J. Cons. int. Explor. Mer, 46: 333–339. 1990

Variation in the hatching length of spring-spawned herring larvae (*Clupea harengus* L.) on Ballantrae Bank in the Firth of Clyde

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Rankine, Paul W., Cargill, Lindsay H., and Morrison, John A. 1990. Variation in the hatching length of spring-spawned herring larvae (*Clupea harengus* L.) on Ballantrae Bank in the Firth of Clyde. – J. Cons. int. Explor. Mer, 46: 333–339.

Variations in the length at hatching of spring-spawned herring larvae are examined. The larvae were caught during a series of intensive plankton surveys in 1987 on Ballantrae Bank in the Firth of Clyde. The results demonstrate that in wild herring, multi-layered egg masses can give rise to larvae with wide-ranging hatching lengths. The results suggest that assumptions regarding fixed hatching length, age–length relationships, and growth rates may not hold for herring larvae originating from multi-layered egg masses.

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Introduction

Many observations have been made on the hatching size and growth rates of herring larvae reared in laboratory experiments and mesocosms (Blaxter, 1956; Gamble *et al.*, 1981; Munk and Rosenthal, 1983). Field data on the growth rates and dispersion of larval herring in the open sea have been derived from patch studies (Henderson *et al.*, 1984; Heath and Rankine, 1989) but the variation in hatching size of wild larvae has never been satisfactorily examined, probably due to the difficulties involved in sampling at the exact time of hatching.

During intensive plankton surveys of the Ballantrae Bank spawning ground in the Firth of Clyde (Ewart, 1884; Parrish *et al.*, 1959) in April and May 1987, newly hatched (<24 h old) yolk sac herring larvae were caught. These larvae were subsequently measured, using a digitizing pad/camera-lucida system, enabling the variation in hatching length of wild spring-spawned herring larvae to be investigated.

Variation in the hatching length of wild herring larvae is of interest in growth-rate studies and also of some importance in the ICES herring spawning stock size estimations from larval abundance data (Anon., 1986). In the back-calculation method used by the ICES working group a fixed hatching length is assumed for all larvae.

Materials and methods

Eleven larval surveys were carried out in the Ballantrae Bank area between 14 and 29 April and 13 and 19 May 1987 (Table 1, Fig. 1). Larvae and plankton were sampled at each station position using a 1 m diameter "drum" net (similar to a bongo net in design) towed at 1 m s^{-1} in an oblique haul from the surface to the seabed. Bottom depths in the area varied from 8 to 25 m. The gear was fitted with a 250 μm mesh net and flow measured with a mechanical flowmeter (Tsurumi-Seiki Kosakusho Co., Ltd). Comprehensive coverage of the spawning area was achieved during each survey.

All herring larvae caught were removed from the plankton and preserved immediately in neutral buffered 4% formaldehyde solution. One month later up to 300 larvae from each sample were measured to the nearest 0.1 mm (standard length) using a digitizing pad and camera-lucida. No corrections were made for shrinkage and therefore larval length data may have been underestimated. The numbers of larvae per 100 m^3 occurring at each station position were then calculated using flowmeter data from each haul.

The 0.1 mm resolution length distributions were summed over each survey period to produce a length distribution which represented the entire larval population present on the Bank on each occasion. The data were then combined into 0.2 mm groups in order to

Table 1. Dates of sampling, total larvae caught and measured, Ballantrae Bank, 1987.

Date	Survey	No. of hauls	Total larvae caught	Total larvae measured
14 Apr	1	15	0	0
15 Apr		13	0	0
16 Apr	2	2	0	0
17 Apr		11	0	0
18 Apr	3	12	0	0
19 Apr	4	13	0	0
22 Apr	5	19	0	0
23 Apr		10	0	0
24 Apr	6	10	94	94
25 Apr	7	17	230	230
26 Apr	8	13	110	110
29 Apr	9	30	21 536[a]	2 630
Total		169	25 678	4 164
13 May		16	9	9
14 May	10	17	48	48
15 May		18	53	53
17 May	11	3	2	2
19 May		21	2	2
Total		75	114	114
Grand total		244	25 792	4 278

[a] 14 000 yolk sac larvae in one sample.

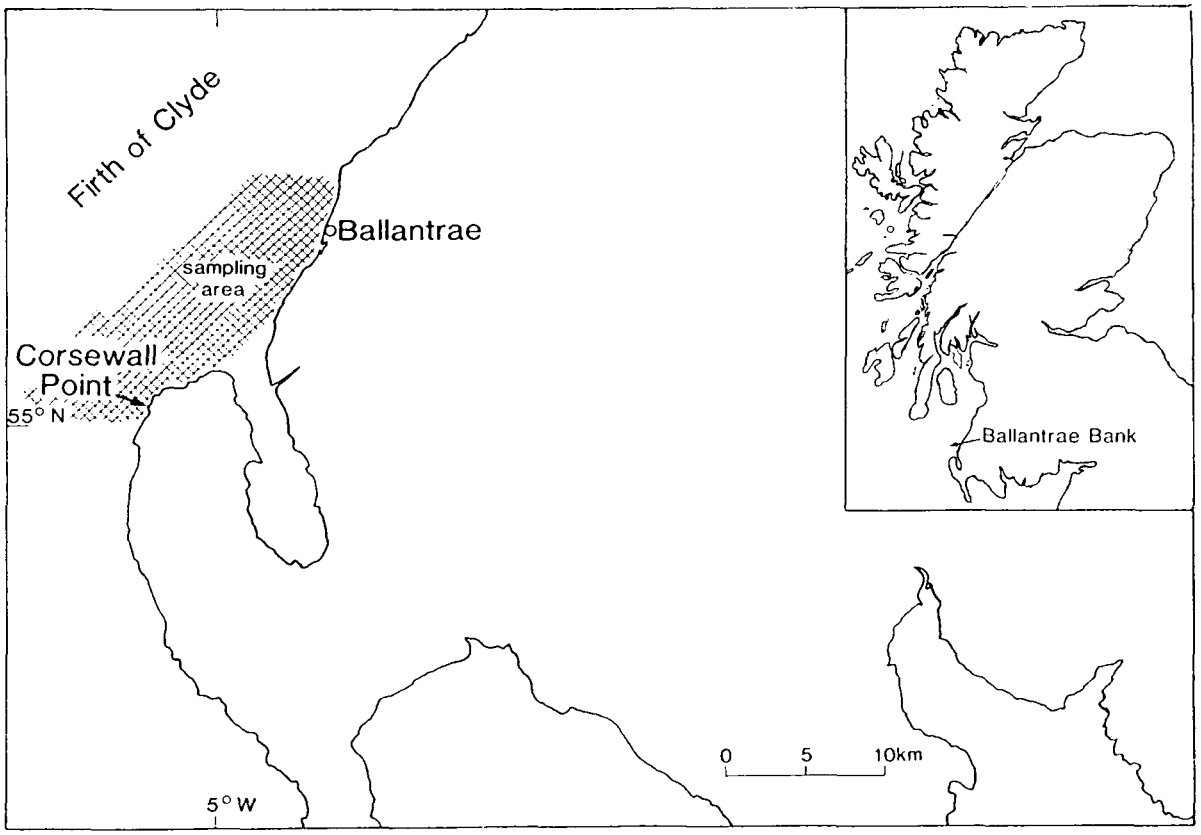

Figure 1. The Ballantrae Bank sampling area. April–May 1987.

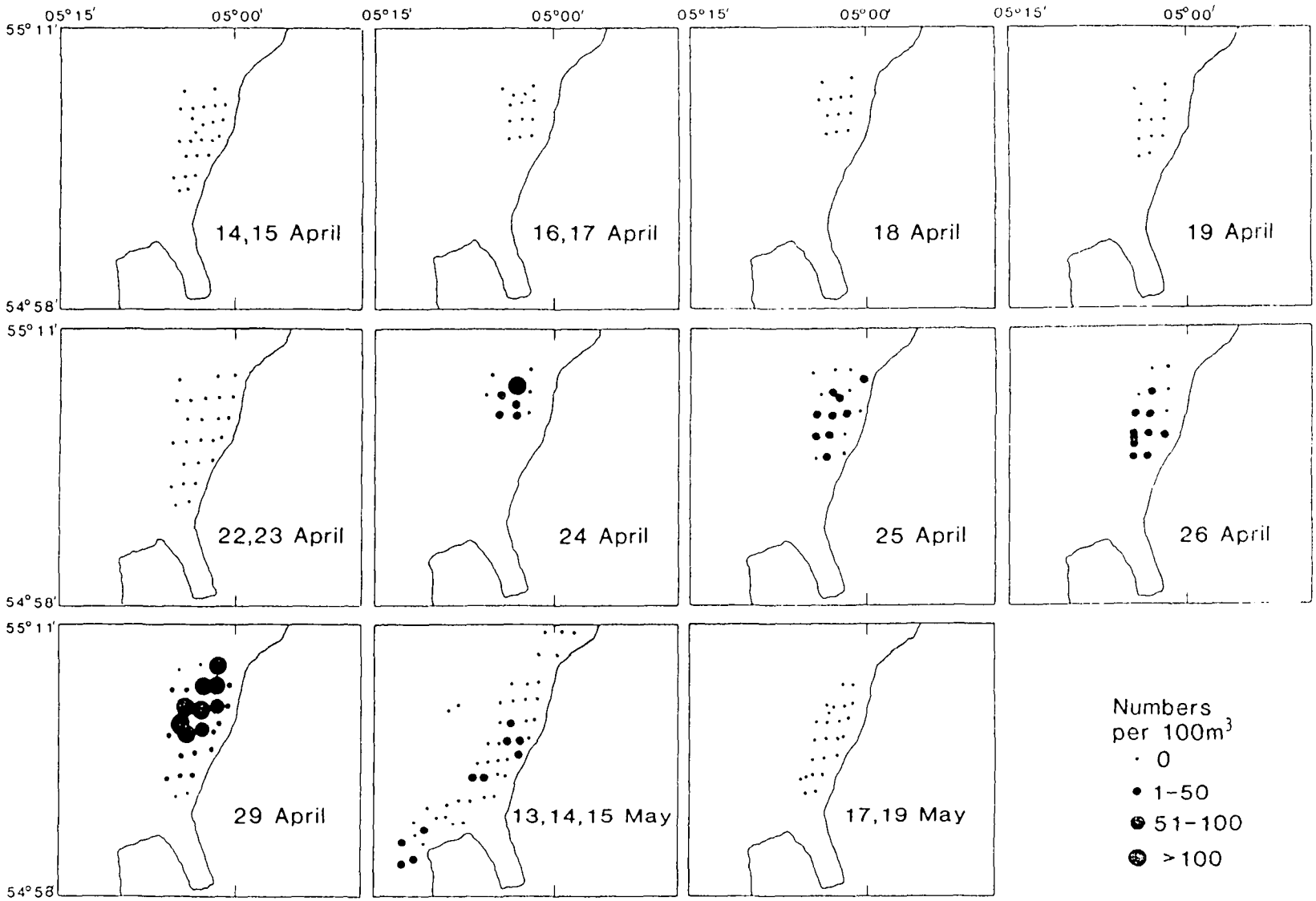

Figure 2. Herring larval distribution, Ballantrae Bank, April–May 1987.

remove localized peaks and troughs. The mean and standard deviations of each length distribution in each of the daily surveys were then identified using an iterative function minimization algorithm (Nelder and Mead, 1965). In order to begin the iteration, initial estimates of the number of distributions present in each survey and their means and standard deviations were made from plots of the original length–frequency data. A constraint on the method was that all components were assumed to be normally distributed.

Results

Larval abundance, distribution and hatching time

Grab sampling prior to 23 April had established the presence of an egg patch of approximately 85 000 m^2 to the northwest of Ballantrae (Rankine and Morrison, 1989). Herring larvae were absent in the samples from 14 to 23 April (Table 1) indicating that no hatching had taken place during this period.

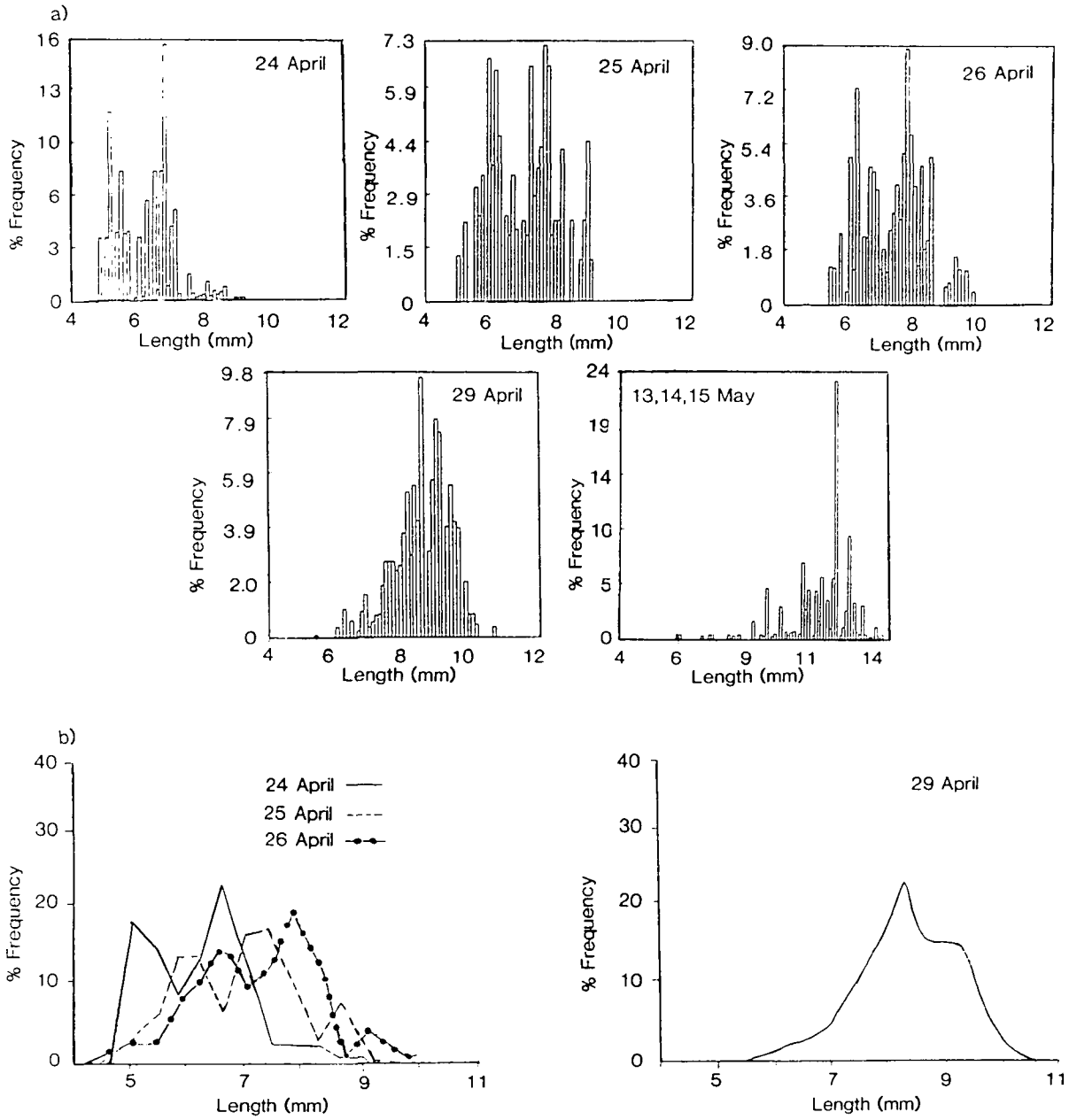

Figure 3. Percentage frequency length distribution of herring larvae 24 April to 15 May 1987: (a) 0.1 mm groups (raw data, not optimized by Nelder–Mead method). (b) 0.4 mm groups (raw data, not optimized by Nelder–Mead method).

Yolk sac larvae were caught in the vicinity of the egg patch on 24 April (Fig. 2). Therefore hatching must have occurred over the previous 24 h. No increase in larval abundance was detected during sampling on 25 and 26 April (Fig. 2). However, by 29 April larval concentrations had increased markedly, indicating that a second, much larger, hatch had occurred (Table 1, Fig. 2).

During later surveys (13–15 May) larvae were found in small numbers in an area extending from the egg patch to south of Corsewall Point (Fig. 2), indicating that larvae had drifted southwards out of the Clyde and into the North Channel by this time. Further surveys carried out during 17 and 18 May were restricted to the area of the bank itself. Very few larvae were caught in these samples, indicating that hatching on Ballantrae Bank had ceased and that all larvae previously found on the bank had been transported out of the area.

Larval length distributions and length increments

A visual inspection of the 0.1 mm grouped data (Fig. 3a) suggested that the length distributions obtained on 24, 25, and 26 April were polymodal. In contrast, the length distribution obtained on 29 April appeared to be unimodal and the much greater numbers of larger larvae (Table 1) completely swamped the distributions of smaller larvae.

The Nelder–Mead method indicated that three overlapping length distributions were present in the data on 24, 25, and 26 April. The three length groups (4.8–5.6, 6.2–6.8, and 6.9–8.5 mm) also appeared to show a daily length increment over the three-day period. Visual inspection of 'raw' 0.4 mm grouped data showed the same trend (Fig. 3b).

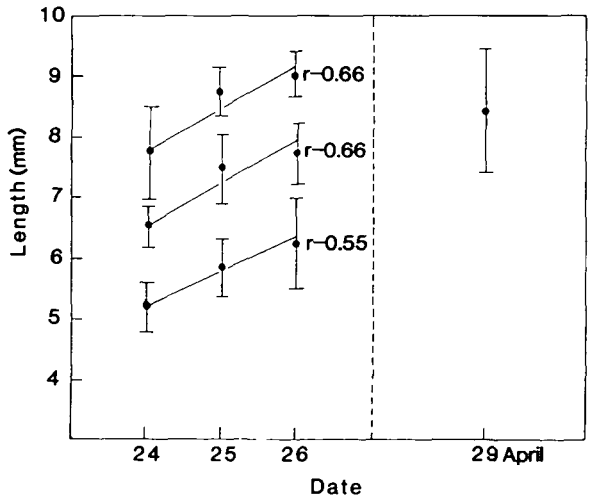

Figure 4. Herring larval mean length and increment by date (optimized data from Nelder–Mead method).

Table 2. Results of the Nelder–Mead optimization technique.

Date	Component	Mean (mm)	s.a.	Proportion
24 Apr 1987	1	5.2	0.29	0.42
	2	6.5	0.30	0.51
	3	7.8	0.75	0.07
25 Apr 1987	1	5.9	0.39	0.42
	2	7.3	0.33	0.46
	3	8.6	0.21	0.11
26 Apr 1987	1	6.3	0.71	0.52
	2	7.7	0.35	0.43
	3	9.0	0.16	0.05
29 Apr 1987	1	8.3	0.80	–

Mean hatching lengths of 5.2 mm, 6.5 mm, and 7.8 mm were estimated from the first hatch on 24 April. The mean lengths of each of these groups were regressed against time giving overall length increases of 0.55 mm day^{-1} for the smallest hatched larvae and 0.60 mm day^{-1} for larvae hatched at 6.5 and 7.8 mm respectively (Fig. 4). On 29 April one modal length was estimated with a mean length of 8.3 mm. The mean length, standard deviation, and relative proportions of each group on each day are given in Table 2.

The identification of component cohorts in the larval distributions obtained from 13 to 19 May proved unsatisfactory due to the low numbers of larvae caught.

Discussion

The hatching lengths of herring larvae may be expected to differ due to variations in the age and condition of adult fish (affecting egg size) and also due to differences between egg micro-environments, which can affect egg development rates. Various authors have carried out egg incubation studies in order to study these effects (Blaxter, 1956; Alderdice and Velsen 1971; Braum, 1973).

In aquarium studies, both Toom (1958) and Blaxter and Hempel (1963) showed that in general large eggs tended to produce large larvae. Conversely, small eggs produce small larvae. Egg and larval sizes were correlated in comparisons between different spawning populations but not within a single spawning group.

Blaxter and Hempel (1963) and Munk and Rosenthal (1983) were unable to demonstrate any relationship between the length of spawning females and larval size at hatching. In fact, both of these studies obtained results which showed a high degree of variability in larval size, even from females within the same population. It cannot therefore be concluded for certain that the small larvae from the 24 April hatch were the progeny of small female fish or that they necessarily hatched from smaller eggs.

Blaxter (1956) found that while higher water temperatures shortened the egg incubation period the

hatching size of spring-spawned larvae remained unaffected. At the time of the first hatch salinity and temperature measurements showed no unusual fluctuations in the Ballantrae area and it was thought unlikely that these factors were responsible for the small larvae observed in the 24 April hatching.

The effects of low oxygen concentrations in the microenvironment around the developing eggs were first noted by Ewart (1884), who found that eggs closely spread on thin gauze, to allow free respiratory and excretory exchange, had a higher hatching success than those prepared on glass slides. A 20% decrease in the mean larval hatching length was observed by Braum (1973) when ambient oxygen levels were lowered from 100% saturation to 40%.

Daykin (1965) asserted that, even at full saturation, the oxygen available to the developing embryo is restricted to that around the surface of the egg membrane. As a consequence the oxygen concentration inside the egg itself will be governed by the amount of uncovered surface membrane, by an oxygen diffusion gradient and by the micro-current system around the egg. Egg layering will therefore seriously affect the surface area available for oxygen exchange. Hourston *et al.* (1981) concluded, in experiments on both naturally and artificially produced spawn, that the incidence of premature hatching of Pacific herring was increased by higher egg densities. Up to 10 egg layers were found in grab samples from the egg patch at Ballantrae. It is possible therefore that the eggs found in the underlying layers of the egg mat suffered from hypoxia, resulting in the premature hatch of small larvae detected on 24 April. Larvae from polluted environments, low in oxygen, also tend to hatch prematurely as stunted "runts" (J. Gamble, pers. comm.).

Marshall *et al.* (1937) observed average length increments of 0.43 mm/day in Clyde larvae over the first 80 days of larval life, which compares favourably with the results obtained in this study for two-day-old larvae. Other authors have obtained daily length increments, in larvae from other areas, which are considerably lower for larvae of this size (0.18 mm day^{-1}, Henderson *et al.* (1984)), after averaging over extended time periods.

In the method used by the ICES Working Group on Herring Larval Surveys to back-calculate larval production figures (Anon., 1986) it is assumed that: (1) all autumn-spawned herring larvae hatch at a standard length; (2) that growth rates are linear (and equal for all hatching sizes); and (3) that a large larva is older than a smaller one.

In this case, clearly, not all of the larvae hatched at the same standard length. Blaxter and Hempel (1963) showed that, on average, larger hatched larvae grew faster than smaller. Thus growth increments may not be equal for all hatching sizes. In addition, at least some of the larger larvae caught on 29 April must be younger, not older, than those caught from the initial hatch (Fig. 4). It would appear therefore that the above assumptions may not hold for larvae originating from multi-layered and possibly poorly oxygenated egg masses.

The results presented here relate to a spring-spawned multi-layered egg mat in an inshore estuarine environment and as such are possibly not typical of autumn-spawned larvae. However, if multiple egg layers are a feature of autumn-spawning grounds then their role in the determination of larval hatching size and in the resulting growth rates, and perhaps survival, of the different spawning populations found offshore remains an important question.

Acknowledgement

The authors thank Miss A. Shanks for her extremely helpful statistical advice, Dr M. Heath for useful discussion, and Dr J. Gamble for technical assistance in the preparation of this paper.

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