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First feeding by larval herring *Clupea harengus* L.

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Abstract

The transition period from endogenous to exogenous feeding by larval herring was investigated in the laboratory for four herring stocks in order to evaluate the chances of survival at the time of first feeding. Observations on larval activity, feeding and growth were related to amount of yolk, visual experience with potential prey organisms prior to first feeding and prey density. Herring larvae did not initiate exogenous feeding until around the time of yolk resorption. The timing of first feeding was not influenced by prior exposure to potential prey organisms during the yolk sac stage. In the light of these observations, the ecological significance of the yolk sac stage is discussed. Initiation of exogenous feeding was delayed by 1-4 days at a low (7.5 nauplii $\cdot$ l^{-1}) compared to a high (120 nauplii $\cdot$ l^{-1}) prey density, but even at prey densities corresponding to the lower end of the range experienced by larvae in the sea, larvae were able to initiate exogenous feeding. There is thus no need to postulate extraordinarily high densities of food in larval nursery areas in order for the larvae to initiate exogenous feeding and the present observations do not support the comprehension that the time of yolk resorption is a particularly 'critical period' for larval herring survival.

Introduction

Marine fish species that propagate by means of planktonic larvae suffer very high mortalities, the majority of which occur prior to recruitment. Fisheries biologists concerned with fish stock recruitment have, therefore, taken considerable interest in trying to understand the processes governing prerecruit mortality.

The period immediate after hatching is a very dynamic life-history stage of marine fishes and, for most species, it is characterised by a change from lecitotroph to planktotroph nourishment. The transition period from endo- to exogenous feeding has been considered a particularly critical period, since scarcity of food at the time the larvae begin to feed could cause catastrophic mortality. The 'critical period' concept, originally introduced by Hjort (1914), states that the year-class strength of fish is largely determined by larval survival at first feeding and, thus, by the availability of food at that time. Since Hjort's work, much effort has been directed towards the testing of this hypothesis. Most field studies have, however, failed to demonstrate a particularly high mortality rate at the time of yolk resorption. However, due to large sampling variability, neither supporting nor contradictory conclusive evidence for the hypothesis can be drawn from field results to date (see review by May 1974).

Most laboratory studies of fish larvae have revealed that significant growth and survival takes place only at food concentrations 1 to several orders of magnitude

higher than the average found in the sea (e.g. O'Connell & Raymond 1970, Laurence 1974, Werner & Blaxter 1981). This has led scientists to suggest that there is either a massive starvation mortality of young fish larvae and/or that larvae depend on a patchy distribution of food, and that only larvae encountering dense food-patches at first feeding will escape starvation mortality (Hunter & Thomas 1974, Lasker 1975, 1981, Houde & Schekter 1978).

Dealing with first feeding herring larvae, Blaxter & Hempel (1963) introduced the concept of 'point-of-no-return' (PNR), referring to the point in time starving larvae are too weak to feed. For herring larvae they found that the duration to PNR varied with egg size and size of the yolk sac at hatching, ranging from about 8 days for larvae with a little yolk sac (e.g. Baltic stock) to more than 20 days for larvae with a large yolk deposit (e.g. Atlanto-Scandian stock). If the larvae do not encounter sufficiently high densities of food within this period, they are bound to die from starvation.

The present study aims at describing behaviour, feeding and growth of herring larvae in relation to density of prey, and in this paper we are specifically dealing with the period from hatching to initiation of exogenous feeding (see Munk & Kiørboe 1985, and Kiørboe & Munk 1985 for a description of the subsequent period). We focus on the lower threshold density of prey at which herring larvae are able to initiate exogenous feeding prior to PNR and on the timing of first feeding in relation to developmental stage and prey density. Finally, we discuss the ecological significance of the yolk sac stage in herring.

Materials and methods

The larvae used were from 4 different stocks. Eggs and sperm were obtained from running adults caught in Præstø Fjord, western Baltic on April 10, 1983 (experiment 1), Ballantrae Bank, Firth of Clyde on March 14, 1984 (experiment 2), the Limfjord, Denmark on April 9, 1984 (experiment 3) and in the Buchan area on August 29, 1984 (experiment 4). On the collection days eggs from one female were spread on glass slides, fertilised with a mixture of sperm from several males and incubated at 8.0 ± 0.1°C and constant light as described by Munk & Rosenthal (1983). Eggs from the Buchan area were initially incubated at 14°C and on arrival to the laboratory in Charlottenlund at 8°C.

Peak hatching occurs 17-18 days after fertilisation at 8°C (Munk & Rosenthal 1983) and on the evening prior to expected peak hatching, the incubation tank was covered by a lid to stimulate hatching. In experiment 1 we were interested in examining larval development in relation to first feeding and two batches of larvae were used; one batch hatching 15 days after fertilization and the other at peak hatching (18 days). To ensure the required quantity of early hatching larvae, hatching in this case was induced by shutting off the water flow in addition to covering the incubation tank with a lid.

After hatching, the larvae were transferred to 180 l black polyethylene tanks at the stocking densities and the densities of copepod nauplii specified in Table 1. Temperature and salinity of the water were 8.0 ± 0.1°C and 27‰, respectively.

Table 1. Larval herring. Incubation temperature, time of hatching and densities of nauplii and larvae used in the four experimental series.

Experiment	Stock	Incubation temperature, °C	Day of hatching after fertilization, days	Larval density, l^{-1}	Food density, l^{-1}
1	Præstø Fjord (spring)	8	15	5.3	100
1	–	–	–	–	0
1	–	–	18	–	100
1	–	–	–	–	0
2	Clyde (spring)	8	17	4.6	120
2	–	–	–	0.4	30
2	–	–	–	–	7.5
3	Limfjord (spring)	8	18	2.9	120
3	–	–	–	0.6	7.5
4	Buchan (autumn)	8-14	13	1.5	7.5
4	–	–	–	–	7.5
4	–	–	–	–	7.5
4	–	–	–	–	120

Artificial illumination was provided by fluorescent tubes yielding 1000-1300 lux at the water surface. A day length of approximately 15 hours was used in experiments 1, 2 and 4, whereas constant light was (erroneously) applied in experiment 3. Gentle turbulence, created by several jets of water in each tank, ensured a homogeneous distribution of food particles.

Each morning, four water samples (0.5-5 l) for nauplii counts were taken from each tank and nauplii from an *Acartia tonsa* monoculture were added to restore the specified nominal densities. Between feedings, the prey density decreased by more than 75 % in experiments 1 and 3, and by 30-50 % in experiment 2 and 4. The nauplii used were stage III-VI, of approx. weight 0.17 μg, width 70-180 μm (excl. appendages) and length 150-210 μm.

Between 10 and 25 larvae were sampled daily 3-6 hours after food addition. The larvae were gently caught in a tube and immediately transferred to a petri dish, whereafter the water was poured off. Standard length and number of food particles in the gut were recorded. The larvae were then rinsed in distilled water, dried at 55 °C for 24 hours, stored in a dessicator and weighed on a Cahn electrobalance within a month. Yolk sacs of some of the larvae in experiments 1, 2 and 4 were dissected away prior to weighing.

To compare larval feeding behaviour for experienced and unexperienced larvae, half the larvae in experiment 1 were allowed to starve. Daily, approximately 50 larvae were gently transferred to tanks containing 100 copepod nauplii per liter. After a 4-hour feeding period the larvae were collected and immediately examined for stomach contents. Standard length and mouth size were measured. The dimension used for the size of mouth was the jaw width. The larvae were placed ventral side up and the width of jaw at the point of articulation was measured.

Observations on larval behaviour were carried out on Clyde larvae exposed to different food densities (experiment 2) using the technique described by Munk & Kiørboe (1985). Swimming activity and attack rate were registered 2-4 times per day in each tank in periods of 10-20 minutes. To calculate attack success at first feeding, 30 feeding attacks were followed up by visual examination of the larval forgut for swallowed nauplii.

Results

Swimming activity and feeding behaviour

During the first days after hatching, the larvae were relatively inactive, swimming for only 35-40 % of the time (Fig. 1a). Swimming in the newly hatched larvae was intermittent, with swimming periods of average 0.8 sec. duration alternating with periods of about 1.5 sec. duration in which the larvae rested in the water. During resting periods, the larvae slowly sink in the water column. At this salinity, inactive yolk sac larvae sink at a rate between 0.55 and 0.35 cm · sec.$^{-1}$ (Blaxter & Erhlich 1974). Thus, swimming activity at this developmental stage prior to initiation of exogenous feeding, can be interpreted as a means of avoiding sedimentation out of the water column, and the activity percentage (35-40 %) is similar to the minimum activity found by Munk & Kiørboe (1985) for older larvae.

At an age of between 5 and 7 days, the swimming activity of Clyde herring larvae increased abruptly to 45-55 %, coinciding with the onset of external feeding for larvae at the high nauplii densities (see below and Fig. 2a). This activity pattern was, however, also observed at the low prey density, where significant feeding did not take place until days 8-10 (see below and Fig. 2a). Thus, the change in swimming activity was not a consequence of exogenous feeding but probably governed by internal stimuli. The effect of increasing the swimming activity at the time of

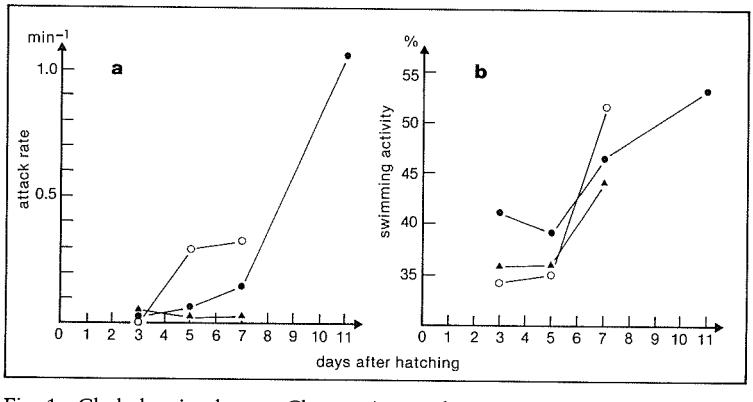

Fig. 1. Clyde herring larvae. Changes in attack rate (a) and swimming activity (b) during the posthatching period. Points represent mean values of observations made during 2 days. ▲ = 7.5 nauplii · l^{-1}; ○ = 30 nauplii · l^{-1}; ● = 120 nauplii · l^{-1}.

first feeding is obvious, since the volume of water searched for potential food particles will increase accordingly.

The prey catching behaviour of feeding herring larvae can be described as follows: when sighting a prey object the larva bends its body into an S-shaped aiming position and subsequently darts forward by straightening the body. Not all aiming positions are followed by attacks and not all attacks are successful. Even prior to first successful feeding, larvae were now and then seen in aiming positions and some of these positions were followed by attacks. The attack rate of Clyde herring larvae was, however, low during the first 3 days after hatching (Fig. 1b). During days 3-7 after hatching, the attack rate increased at the high prey densities, reaching about 1 attack · min^{-1} 11 days after hatching at 120 nauplii · l^{-1}. At this prey density, the attack success (percentage of attacks leading to capture) was 40% one day after initiation of feeding. The attack rate of larvae at 7.5 nauplii · l^{-1} was still very low 7 days after hatching (Fig. 1b).

Feeding incidence in relation to age and prey density

The variation recorded above in attack rate of Clyde herring larvae was closely related to variation in feeding incidence (the percentage of larvae that had initiated exogenous feeding) (Fig. 2a). Exogenous feeding had already commenced at the highest prey densities (30 and 120 nauplii · l^{-1}) on day 4 when observations on gut contents were begun. Feeding incidence subsequently rapidly increased, by day 6 to more than 70%. Clyde herring larvae were also able to initiate external feeding at the low prey density (7.5 nauplii · l^{-1}) although first feeding was delayed by 3-4 days. For Limfjord larvae (Fig. 2b) and Buchan larvae (Fig. 2c) the same general pattern emerged: At the high prey density, Limfjord larvae had initiated external feeding on day 3 when the observations started and first feeding Buchan larvae were also observed on day 3. Thereupon, feeding incidence increased to more than 90% at day 6 in Buchan larvae and 100% at day 5 in Limfjord larvae. Larvae from

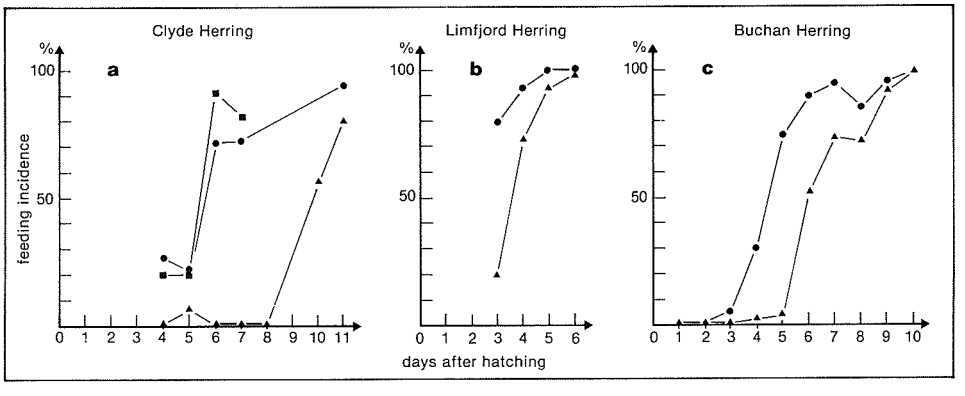

Fig. 2. Larval herring. The change in feeding incidence (percentage of larvae with food in the gut) at different food densities and for different herring stocks. a: Clyde; b: Limfjord; c: Buchan. ▲ = 7.5 nauplii · l^{-1}; ■ = 30 nauplii · l^{-1}; ● = 120 nauplii · l^{-1}. For Buchan larvae at 7.5 nauplii · l^{-1} points represents means of three replicates.

both of these two stocks were also able to initiate first feeding at the low prey density (7.5) but again external feeding was somewhat delayed: by 2-3 days in Buchan larvae and 1-2 days in Limfjord larvae in comparison to the larvae held at the highest prey densities. At the high prey densities, Clyde larvae initiated feeding while there was still significant amounts of yolk left (Fig. 3a), whereas the yolk reserves had been totally exhausted at the low prey density before first feeding took place. In the Buchan and Limfjord larvae, all yolk had been used prior to first feeding, both at 120 and 7.5 nauplii $\cdot l^{-1}$. Data on feeding incidence for all stocks are summarized in Table 2, where size at hatching, relative size of yolk sac and age at 50% feeding incidence are shown. Larval weight at hatching and both relative and absolute size of yolk reserves decrease in the order Clyde–Buchan–Limfjord–Præstø. The general trend is that the smallest larvae commenced exogenous feeding first and had the shortest delay of first feeding at the lowest compared to the highest prey density.

Changes in larval weight during the first feeding period

Changes in larval weight during the first feeding period are shown in Fig. 3. From hatching to the end of the yolk sac stage, there was a steady decrease of total prolarval weight representing respirative losses due to basic metabolism, activity and conversion of yolk to tissue. For Præstø, Buchan and Clyde larvae, gross efficiencies of yolk to tissue conversion during the yolk sac period of 52-59%, 53% and 67%, respectively can be calculated (increase in weight of larval tissue during yolk sac period/decrease in weight of yolk sac $\times$ 100%). From the onset of external feeding, larvae at the highest prey densities (120 nauplii $\cdot l^{-1}$) increased their

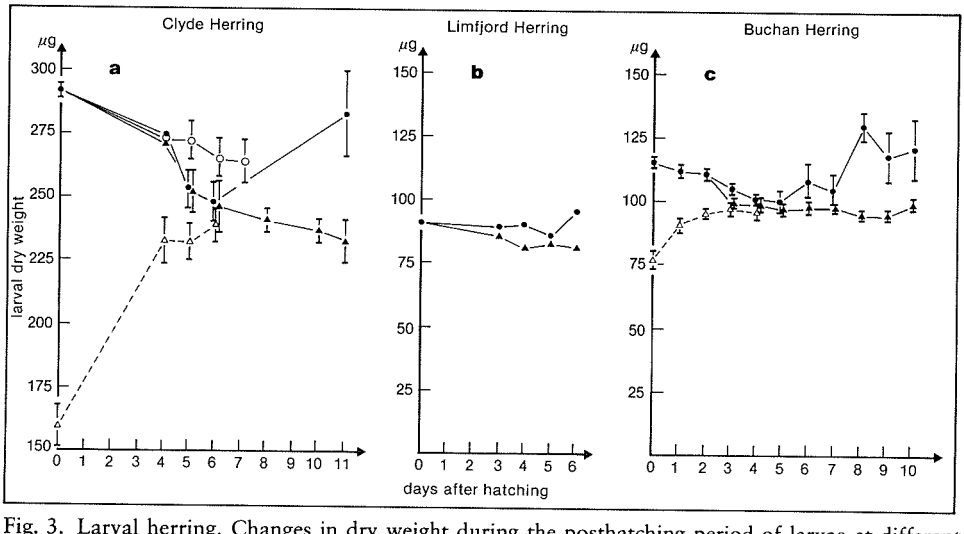

Fig. 3. Larval herring. Changes in dry weight during the posthatching period of larvae at different food densities and for different herring stocks. a: Clyde; b: Limfjord; c: Buchan. ▲ = 7.5 nauplii $\cdot l^{-1}$; ○ = 30 nauplii $\cdot l^{-1}$; ● = 120 nauplii $\cdot l^{-1}$. Points represent average values, bars 95% confidence limits. For Buchan larvae at 7.5 nauplii $\cdot l^{-1}$ data from three replicates are pooled. Broken lines = weight of larva; full lines = total prolarval weight (incl. yolk).

weights. Since the present investigation covered only the first feeding period, the experiments were terminated too early to ascertain whether Clyde and Limfjord herring larvae would eventually gain weight at the lowest prey densities. This was possible only for the Buchan larvae, where there was a slight increase in weight during the end of the period (Fig. 3c). The increase was statistically significant ($p<5\%$) for one of the three replicates.

Significance of visual experience for initiation of exogenous feeding

To decide whether or not prior exposure to potential prey organisms influences the timing of first feeding, feeding incidence of visually experienced and unexperienced larvae were compared. Data from larvae hatched from the same batch of eggs, but at two different points in time (15 and 18 days after fertilisation, respectively) were utilized (Fig. 4a). The initial response in feeding incidence was similar

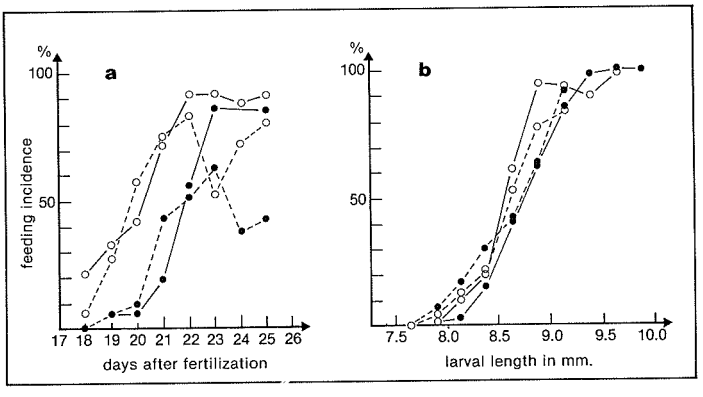

Fig. 4. Larval herring. Præstø stock. Changes in feeding incidence for early (○) and late hatchers (●) as a function of age (a) or length (b). Broken line: unexperienced larvae; full line: experienced larvae.

for experienced and unexperienced larvae in both groups. However, feeding incidence tended to decrease with time in the unfed groups, in particular in the last hatching group. This is due to starvation and approach of PNR in the unfed groups, and cannot be ascribed to lack of experience. It is, therefore, concluded that visual experience has no effect on the timing of first feeding.

Timing of first feeding in relation to developmental stage

The experiments presented in Fig. 4a were also designed to give an impression of the effect of developmental stage on the timing of first feeding. The larvae used to compile Fig. 4 were of similar age relative to time after fertilization. However, the early hatchers hatched at a comparatively less developed stage and were smaller in size with larger yolk reserves than the late hatchers (see Table 2). The three day delay in hatching time was accompanied by a delay of about two days in the initiation of exogenous feeding (Fig. 4a). Since there was no effect of visual experience, this indicates that different degrees of maturation may be the cause of the

Table 2. Larval herring. Weight at hatching, % yolk of total prolarval weight at hatching, days after hatching of 50 % feeding incidence (FI) at 120 and 7.5 nauplii $\cdot l^{-1}$ and delay of feeding at low vs. high prey density.

Stock	Weight at hatching, μg	Yolk, %	50 % FI 120 n $\cdot l^{-1}$, days	50 % FI 7.5 n $\cdot l^{-1}$, days	Delay, days
Clyde	291.2	45	5.5	10	4.5
Buchan	115.0	33	4.5	6.5	2
Limfjord	91.0	nd	<3	3.5	1[b]
Præstø Fjord, 15 d	91.7	22	4.5[a]	nd	nd
Præstø Fjord, 18 d	84.0	9	3.5[a]	nd	nd

a, determined at 100 nauplii $\cdot l^{-1}$
b, at 80 % feeding incidence
nd, not determined

delayed feeding. Replotting the feeding incidence data in Fig. 4a relative to larval length rather than age removes the differences between the groups (Fig. 4b). For larvae of this stock 50 % feeding incidence takes place at a larval length of about 8.6 mm, indicating that the developmental stage at which first feeding takes place can be related to larval length, even though larval length *per se* may be of minor importance. The mouth size was directly related to length, and the average jaw size at 50 % feeding incidence was 0.35 mm.

Discussion

The timing of first feeding depends on the developmental stage of the larvae and on the availability and abundance of potential food organisms.

Prey density

The preferred food of young herring larvae is copepod nauplii (Checkley 1982). The concentration of copepod nauplii in the Buchan area in mid September 1984, at the centre of a patch of first feeding herring larvae was about 10-20 nauplii $\cdot l^{-1}$ (preliminary, unpublished data). In general, the concentration of copepod nauplii in open and partially closed seas is in the range of 5-80 nauplii per liter, whereas concentrations in fjords and sheltered bays may exceed several hundreds per liter (see data in Laurence 1982). The present experiments have shown that herring larvae of all the stocks examined were able to initiate exogenous feeding even in the lower range of food densities experienced in their natural habitats and that the magnitude of the delay in timing at the low prey density was well within the time available prior to PNR (Table 2).

After first feeding, larvae at the highest prey density gained weight and this was also the case for the Buchan larvae at the lowest prey density, even though the growth rate was much lower. This is in accordance with the findings of Kiørboe & Munk (1985) for slightly older herring larvae. The conclusion that herring larvae are able to initiate feeding and subsequently grow at food concentrations in the

lower range of what they experience in the sea, has also been arrived at from experiments in large, predator-free enclosures (e.g. Øistad & Moksness 1981, Gamble *et al.* 1981, Paulsen *et al.* 1983, Gamble 1984). In contrast to these experiments, however, a homogeneous distribution of food particles was ensured in our study by the application of a gentle mixing of the water column in the experimental tanks. It is, therefore, not necessary to postulate extraordinarily high densities of prey organisms or a patchy distribution of food in the sea in order for herring larvae to escape massive starvation mortality.

In addition to a direct influence on larval mortality due to starvation, food density can interfere with survival through its influence on larval growth. A lowering of the food density results in retardation of the growth rate (Fig. 3a-c). This will prolong the duration of the larval stage and thus increase the total mortality experienced during this stage.

The same picture may, however, be drawn for older larvae, (Kiørboe & Munk 1985) and is consequently not a special feature of first feeding larvae. In conclusion then, none of our observations support the expectation of a particularly high mortality rate or a particularly 'critical period' at the time of yolk resorption in larval herring.

Developmental stage

Herring larvae hatch at a relatively advanced developmental stage with apparently functional eyes (pigmented), jaws and guts. However, even when offered a plentyful food supply, they do not initiate external feeding until 2-6 days after hatching, slightly before or at the time of yolk sac resorption (Table 2). This developmental stage can be described by larval length (Fig. 4b), which is probably indicative of the motoric performance of the larvae, since swimming ability/activity increases abruptly at the time of first feeding (Fig. 1a). At first feeding, the attack success is quite low, 40 % in Clyde herring larvae, but in the upper range of success estimates of first feeding herring larvae hitherto reported (e.g. Rosenthal & Hempel 1970: 10-40 %; Blaxter & Staines 1971: 5 %). At a larval age of 10-15 days, attack success increases to 60-75 % for the stocks here considered (Munk & Kiørboe 1985). The initial low and subsequently increasing attack success, likewise, indicates that additional maturation of nervous coordination or control takes place after hatching and prior to first feeding. In addition, the digestive system develops until first feeding. During the last few days of the incubation period and, in particular, during the first days following hatching, the embryo/prolarva synthesize the digestive enzyme trypsin, and the amount of the larval enzyme peaks at the time of the first feeding (B.H. Pedersen and K. Hjelmeland, pers. comm.). Thus, in spite of the apparent advanced developmental stage at hatching, herring larvae are not able to initiate exogenous feeding until motoric performance, nervous control and digestive capability have been more fully matured.

The ecological significance of the yolk sac stage

Herring larvae apparently obtain no advantage through visual experience during the yolk sac stage and are not able to initiate exogenous feeding until some matura-

tion has taken place, i.e. around the time of yolk sac absorption: What, then, is the ecological significance of the yolk sac stage, and how is the striking between-stock variation in egg size and yolk sac size at hatching to be understood?

Egg size in the different herring spawning stocks of the North Sea varies by a factor of about 3 (e.g. Blaxter & Hempel 1963, Zijstra 1973). Zijstra (1973) and others have considered the factors controlling egg size and concluded that egg size is, to a large extent, genetically fixed rather than under the influence of environmental factors such as food supply in the nursery grounds of the adult stock. In addition, the total energy investment in eggs (gonads) for a herring of a given size is relatively constant between stocks (Ware 1980, Sinclair & Tremblay 1984). Variation in egg size must, therefore, be interpreted in the light of the environmental conditions encountered by the newly hatched larvae and the optimal egg size considered as the compromise between maximum numbers of offspring (decrease with egg size) and maximum survival of larvae (assumed to increase with egg size).

Larval size at hatching varies according to egg size but not to the same extent, since larger larvae also hatch with a relatively larger yolk sac (Blaxter & Hempel 1963). The relative size of the yolk sac, thus, varies by a factor of about 7 between herring stocks, constituting between 10 and 70 % of total prolarval weight (Blaxter & Hempel 1963, Elridge *et al.* 1977, present study). This variation becomes even more striking when compared to the constancy of yolk sac size in species with pelagic eggs (e.g. pacific sardine: 70 % yolk at hatching, Lasker 1962; sole: 63 %, Flüchter & Pandian 1968; tautog: 65 %, Laurence 1973; Southern pigfish: 58 %, Robertson 1974; yellowtail flounder: 73 %, Howell 1980) and has prompted considerable speculation as to the adaptive significance of the yolk deposit and the spawning strategy of herring (e.g. Blaxter & Hempel 1963, Hempel 1965, Hempel & Blaxter 1967, Mann & Mills 1979, Sinclair & Tremblay 1984).

The most widely accepted suggestion is that a large yolk supply of the newly hatched larva increases the time to PNR, and is, therefore, an adaptation to a harsh environment and a poor food supply in the larval nursery area. This is supported by the general tendency in the North Sea of winter and spring (i.e. in periods of low food availability) spawned eggs to be larger than eggs spawned during autumn (Blaxter & Hempel 1963, Hempel 1965, Hempel & Blaxter 1967).

In light of results from this study, this explanation seems unlikely. The larvae do not feed during the yolk sac stage, and the time from yolk resorption to PNR is similar for large and small sized herring larvae (e.g. 6 days in the large sized Clyde herring larvae and 5 days in the much smaller Blatic larvae; Blaxter & Hempel 1963). The only potential advantage of large relative to small larvae in a food deprived environment is that they, due to a better swimming performance, may search a larger volume of water for food. This does not, however, explain the variation in yolk sac size between herring stocks or the ecological significance of having a yolk sac at all.

A more likely explanation of the ecological significance of the yolk sac stage is that the yolk reserve allows the larvae to be transported from the hatching to the feeding area, in cases where these do not coincide, and that variation in size of the

yolk sac may be related to the distance or transportation time between these two.

The herring spawns its eggs demersally and only certain areas are suitable as spawning grounds. Herring normally spawn on gravel and sand bottoms (de Groot 1980) where the water currents/movements are strong enough to ensure a sufficient supply of oxygen to the eggs. There are, therefore, certain limits to the choice of the spawning ground that are independent of the demands to the food supply of the subsequently hatching larvae. Thus, in tidal areas, herring seem to spawn in the tidally energetic, mixed zone rather than in the transition zone between mixed and stratified water (Iles & Sinclair 1982, Sinclair & Tremblay 1984), even though food abundance in the transitional zone is apparently much higher than in the mixed zone (e.g. Flodgate *et al.* 1981, Dagg & Turner 1982, Richardson *et al.* 1984). Transportation of herring larvae to the richer transitional zone subsequent to hatching in the mixed zone has been observed in the area to the west of the Outer Hebrides (Mike Heath, pers. comm.). There is not much supporting evidence for a relation between yolk sac size and transportation time. It is, however, striking that populations spawning in shallow, sheltered fjords, where spawning and larval feeding grounds coincide, invariably have very small eggs and yolk deposits at hatching (e.g. Blaxter & Hempel 1963, Hempel & Blaxter 1967; see also Table 2), whereas populations spawning in tidal areas, where this may not be the rule, all have larger yolk sacs. In conclusion, then, the function of the yolk deposits in larval herring is therefore to allow transportation of the larvae from hatching to nursery ground, rather than to prolong the period available for initiation of exogenous feeding.

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