In both years, however, the larvae were calculated to have been hatched in late March, indicating favourable survival conditions for the larvae that hatched in this period during both years. The back-calculated growth rate in the two years peaked (0.37–0.41 mm d^{-1}) between the ages of 30 and 40 days, and decreasing to between 0.24 and 0.29 mm d^{-1} until the end of the observations (age 60 days). At 60 days the herring were at a size suitable for schooling. The average daily length increment of the sampled larvae was estimated at 0.32 mm d^{-1}.

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

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Introduction

There was almost no recruitment in Norwegian spring-spawning herring from 1967 to 1982. In 1983, however, recruitment was similar to the average recruitment of the year-classes before 1967. The spawning stock in 1983 was about 0.5 million metric tons (t), compared to more than 2.5 million t in the years before 1967 and as high as 13.9 million t in 1955 (Anon., 1991; Dragesund and Ulltang, 1978). Since 1983 the year-class strength has been far below that of the 1983 year-class, but, above that for the year-classes from 1967 to 1982. The spawning stock of the Norwegian spring spawning herring has increased since 1987, and 91% of the spawning stock in 1989 (1.5 million t) were from the 1983 year-class (Anon., 1991). In the process of rebuilding the Norwegian spring-spawning herring, it is important to understand the recruitment mechanisms for the species, as also concluded by Toresen (1990). Dragesund (1970) discussed important factors affecting recruitment in Norwegian spring-spawning herring. He concluded that strong year-classes seemed to occur when there was widespread distribution of spawning, long duration of the spawning period and rapid dispersion of larvae from the spawning ground.

Hypotheses to explain the variation in year-class strength have been reviewed by Anderson (1988). He concluded that a growth–mortality hypothesis provides a rational framework for future research. This hypothesis, which proposes an inverse relationship between growth and mortality, has been discussed in more detail by Beyer (1989) and Houde (1987). Both authors indicate that mortality rate can be estimated by back-calculating the growth rate. Houde (1987) suggests the use of otolith analysis to estimate the growth rate of marine fish larvae. A recent mesocosm experiment concluded that the growth increments in the otoliths of Norwegian spring-spawned herring are formed daily (Moksness, 1992). The estimated age and daily growth rate can be used to determine the hatching-date distribution and the growth history of the recruits (Methot, 1983; Butler, 1989). If the age structure and daily growth rate of the fully recruited year-class is compared with other parameters, like the actual hatching and daily growth rate distributions, temperature, drift, microzooplankton and predator abundance, one can move further towards solving the questions about recruitment variability.

In the present study, the hatching-date distribution and daily growth rate have been back-calculated from otolith microstructure of 2-month-old herring larvae. The objective of the study was to compare the back-calculated hatching-data distribution with the hatching that actually took place over the spawning grounds 1–2 months earlier and to back-calculate their daily growth rate.

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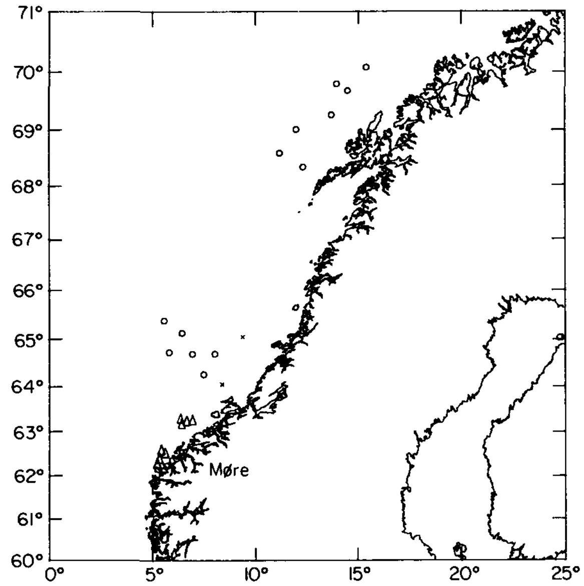

Figure 1. Sampling locations of Norwegian spring-spawned herring yolksac larvae (△ = hatching investigation) and 2-month-old larvae in 1985 (○) and 1989 (×).

Material and methods

Yolksac and early post yolksac larvae

Yolksac herring larvae were sampled off Møre (62–63.5°N) in the middle of April 1985 from RV "Eldjarn", and in 1989, twice a week during March and April from RV "Opal" (Fig. 1). The larvae were sampled with 0.5 m^2 diameter conical dip-nets with a mesh size of 375 μm. The nets were hauled to the surface from 150 m at a speed of 0.5 m s^{-1}. The larvae were sampled from non-filtering cod ends and 50 larvae were measured to nearest mm below. The larvae were preserved in 2% formaldehyde and staged according to Doyle (1977). The hatching curve in 1985 was calculated from data from the mid-April cruise and in 1989 from the cruises in March and April. Stage duration was set according to Bjørke *et al.* (1986), and the actual number of newly hatched herring larvae were later back-calculated from the number of larvae in different stages with a 10% daily mortality rate (Christensen, 1985).

Larvae

The 2-month-old herring larvae were sampled during two different cruises on the Norwegian continental shelf, north of 64°N, in May 1985 and 1989 (Fig. 1) from RV "Eldjarn". The gear used was a mid-water capelin trawl with a 10-m fine meshed (8 mm) net inside the cod end. In 1985 the larvae were frozen, while in 1989, the larvae were preserved in 80% buffered ethanol shortly after capture. The sagittae from each herring larva were removed and mounted on a glass slide for later examination with light microscopy. The examination and measurements of the sagittal microstructure used the techniques described by Moksness and Wespestad (1989). To estimate the real age of the larvae, 10 days were added to the number of increments counted to compensate for the yolksac stage (Moksness, 1992). Correction for shrinkage due to preservation in 80% alcohol was 40% for dry weight and 4% for standard length (Moksness, unpubl. data). Correction for shrinkage in standard length due to freezing was 8% (Townsend and Graham, 1981; Hay, 1982). No correction due to damage from net sampling was made. Average standard length at hatching was set to 9.5 mm (Moksness, unpubl. data). The standard length of the larvae examined ranged from 16.9 to 37.1 mm. The total number of larvae examined was 260.

To establish the relationship between standard length of the larvae and the otolith radius, data from a total of 45 larvae (9.1–12.2 mm) originating from the 1990 year-class of the Norwegian spring-spawning herring and used in a mesocosm experiment (Moksness, 1992) were used. JMP 1.04, SAS Institute Inc., was used in estimation of the polynomial model.

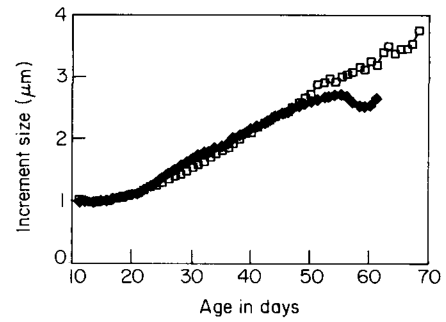

Figure 2. The average otolith increment width (μm) measured in the 1985 (□) and 1989 (■) year-classes.

Results

The average temperatures at 20 m depth in the Norwegian Coastal current are typically 5–6°C over the spawning beds in April, and 7°C on the coastal banks in May. A comparison shows approximately one degree higher temperature in 1989 than in 1985 during May.

Otolith microstructure

The mean increment widths are given in Figure 2. There were only minor and non-significant differences in the

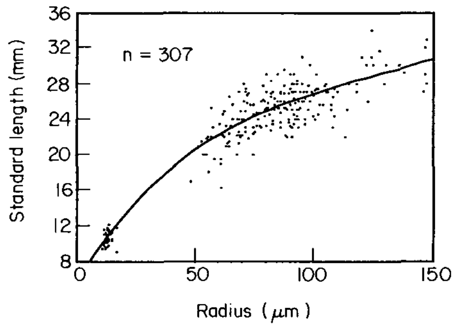

Figure 3. Standard length (SL; mm) plotted against otolith radius (R; µm). $SL = 5.543 + 0.435*R - 3.43e-3*R^2 + 1.41e-5*R^3 - 2.06e-8*R^4$, $r^2 = 0.93$. Each of the parameters is significant with absolute *t*-values between 5.2 and 16.4.

average increment size (*t*-test, age 30 days; $t = -0.616$; Zar, 1974, pp. 105–107) for the two year-classes examined. The relationships between standard length of the larvae and the otolith radius are shown in Figure 3. The relationships given are only valid for Norwegian spring-spawned herring larvae up to a maximum standard length of 30 mm.

Hatching period

The observed hatching-dates of Norwegian spring-spawned herring larvae off Møre in 1985 and 1989 are given in Figures 4 and 5. The mean hatching-dates in the 2 years were significantly different (*t*-test; *t*-value $= -25.563$; d.f. = 1576). In 1985 the hatching started in the middle of March, and reached a peak in late March. In 1989 the hatching was approximately 1 week later with peak hatching in early April. The observed hatching in 1985 and 1989 was compared with the back-calculated hatching distribution of the 2-month-old larvae of the same year (Figs 4, 5). In 1985 the observed and back-calculated mean hatching-date did not differ significantly (*t*-test; $t = -1.516$; d.f. = 1215), indicating that the 2-month-old larvae originated from the entire hatching period. In 1989, however, the back-calculated hatching-dates were significant earlier than the observed (*t*-test; $t = 18.678$, d.f. = 619), indicating that the surviving larvae came from the earlier part of the hatching period. The back-calculated hatching periods of the surviving larvae in 1985 and 1989 were identical (*t*-test; $t = 0.915$; d.f. = 261) indicating that the last part of March was most favourable for survival in both years. In 1985 there was no significant difference in the back-calculated mean hatching-date for larvae caught in the northern (north of 68°N) or southern (between 64 and 66°N) region of the coast (*t*-test; $t = 0.293$; d.f. = 76) indicating that these larvae originated from the same area.

Growth rate

The back-calculated daily growth rate based on the increment width in the otoliths is shown in Figure 6. In both years, maximum growth rate (0.37–0.41 mm d^{-1}) took place at age 30–40 days. Subsequently the growth rate decreased to between 0.24 and 0.29 mm d^{-1} until the end of the observations (age 60 days). In this period (age 40–60 days) the larvae increased their standard length from 21.1 and 21.2 mm to 27.0 and 26.8 mm, in 1985 and 1989, respectively. The results given in Figure 6 indicate a higher growth rate within the first 40 days from hatching in the 1989 year-class compared to the 1985 year-class. However, the observed difference was not significant (*t*-test, age 30 days; $t = -0.822$; Zar, 1974, pp. 105–107). In both years the sampled larvae had equal average growth rate (0.32 mm d^{-1}; *t*-test, $t = -0.881$, d.f. = 258).

Discussion

In the period 1985 to 1989 the spawning stock of Norwegian spring spawners increased from 0.6 to 1.5 million t (Anon., 1991). There was also an increase in the year-class strength from 1985 to 1989 and the logarithmic index of the two year-classes was 0.23 and 0.58, respectively (Anon., 1989). This gives some support to the indications made by Dragesund and Nakken (1973) and Lambert (1990), that there is a relationship between the parent stock size and recruitment. They also concluded that such a relationship would only be valid when favourable conditions exist during spawning and hatching. In the present study hatching was observed over the spawning grounds more frequently in 1989 than in 1985. The observed hatching period in 1985 is supported by Krysov and Ergakova (1989), who constructed a separate hatching curve of Norwegian spring-spawned herring larvae. From their study it is evident that the main hatching took place in the period 15 March to 5 April, identical to the observations in this study. The observed significant difference in spawning periods, a week later in 1989 than in 1985, is most likely explained by differences in the spawning stock for those two years. The 1985 spawning stock wintered off Møre (62°N) prior to spawning, while the 1989 spawning stock, consisting mainly of the 1983 year-class, which were spawning for the first or second time, wintered in the Vestfjord (68°N) prior to spawning (I. Røttingen, Institute of Marine Research, pers. comm., 1991). Differences in temperature prior to spawning and age structure in the spawning stocks probably caused the observed differences in spawning periods in those two years. The highest number of recruits per unit of the spawning stock was seen in 1985. In that year the larvae caught in May originated from the entire observed hatching period. In 1989 the larvae caught in May came from the early part of the hatching period, indicating

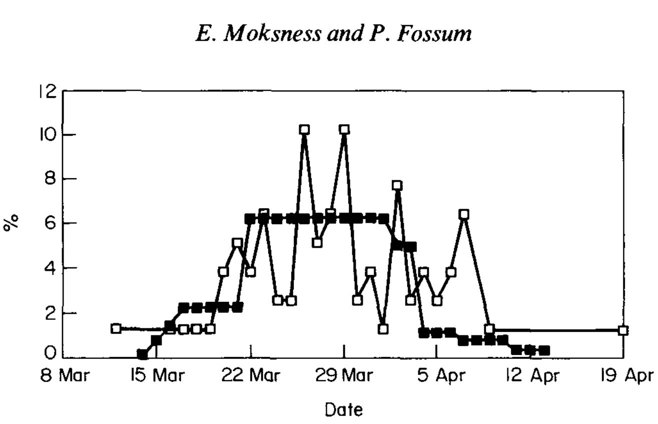

Figure 4. Hatching distributions of 1139 Norwegian spring-spawned herring larvae sampled in April (■) and back-calculated from 78 larvae sampled in May (□) 1985. The average hatching-dates were 27 March and 28 March, respectively.

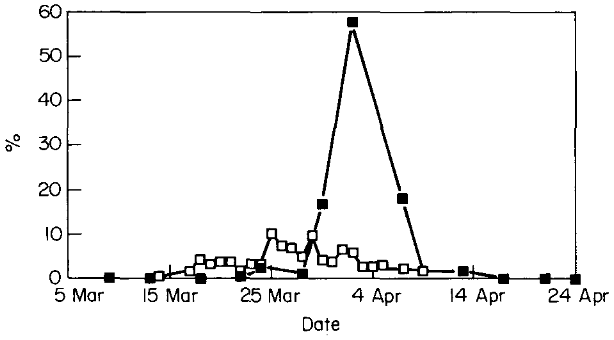

Figure 5. Hatching distributions of 439 Norwegian spring-spawned herring larvae sampled in March–April (■) and back-calculated from 182 larvae sampled in May (□) 1989. The average hatching-dates were 2 April 1989 and 28 March 1989, respectively.

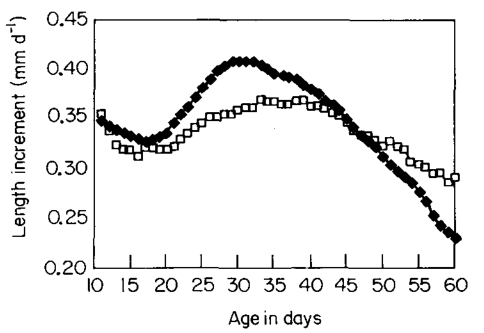

Figure 6. Back-calculated length increment (mm d^{-1}) of the sampled herring larvae in May 1985 (□) and 1989 (■).

higher survival of those larvae. The results indicate that survival was highest in both years among those larvae hatched during late March. It is impossible to link these findings to density and timing of the spring bloom, since these results are not supported with data on prey abundance in those two years. However, the mismatch in hatching-data distribution between larval production and the surviving larvae in 1989 indicate the importance of a polymodality in the age structure of the spawning stock, as concluded by Lambert (1990).

Dragesund and Nakken (1971, 1973) investigated the mortality of the Norwegian spring-spawned larvae of the 1967 to 1969 year-classes. Besides a heavy predation mortality during the egg stage (>95%), they estimated that between 70 and 95% of the herring larvae died during the first 20 days after hatching. In addition to mismatch between first feeding larvae and their prey, the growth rate in this early period might be of importance for survival, as suggested in the growth-mortality hypotheses of Beyer (1989) and Houde (1987). In the present study, growth rate was back-calculated from otolith microstructure, a method which has been reported to provide accurate and precise estimates (Campana and Moksness, 1991). The back-calculation of length in this study indicates a general trend in the growth history of the juveniles from both years. Maximum growth rate (0.37–0.41 mm d^{-1}) was back-calculated to take place at age 30–40 days. Subsequently the growth rate decreased to between 0.24 and 0.29 mm d^{-1} until the end of the observations (age 60 days). The latter correspond to a length above 26 mm, indicating that the fish had probably started to school. The observed growth pattern is in accordance with earlier observations both on Atlantic herring in the Gulf of Maine–Georges Bank region (Lough *et al.*, 1982) and on a tropical herring (Thorold, 1988). In both papers a

Gompertz growth curve was fitted to the data, while in the present paper the growth curve was established from the fish length–otolith radius relationship. However, more data should be added to the fish length–otolith radius relationship in the future, to improve the relationship and thereby give more accurate estimates of daily growth rate. For the two year-classes, average growth rates did not differ significantly, supporting the indication by Butler (1989), that similarity of back-calculated larval growth rate from the survivors may be a result of the interaction of growth and mortality. The observed higher growth rate within a short period in the 1989 year-class might have been caused by the 1 degree higher temperature in 1989 compared to 1985. Houde (1989) reported that a 1 degree increase in temperature will cause on average a 1% increase in specific growth rate.

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