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# Description of the Early Development of the Halibut *Hippoglossus hippoglossus* and Attempts to Rear the Larvae Past First Feeding

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## Abstract

Rearing experiments on the halibut *Hippoglossus hippoglossus* (L.) were carried out using gametes from parents caught at a depth of 600 to 700 m off the Norwegian coast in February 1980. After fertilization, the average egg diameter was 3.08 mm, average dry weight 1 038 $\mu$g and neutral buoyancy was at 36.5‰ S. The eggs hatched after 20 d at 4.7 °C, 18 d at 5 °C and 13 d at 7 °C. Survival to hatching was better when antibiotics were used. At hatching the larvae were 6.4 mm long, there were no functional eyes or mouth, but prominent neuromast organs were present. Resorption of yolk lasted 50 d at 5.3 °C; the eyes and mouth were then functioning and the larva was about 11.5 mm long. The larvae were offered zooplankton as food, but with little success in initial feeding. A few larvae fed and grew in 2 500-litre plastic bags, one reaching a length of 24 mm after 90 d.

## Introduction

Rearing experiments with halibut larvae, *Hippoglossus hippoglossus* (L.), have been carried out at intervals in various research laboratories, but without much success (Rollefsen, 1934; Forrester and Alderdice, 1973; Solemdal *et al.,* 1974). The most successful experiment so far was carried out in Norway in 1974 (Solemdal *et al.,* 1974), when the larvae were kept alive for 60 d. The unusual development of this species during yolk resorption as a result of the large egg and long incubation period was then observed. In the present experiment, different types of systems were tested for incubation of the eggs and for holding the larvae during the long period until the first feeding stage was reached. Feeding experiments were then started. During development, observations were made on the anatomy and growth of the larvae.

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Some results in this paper have previously been presented in a report to ICES, statutory meeting (Øiestad and Haugen, 1980).

## Materials and Methods

Spawning halibut [*Hippoglossus hippoglossus* (L.)] were obtained by gill net in a fjord north of Bergen in February 1980 at a depth of 600 to 700 m. A female and a male halibut were caught and stripped on board. After artificial fertilization the eggs were brought to the State Biological Station Flødevigen outside Arendal in southern Norway, where they arrived 14 h later. The eggs were incubated in 25 one-litre plastic beakers in darkness in a refrigerator at 4.7 °C. The salinity of the water was increased to about 37‰ using NaCl in order to make the eggs float. Antibiotics were added according to the dosage suggested by Shelbourne (1963).

After 3 d, some of the eggs were transferred from the beakers and incubated in 1-litre glass jars kept in water baths at 5° and 7 °C. The jars were covered with a glass plate and kept in darkness. Each water bath contained 3 jars, and to two of the jars antibiotics were added. The salinity in all jars was about 37‰. About half the water was changed each day and dead eggs and larvae were removed. The larvae which hatched were kept there until total mortality had occurred.

Another group of eggs was transferred 3 d after fertilization and incubated in darkness in Dannevig's fish egg incubator (Dannevig, 1910), which is an open circulation system in which the salinity and temperature were maintained at 34.5‰ and 5 °C. The eggs were held in suspension most of the time by the shaking system of the incubator (Dannevig, 1910). Dead eggs were not removed during incubation in this system.

Rollefsen (1934) and Lønning *et al.* (1982) have published photographs of the egg stages. The last part of the incubation period is presented in more detail in our

paper. In our experiments, egg development was classified according to Westernhagen's egg division scale (von Westernhagen, 1970).

Larvae hatched in the refrigerator were transferred to two 10-litre buckets containing seawater of 37‰ salinity and treated with antibiotics. They were kept in the refrigerator at 5.3 °C. Larvae were frequently sampled from the buckets for staging, for measuring neutral buoyancy and for description of swimming behaviour. At the ages of 38, 44 or 53 d post-hatching, groups of larvae were transferred to 8-litre and 140-litre jars containing water of 37‰ salinity for feeding on natural zooplankton followed by gut inspection. The zooplankton was collected by net hauls in the bay outside the station. The mesh size of the net was 90 $\mu$m and only the fraction passing a 500 $\mu$m sieve was added to the feeding jars. The food organisms were mainly rotifers and different stages of calanoid copepods. The food density was not monitored. The water in the jars was not changed, nor were antibiotics used. Fifty larvae at an age of 38 d were also added to each of two black plastic bags. These were 2 m deep, cylindrical in shape, with a conical bottom and each held 2 500 litres of seawater of 34.5‰ S. The salinity was increased in the bottom water to about 35‰. The plastic bags were supplied with an inoculum of zooplankton 1 wk before larval transfer. The zooplankton was collected and sieved as described for the feeding experiments in the laboratory. Food density was not monitored.

The larval age is given in days from 50% hatching, all measurements being carried out on larvae preserved in 4% formalin (a saturated solution of formaldehyde in water diluted ten times with 15‰ S sea water) unless otherwise indicated. Length is given from the snout to tip of the notochord. Dry weight measurements were made to an accuracy of $\pm$ 1 $\mu$g after 48 h in an oven at 60 °C. The egg weight was measured after dissecting off the chorion and the yolk sac and larval body were weighed separately after dissection. All photographs except those on neuromasts were taken on living anaesthetised larvae. Some conventional histology was carried out on the larval stages, especially on the sense organs. Scanning electron microscopy was used to investigate the neuromast organs.

In the calculations of energy content of yolk sac and larval body, 6 000 cal $g^{-1}$ for yolk sac and 5 000 cal $g^{-1}$ for larval body were used in accordance with Laurence's (1969) values for largemouth bass. The decrease in total caloric content of the larvae due to metabolism was compared with the metabolism of plaice larvae as observed by De Silva and Tytler (1973) for both unanaesthetised and anaesthetised larvae from the yolk sac stage to metamorphosis. Their values were converted to 5 °C applying a $Q_{10}$ of 2 and, as indicated by the authors, unanaesthetised metabolism was considered to correspond with routine metabolism and anaesthetised to correspond with basal metabolism. The dry weight of the yolk sac apparently increased from hatching to Day 15 post-hatching, but this is assumed to be a sampling error, so for this 2 wk period the estimated dry weight was calculated assuming basal metabolism during this period. In these calculations, basal metabolism for plaice larvae of the same weight was applied.

## Results

### Eggs

The mortality curve of the *Hippoglossus hippoglossus* eggs in the refrigerator is shown in Fig. 1 A. About 50% of the eggs hatched, the heaviest mortality occurring from the initial migration of the germinal disc (Day 3) to the closure of the blastopore (Day 10); from then onwards negligible mortality occurred until hatching, when it again increased. Although antibiotics were added and the water was changed daily, the water smelt stale at the end of the incubation period. The chorion was also opaque, in contrast to the eggs incubated in the Dannevig open-water circulation. The mortality in this system was not measured, but seemed to be less than in the stagnant system.

The mortality to hatching in the water baths was 100% at 5 °C and 50% at 7 °C in the jars without antibiotics added (Fig. 1 B, C), while it was only 20 to 40% at 5 °C and 15 to 30% at 7 °C with antibiotics added. The mortality for the first 3 d after transfer to the jars was zero or very low, but rather high for the next few days, as also observed in the refrigerator.

The average live egg diameter was 3.08 mm (SD 0.03; $n = 16$) and neutral buoyancy was found in sea water of salinity 36.5‰. The average dry weight of halibut eggs just after fertilization was 1 038 $\mu$g (SD 21; $n = 23$) excluding the chorion. Just before hatching the average dry weight of the egg (embryo plus yolk) was 740 $\mu$g (SD 10; $n = 5$) and in addition the average dry weight of the chorion was 106 $\mu$g (SD 8; $n = 7$).

The stages at different age for eggs incubated at 5° and 7 °C are shown in Fig. 2 for the period after gastrulation until beginning of hatching, and some stages are illustrated in Fig. 3 A–D. The embryo was unpigmented. At Stage 3$\beta$, the body of the embryo started to bend in the gut region (Fig. 3 A–C). This bending only disappeared during late incubation (Fig. 3 D), and the newly hatched larva had a straight body (Fig. 3 E). Incubation time to 50% hatching was 20 d at 4.7 °C and 18 and 13 d at 5° and 7 °C, respectively, with hatching starting about 2 d before.

### Larvae

The larvae hatched with a very large yolk sac; yolk resorption was complete after about 50 d post-hatching at 5.3 °C. The newly hatched larva had no pigmentation of eye or body, the gut was straight and without a lumen and the mouth was not opened (Fig. 3 E). The results below refer to development at 5.3 °C unless otherwise stated.

*Eye Development.* Pale pigmentation started along the margin of the eyes after about 2 wk (Fig. 3 F), and a light

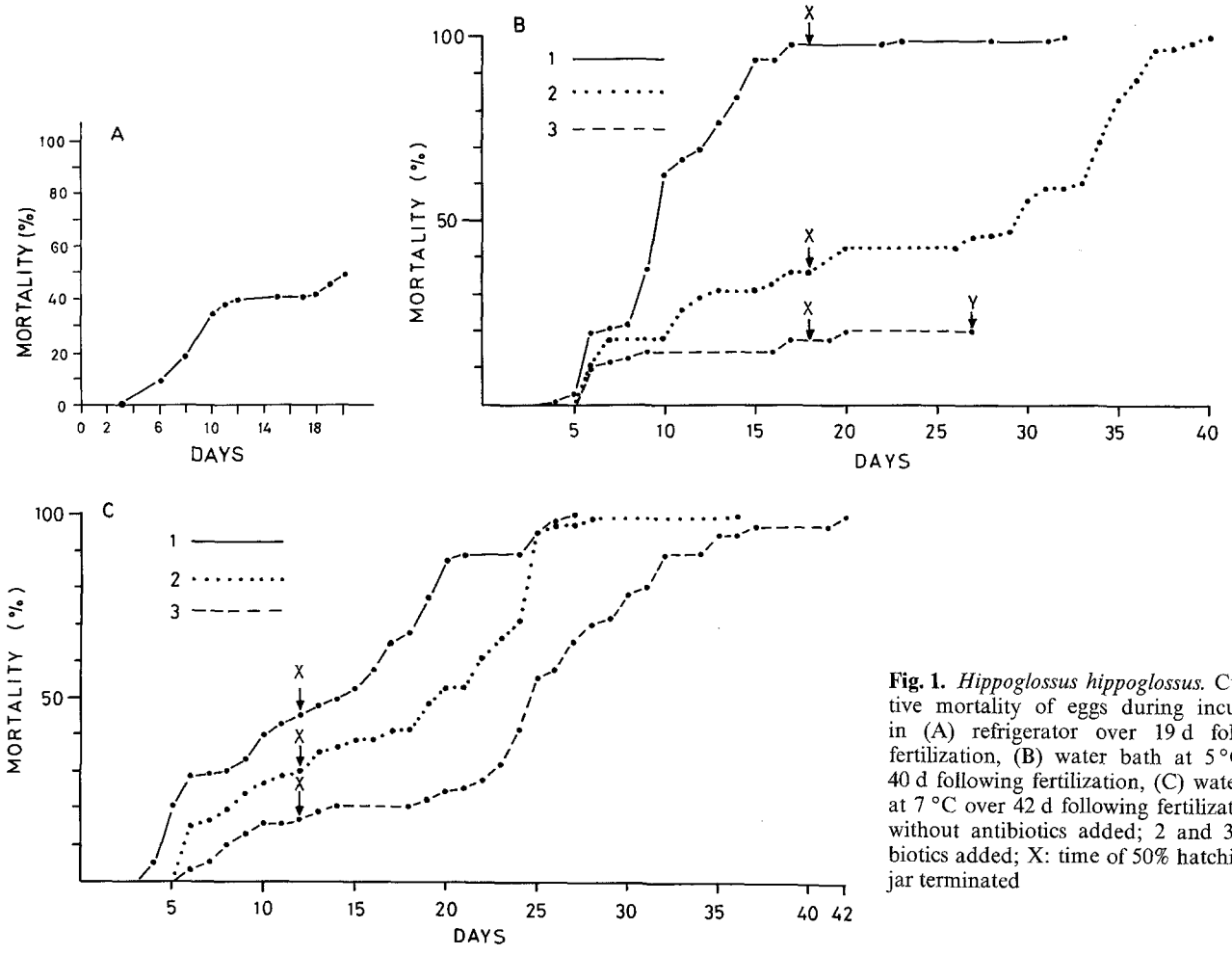


**Fig. 1.** *Hippoglossus hippoglossus.* Cumulative mortality of eggs during incubation in (A) refrigerator over 19 d following fertilization, (B) water bath at 5 °C over 40 d following fertilization, (C) water bath at 7 °C over 42 d following fertilization. 1: without antibiotics added; 2 and 3: antibiotics added; X: time of 50% hatching; Y: jar terminated

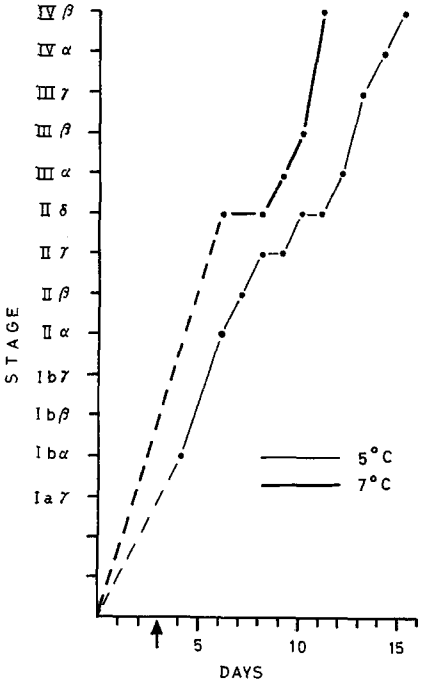


**Fig. 2.** *Hippoglossus hippoglossus.* Duration of developmental stages of eggs at 5° and 7 °C over 16 d following fertilization. Arrow shows day of transfer to experimental condition

brown pigmentation covered the whole eye after the third week. Within the next week the eyes turned black (Fig. 3 G). The duration of the process is indicated in Fig. 4 C. At 7 °C the eyes turned black within 14 d. Conventional histology showed a fully developed lens and retina by Day 30 at 5.3 °C. The retina comprised single cones with long nuclei. No rods were present.

*Mouth Development.* The mouth opens after 3 wk, and from that time the mouth is widely opened and cannot be closed (Fig. 3 G). Further development of the lower jaw makes it possible for the first larva to close its mouth after 25 d. The lower jaw points upwards and forward at an angle of about 45° to the horizontal body axis (Fig. 3 I). At 7 °C the mouth opens after 14 d, but no data were obtained on time to develop a functional mouth at this temperature. At the end of the yolk sac stage, 70% of the larvae had a functional mouth (Fig. 4 B).

*Gut Development.* After 4 wk, the rectum started to develop and also the lumen in that area (Fig. 3 G). Within the next 10 d the lumen in the rest of the gut was developed and the gut started to bend (Fig. 3 H), and within the following week the rotation of the gut was complete (Figs. 3 I and 4 A).

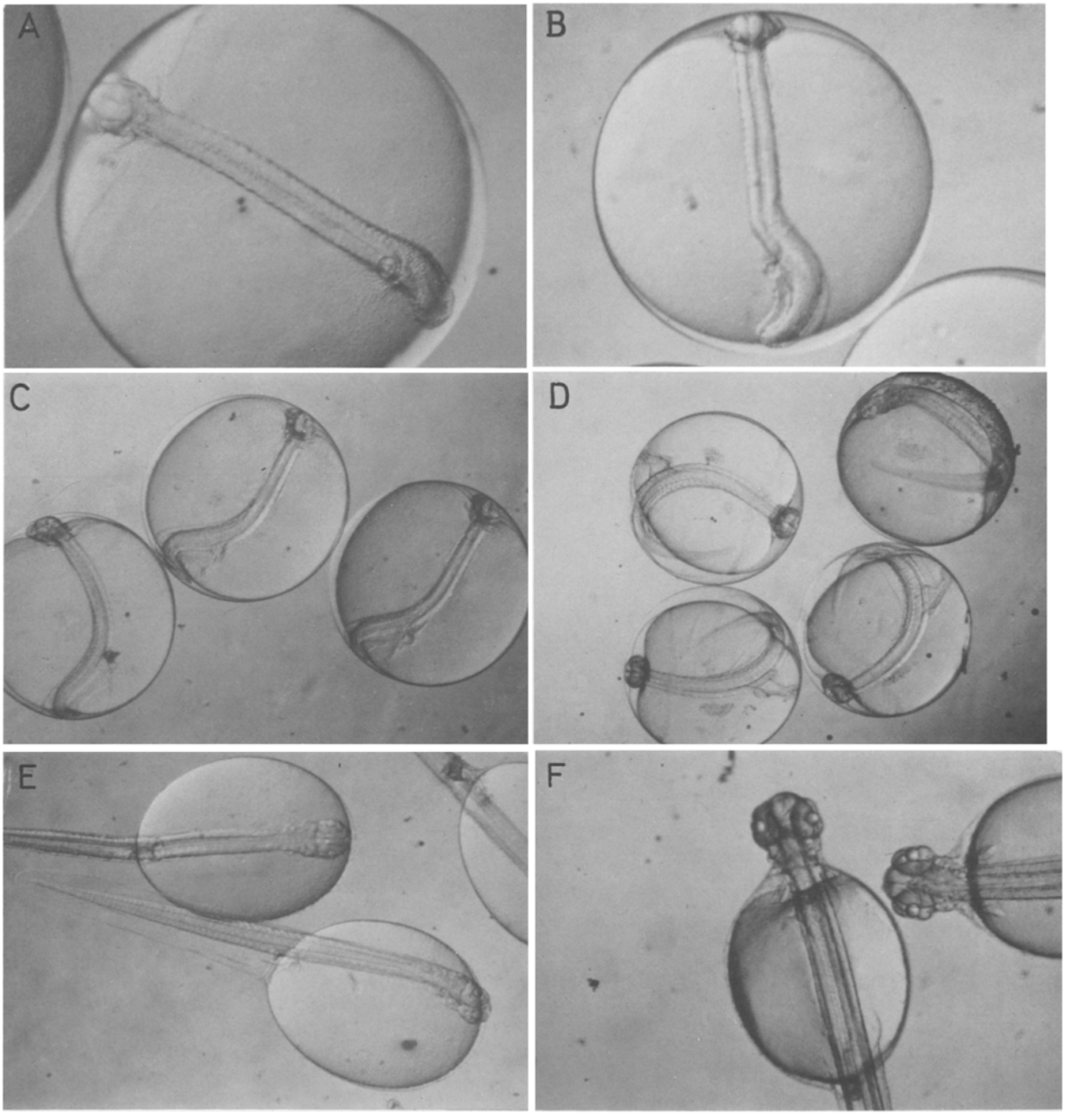


**Fig. 3.** *Hippoglossus hippoglossus.* (A) – (D) Halibut eggs at different stages: (A) $3\beta$, (B) $3\gamma$, (C) $4\alpha$, (D), $4\beta$; average egg diameter is 3.08 mm. (E – J) Halibut larvae: (E) newly hatched, about 6 mm long; (F) with pale eye pigment, about 20 d post-hatching, length 9.5 mm; (G) with fully pigmented eyes, mouth wide open and cannot be shut, rectal lumen, primitive heart, and small liver, about 30 d after hatching, length 10.8 mm; (H) with partially bent gut and with connection between liver and yolk sac, about 40 d after hatching, length 11.2 mm; (I) with functional mouth and rotated gut, about 50 d after hatching, length 11.5 mm; (J) with differentiated heart connected with liver, about 40 d after hatching, length 11.2 mm. (K) Transverse section of neuromast organ (scale bar = 50 $\mu$m). (L) Scanning electron microscopy of neuromast organ (scale bar = 1 $\mu$m)

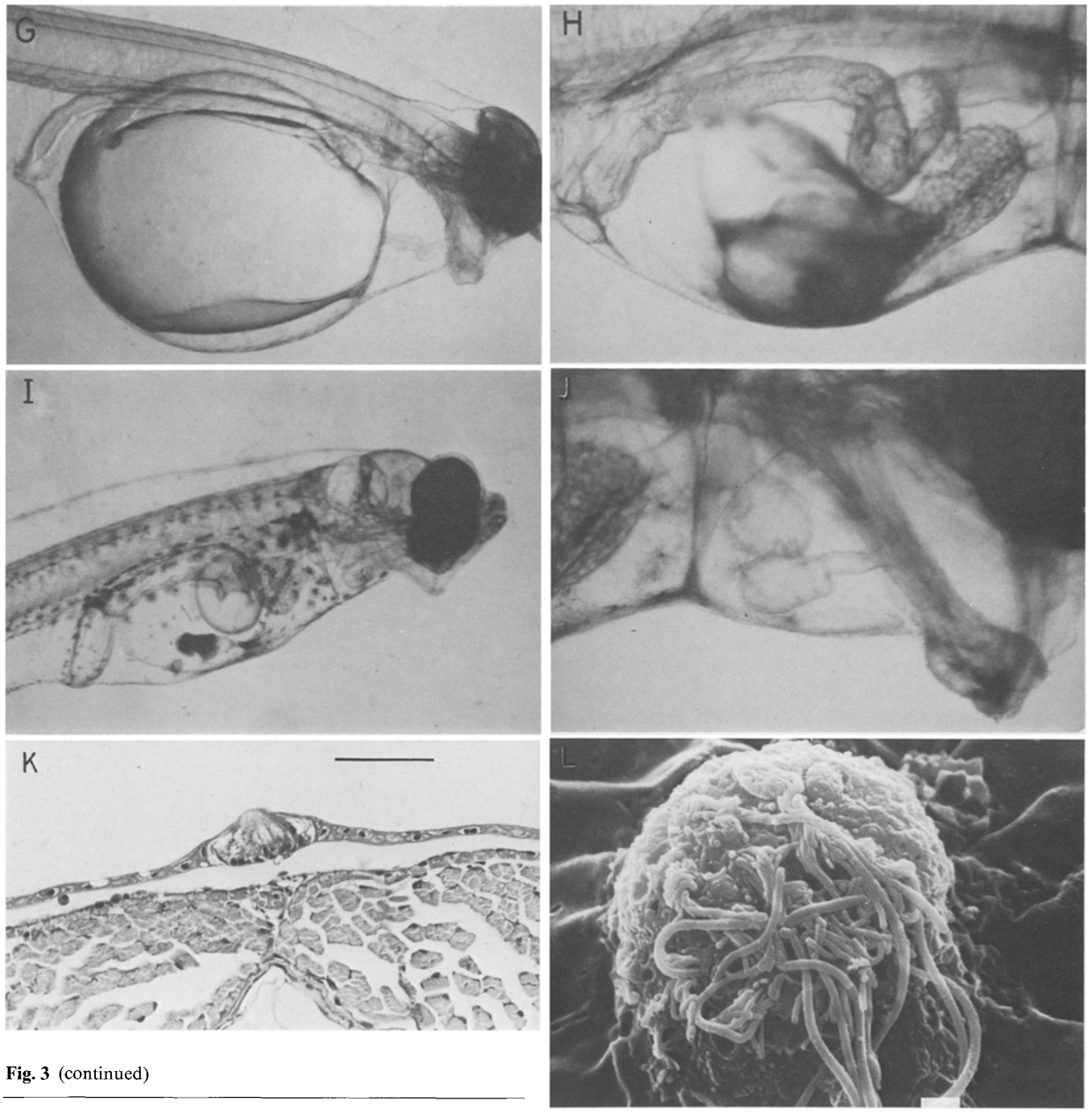


**Fig. 3** (continued)

*Heart Development.* Two stages of the development of the heart are shown, an earlier one in Fig. 3 G and a later one at the end of the yolk sac stage where the heart is fully differentiated with distinct chambers (Fig. 3 J).

*Liver Development.* The liver, which was situated on top of the yolk sac, was a very small organ during the first part of the yolk sac stage and the developmental rate was very slow. The connection between the liver and the yolk sac was clearly seen just before the total resorption of the yolk (Fig. 3 H). At the end of the yolk sac stage the liver was situated in front of the coiled gut (Fig. 3 I). A connection between the heart and the liver is seen in Fig. 3 J.

*Body Pigmentation.* The first pigmentation occurred after 5 to 6 wk, mainly on the dorsal part of the primordial fin. Between Days 40 and 50, the chromatophores were laid down mainly as ventral, lateral and dorsal lines along the larval body, and were also found in the gut region.

*Neuromast Organs.* Very prominent conical humps could be seen in the mid-lateral position on either flank of the larvae, increasing from 2 to 4 at hatching to 11 to 12 at the end of the yolk sac stage. A histological view in transverse section is shown in Fig. 3 K. Scanning electron microscopy (Fig. 3 L) showed the characteristic kinocilia and sterocilia of a free neuromast organ.

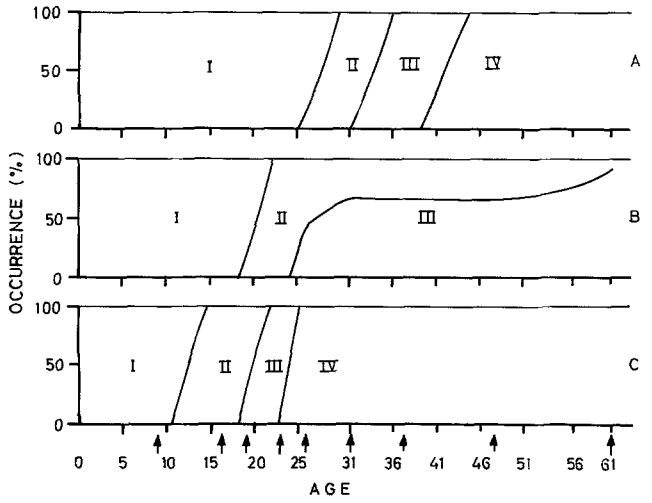


**Fig. 4.** *Hippoglossus hippoglossus.* Organ development of larvae in refrigerator; age is in days post-hatching; arrows show days of sampling. (A) Development of gut; I: straight gut without any differentiation, II: straight gut with start of rectum formation, III: gut bent and with lumen, distinct rectum, IV: coiled gut. (B) Development of mouth; I: mouth not open, II: mouth open or widely open, III: mouth shut or can be shut. (C) Development of eyes: I: unpigmented eyes, II: pale pigment on edge of eyes, III: pale pigmentation of most of eyes, IV: dark pigmentation of eyes

*Mortality.* The mortality pattern of the larvae in the refrigerator is shown in Fig. 5. Two long periods of slow mortality (2% and 6.8% $d^{-1}$) were observed, interspersed with two short periods of high mortality (11% and 22% $d^{-1}$). The heavy mortality from Days 8 to 13 was partly due to an accident when changing water. The survival to Day 30 was 35% and the last larvae died on Day 61.

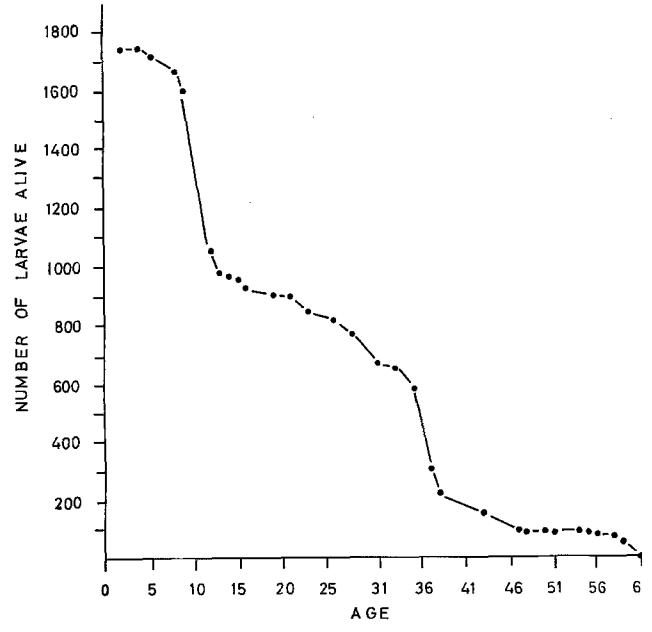


**Fig. 5.** *Hippoglossus hippoglossus.* Mortality of larvae in buckets in refrigerator. Age is in days post-hatching

In one of the plastic bags started in April on Day 39, one larva was caught on 28 April (Day 54), and two larvae survived to metamorphosis (Day 90); see example in Fig. 6.

All larvae in the Dannevig's fish egg incubator died within a few days after hatching due to the shaking and water circulation in this system. In the water baths, the initial larval mortality was slight for the larvae in the jars with antibiotics (Fig. 1 C). About Day 20 a mass mortality occurred in the two jars with antibiotics at 7 °C and about 10 d later in the three jars at 5 °C (Fig. 1 B, C). Due to the small number of larvae in the system, regular sampling for staging was not carried out at either of these temperatures.

The larvae provided with natural zooplankton in feeding jars in the laboratory, died within a few days and none of these larvae was observed with food in the gut.

*Larval Growth.* The mean fixed length at hatching was 6.4 mm (SD 0.24) (live length 6.7 to 7.1 mm) and increased to 11.5 mm (SD 0.40) on Day 50 in the refrigerator (Fig. 7). This gives a daily length increment (DLI) of 0.1 mm during yolk sac resorption (to Day 50), but most of the increase took place to Day 30 (DLI was 0.15 to Day 30, Fig. 7). The halibut larva caught in one of the plastic bags on 28 April (54 d post-hatching) had a length of 12.0 mm, giving a DLI of 0.11 mm from 12 April (38 d post-hatching). The larvae held in the laboratory feeding jars in the same period had a DLI of 0.03 mm [from 11.17 mm (SD 0.64) to 11.53 mm (SD 0.40)]. Another larva from the same bag captured on 27 May (93 d post-hatching) had reached a standard length of 24.2 mm (total length of 29 mm), giving a DLI since release in the bag (12 April) of 0.29 mm. The myotome height of the larvae in the refrigerator increased from 0.38 to 0.76 mm at end of the yolk sac stage and the largest diameter of the eye increased from 0.37 to 0.73 mm at the end of the yolk sac stage (Fig. 8). The observed myotome height and eye diameter of the larvae caught in the plastic bag on Day 54 are also indicated in Fig. 8, and a considerable increase in both is demonstrated.

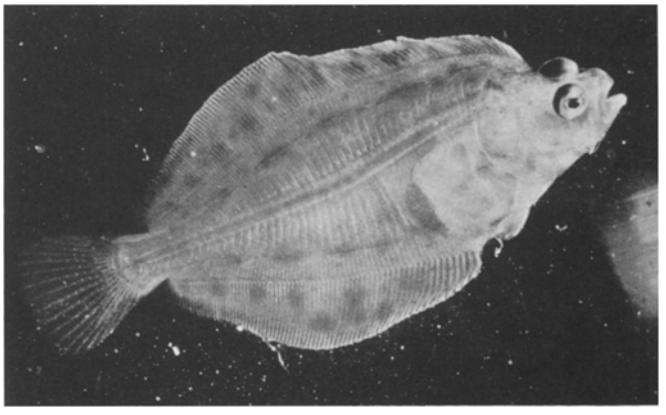

**Fig. 6.** *Hippoglossus hippoglossus.* 90 d-old juvenile from plastic bag experiment, length 24 mm

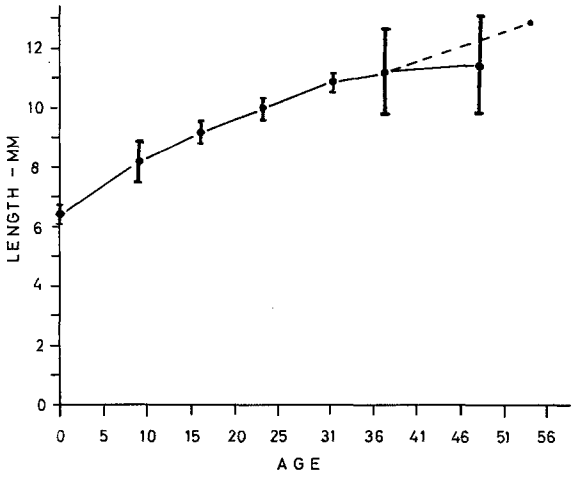


**Fig. 7.** *Hippoglossus hippoglossus.* Mean length of larvae in refrigerator (length of halibut larva from plastic bag on 28 April is also shown by dashed line). Age is in days post-hatching. Vertical bars are 95% confidence limits

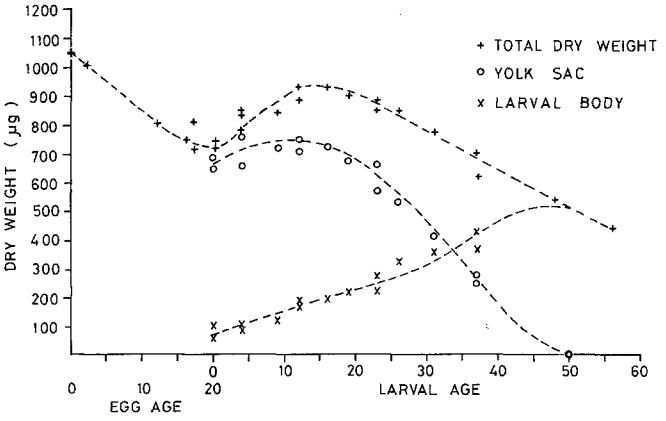


**Fig. 9.** *Hippoglossus hippoglossus.* Total dry weight of eggs (less chorion) and larvae (+), dry weight of yolk sac from hatching to yolk absorption (○), and of larval body from hatching to Day 60 (×). Yolk sac weights are true, not estimated (see "Materials and Methods")

The dry weight of the larval body increased from an average of about 80 $\mu$g at hatching to about 515 $\mu$g at the end of the yolk sac stage at Day 50 (Fig. 9 and Table 1), giving a specific growth rate (SGR) of 3.7%. In the same period, the yolk sac decreased from an average of 823 $\mu$g at hatching (Table 1) to zero, which gives a conversion ratio of yolk to larval body of 53%. At hatching the larva made up only 9% of the total dry weight; on Day 30, when most organ systems were functional, the larva made up 45% of the total dry weight and 10 d later 73% (Table 1).

The halibut larva captured in the plastic bag on 28 April (larval age 54 d) had a dry weight of 1 020 $\mu$g, giving a SGR of 5% since 12 April (larval age 38 d).

*Metabolism.* The change in energy content of yolk sac and larva from hatching to the end of the yolk sac stage made it possible to calculate the reduction in total energy content and, indirectly, to calculate the total metabolism (see Table 1).

These calculations have been compared with routine and basal metabolism for plaice (*Pleuronectes platessa* L.) at 5 °C in Fig. 10. From Days 30 to 45, the routine metabolism of halibut larvae was almost twice the routine metabolism of plaice. Before Day 28 and after Day 48, the routine metabolism of halibut lay between the basal and routine metabolism of plaice.

*Behaviour.* The swimming pattern from Day 20 onwards was characterized by cruising and bending and by burst-swimming when disturbed. The larva could also remain motionless for a few minutes. When bending the larva formed a "U" shape and could maintain this position for

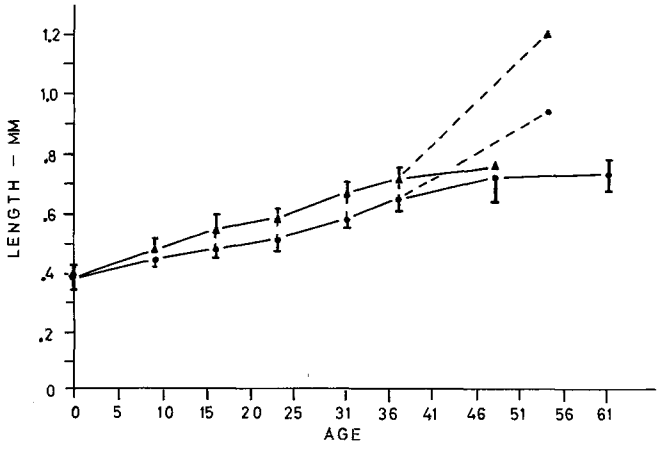


**Fig. 8.** *Hippoglossus hippoglossus.* Mean myotome height measured behind anus (▲) and mean largest eye diameter (●) from larvae in refrigerator (myotome height and eye diameter of larvae from plastic bag on 28 April are also shown by dashed lines). Age is in days post-hatching. Vertical bars are 95% confidence limits

**Table 1.** *Hippoglossus hippoglosus.* Dry weight changes with age (in days from hatching) of larval body and corresponding calorific values, and the calculated decrease of calorific value in each 5 d period. Total dry weights to Day 15 are estimated (see "Materials and Methods"). Yolk sac wt = total wt minus larval body wt

| Age (d) | Dry weight ($\mu$g) | | | Energy (cal) | | |
|---|---|---|---|---|---|---|
| | Total | Larval body | % of total | Larval body | Total | De-crease |
| 0 | 903 | 80 | 9 | 0.40 | 5.34 | – |
| 5 | 890 | 105 | 12 | 0.53 | 5.24 | 0.10 |
| 10 | 880 | 145 | 16 | 0.73 | 5.14 | 0.10 |
| 15 | 870 | 185 | 21 | 0.93 | 5.04 | 0.10 |
| 20 | 850 | 230 | 27 | 1.15 | 4.87 | 0.17 |
| 25 | 830 | 290 | 35 | 1.45 | 4.69 | 0.18 |
| 30 | 780 | 350 | 45 | 1.75 | 4.33 | 0.36 |
| 35 | 705 | 405 | 57 | 2.03 | 3.83 | 0.50 |
| 40 | 630 | 460 | 73 | 2.30 | 3.32 | 0.51 |
| 45 | 560 | 510 | 91 | 2.55 | 2.82 | 0.47 |
| 50 | 515 | 515 | 100 | 2.58 | 2.58 | 0.27 |
| 55 | 465 | 465 | 100 | 2.33 | 2.33 | 0.25 |
| 60 | 350 | 350 | 100 | 1.75 | 1.75 | 0.58 |

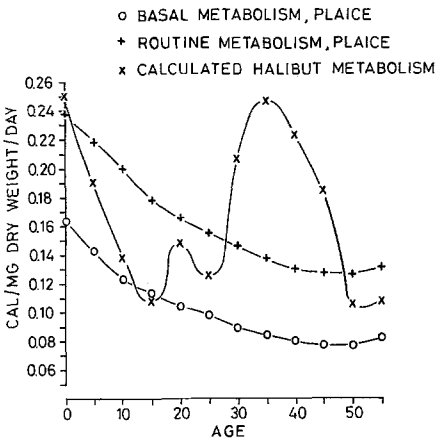


**Fig. 10.** *Hippoglossus hippoglossus.* Calculated total metabolism per mg dry weight of larvae based on dry weight reduction from hatching to Day 60, compared with basal and routine metabolism of equal-sized plaice (*Pleuronectes platessa* L.) larvae at 5 °C (calculated from De Silva and Tytler, 1973). Age is in days post-hatching

minutes at a time with the tip of the tail vibrating vigorously. It would then start swimming again or bend in the opposite direction.

The metamorphosed halibut fry in the plastic bag swam pelagically in an upright position and were not observed settling on the wall or bottom. A sigmoid body shape was observed when the fry approached a prey organism, followed by snapping. When one of them was transferred to the laboratory, it settled to the bottom, only occasionally swimming along the wall of the 140-litre jar.

Neutral buoyancy was found in sea water of 35.8‰ S at hatching, 34.8‰ S on Day 12, and in 36.4‰ S on Day 35.

## Discussion

The high salinity giving neutral buoyancy in *Hippoglossus hippoglossus* eggs found in the present study, and also reported by Solemdal *et al.* (1974), and Lønning *et al.* (1982), seems to result from a high content of organic matter, the dry weight of the eggs being about 10% of the wet weight. This occurs despite the ability of the egg to regulate the tissue osmotic pressure well below that of sea water Riis-Vestergaard, 1982). Since the salinity of the sea water along the Norwegian coast does not exceed 35‰, it seems possible that halibut eggs develop near or on the sea bed. This possibility is still open to further investigation, since Devold (1943) found halibut eggs in pelagic plankton samples. In addition, among the 10 ripe halibut females tested by Solemdal (personal communication, Institute of Marine Research, Bergen) one gave eggs with a neutral buoyancy equivalent to 34.7‰ S. Further results from 1982 support this observation since two captured females had eggs which floated in 35‰ S.

Recently, Haug *et al.* (1982) made plankton surveys off the north coast of Norway using a bottom sampler and midwater trawl. No halibut eggs were found on the sea bed, but 53 were found floating bathypelagically at depths from 70 to 200 m, and a few as deep as 350 m. They seem to be mostly at depths where there were substantial temperature and salinity gradients, from 4° to 7 °C and 34 to 35‰ S, respectively.

Lønning *et al.* (1982) have carried out both light and electron microscope studies of halibut eggs, and they conclude that both the morphology and ultrastructure of halibut eggs and embryos, plus their development, resemble that of other pelagic eggs.

The survival of eggs and larvae depended partly on the conditions of the experiment. The best egg survival was obtained in the water baths at 5° and 7 °C with the use of antibiotics and these also yielded low initial larval mortality. Egg mortality was greater before closure of the blastopore, which has been reported earlier (Rollefsen, 1934; Forrester and Alderdice, 1973).

It seems likely that a stagnant system with antibiotics, increased salinity to float the larvae, frequent disturbance when removing dead larvae or changing the water may have caused stress and ultimate mortality. There was a suggestion that the quality of the eggs at hatching was best in the Dannevig open circulation system. However, the only survival to feeding and metamorphosis occurred with two larvae in the plastic bags with natural zooplankton as food. The very long period for development at 5 °C may be undesirable in artificial rearing conditions and it is possible that an increase of temperature to 7 °C or higher may be advantageous in future experiments.

The developmental changes observed agree in general with earlier results. Both Rollefsen (1934) and the present results indicate that the eye pigmentation starts later in European halibut than in Pacific halibut which develop pigmentation at 2 to 4 d post-hatching according to Forrester and Alderdice (1973). The eye is not fully functional, as judged histologically, until about 30 d post-hatching at 5.3 °C. The prominent neuromast organs, present from hatching, have not been reported before and clearly endow the larvae with some sensory capability before the development of vision.

The development of the mouth seems similar to that of Pacific halibut (Thompson and van Cleve, 1936; Forrester and Alderdice, 1973), being rudimentary at hatching, non-closing during an intermediate period and functioning, as the lower jaw develops, only 3 to 4 wk post-hatching. Thus, the eyes and mouth became functional about the same time, so preparing the larva for feeding. The gut does not appear to be functional until about 1 wk later so that the anatomical evidence suggests the larva can feed and assimilate food 28 to 35 d post-hatching at 5 °C. This is a very long period compared with other marine fish larvae investigated in the North-East Atlantic (Russell, 1976).

At this first feeding stage, the typical larva still has a yolk sac weighing about 250 $\mu$g, a body weight of 370 $\mu$g and a body length of 11 mm. Calculations show that the metabolic rate up to this stage (Day 25) lies between the

basal and routine metabolism of plaice larvae (Fig. 10). The metabolic rate of halibut larvae increases sharply, however, after Day 25, and reaches a level almost double the routine metabolic rate of larval plaice. This is the period when the halibut larva becomes fully equipped to feed from the aspect of its sense organs, mouth and gut.

The halibut with its very large eggs and long period of larval development is very unusual compared with most other marine teleosts. The high density of the egg, causing it to sink in sea water, may be an adaptation to reduce mortality, since it is probably less vulnerable to predation on or near the sea bed than in the pelagic zone.

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