Comparison of Somatic and Otolith Growth in North Sea Herring (*Clupea harengus* L.) Larvae: Evaluation of Growth Dynamics in Mesocosms

Erlend Moksness, Kjetil Rukan, Lars Ystanes,
Arild Folkvord, and Arne Johannessen

ABSTRACT: Autumn-spawned North Sea herring eggs were fertilized artificially, incubated in the laboratory, and released into two mesocosms (A and B) in September 1991 as 1-d-old larvae (hatched within 24 h). The duration of the experiments was 60 d. The released larvae experienced a high initial temperature (~ 18°C) in both mesocosms; the temperature decreased to approximately 10°C at the end of the experiments. The temperature in mesocosm A was on average 0.7°C higher compared to mesocosm B. The prey density was higher initially in mesocosm B (>1 l^{-1}) compared to mesocosm A (<0.1 l^{-1}). The situation reversed around day 23, resulting in higher prey densities in mesocosm A (>3 l^{-1}) compared to mesocosm B (1 l^{-1}). Differences in the somatic and otolith growth rates of the herring larvae were observed, reflecting the pattern of prey densities in the two mesocosms. However, changes in the otolith growth rate showed a delayed response to changes in the body growth rate. The results show that starving and slow-growing herring larvae have a relatively higher otolith growth rate than somatic growth rate. Both the somatic and otolith growth rates increased with increasing prey density; however, they were affected inversely by temperature. The thermally stable marine environment indicates that decoupling of otolith and body growth rates caused by temperature alone will be of only limited importance. When back-calculating to a previous body size, decoupling might not be a serious problem above a minimum body growth rate (>0.19 mm d^{-1}) in herring larvae, but the problem may arise when starved and slow-growing herring larvae are included.

Introduction

Autumn-spawned North Sea herring and Norwegian spring-spawning herring are important components of the pelagic fish community in Norwegian and adjacent waters. However, both stocks have experienced a drastic decline in stock biomass during the past 30 yr. The autumn-spawned North Sea herring recovered during the late 1970s and the 1980s (International Council for the

Exploration of the Sea 1992a). The larger of the two stocks, the Norwegian spring-spawning herring, was estimated to be as high as 13 million tons in spawning biomass before it collapsed in 1969. On average the stock produced abundant year-classes every 10 yr (Hamre 1990). However, between 1961 and 1982, only poor year-classes have been produced. Since then, strong year-classes have been reported in 1983, 1991, and 1992 (International Council for the Exploration of the Sea 1992b).

Since Hjort (1914) presented his hypothesis about what causes strong and weak year-classes in marine fish, with special reference to the Norwegian spring-spawning herring, several new hypotheses have been presented (Anderson 1988). Of these, the inverse growth rate-mortality rate hypothesis (Ware 1975; Shepherd and Cushing 1980) has been suggested as a rational framework for future research (International Council for the Exploration of the Sea 1992c). The hypothesis has been recently elaborated by Beyer (1989) and Houde (1987), who modelled size-specific and growth-rate-dependent processes on recruitment. However, to test whether size-specific processes or fluctuations in growth rate during the larval period contribute to recruitment variability, true individual larval growth rates need to be back-calculated.

Pannella (1971) originally proposed the use of otolith microstructure to back-calculate growth rates under two assumptions: first, that the increments are formed daily, and second, that the increment widths reflect somatic growth. For Norwegian spring-spawning herring it has been validated that one increment is formed every day in the sagitta from the end of the yolk-sac stage (Moksness 1992b) and that precision in age determination is high (Campana and Moksness 1991). The relationship between otolith size and body size has been reported to be uncoupled for several species (Bradford and Geen 1987; Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989; Wright et al. 1990), indicating that back-calculation of body growth rate based upon otolith increment widths might be biased. Secor and Dean (1992) reported that otolith and body growth are not equally affected by the feeding regime. Similar observations have been reported for Norwegian spring-spawned herring larvae (Moksness 1992b), also indicating an uncoupling in the relationship of otolith size to body size. However, results from a field investigation of North Sea autumn-spawned herring larvae indicated that uncoupling did not occur due to differences in the somatic growth rate (Moksness 1992a).

The objective in the present study was to examine the effect of changes in the body and otolith growth rates of herring larvae on the relationship of otolith size and fish size. Earlier observations have indicated that examination of such relationships from laboratory data might not be fruitful (Moksness et al. 1987), since herring larvae seldom obtain a sufficient growth rate even at high prey densities. Mesocosm systems for rearing marine fish larvae have been shown to better approximate the open sea environment than have laboratory conditions (Øiestad 1990). Adequate growth and survival of fish larvae have been obtained, even at low food levels, which make mesocosm systems appropriate for verification studies of growth dynamics in fish larvae (Øiestad 1990). Therefore, the experiments were carried out in two outdoor mesocosms. The larvae used came from autumn-spawned North Sea herring.

Methods

Eggs from autumn-spawned North Sea herring were artificially fertilized at Marine Laboratory, Aberdeen, United Kingdom, on 23 August 1991. The eggs were transported to the Institute of Marine Research, Flødevigen Marine Research Station, the same day and placed in hatching boxes

supplied with circulating seawater. The temperature and salinity during incubation varied between 12.9-13.4°C and 34.0-34.2‰, respectively. Peak hatching occurred between 31 August and 2 September. Newly hatched herring larvae were collected every morning from the incubation boxes and transferred to 40-l cylinders placed in a water bath. Larvae collected over a 24-h hatching period were grouped together.

On 2 September, approximately 18,000 one-day-old herring larvae were released into a large outdoor mesocosm (mesocosm B: 2,500 m^3 volume, 1,000 m^2 surface area, 3.0 m maximum depth). On 3 September, approximately 5,000 one-day-old herring larvae were released into a second outdoor mesocosm (mesocosm A: 2,500 m^3 volume, 600 m^2 surface area, 5.0 m maximum depth).

The herring larvae were sampled daily by hauling a two-chambered plankton net (500-μm mesh) diagonally across the mesocosms. The captured herring larvae were immediately preserved in 95% ethanol. Weekly estimates of zooplankton density were obtained from pump samples taken from depths of 0 m, 0.5 m, 1 m, 2 m, and 3 m. Water was pumped from each depth for a short period prior to filtering a 100-l sample through a 90-μm plankton net. Samples were preserved in 4% formalin and examined later using a binocular microscope and counting chamber. Temperature was measured every day at each depth and a mean temperature of the water column was calculated. Salinity and oxygen were measured at these depths once a week. A detailed description of the methods involved are given in Wespestad and Moksness (1990). The examination and measurements of the larvae started not earlier than 3 wk from sampling and were performed according to Wespestad and Moksness (1990). The sagittal otolith microstructure was examined according to Moksness and Wespestad (1989). The otoliths were read at 1200X magnification using a light microscope, and increments were measured using a digitizer.

All larvae were alive at preservation, therefore, no correction due to damage from net sampling was made. No correction for shrinkage due to preservation in ethanol was made. Initial average standard length and dry weight were measured to 8.0 mm and 0.057 mg respectively. Growth rates, given in Table 1, were calculated as follows:

Specific Growth Rate (SGR; % d^{-1}; Houde and Schekter 1981)

$$SGR = (\exp(\ln(Wt_2) - \ln(Wt_1)) / (t_2 - t_1)) - 1)\ 100$$

where Wt_1 and Wt_2 are average dry weights of the larvae at days t_1 and t_2.

Daily length increment (DLI; mm d^{-1})

$$DLI = (SL_2 - SL_1) / (t_2 - t_1)$$

where SL_1 and SL_2 are mean standard lengths of the larvae at days t_1 and t_2.

Daily otolith increment (DOI; μm d^{-1})

$$DOI = (RAD_2 - RAD_1) / (t_2 - t_1)$$

where RAD_1 and RAD_2 are mean otolith radii at days t_1 and t_2.

Table 1. Average body and otolith growth rates of larval herring in mesocosms during the two periods T1 (1-21 d) and T2 (22-60 d).

	Mesocosm	T1	T2
Daily length increment (mm d^{-1})	A	0.16	0.36
	B	0.69	0.10
Specific growth rate (% d^{-1})	A	4.00	9.71
	B	13.11	3.82
Otolith growth rate (μm d^{-1})	A	0.47	2.64
	B	1.88	2.01

Results

The temperature in both mesocosms decreased linearly from 18°C to 10°C during the experiment (Fig. 1). On average, the temperature in mesocosm A was significantly higher (0.7°C) compared to mesocosm B (t-test; t = −5.827, df = 46, p = 0.0001). The salinity was between 30‰ and 33‰ and oxygen saturation was above 80% at all times. The production of phytoplankton was low in mesocosm A (below 5 μg l^{-1}) throughout the whole experiment compared with the production in mesocosm B (between 5 μg l^{-1} and 35 μg l^{-1}). Composition of available prey organisms for the herring larvae in the two mesocosms was similar: predominantly copepod nauplii, calanoid copepods, and harpacticoid copepods. The density was initially less than 0.1 l^{-1} in mesocosm A, but increased to more than 3 l^{-1} by the end of the experiment (Fig. 2). In mesocosm B, the prey density was between 1.0 l^{-1} and 1.5 l^{-1}, except during an initial period, when it was over 3.0 l^{-1} (Fig. 2). The crossing in prey densities in the mesocosms took place around day 23.

Body and Otolith Growth

At the beginning of the experiment, herring larvae of the same age were larger in mesocosm B compared to mesocosm A. There was, however, a shift in growth rate in both mesocosms in the latter part of the experiment (Fig. 3); larvae in mesocosm A showed improved growth and those in mesocosm B slowed growth.

The pattern of otolith growth (Fig. 4) was similar to that observed for growth in body length, with a significantly higher average growth rate during the first part of the experimental period in mesocosm B compared to mesocosm A, and vice versa in the latter part (Table 1).

Daily larval length increment and otolith increment in the two mesocosms were calculated based upon the polynomial equations:

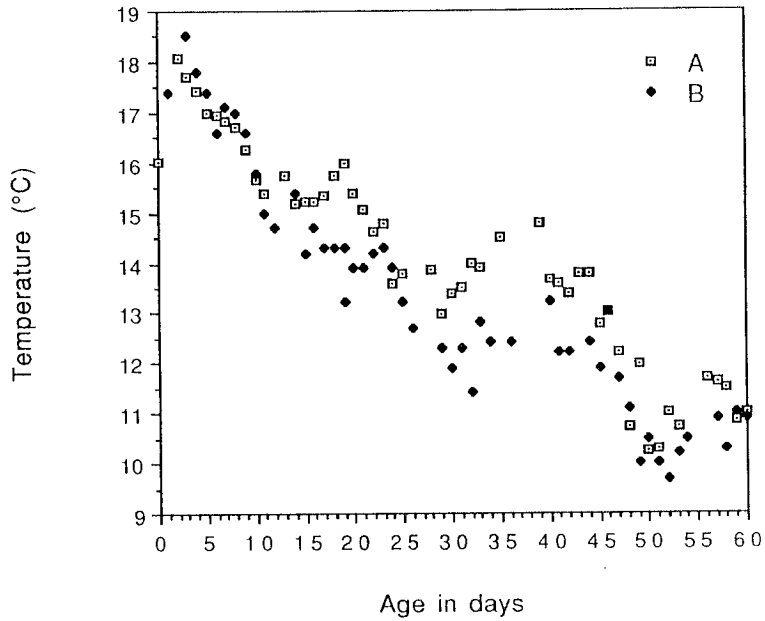

Fig. 1. The relationship between calculated average temperature (T) in mesocosms A and B, and age of the herring larvae.

Larval length increment (Fig. 3)

mesocosm A: $y = 7.6697 + 0.53791x - 0.055812x^2 + 0.0027884x^3 - 0.000049406x^4 + 0.00000028869x^5$ $r^2 = 0.964$

mesocosm B: $y = 5.8158 + 0.99695x - 0.020566x^2 + 0.00014243x^3$ $r^2 = 0.856$

Otolith increment (Fig. 4)

mesocosm A: $y = 19.574288 - 1.700334 + 0.09471111x^2 - 0.00060007x^3$ $r^2 = 0.943$

mesocosm B: $y = 18.1112 - 2.593x + 0.35511x^2 - 0.0095768x^3 + 0.000081257x^4$ $r^2 = 0.817$

The pattern in calculated average increment widths based upon measurements from the examined otoliths were similar to the time derivative of otolith radius using the polynomial equations in Fig. 4, indicating that the polynomial equations gave a reasonable description of the otolith growth in

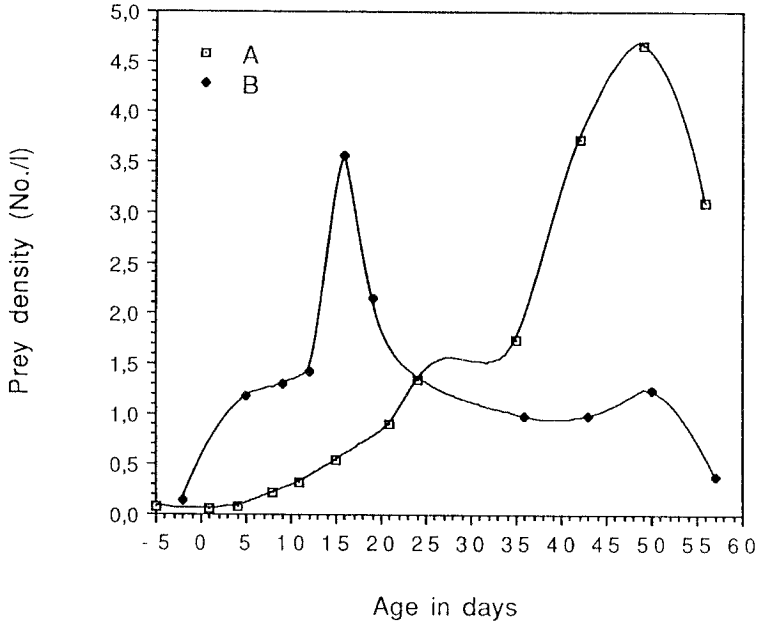

Fig. 2. Mean density (number per liter) of prey organisms for the larval herring in the mesocosms. Lines are spline smoothed.

the two experiments. The differences (mesocosm B minus mesocosm A) in the daily length increment and the otolith increment, as predicted from the time derivative of the polynomial equations (Figs. 3 and 4), are shown in Fig. 5. The results indicate that the larvae in mesocosm B had a higher somatic growth rate from age 0 to 21 d, compared to larvae in mesocosm A; better somatic growth was observed in mesocosm A compared to B in the period following day 21. Therefore age 21 d was chosen as the border line between the two periods in the analyses of body growth in this experiment. A similar change in otolith growth rate took place around day 27 (Fig. 5), indicating a delayed response of approximately 1 wk relative to the body growth rate.

Body Size and Otolith Size Relationships

The relationships between fish and otolith sizes are given in Figs. 6 through 9, and the results from the statistical tests are given in Table 2. No trends in the residuals were found in the regressions except in the otolith versus dry weight regression of T1 in mesocosm B, where a marked curvilinear trend was observed. A new analysis was conducted using only the individuals from mesocosm B with a dry weight less than 0.33 mg, corresponding to the weight range present in

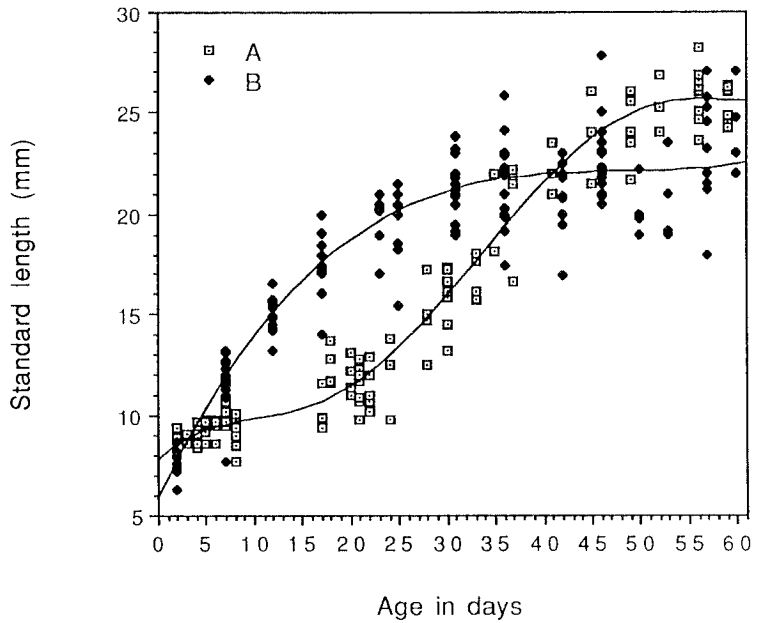

Fig. 3. Measured standard length (mm) from individual herring sampled in mesocosms A and B, with polynomial lines fit to the data.

mesocosm A (Table 2). The results show that when comparing same-size herring larvae under slow-growing and fast-growing conditions, the slow-growing larvae have a larger otolith radius. The difference varied between 10% and 20%. To examine which factors affected the body and otolith growth rate, the following multiple regression equations were obtained by a stepwise regression procedure:

$$Y = a + bX1 + cX2 + dX3$$

where Y is either body (DLI) or otolith (DOI) growth rate, X1 = larval standard length (mm), X2 = average temperature (°C), and X3 = average prey density (no. l^{-1}). Data from both mesocosms were combined. Running the model, neither body nor otolith growth rate were significantly influenced by the fish size and this parameter was therefore ignored during later analyses. The following results emerged from the analyses:

$$DLI = -1.198 + 0.0939\ (\text{temperature}) + 0.120\ (\text{prey density}) \qquad r^2 = 0.46 \quad n = 20$$

$$DOI = 2.889 - 0.124\ (\text{temperature}) + 0.572\ (\text{prey density}) \qquad r^2 = 0.84 \quad n = 20$$

Table 2. Results of ANCOVAs comparing slopes and intercept values between mesocosms A and B (Figs. 6-9). df = degree of freedom, S = significant ($p < 0.05$), NS = not significant, OR = otolith radius, SL = standard length, DW = dry weight. * recalculated based on residual analysis (ln(DW) < −1.1).

	Period	Relationship	Figure	F	df	
Slope	T1	ln(OR) – SL	6	6.44	121	S
	T1	ln(OR) – ln(DW)	7	0.18	120	NS
	T1*	ln(OR) – ln(DW)	7	8.50	95	S
	T2	ln(OR) – SL	8	0.04	157	NS
	T2	ln(OR) – ln(DW)	9	3.62	155	NS
Intercept	T2	ln(OR) – SL	8	17.56	158	S
	T1*	ln(OR) – ln(DW)	7	21.89	121	S
	T2	ln(OR) – ln(DW)	9	50.46	156	S

Table 3. Variance component in the multiple regression models. DLI = daily growth rate in body length; DOI = daily growth rate in otolith radius.

Dependent Variable	Source	Sum of Squares	% of Variance Explained
DLI	Regression	0.619	51.3
	Temperature	0.332	27.5
	Prey	0.286	23.7
	Total	1.205	
DOI	Regression	13.254	84.4
	Temperature	12.24	78.0
	Prey	1.01	6.4
	Total	15.699	

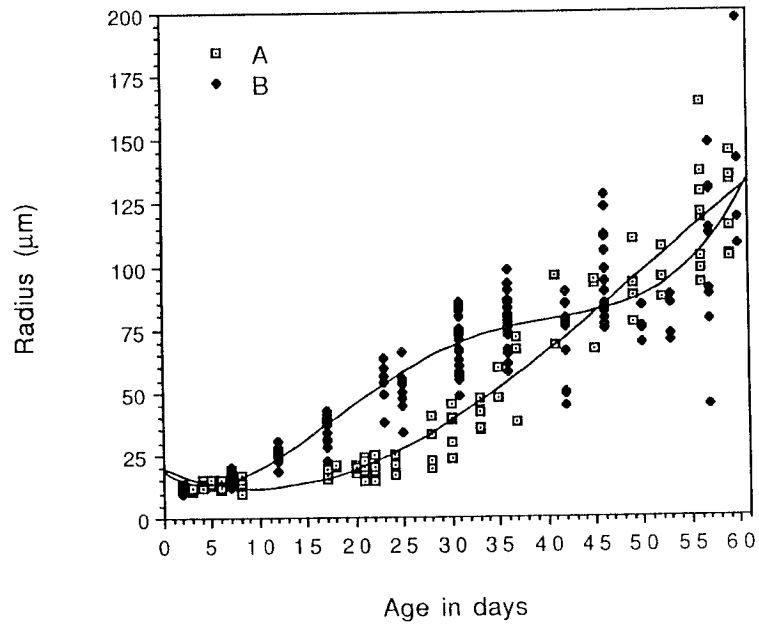

Fig. 4. Measured otolith radius (µm) from individual herring sampled in mesocosms A and B. The lines are polynomial fit to the data.

All parameters in the two regressions were significantly different from zero ($p < 0.05$). The sign of parameters for prey density indicate that both body and otolith growth rate increased with increasing prey density. For temperature, however, the sign of the parameters were opposite, indicating that body and otolith growth rate were affected inversely by temperature. Temperature explained most of the variance in the models (Table 3).

Discussion

Otolith microstructure has been documented as a reliable method to age and back-calculate the hatching date of individual herring larvae (Campana and Moksness 1991; Moksness 1992b). As reported by Pannella (1971), the second valuable application of otolith microstructure is to determine the size distribution of survivors at some date prior to sampling. Houde (1987) suggested that this could be an important tool in the evaluation of size-dependent mortality in larval fish populations, but such an approach is only valid when there is a close relationship between body and otolith growth rates. A fundamental basis for using otolith microstructure is the formation of

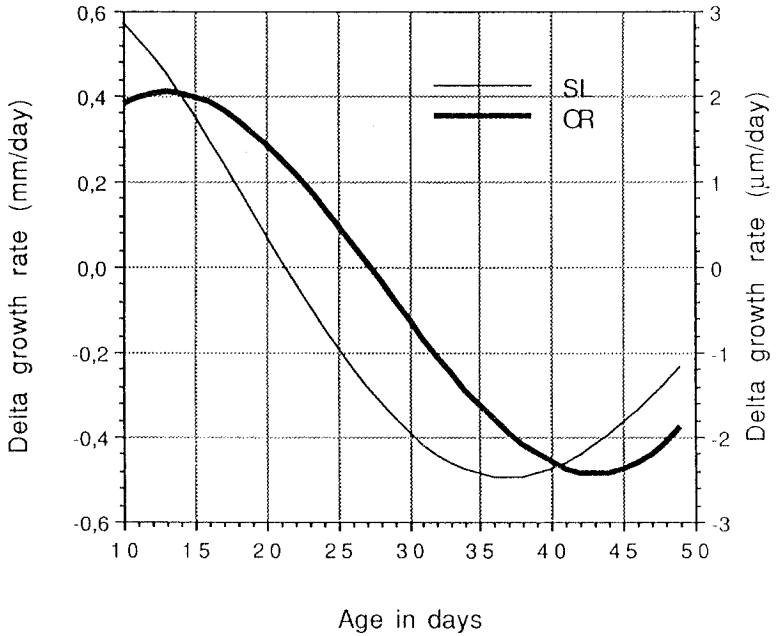

Fig. 5. Differences in body growth rate (SL; mm d^{-1}) and otolith growth rate (OR; μm d^{-1}) between the two mesocosms (B-A).

daily increments at high, medium, low, and zero body growth rates. However, at body growth rates equal to or less than zero, the otolith growth rate will still be positive, resulting in larger otoliths in these larvae compared to the same-size larvae that have positive growth rates. In addition, for larvae having a positive body growth rate, the ratio of otolith size to fish size might decline with increasing growth rate (Secor et al. 1989) and thereby result in growth-rate-dependent decoupling. Alternatively, the decoupling may only take place below a specific low, but positive, body growth rate.

The main conclusion from the present study is that slow-growing herring larvae have larger otoliths compared to the same-size herring larvae under good food conditions and that the difference could be as large as 20%. In addition, temperature and prey density turned out to be prime factors in the modeling of body and otolith growth rates, while fish size was not. Mosegaard et al. (1988) reported that in Arctic char (*Salvelinus alpinus*) the body and otolith growth rates were effected differently depending on the temperature (8-19°C) at which the fish were kept. However, the decoupling did not change proportionally to changes in temperature. In the present study, autumn-spawned North Sea herring larvae were released into two separate mesocosms at temperatures (~ 18°C) more than 5°C above what these larvae normally experience in nature (Richardson

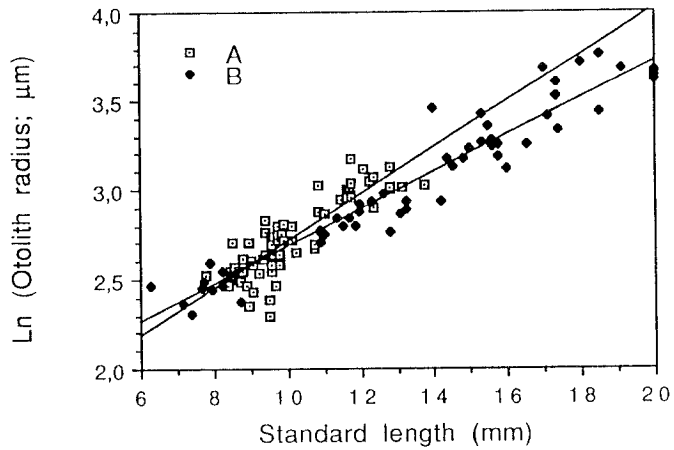

Fig. 6. Relationship between standard length (SL) and otolith radius (OR) of the herring larvae in mesocosms during period T1. Mesocosm A: ln (OR) = 1.401 + 0.131 SL, r^2 = 0.747 (n = 69); mesocosm B: ln (OR) = 1.631 + 0.104 SL, r^2 = 0.925 (n = 56).

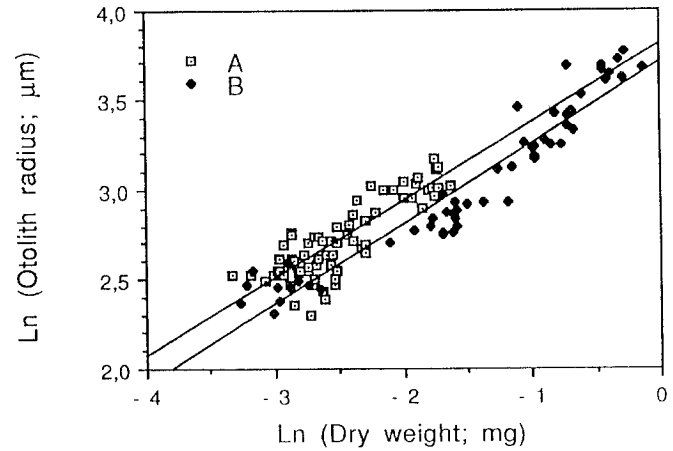

Fig. 7. Relationship between dry weight (DW) and otolith radius (OR) of the herring larvae in mesocosms during period T1. Mesocosm A: ln (OR) = 3.786 + 0.429 ln (DW), r^2 = 0.704 (n = 69); mesocosm B: ln (OR) = 3.695 + 0.447 ln (DW), r^2 = 0.908 (n = 55). Because of the observed trend in the residuals (mesocosm B), the new regression (ln DW < -1.1) gave ln (OR) = 3.361 + 0.307 ln (DW), r^2 = 0.881 (n = 30).

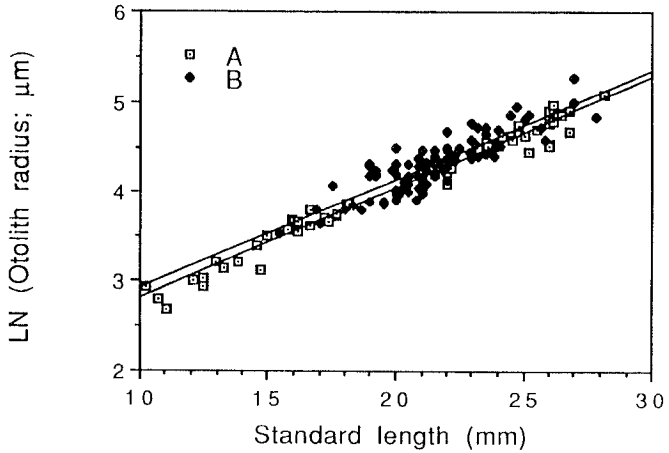

Fig. 8. Relationship between standard length (SL) and otolith radius (OR) of the herring larvae in mesocosms A and B during period T2. Mesocosm A: ln (OR) = 1.541 + 0.124 SL, r^2 = 0.975 (n = 58); mesocosm B: ln (OR) = 1.672 + 0.123SL, r^2 = 0.744 (n = 103).

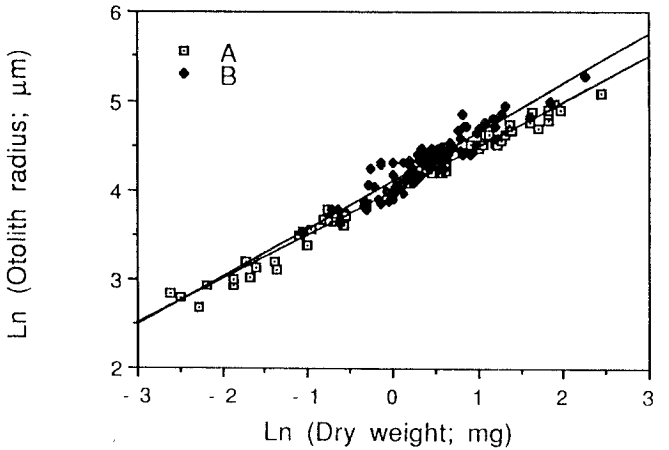

Fig. 9. Relationship between dry weight (DW) and otolith radius (OR) of the herring larvae in mesocosms A and B during period T2. Mesocosm A: ln (OR) = 3.983 + 0.496 ln (DW), r^2 = 0.986 (n = 56); mesocosm B: ln (OR) = 4.096 + 0.539 ln (DW), r^2 = 0.851 (n = 103).

et al. 1986). The unusually high temperatures did not result in higher mortality rates compared to previous mesocosm studies (Moksness 1992b). The high temperatures resulted in accelerated development, and the larvae used their yolk within a few days of hatching. However, the influence of temperature on body and otolith growth rates was different, indicating a more complex relationship than decoupling alone due to different body growth rates. The thermally stable marine environment experienced by herring larvae both in the North Sea and at the Norwegian shelf, with less than 3°C difference within the respective areas and limited temperature changes within the first months from hatching (Richardson et al. 1986; Moksness and Fossum 1992; K. Richardson, Danish Institute of Marine Research, personal communication 1993), indicates decoupling caused by temperature alone is of limited importance.

Both body and otolith growth rates were positively influenced by prey density, but there was a lagged response of about 7 d in otolith growth rate to changes in body growth rate. A lagged effect of feeding on deposition of increment width has previously been suggested by Secor et al. (1989); they observed that feeding regime not only affected the body growth rate but also the relationship between the otolith and body growth rates. The process of decoupling resulting from changes in the body growth rate is limited to approximately 7 d. A similar time lag has been observed in the RNA : DNA ratio (Ueberschär and Clemmensen 1992) when herring larvae are starved, indicating that increment widths and the RNA : DNA ratio may be affected by similar mechanisms. They concluded that the RNA : DNA ratio could be a good indicator of the nutritional condition in wild-caught herring larvae. This leads to the conclusion that increment widths probably could be a good indicator of larval nutritional condition or recent growth rate, as also suggested by Suthers et al. (1992) for pelagic juvenile cod. Combining the two techniques might be valuable in future recruitment studies. The RNA : DNA technique could be used beneficially on the young herring larvae to identify moribund individuals, and the otolith microstructure technique could be used on older larvae to back-calculate their sizes at some previous date.

The present study lacks the data necessary for a comparison of the otolith size to fish size ratio from herring larvae growing at different, but constant, rates. However, field investigations on autumn-spawned North Sea herring larvae (Moksness 1992a) did not show any significant difference in this ratio when comparing fast-growing (0.37 mm d^{-1}) and slow-growing (0.19 mm d^{-1}) larvae before metamorphosis. Comparing average growth rate within the first 2 mo of hatching for five different year-classes of Norwegian spring-spawned herring larvae, Fossum and Moksness (1994) concluded that there was little difference in the growth rate between one year-class and another (e.g., 0.31 mm d^{-1} in 1990 and 0.28 mm d^{-1} in 1991). Comparing the otolith size to fish size ratio for the year-classes 1990 and 1991 did not result in any significant statistical difference between the two. Another investigation in the North Sea (Munk 1993) showed that sprat larvae (5-23 mm) growing at different rates (0.19-0.31 mm d^{-1} and 0.43-0.46 mm d^{-1}) did not have significant differences in the body size to otolith size ratio. These observations indicate that decoupling might not be a serious problem above a minimum body growth rate, but problems may arise when starved or slow-growing larvae are sampled.

The bias in back-calculating previous size (due to decoupling) may be less than biases introduced when obtaining larval size through sampling. Gear treatment alone has been estimated to result in more than 10% shrinkage in length and 30% in dry weight (McGurk 1985). In addition, herring larvae shrink about 4% (0-10%) in standard length and about 40% in dry weight when preserved in alcohol (Moksness unpublished data). A similar shrinkage in length and about 20-30% shrinkages in dry weight have been reported when larvae are preserved in formaldehyde (Schnack

and Rosenthal 1978; Hay 1982, 1984). The shrinkage decreases with increasing larval size, resulting in greater bias among the younger herring larvae. Correct measurements of larval herring size in field studies are not easy to obtain, and the size estimates might be more biased than the estimates of larval size based on back-calculation from otolith microstructure. In addition, when comparing the ontogenetic variation in otolith size and body size, one must keep in mind the behavioral aspects of larval avoidance to approaching sampling gear. With increasing fish size, gear-selective bias becomes more and more prominent and results in selection of weaker and slower growing larvae (Heath and Dunn 1990). Larvae in this experiment had attained lengths above 20 mm, and we would therefore expect avoidance with the use of the present sampling gear.

Several approaches have been suggested to back-calculate previous fish size from otolith microstructure (see Campana 1990; Secor and Dean 1992). An additional approach, as previously suggested by Secor and Dean (1989), is to include a size-dependent minimum increment width that will be formed independently of body growth rate. Any increment width above such a minimum will be proportional to the positive body growth rate. Future otolith microstructure examinations should therefore include analyses of individual otolith growth trajectories in response to ontogenetic and enviromental effects. Examination of these trajectories will identify periods of starvation or low body growth rate and thereby indicate how precise the back-calculated procedure will be.

ACKNOWLEDGMENTS

We would like to thank the technical assistants Marit Bodvin, Inger Henriksen, and Vetle Madsen at the Institute of Marine Research, Flødevigen Marine Research Station, for an excellent job during the fertilization and incubation of the herring eggs, for participating in the mesocosm experiment, and for reading the otoliths. We are also grateful to colleagues at the Marine Laboratory, Aberdeen, United Kingdom, who kindly provided us with eggs and sperm from the herring. Partial funding for this project was provided by the Norwegian Fishery Research Council.

LITERATURE CITED

Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science* 8: 55-66.

Beyer, J. 1989. Recruitment stability and survival - Simple size-specific theory with examples from the early life dynamics of marine fishes. *Dana* 7: 45-147.

Bradford, M.J. and G.H. Geen. 1987. Size and growth of juvenile chinook salmon back-calculated from otolith growth increments, p. 453-462. *In* R.C. Summerfelt (ed.), Age and Growth of Fish. Iowa State University Press, Ames, Iowa.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Science* 47: 2219-2227.

Campana, S. and E. Moksness. 1991. Accuracy and precision of age and hatch date estimates from otolith microstructure examination. *ICES Journal of Marine Science* 48: 303-316.

Fossum, P. and E. Moksness. 1995. Recruitment processes of the strong 1991 year-class of Norwegian spring-spawning herring (*Clupea harengus* L.) derived from otolith microstructure examination, p. 467-479. *In* D.H. Secor, J.M. Dean, and S.E. Campana (eds.), Recent Developments in Fish Otolith Research, University of South Carolina Press, Columbia, South Carolina.

Hamre, J. 1990. Life history and exploitation of the Norwegian spring-spawning herring, p. 5-39. *In* T. Monstad (ed.), Biology and Fisheries of the Norwegian Spring-Spawning Herring and Blue Whiting in the Northeast Atlantic. Proceedings of the Fourth Soviet-Norwegian Symposium, Bergen, 12-16 June 1989.

Hay, D.E. 1982. Fixation shrinkage of herring larvae: Effects of salinity, formalin concentration, and other factors. *Canadian Journal of Fisheries and Aquatic Science* 39: 1138-1143.

Hay, D.E. 1984. Weight loss and change of condition factor during fixation of Pacific herring, *Clupea harengus pallasi,* eggs and larvae. *Journal of Fish Biology* 25: 421-433.

Heath, M. and J. Dunn. 1990. Avoidance of a midwater frame trawl by herring larvae. *Journal du Conseil Conseil International pour l'Exploration de la Mer* 47: 140-147.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Viewed in light of biological research. *Rapport et Procés-Verbaux des Reunions Conseil International pour l'Exploration de la Mer* 20: 1-228.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium* 2: 17-29.

Houde, E.D. and R.C. Schekter. 1981. Growth rates, rations, and cohort consumption of marine fish larvae in relation to prey concentration. *Rapport et Procés-Verbaux des Reunions Counseil International pour l'Exploration de la Mer* 178: 441-453.

International Council for the Exploration of the Sea. 1992a. Report of the herring assessment working group for the area south of 62°N. Council Meeting, International Council for the Exploration of the Sea, Copenhagen, Denmark. (Assess:11).

International Council for the Exploration of the Sea. 1992b. Preliminary report of the international 0-group fish survey in the Barents Sea and adjacent waters in August-September 1992. Council Meeting, International Council for the Exploration of the Sea, Copenhagen, Denmark. (G:82).

International Council for the Exploration of the Sea. 1992c. Report of the working group on Recruitment Processes. Fuengirola, Spain, 23-26 June 1992. Council Meeting, International Council for the Exploration of the Sea, Copenhagen, Denmark. (L:6).

McGurk, M.D. 1985. Effects of net capture on the postpreservation morphometry, dry weight, and condition factor of Pacific herring larvae. *Transactions of the American Fisheries Society* 114: 348-355.

Moksness, E. 1992a. Differences in otolith microstructure and body growth rate of North Sea herring (*Clupea harengus* L.) larvae in the period 1987-1989. *ICES Journal of Marine Science* 49: 223-230.

Moksness, E. 1992b. Validation of daily increments in the otolith microstructure of Norwegian spring-spawning herring (*Clupea harengus*). *ICES Journal of Marine Science* 49: 231-235.

Moksness, E., J. Butler, and R.L. Radtke. 1987. Estimation of age and growth rate in Norwegian spring-spawning herring (*Clupea harengus*) larvae and juveniles. *Sarsia* 72:341-342.

Moksness, E. and P. Fossum. 1992. Daily growth rate and hatching-date distribution of Norwegian spring-spawning herring (*Clupea harengus* L.). *ICES Journal of Marine Science* 49: 217-221.

Moksness, E. and V. Wespestad. 1989. Aging and back-calculating growth rate of Pacific herring (*Clupea harengus pallasi)* larvae by reading daily otolith increments. *Fisheries Bulletin, U.S.* 87: 509-518.

Mosegaard, H., H. Svedäng, and K. Taberman. 1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus aplinus)* as an effect of differences in temperature response. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1514-1524.

Munk, p. 1993. Differencial growth of larval sprat (*Sprattus sprattus*) across a tidal front in the eastern North Sea. *Marine Ecology Progress Series* 99: 17-27.

Øiestad, V. 1990. Specific application of meso- and macrocosms for solving problems in fisheries research, p. 136-154. *In* C.M. Lalli (ed.), Enclosed Experimental Marine Ecosystems: A Review and Recommendations. Springer-Verlag, New York.

Pannella, G. 1971. Fish otoliths: Daily growth layers and periodical patterns. *Science* 174: 1124-1127.

Reznick, D, E. Lindbeck, and H. Bryga. 1989. Slower growth results in larger otoliths: An experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* 46: 108-112.

Richardson, K., M.R. Heath, and N.J. Phil. 1986. Studies of larval herring (*Clupea harengus* L.) patch in the Buchan area. I. The distribution of larvae in relation to hydrographic features. *Dana* 6: 1-10.

Schnack, D. and H. Rosenthal. 1978. Shrinkage of Pacific herring larvae due to formalin fixation and preservation. *Berichte der Deutschen Wissenschaftlichen Kommission fuer Meeresforschung* 26: 222-226.

Secor, D.H. and J.M. Dean. 1989. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis* (Walbaum). *Canadian Journal of Fisheries and Aquatic Sciences* 46: 113-121.

Secor, D.H. and J.M. Dean. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis. Canadian Journal of Fisheries and Aquatic Sciences* 49: 1439-1454.

Secor, D.H., J.M. Dean, and R.B. Baldevarona. 1989. Comparison of otolith growth and somatic growth in larval and juvenile fishes based on otolith length/fish length relationship. *Rapport et Procés-Verbaux des Reunions Conseil International pour l'Exploration de la Mer* 191: 431-438.

Shepherd, J.G. and D.H. Cushing. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. *Journal du Conseil Conseil International pour l'Exploration de la Mer* 39: 160-167.

Suthers, I.M., A. Fraser, and K.T. Frank. 1992. Comparison of lipid, otolith, and morphometric condition indices of pelagic juvenile cod, *Gadus morhua*, from the Canadian Atlantic. *Marine Ecology Progress Series* 84: 31-40.

Ueberschär, B. and C. Clemmesen. 1992. A comparison of the nutrition condition of herring larvae as determined by two biochemical methods - Tryptic enzyme activity and RNA : DNA ratio measurements. *ICES Journal of Marine Science* 49: 245-249.

Ware, D.M. 1975. Relation between egg size, growth, and natural mortality of larval fish. *Journal of the Fisheries Research Board of Canada* 32: 2503-2512.

Wespestad, V. and E. Moksness. 1990. Observations on the early life history of Pacific herring (*Clupea harengus pallasi)* from Bristol Bay, Alaska, in a marine mesocosm. *Fisheries Bulletin, U.S.* 88: 191-200.

Wright, P.J., N.B. Metcalfe, and J.E. Thorpe. 1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L.: Evidence against coupling. *Journal of Fish Biology* 36: 241-249.