Differences in growth pattern between spring and autumn spawned herring (*Clupea harengus* L.) larvae

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Otolith and somatic growth of herring (*Clupea harengus* L.) larvae were studied in laboratory experiments (500-litre tanks) in autumn 1995 and spring 1996. The larvae were kept at 8 °C and offered natural zooplankton at low (20-40 prey l^{-1}) or high prey densities (1200-2000 prey l^{-1}), and simulated seasonal photoperiods were used. Mean growth rates in length were higher in spring than in autumn both when offered low (0.12 mm d^{-1} v. 0.08 mm d^{-1}) and high (0.35 v. 0.24 mm d^{-1}) prey densities. Average weight-specific growth rates (G) were 1.7 % d^{-1} at low and 6.7 % d^{-1} in the high density groups. Autumn spawned larvae showed a dome-shaped growth pattern with a maximum in growth about 3-4 weeks post hatching, whereas spring spawned larvae grew at approximately constant rates during the same period. Daily mortality rates were less than 2.5 % in all groups. Otolith radii were not significantly different at similar lengths in autumn- and spring-spawned larvae.

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INTRODUCTION

Autumn and spring spawning herring stocks occur normally as components of the pelagic fish community in Norwegian and adjacent waters, and may overlap in nursery and feeding areas (Moksness & Fossum 1991; Fossum & Moksness 1993). Atlantic herring larvae of different seasonal origin may therefore coexist despite basic differences in early environmental history. Ambient temperature, food and day length may generate differences in stock characters between seasons. Herring larvae metamorphose to juveniles between April and October and the larval period lasts from 3 to 11 months (Sinclair & Tremblay 1984). This period is longer in autumn spawned larvae than in spring spawned ones due to slower growth rates (Moksness & Fossum 1991). Can differences in photoperiod explain the differences in somatic and otolith growth observed in nature?

In autumn the production in stratified areas is low prior to destabilisation with even lower production during the winter when also light conditions decrease (Sinclair & Tremblay 1984). Suboptimal growth conditions are therefore likely to evolve adaptations for survival. It is widely argued that growth in fishes should be maximised during the early life (e.g. Hare & Cowen 1997). Faster growing and more rapidly developing larvae attain larger size at any given age, thus having also lower risk of mortality. Whether rapid-growing larvae have survival advantages over those that grow more slowly is unclear. Several investigations have reported that otolith growth is highly correlated with somatic growth (e.g. Neilson & Geen 1982), whereas others claim that otolith growth and somatic growth are not as tightly coupled as models often assume (Brothers 1995). Studies on food dependent otolith growth are numerous (e.g. Gleason & Bengtson 1996), and several studies have examined the effect of photoperiod (e.g. Suthers & Sundby 1996). Suthers & Sundby (1996) suggested that in the short northern summer fast growth was necessary for overwinter survival in cod, and this was assumed to be achieved due to more time available for feeding.

The aim of this study was to compare otolith and somatic growth between progeny of autumn and spring spawning herring offered optimal and suboptimal food conditions. Genetic influence is not considered in this study. Herring larvae used in the present experiments were obtained from two populations spawning off western Norway in different seasons. The experiments were performed during autumn and spring under similar food concentrations and temperature regimes, but with simulated seasonal photoperiods.

MATERIAL AND METHODS

Collection of material

Adult herring with running gonads were collected from spawning grounds west of Bergen (Sotra; local autumn spawners) and at a bank area off south-west Norway (Karmøy, 59°13'N, 05°08'E; Norwegian spring spawners). The autumn samples were collected by gillnets and the spring samples were caught by trawl (RV *Michael Sars*), and transported alive to Bergen in containers with running water.

Laboratory experiments

Eggs from one female (autumn) or two females (spring), respectively, were stripped onto plastic sheets and fertilised with milt from 6 males. Eggs were incubated in running filtered seawater at mean temperatures (± SD) of 10.1 °C (± 0.2) and 8.0 °C (± 0.2) in autumn and spring, respectively, and the salinity ranged from 33-34. In autumn 350 and in spring 650 larvae were transferred on day 0 (5 October 1995 and 11 April 1996) to each of 4 fibreglass tanks (1 × 1 × 0.6m) filled with 500 l filtered seawater. Two hundred larvae were transferred to each of two unfed groups (5-litre buckets), which were used for viability controls. The tanks had perforated tubes at the bottom for aeration, which supported water mixing. The oxygen saturation was maintained above 80 % in the tanks. Temperature was monitored once or twice per day, and salinity and oxygen were measured weekly in all groups.

The experiments were set up with temperature maintained constant at 8 °C × 2 nominal predetermined food densities (high = 2000 (1200 in spring 1996) and low = 20 (40 in spring 1996) prey l^{-1}). Available prey numbers per larva was therefore of about 1500 and 30 prey per larva at high and low feeding groups, respectively. Algae (*Rhodomonas* sp. and *Isochrysis* sp.)(3 l) were added to each tank from day 3. From day 4, natural zooplankton (Day 4-21: 80-250 µm size fraction, Day 22-35: 80-500 µm) was added daily to obtain the predetermined level given for each individual tank. Zooplankton was collected from local seawater (salinity: 33) at 3 m depth, and filtered through a UNIK filtering device. Dead fish larvae were siphoned and removed every morning. Until day 18, two replicates were conducted in spring experiments. Simulated photoperiods for the natural season and latitude (60°25'N, 5°20'E) were maintained throughout both experiments. Two double 36 W fluorescent roof lamps (LUMA Aura) were applied as light sources. Light intensities at noon were measured at the uncovered tank water surface with values of 5.03-8.38 µmol m^{-2} s^{-1}. White plexiglass lids (3mm), placed on top of the tanks, provided diffuse light and reduced the light intensity by additionally 21 %. In autumn, the experiment started about 2 weeks after autumnal equinox, and in spring it commenced about 3 weeks after vernal equinox. From hatching to termination of the experiments, day length decreased nearly linearly from 13 to 10 hours per day in autumn, whereas in spring day length increased from about 16 to 20 h. The experiments were terminated on day 35 (9 November 1995) in the autumn experiment and on day 46 (27 May 1996) in the spring experiment. Only data for the first 35 days were used in the analyses. Twenty-four herring larvae were sampled on each sampling day, of which eight were used for otolith analysis. Sampling was performed on day 0, 4, 7, 14, 21, 28, and 35 in the autumn experiment and on day 0, 4, 11, 18, 21, 25, 28, 32, and 35 in spring 1996. The experimental set-up and operating procedures are the same as described in Folkvord & al. (2000).

Larval and otolith analyses

Live standard length (SL, n = 1701), developmental stage (Doyle 1977) and dry weight (DW; n = 722) of larvae preserved on liquid nitrogen and otolith measures (96 % alcohol or nitrogen preserved material) were obtained using the same procedures as described in Folkvord & al. (2000). Average radii were used when data on both sagittae were available (n = 553).

All statistical analyses were performed with Statistica for Windows (StatSoft Inc., 1995). Analysis of covariance (ANCOVA) was used to test for differences in slopes and intercepts between groups of the relationships: SL v. age or ln sagittal radius v. SL with age and SL as the covariates, respectively. The analyses were restricted to common size ranges between larval groups.

RESULTS

Standard length

Initial mean standard live length (SL) (± SD) at hatching was lower in autumn (8.0 ± 0.5 mm; n = 48) than in spring (9.6 ± 0.3 mm; n = 66). Mean growth rates in length were estimated from linear regressions at high ($r^2 \geq 0.94$, $p < 0.01$) and low prey levels ($r^2 \geq 0.66$, $p < 0.01$). At high prey levels mean growth rates of the larvae were 0.24 and 0.35 mm d^{-1} in autumn and spring, respectively, and 0.08 and 0.12 mm d^{-1} in corresponding low density groups. In starving control groups, autumn and spring mean growth rates were 0.06 and 0.09 mm d^{-1}, respectively. Growth stagnation in length occurred after about 2 weeks with a subsequent drop in length. At low and high food levels, growth rates in length were significantly higher in spring than in autumn spawned larvae (ANCOVA, $p < 0.01$) (Fig. 1). Within any season, mean growth rates increased significantly with prey levels (ANCOVA, $p < 0.05$).

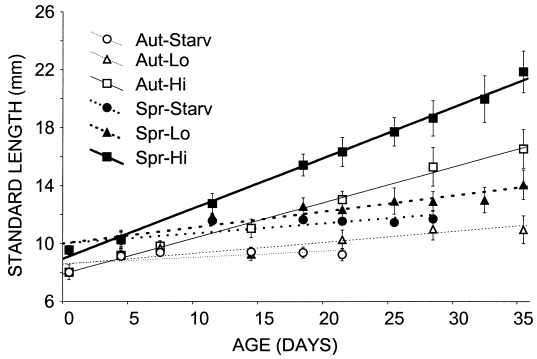

Fig. 1. Mean age-specific length growth (± 2 SD) of herring larvae in autumn and spring at different prey densities (0 l^{-1} (starvation controls), low (20-40 l^{-1}) and high (1200-2000 l^{-1})). Linear regressions were fitted for autumn (Aut) and spring spawned (Spr) larvae at high (Aut-Hi: $L = 8.1 + 0.24 \cdot d$ ($r^2 = 0.94$, $n = 223$, $p < 0.01$), Spr-Hi: $L = 9.3 + 0.35 \cdot d$ ($r^2 = 0.95$, $n = 317$, $p < 0.01$)) and low prey densities (Aut-Lo: $L = 8.5 + 0.08 \cdot d$ ($r^2 = 0.66$, $n = 216$, $p < 0.01$), Spr-Lo: $L = 10.0 + 0.12 \cdot d$ ($r^2 = 0.75$, $n = 305$,) and for unfed larvae (Aut-Starv: $L = 8.4 + 0.06 \cdot d$ ($r^2 = 0.42$, $n = 154$, $p < 0.01$), Spr-Starv: $L = 9.9 + 0.09 \cdot d$ ($r^2 = 0.69$, $n = 249$, $p < 0.01$)).

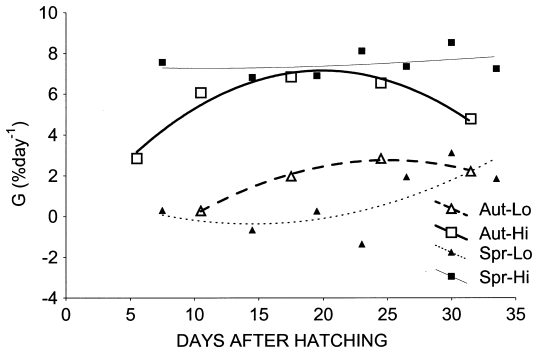

Fig. 2. Mean weight-specific growth rates (G) of post yolk-sac herring larval groups in autumn and spring at two different prey regimes (low: 20-40 l^{-1} and high: 1200-2000 l^{-1} prey densities). $G\ (\%\cdot d^{-1}) = (e^g - 1)\cdot 100$, of which g is the instantaneous growth rate, $g = (\ln DW_2 - \ln DW_1)/(t_2 - t_1)$, where ln DW is the logarithmic ($\log_e$) mean dry weight of individuals in each tank population at respective time periods t_1 and t_2. Weight-specific growth rates (G) were averaged over up to three consecutive sampling dates and weighted equally. Curves were fitted using the least squares method.

Growth patterns

Curves describing smoothed average weight-specific growth rates (G) of post yolk-sac individuals in the population followed different patterns in spring and autumn spawned herring larvae. In spring, the G of herring larvae fed high and low prey levels were relatively constant at about 7 % d^{-1} and 1.5 % d^{-1}, respectively. At low prey levels, growth stagnation occurred during the first 3 weeks ($G \approx 0$ % d^{-1}), with subsequently increasing growth rates induced by significant size-selective mortality in the tank and improving prey conditions for the surviving larvae. In autumn, however, G followed dome-shaped curves for both feeding groups, increasing just after start of feeding towards a well defined maximum about 20 days after hatching for the high prey level group and about five days later for those fed at low densities with maximum values of about 7 % and 3 % d^{-1}, respectively (Fig. 2).

Survival

High survival rates (85-92 %) of herring larvae were observed by the end of the experiments at high prey levels in both seasons with daily mean mortality rates less than 0.4 %. At low prey levels, 43-49 % of the larvae survived by the end of the experiments, yielding mean mortality rates of 1.5 - 2.4 % d^{-1}.

Somatic versus otolith growth

Length-specific otolith size relationships were apparently non-linear ($r^2 > 0.92$) (Fig. 3), and no significant differences were found between fed herring larvae in the common length range 9-14 mm (ANCOVA; covariate: SL; $p > 0.25$).

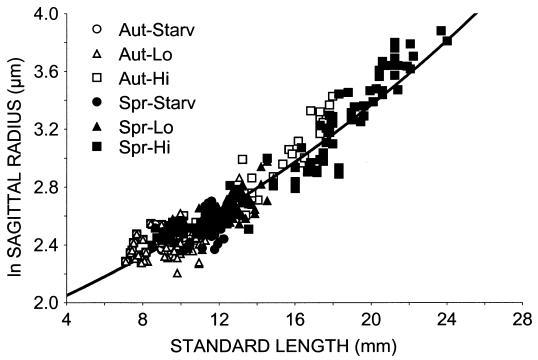

Fig. 3. Length-specific size of larval herring otoliths (ln Sagittal radius) in autumn and spring at (low (20-40 l^{-1}) and high (1200-2000 l^{-1}) prey densities. A common regression curve was fitted for all larvae ($y = 1.81 \cdot \exp(0.031x)$). Symbols as in Fig. 1.

DISCUSSION

Age-specific length growth rates were higher in spring than in autumn at similar temperature and prey densities. The generally larger size at hatch of herring in spring compared to autumn was maintained between the two populations throughout the experimental period. Differences due to lower experimental incubation temperature in spring cannot be neglected (Høie & al. 1999; Johnston

& al. 1998), but seasonal differences in egg size are common (Blaxter & Hempel 1963). The growth rates in length at high prey levels were comparable with those obtained for herring at similar ages in laboratory (Checkley 1984; Kiørboe & Munk 1986), in mesocosm experiments (Øiestad 1983; Gamble & al. 1985) and *in situ* (Moksness 1992; Moksness & Fossum 1992; Fossum & Moksness 1993). Experimental growth (otolith and somatic) and survival curves of herring larvae were found to reach asymptotic levels at prey densities of 100-300 prey l^{-1} (Werner & Blaxter 1980; Blom unpubl.), compared to more than 1200 prey l^{-1} in our experiments, which therefore should induce optimal feeding conditions of the high prey level groups. In the experimental groups offered low prey levels, similar prey numbers were available per larva in each season and high survival success was obtained, which reconfirm the high capability of larval herring to tolerate deteriorating food conditions in a predator-free environment (Øiestad 1985). The increased length range with age of herring larvae at low prey levels is probably a reflection of size hierarchy (Ehrlich & al. 1976), which implies that some larvae are better fit for growth at suboptimal conditions compared to their smaller siblings (Moksness & Wespestad 1989).

Herring larvae, like most fish larvae, are visual feeders, and potential food consumption is therefore limited by the number of hours of light available for feeding (Blaxter 1966), which varies between seasons. On average more than 50 % longer day length was available for feeding in spring than in autumn. Higher daily food intake in spring for larvae of similar size may therefore explain the differences. The temperature applied in the experiments, 8 °C, was a compromise between the natural conditions experienced by herring larvae in autumn and spring. Temperatures of at least 10-11 °C in October decreasing to 7-8 °C in November are common in the North Sea and Skagerrak as well as in other similar natural habitats of autumn spawned larvae (Gamble & al. 1985; Richardson & al. 1986). In April-May, however, 8 °C are higher than normally experienced in spawning and nursery areas (Moksness & Fossum 1992; Johannessen & al. 1995). Thus, it may be inferred that higher *in situ* temperatures in autumn are expected to generate higher somatic growth rates than obtained in this experiment, whereas lower *in situ* temperatures will induce lower rates for spring spawned larvae. Gamble & al. (1985) assumed that lower growth rates in autumn spawned herring larvae were due to declining zooplankton abundance which is consistent with low production in stratified areas prior to destabilisation and during the winter the production will decrease even more (Sinclair & Tremblay 1984). In order to cope with the harsh conditions encountered in nature by autumn spawned larvae prior to the onset of the winter, our results suggest that autumnal and vernal larval groups apply different growth strategies to compensate for differences between seasons.

Growth patterns

Dome-shaped weight-specific growth patterns (G) with clearly defined maxima 3-4 weeks after hatching were observed in autumn spawned larval groups, whereas in spring spawned groups the corresponding G was relatively constant and less dynamic during most of the experimental period. Given food conditions in excess, it seems unlikely that prey size and quality should induce any growth optimum. For low prey level groups, however, the influence of zooplankton quality on larval growth is not so clear. Gallego & al. (1996) suggested that rapid initial growth of early larvae may be an adaptation to compensate for suboptimal food supply and Kiørboe & Munk (1986) found that large sized larvae of autumn spawned herring of similar age (1-3 weeks) were more efficient in transforming ingested matter into growth. Over-winter survival in temperate species is thus suggested to be size-dependent, with low energy reserves of small fish more likely to result in starvation (Oliver & al. 1979; Henderson & al. 1988). Kiørboe & Munk (1986) suggested that different growth efficiencies were not related to geographical origin, meaning that stock or genetic differences are insignificant. They did not, however, consider day length to be important. Suthers & Sundby (1996) suggested that improved growth conditions of cod larvae in the Barents Sea than off Newfoundland were mainly due to longer photoperiods. It remains therefore to verify whether herring larvae of pre-winter cohorts apply other growth strategies for survival in the first weeks after hatching than at other seasons.

Otolith size increased exponentially with increasing body length, as also suggested by e.g. Secor & Dean (1992), but no differences were observed between groups of herring larvae in the narrow length range considered. This is in contrast to findings that slow growing larvae have larger otoliths at the same lengths (Secor & Dean, 1989; Reznick & al. 1989), but an extension of the studied larval length range would probably make any likely differences more evident.

The influence of genetic factors in the evolution of life history strategies and how they are related to photoperiod and other seasonal, environmental cues should be encouraged in future experiments.

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