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Effects of a transitory, low food supply in the early life of larval herring (*Clupea harengus*) on mortality, growth and digestive capacity

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Abstract. In order to assess possible effects of a transitory, low food supply on later development, three groups of Clyde herring larvae (*Clupea harengus* L.) were exposed in 1989 to different feeding regimes immediately after yolk resorption. Group 1 received a high daily ration of 80 copepods larvae^{-1} for 31 d, Group 2 a low daily ration of 15 copepods larva^{-1} for 10 d followed by a high ration (80 copepods larva^{-1}) for 21 d and Group 3 a low ration of 15 to 20 copepods larva^{-1} for 31 d. After 31 d of feeding, digestive capacity, expressed as the sum of trypsin and trypsinogen, was markedly reduced in Group 2 compared to Group 1, while Group 3 had an even lower digestive capacity. After the switch from low to high ration Group 2 exhibited compensatory growth and caught up with Group 1 both in standard length and content of soluble protein. Group 3 had the lowest growth rates. Mortality was equal in Groups 1 and 2, while Group 3 showed an excess mortality of 40% of the start population. Although Group 2 larvae had caught up with Group 1 in growth at the end of the study, content of trypsin and trypsinogen in Group 2 was only half of that found in Group 1. Thus, comparing effects of a short period of food limitation on future growth, mortality and content of digestive enzymes, the study indicates content of trypsin and trypsinogen to be the most sensitive variable for detection of food limitation in the early stages of exogenous feeding.

Introduction

Since Hjort (1914) introduced the concept of the "critical period" in the early post-yolk-sac life of marine fish larvae, much effort has been directed towards diagnosing starving from non-starving larvae in several species of marine fish. Morphological, histological and chemical studies revealed that starvation led to structural degeneration of organ systems such as gut and liver (Ehrlich et al. 1976), musculature and pancreas (O'Connell 1976), and biochemically to immediate mobilization of protein, from which energy was mainly derived (Ehrlich 1974). Recently, content of trypsinogen in the pancreas and of trypsin in the intenstine has been used to monitor ontogenetic changes as well as effects of starvation or food limitation on pancreatic function in larval herring (Pedersen et al. 1987, Hjelmeland et al. 1988, Pedersen and Hjelmeland 1988). Also trypsin-like activity was used as indicator of nutritional status in larvae of turbot and herring (Ueberschär 1988).

The aim of the present study was to assess whether or not a transitory period of food limitation, as opposed to total starvation, during the "critical period" would have effects on later development in larval herring. The criteria used to detect possible adverse effects of a short period of low ration were changes in mortality, growth (length and content of soluble protein) and amount of trypsin and trypsinogen relative to these parameters in larvae offered a constant high or low ration.

Materials and methods

Herring

Eggs from one female Clyde herring (*Clupea harengus* L.) were artificially fertilized with sperm from several males and incubated at ca 7 °C until hatching was induced 20 d after fertilization as previously described (Pedersen et al. 1987). A total of 1005 newly hatched larvae were transferred to three experimental tanks (3 × 335 fish) of 50 l. The water temperature was ca 8.5 °C (Table 1), salinity was 30.2‰, and the light period was 15 h, light intensity at the water surface being 30μE m^{-2} s^{-1}. Nauplii of the copepod *Acartia tonsa* were added to the tanks 4 d after hatching, when yolk absorption was almost complete, and the fish immediately started to feed. From the time of first exogenous feeding (Day 4) larvae in each tank were subjected to a specific feeding regime (Table 1). Group 1 was offered a high daily ration, i.e. 60 copepods larva^{-1} Days 4 to 6, rising to 80 copepods larva^{-1} Days 7 to 35. Group 2 was exposed to a low daily ration of 15 copepods larva^{-1} during the first 10 d of exogenous feeding (Days 4 to 13) and was then switched to a high ration (80 copepods larva^{-1}) Days 14 to 35. Group 3 was maintained at 15 to 20 copepods larva^{-1} throughout the experiment.

Cultivated *Acartia tonsa* were fed *Rhodomonas* sp., filtered (45 μm mesh), and cooled before being offered to herring. Larvae

Table 1. *Clupea harengus.* Rearing conditions for three groups of larvae

	Ration (no. copepods fish^{-1} d^{-1})	Period post-hatching	Temp. (°C)
Group 1	80	4–35	8.6 (SD 0.4)
Group 2	15	4–13	8.5 (SD 0.5)
	80	14–35	
Group 3	15	4–24	8.4 (SD 0.5)
	20	25–35	

Table 2. *Clupea harengus. A*: Mean prey density (copepods l^{-1}) after food addition. With constant ration, samplings of larvae decrease prey concentration. Days 4 to 13 is the low ration period of Group 2, and the last two periods each contain two samplings. *B*: Mean amount of uningested prey (copepods l^{-1}) before food addition. Periodicity is adjusted according to occurrence of high amounts of uneaten prey in Groups 1 and 2

Period (d post-hatching)	Group 1	Group 2	Group 3
A			
4–13	441	92	89
14–25	434	450	77
26–34	313	330	48
B			
5–14	27	3	5
15–23	65	154	4
24–34	2	7	4

were offered nauplii during the first week of exogenous feeding followed by varying mixtures of nauplii and young copepodites. Daily food additions were based on prey number in fish tanks prior to addition (following gentle horizontal mixing, subsamples totalling 1 l were taken vertically through the water column at 20 random positions) and on estimates of number of fish in each tank (number of fish stocked in tank minus number of sampled or dead fish). Mean food densities after adjustment are given in Table 2 A. Low amounts of food were generally left in tanks prior to daily adjustment of prey number. Except for periods mentioned below, the daily amount of uneaten prey was a few copepods l^{-1}. However, during the start of exogenous feeding (Days 5 to 14) Group 1 was unable to ingest all of the offered prey (Table 2 B). Also, from Day 15 to 23, which includes a period with water quality problems, appetite was reduced in Groups 1 and 2, but more so in Group 2 (Table 2 B), in which mean, daily amount of uningested prey constituted ca ⅓ of the offered ration.

Water exchange in fish tanks occurred only during prey adjustments. On Day 16, however, bottom water in all tanks smelled, and corrective procedures were taken, i.e. immediate exchange of ca ¼ of the water volume followed by daily, vigorous bottom cleaning. Water quality problems could no longer be detected from Day 20 onwards.

Sampling

Both at hatching and at first exogenous feeding (Day 4), five larvae from each tank were sampled for individual determination of live standard length, soluble protein content and content of the sum of trypsin and trypsinogen. Subsequently, on Days 14, 21, 26, 29 and 35 after hatching, 15 fish from each tank were sampled for analysis. Fish were caught individually, pipetted onto a cellophane-covered glass slide, and the surrounding seawater removed with a pointed capillary tube. Live standard length was measured using an ocular micrometer. The cellophane was cut, leaving the fish on a strip which was transferred to an Eppendorf tube. Samples were frozen and stored at −30 °C until analysis for content of enzyme and water soluble protein. Samples for quantification of enzyme and water soluble larval protein were prepared by adding 600 µl of phosphate buffered saline to each Eppendorf tube. The sample was then homogenized with a Branson sonifier B-12 and the homogenate divided into equal volumes in two vials and frozen.

Content of trypsin and trypsinogen in individual herring larvae was analyzed by a trypsin radioimmunoassay in which the anti-herring-trypsin antibody reacted with both the pancreatic form (trypsinogen) and the intestinal form (trypsin) of the enzyme (Hjelmeland and Jørgensen 1985). The linear range of the radioimmunoassay standard curve was 0.3 to 30 ng trypsin. For measurements of water soluble protein, vials of thawed, sonicated larvae were subjected to Vortex mixing and centrifuged at $10\,000 \times g$ for 10 min. Soluble protein in the supernatant was determined according to Bradford (1976) by the macromethod of the Bio-Rad protein assay kit (Bio-Rad Laboratories). Bovine serum albumin was used as standard. Means of distributions (length, protein and enzyme content, respectively) were compared by Student's *t*-test (equal variances) or by Welch's approximative *t*-method (unequal variances). The null hypothesis (H_0: $\mu_A = \mu_B$) was rejected at the 0.05 level.

Results

Content of trypsin and trypsinogen in larval *Clupea harengus*

Enzyme content (Fig. 1) rose six-fold during the yolk sac stage (Days 0 to 4). At hatching and at first feeding (Day 4), respectively, enzyme content did not differ significantly between tanks. From Day 4 to 14 a significant decline in enzyme content was observed in all groups. On Day 21 Group 1 had increased in enzyme to a level not different from the content on Day 4, and it contained significantly ($p < 0.001$) more trypsin and trypsinogen than Groups 2 and 3.

It is noteworthy that Group 2 did not increase its enzyme content during the start of the high ration period (Days 14 to 21).

On Day 26, the enzyme content of Group 1 exceeded that of Group 2 ($0.01 > p > 0.001$), which in turn had a higher level of trypsin and trypsinogen ($p < 0.001$) than Group 3. The same ranking of mean enzyme content (Group 1 > Group 2 > Group 3) was apparent on Day 29. However, mean enzyme level in Group 1 did not significantly differ from mean enzyme content in Group 2, whereas Group 3 had a significantly lower enzyme content than the two other groups ($0.05 > p > 0.02$ and $p < 0.001$ compared to Group 2 and 1, respectively).

On Day 35, Group 1 exhibited an enzyme content almost twice as high ($p < 0.001$) as that of Group 2. Both Group 1 ($p < 0.001$) and Group 2 ($0.01 > p > 0.001$) had increased their content of enzyme relative to the level at first exogenous feeding (Day 4). Group 3 had the lowest ($p < 0.001$) enzyme content on Day 35, and had lost enzyme ($p < 0.001$) compared to Day 4.

Larval standard length

Live standard lengths are shown in Fig. 2. Significant growth was observed during the yolk sac stage. From

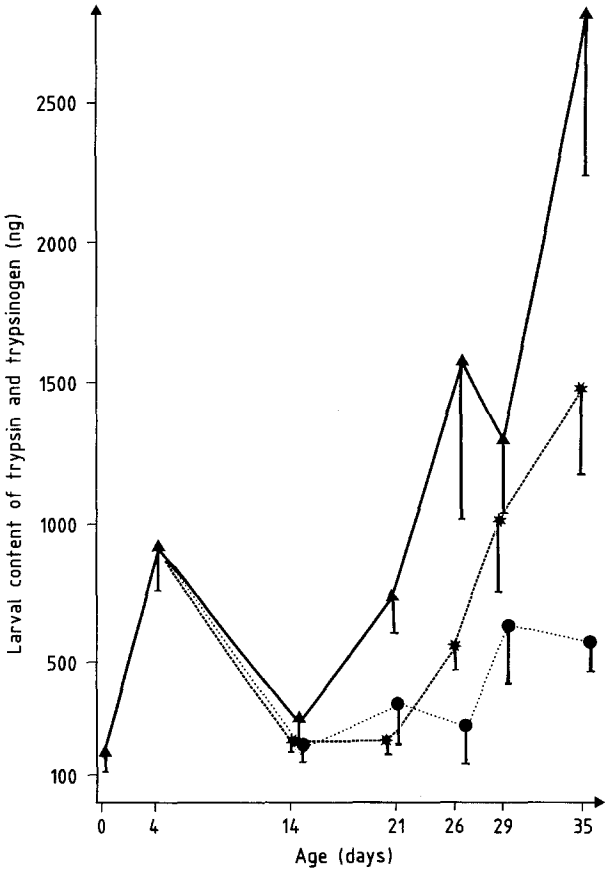

Fig. 1. *Clupea harengus.* Sum of trypsin and trypsinogen (mean −95% CL) versus days after hatching for larvae exposed to different feedings regimes. Group 1: high ration (▲——▲), Group 2: low and high ration (*-------*), Group 3: low ration (●·····●)

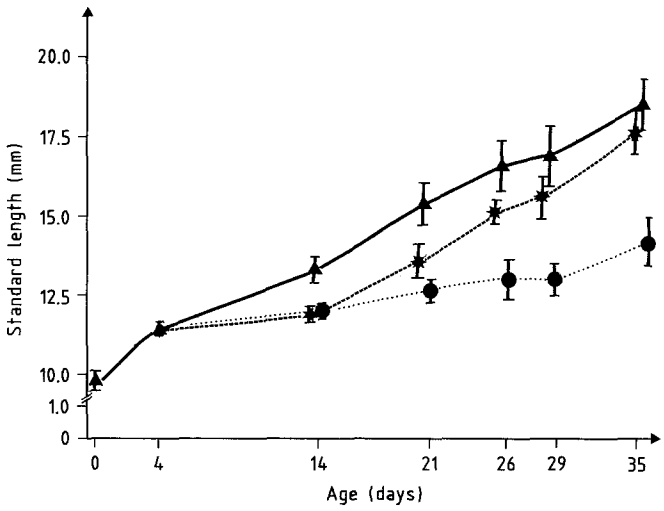

Fig. 2. *Clupea harengus.* Live standard length (mean ±95% CL) for larvae exposed to different feeding regimes. See Fig. 1 for further details

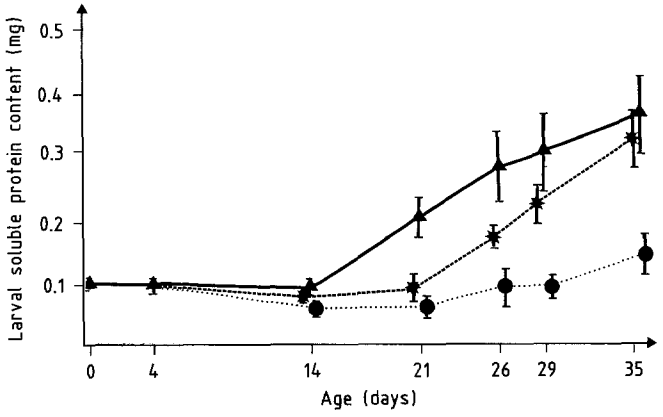

Fig. 3. *Clupea harengus.* Content of soluble protein (mean ±95% CL) of larvae exposed to different feeding regimes. See Fig. 1 for further details

Day 4 to 14, all groups increased in length ($p<0.01$). On Day 14, Group 1 was longer ($p<0.001$) than the two low ration groups, which did not differ in length. During the first high ration period in Group 2 (Days 14 to 21) all groups significantly ($p<0.01$) increased in length. On Days 21, 26 and 29 Group 1 was longer ($p<0.001$, $0.01>p>0.001$ and $0.02>p>0.01$, respectively) than Group 2, which in turn had increased in length ($p<0.01$) relative to the low ration Group 3. At the end of the experiment (Day 35), mean length did not differ significantly between Groups 1 and 2, whereas Group 3 exhibited a significantly ($p<0.001$) shorter length. During the whole period of exogenous feeding (Days 4 to 35), all three larval groups increased in mean length. Mean growth rates of the three groups are shown in Table 3. Growth rates from the end of the yolk sac stage to Day 35 were approximately twice as high in Groups 1 and 2 as in the survivors of the low ration Group 3. In Group 2, mean growth rate increased about seven times from the low ration to the high ration period.

Table 3. *Clupea harengus.* Larval growth rates. Numbers in parentheses are the highest growth rates observed during compensatory growth in Group 2 from Day 21 to 35

Period (d)	Group	Growth rate (mm d^{-1})	Growth rate (μg protein d^{-1})
4–35	1	0.23	8.52
	2	0.20	7.23
	3	0.09	1.42
4–14	1	0.18	−0.60
	2	0.04	−1.60
	3	0.06	−3.60
14–35	1	0.25	12.86
	2	0.27 (0.29)	11.43 (16.43)
	3	0.10	3.81

Larval content of soluble protein

Larval content of soluble protein as a function of age and feeding regime is shown in Fig. 3. At hatching and at first feeding (Day 4), respectively, there was no difference in larval protein content between tanks. From Day 4 to 14, larval protein content in the low ration Groups 2 and 3 decreased ($p<0.001$), while the high ration Group 1 had a protein level which did not differ significantly from the content on Day 4. During the first week of high ration

Table 4. *Clupea harengus*. Number of live fish at hatching and at the end of the experiment for each group

	Hatching	Day 35	
		Actual	Nominal
Group 1	335	166	157
Group 2	335	162	173
Group 3	335	40	79

(Days 14 to 21) Group 2 did not significantly increase its protein content, and neither did Group 3. Group 1, however, significantly increased ($p<0.001$) in protein during this period. On Days 21, 26 and 29 Group 1 had a higher protein content than Group 2 ($p<0.001$, $p<0.001$ and $0.02>p>0.01$, respectively), which in turn exceeded the protein level of Group 3 ($0.05>p>0.02$, $p<0.001$ and $p<0.001$, respectively). On Day 35, however, there was no significant difference in protein content between Groups 1 and 2, while Group 3 contained significantly ($p<0.001$) less protein than the other groups.

During the whole period of exogenous feeding (Days 4 to 35) all three groups of fish had increased in protein content, Group 1 almost four times (no overlap), Group 2 more than three times (no overlap) and Group 3 almost one and a half times ($0.01>p>0.001$). Mean protein growth rates are shown in Table 3. Growth rates from Day 4 to 35 were ca six times faster in Groups 1 and 2 compared to Group 3. Mean growth rate in Group 2 rose ca eight-fold from the period of low ration (Days 4 to 14) to the period of high ration (Days 14 to 35).

Specific content of trypsin and trypsinogen

From hatching to Day 14, when larval protein content was low and stabile (Fig. 3), specific enzyme content (μg trypsin + trypsinogen mg^{-1} soluble protein) oscillated as did enzyme content (Fig. 1). Peak specific enzyme content, ca 10 $\mu g\ mg^{-1}$, was observed on Day 4 followed by a decline to ca 3 $\mu g\ mg^{-1}$ on Day 14. The specific enzyme content on Day 35 in Group 1 was 8 $\mu g\ mg^{-1}$, as compared to 4.5 $\mu g\ mg^{-1}$ in Groups 2 and 3.

Survival

Table 4 shows the number of larvae at stocking and the number of fish left after the final sampling on Day 35. Survival in Groups 1 and 2 was almost identical, while Group 3 exhibited a mortality in excess of that of the other groups of ca 125 larvae, corresponding to ca 40% of the initial population. Table 4 also gives the number of larvae believed to be alive in each tank on Day 35, i.e. the nominal number of surviving fish. Nominal and actual numbers were close for Groups 1 and 2. In Group 3, however, the nominal number used for food adjustments was twice the actual number of surviving fish. Therefore, rations provided to the survivors in Group 3 were higher than intended. A consequence of this may be the tendency in Group 3 to increase in length, protein and enzyme content towards the end of the experiment.

Discussion

Enzyme content in *Clupea harengus*

In the present study effects of unfavourable food conditions during the first 10 d of exogenous feeding could be traced by measurements of trypsin and trypsinogen during the following 3 wk. From Day 14 onwards, Groups 2 and 3 exhibited a lower enzyme content than Group 1, and although Group 2 gradually increased its enzyme content to a level higher than found in Group 3, Group 2 only reached an enzyme level half of that seen in Group 1 at the end of the experiment. As Group 2 at that time had caught up with Group 1 in growth, unfavourable feeding conditions in the early life history of herring larvae seem to be reflected more clearly in enzyme measurements than in conventional growth parameters.

During early life, in the yolk sac stage, a sharp increase in content of trypsin and trypsinogen has previously been demonstrated in other stocks of herring larvae (Pedersen et al. 1987). During this phase enzyme synthesis is rapid and enzyme secretion presumably negligible. In the present study larval trypsinogen synthesis averaged at least 200 ng d^{-1} in the yolk sac period bringing trypsinogen content up to 1% of larval soluble protein. At the start of exogenous feeding enzyme content decreased irrespective of feeding regime. This food-independent fall in enzyme confirms earlier findings in other stocks of larval herring (Pedersen et al. 1987) and in larval cod (Hjelmeland et al. 1984), and seems to be a consequence of a programmed development.

In the period following the food-independent fall in content of trypsin and trypsinogen, the present study shows ration-dependent differences in enzyme content between Groups 1 and 3 from Day 14 onwards. In a previous study (Pedersen et al. 1987) herring larvae reared at two constant prey densities exhibited a prey-density-dependent rise in content of trypsin and trypsinogen in the period from Day 13 to 24 after hatching. At least two explanations may be suggested for such food-dependent differences in enzyme content. First, Giorgi et al. (1985) have shown that trypsin-like enzyme activities and amounts of trypsinogen-mRNA rose with increasing protein intake in rat. Hence, the rate of trypsinogen synthesis in fish larvae might be directly correlated to ration-dependent amounts of mRNA for trypsinogen. Second, degenerative processes due to starvation decreased content of pancreatic enzyme granules in fish (Umeda and Ochiai 1975, O'Connell 1976), a process which would cause a reduction in available trypsinogen.

An apparent latency period for induction of protein synthesis was indicated during the first week of high ration (Days 14 to 21) in Group 2, as neither content of enzyme nor of soluble protein rose significantly. However, the lack of response in protein synthesis to larval exposure to a higher ration may have been caused by the

deteriorating water quality, as the larvae did not eat up their full ration in the period from Day 15 to 23 (Table 2 B). If the apparent latency period was due to the transitorily, decreased water quality it is the only detectable consequence thereof, as protein synthesis from Day 21 onwards was extremely high and resulted in catch-up growth in Group 2 (see below). Neither was mortality in Group 2 larvae negatively affected.

Growth

In the Buchan area (northwestern North Sea), larval growth rates ranged between 0.13 to 0.24 mm d^{-1} (Kiørboe et al. 1988). Field growth rates were thus close to growth rates observed in this study during the period of exogenous feeding (0.09 to 0.23 mm d^{-1}). In the laboratory, maximum specific growth rates for larval Clyde herring older than 10 d were ca 0.07 (Kiørboe et al. 1987) which is comparable to the maximal specific increase in soluble protein content (protein increment divided by average protein content and duration of measuring period) of 0.06 found in Group 1 from Day 14 to 35. During this period Group 2 caught up with Group 1, and therefore growth in these two groups does not seem to have been limited by food availability.

Comparing Groups 1 and 2 from Day 14 onwards, it is apparent that ingested food in Group 2 was channelled into rapid somatic catch-up growth as has been demonstrated in older fish and other animals (Wilson and Osbourn 1960, Bulow 1970, Weatherly and Gill 1981, Dobson and Holmes 1984, Ashworth 1986, Pitts 1986, Miglavs and Jobling 1989). During catch-up growth following transfer from restricted to satiation feeding in 1-yr-old *Salvelinus alpinus* both hyperphagia and an improved food conversion efficiency were observed (Miglavs and Jobling 1989). Growth data in the present study indicate that Group 2 larval herring markedly improved their food conversion efficiency after exposure to high ration, as amount of uningested prey was either higher than (Days 15 to 23) or similar to (Days 24 to 34) that of Group 1 (Table 2 B). It is noteworthy that Group 2 larvae were able to exhibit catch-up growth even in spite of the reduced food intake accompanying the period with decreased water quality. Balance between anabolic and catabolic processes in Group 2 fish may therefore have been altered following the shift in feeding regime, as has been suggested for other species (Miglavs and Jobling 1989). The present study also implies that Group 2 larvae did not build up a digestive capacity, expressed as content of trypsin and trypsinogen, such as found in fish at a constant high ration. As amount of enzyme spent on digestion in Group 2 would be less than or equal to that of Group 1 from Day 14 onwards, synthesis of trypsinogen in Group 2 was depressed compared to Group 1. Overall protein synthesis in Group 2 was, however, not slowed down by the period of low food availability, as increase in protein content was rapid, and faster than that of Group 1.

Although, at the end of the study, Group 2 exhibited a markedly reduced digestive capacity relative to that of Group 1, growth and mortality rates of Group 2 larvae suggest that their digestive potential would suffice with respect to current environmental circumstances. It is possible, however, that larvae belonging to Group 2 would be less robust than Group 1 fish if confronted with adverse feeding conditions in the future, and that their digestive capacity might deteriorate rapidly to a level not compatible with continuous growth. As Clyde larvae belong to the winter-spring spawning stocks, characterized by large eggs and hence large larvae at hatching (Blaxter and Hunter 1982), effects of a transitory, low food supply immediately after yolk resorption may have greater impact on future growth and survival potential in the smaller larvae belonging to other stocks.

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