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Changes in buoyancy and activity during starvation of cod larvae (Gadus morhua L.).

by

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Introduction

In 1914 Hjort stated his hypothesis about the critical period in the early life history of fish larvae. Hjort (1914, 1926) established that the year-class strength of Norwegian herring and cod stocks varied widely and that it was determined early in the larval life-history. According to Hjort one of the main factors affecting survival through this stage was the lack of food at the time larvae began to feed.

It is perhaps surprising how little is known about the ecology of cod larvae. This is apparently due to the considerable difficulties of rearing cod larvae in the laboratory. These problems are still not solved.

Fish larvae will reach a state of starvation shortly after yolk resorption where they will inevitably die even if food suddenly becomes available. This "point-of-no return" (PNR) is described by Blaxter & Hempel (1961) where 50 per cent of the larval population are too weak to feed if food becomes available. The fish larvae may live for a long period beyond the PNR and even exhibit feeding behaviour after they have passed a point in time when they are irreversibly starved (Lasker et al., 1970). Ecologically the point of irreversible starvation is a more important time to establish than the moment of death.

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The determination of the PNR is based on measuring mortality rates of fish larvae deprived of food for varying lengths of time, (Lasket, et al., 1970). This obviously requires successful rearing of the larvae involved. However, Blaxter & Ehrlich (1974) have described a method where the rearing problems can be avoided and the PNR can still be determined. They found it possible to do this by studying the changes in activity and buoyancy of herring and plaice larvae during starvation.

In this report we describe the changes in activity and buoyancy of the larval cod, *Gadus morhua* L., from hatching to subsequent death from starvation in an attempt to determine the PNR. The observations will be combined with results of field studies on cod larvae, see (F:34) this meeting.

MATERIALS AND METHODS

Materials

Artificially fertilized eggs of Arcto-Norwegian cod were obtained in March from the Lofoten area. Eggs from different females were kept separate and were sent by air to the Institute of Marine Research, Bergen, the day after fertilization.

Incubation

The fertilized eggs were incubated in perspex cylinders 15 cm in diameter and 22 cm deep. The incubators were placed in each of five thermostats. Before entering the cylinders the sea water was filtered through 50 - and 10 μ filters. The gas surplus was removed under atmospheric pressure in a horizontal tube. The water then entered and left the incubator cylinders through siphons (see Figs. 1 and 2). The temperature was kept constant at 5^{o}C, and throughout the experiment the salinity was 34 - 34.7 $^{o}/oo$.

Buoyancy

Thirteen 250 ml glass cylinders containing sea water graded in 0,5 $^{o}/oo$ salinity steps from 28 to 34.5 $^{o}/oo$ were placed in a thermostat with a constant temperature of 5^{o}C. The salinities were made up by adding

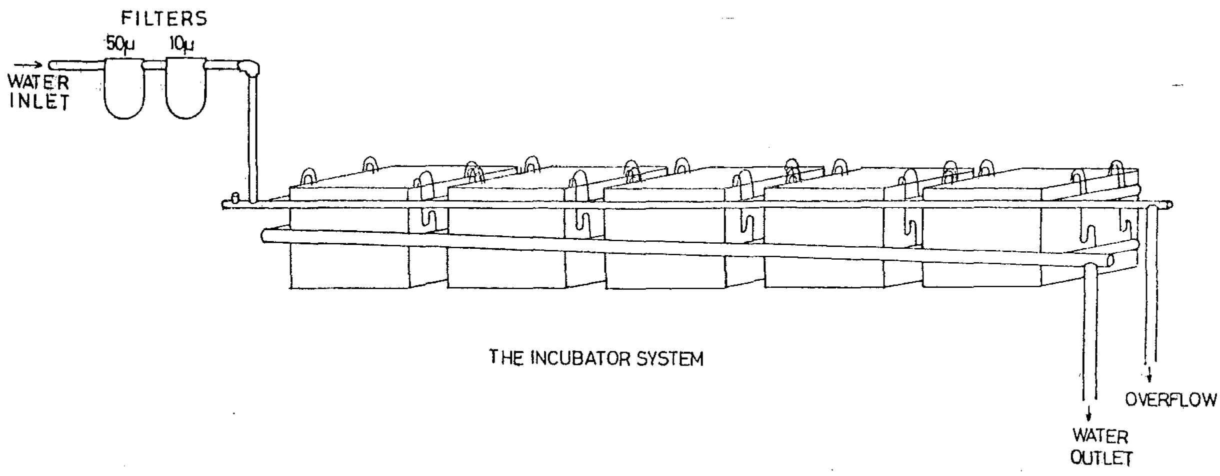

Fig. 1.

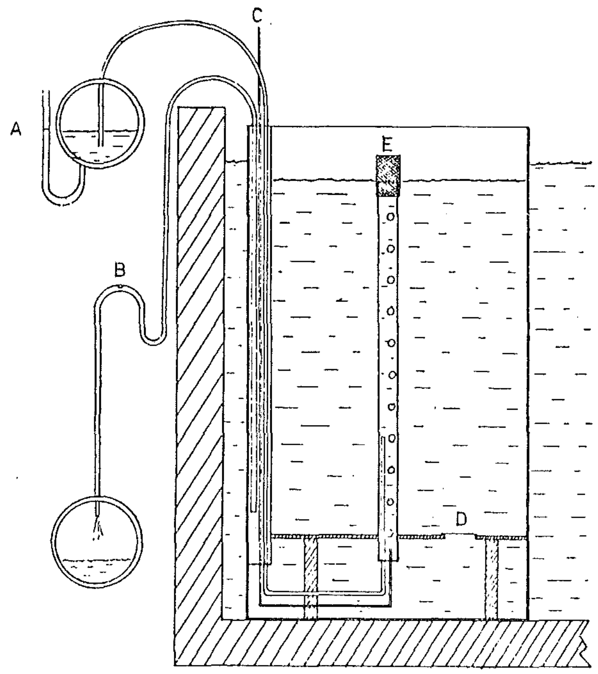

Fig. 2. Cross section of part of a thermostat containing one incubation cylinder. The system for regulating the water flow is also shown.

A : Inlet level control. B : Air hole regulating the outflow level.

C : Air tube. D : Bottom sieve. E : Airlift.

distilled water to sea water of 34.7 ^{o}/oo salinity. Thirty larvae were anaesthetized in 1:20 000 MS 222, and 10 larvae were transferred to each of three cylinders. In all instances the larvae were rinsed in the same salinity as that of the experimental cylinder. The neutral buoyancy of the larvae was assessed according to the method of Solemdal (1971).

Activity

The response of 50 larvae to different light intensities was observed in a vertical perspex tube 130 cm high and 15 cm in diameter. The vertical tube was contained in a light-proof observation chamber over which was placed an artificial light source with two lamps. The intensity of one of these lamps, a 1000 W halogen lamp, could be varied by an adjustable auto transformer (0 - 220 V). The other lamp was a 60 W tungsten lamp with an infrared filter. The light intensity was measured at the bottom of the tube. The tube was protected against the light source and the surrounding air by a perspex cooling jacket. In darkness the larvae were observed by an infrared sensitive television camera (Fig. 3).

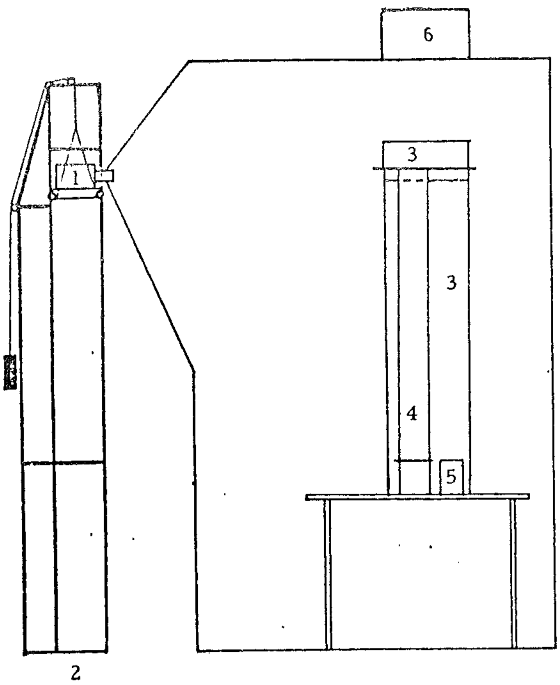

Fig. 3. Outline of the observation chamber
1 : Infrared sensitive television camera. 2 : Camera stand.
3 : Cooling jackets. 4 : Activity chamber. 5 : Photometer.
6 : Light source.

The larval reactions to changes in light intensity was observed after adaption to 14 hours of darkness, when the light was slowly increased from 0 to 80 000 lux followed by a slow reduction to 1000 lux. The amount of larvae showing swimming behaviour associated with searching for food was observed for 15 minutes after two hours adaption to light (1000 lux) (see Table 2). The larval activity and swimming behaviour was observed daily from hatching to subsequent death from starvation.

RESULTS

Buoyancy

Changes in neutral buoyancy of cod larvae from two different females from hatching through the yolk-sac stage to subsequent death from starvation are shown in Fig. 4. After hatching there was a steady increase in the specific gravity of the larvae. The larvae were neutrally buoyant at about 28^{o}/oo salinity at hatching, and they were heaviest at yolk resorption where they were neutrally buoyant at about 34.5^{o}/oo salinity. After the period of yolk resorption the specific gravity decreased and reached a minimum about 13-14 days after hatching where the larvae were neutrally buoyant at about 31-30^{o}/oo salinity. When the larvae became moribund the specific gravity increased again and as the larvae died osmoregulation probably failed and they were negatively buoyant in 34.7^{o}/oo salinity.

Activity

The percentage of larvae at the surface after 14 hours adaption to darkness from hatching through the period of yolk resorption and death from starvation, is shown in Fig. 5. At hatching, 100 per cent of the larvae were at the surface. One day after hatching the number of larvae at the surface decreased, reaching a minimum of less than five per cent on the fourth day after hatching. From this period on, the percentage increased until the thirteenth day after hatching, when more than 80 per cent of the larvae were found at the surface after a period of 14 hours adaption to darkness. On the fourteenth day there was a significant change as the larvae died and sank to the bottom of the tube (Fig. 5, dotted line). Three days later all the larvae were dead.

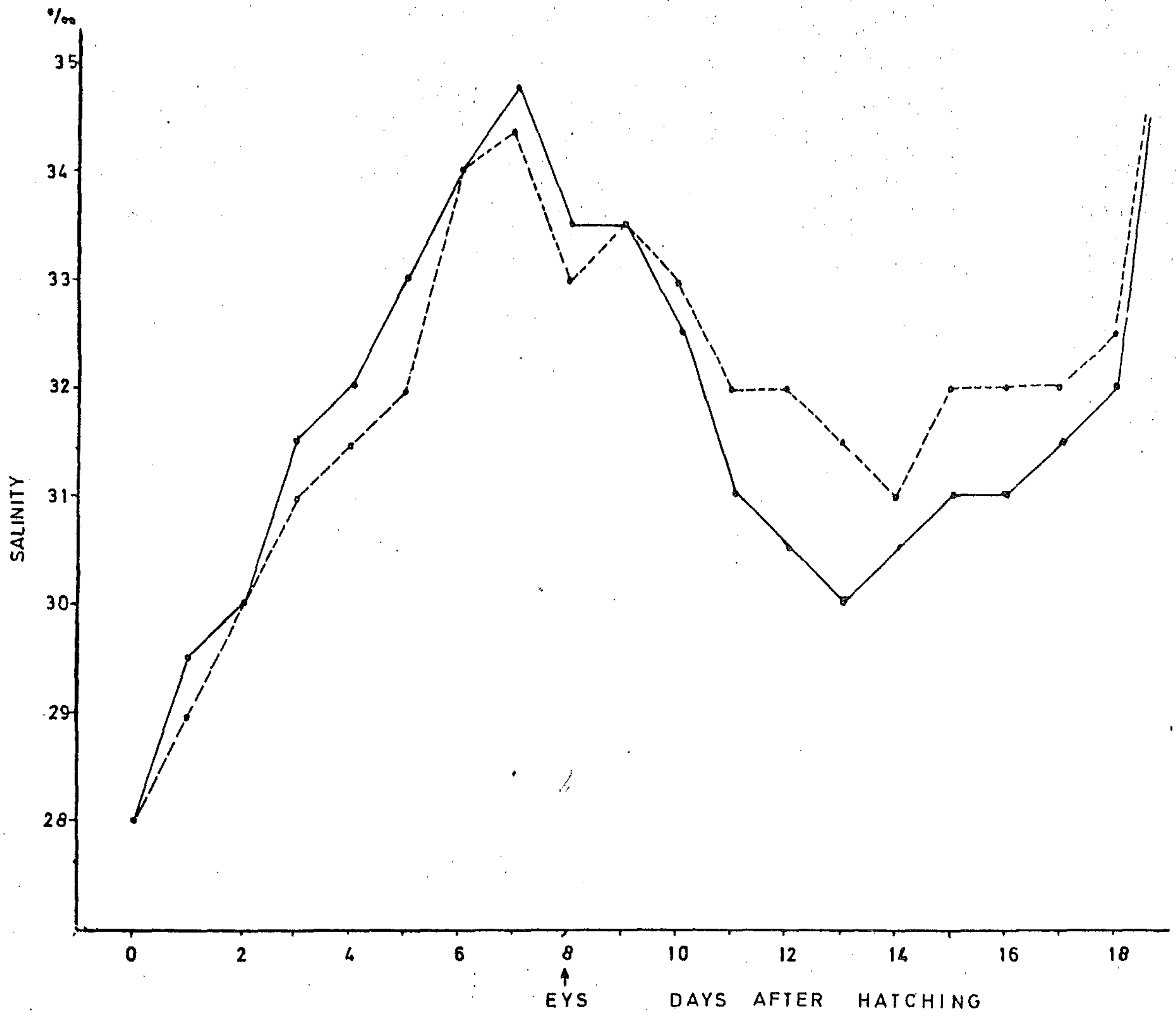

Fig. 4. Changes in neutral bouyancy in the cod larvae from hatching to death from starvation ——— and ------- are based on larvae from two different female fish.

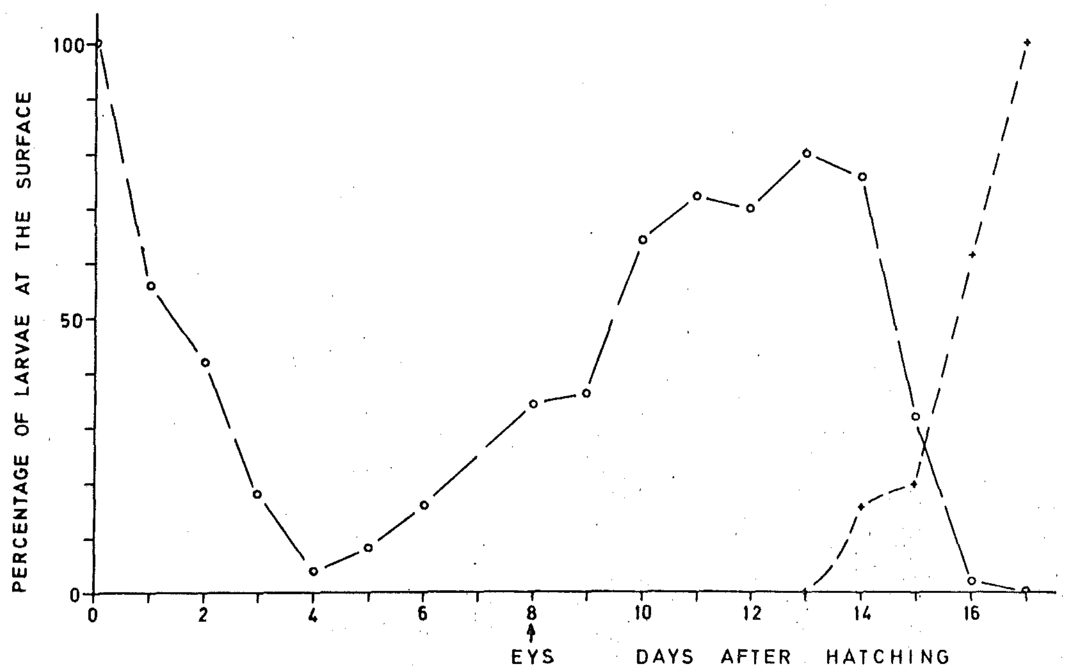

Fig. 5. Percentage of starving cod larvae at the surface from hatching until death from starvation. ------- Percentage of dead larvae on the tube.

The percentage of larvae at the surface (0 - 5 cm), of the column and at the bottom (125 - 130 cm) of the tube after two hours adaption to light at 1000 lux is shown in Fig. 6. From the second day after hatching to the tenth day, about 80 to 90 per cent were found in the column and on the bottom of the tube. Only between 10 and 20 per cent remained at the surface. On the eleventh day the activity of the larvae seemed to decrease and from this day on an increasing number of larvae were found at the surface even after two hours adaption to light. A maximum of 40 per cent was found at the surface on the thirteenth day after hatching. The larvae were then probably becoming truly moribund, because from this stage on they disappeared from the surface and column and were found dying or dead on the bottom. Four days later all 50 larvae were dead.

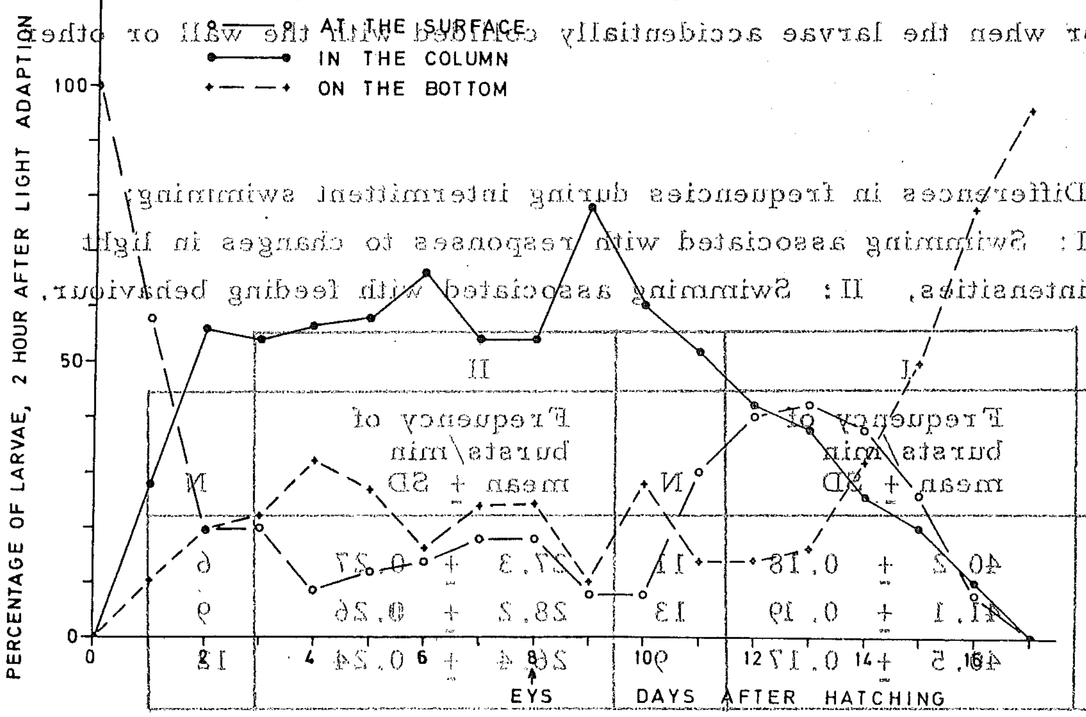

Fig. 6. Larval response to light, from hatching until death from starvation.

Swimming behaviour

During the first 48 hours of larval life the cod larvae exhibited little locomotory activity. Most of the time they floated motionless at the surface. At the end of the second day their activity increased. Three different swimming patterns were observed. The distinctive feature of two of these patterns was that the larvae executed a brief but intense burst of swimming where the tail and body beat from side to side. This burst of swimming lasted for less than one second. The frequency of the two intermittent swimming patterns was different. The highest frequency was associated with active swimming up and down the water column in response to changes in light intensity. The lowest frequency was observed when the larvae started showing feeding behaviour, and was closely associated with larvae searching for food. The frequency typical for these swimming patterns is shown in Table 1. The third characteristic swimming pattern was an avoidance or escape reaction. The larvae swam continuously for several seconds. This reaction was strongly stimulated when tapping the wall of the tube, or when the larvae accidentially collided with the wall or other larvae.

Table 1. Differences in frequencies during intermittent swimming; I: Swimming associated with responses to changes in light intensities, II: Swimming associated with feeding behaviour.

	I		II	
Age in days	Frequency of bursts/min mean ± SD	N	Frequency of bursts/min mean ± SD	N
3	40.2 ± 0.18	11	27.3 ± 0.27	6
4	41.1 ± 0.19	13	28.2 ± 0.26	9
9	40.5 ± 0.17	9	26.4 ± 0.24	12

The larval activity in the dark was studied by using infrared light and an infrared sensitive television camera. After 8 hours adaption to light the intensity was slowly reduced to 0 lux and the IR - light was turned on. The larval swimming activity was significantly reduced and as the larvae were positively buoyant in 34.7°/oo salinity sea water, they slowly rose to the surface. If, on the other hand, the light was slowly increased from 0 to 80 000 lux after 14 hours adaption to darkness and then slowly reduced again to about 1000 lux, the larvae (more than 2 days old) would swim actively towards the surface. This was used to test the response of the larvae to changes in light intensity (Table 2).

The changes in the larval locomotory activity and responses to change in light intensity are given in Table 2 as percentage of larvae showing the above described activities from hatching to subsequent death from starvation.

Table 2. The activity of 50 cod larvae from hatching to subsequent death from starvation showing I: The percentage of larvae performing intermittent swimming associated with responses to changes in light intensity and II: Intermittent swimming associated with feeding behaviour. The percentage of passive unspecified larvae also includes larvae in the "head down" position.

	Activity		Passive		
Age in Days	Per cent intermittent swimming I	Per cent intermittent swimming II	unspecified	"Head" down	Dead
1	0	0	100	0	0
2	48	0	52	0	0
3	80	60	20	0	0
4	93	72	7	0	0
5	91	91	9	0	0
6	89	89	11	0	0
7	85	85	15	0	0
8	85	85	15	0	0
9	92	90	8	0	0
10	92	78	8	0	0
11	71	64	29	0	0
12	60	43	40	0	0
13	57	31	43	6	0
14	23	23	61	26	16
15	19	19	61	32	20
16	0	0	38	16	62
17	0	0	0	0	100

At hatching the cod larvae did not respond to changes in light intensity. After 14 hours adaption to darkness the light was slowly increased from 0 to 80 000 lux and all the larvae then floated more or less motionless at the surface.

The activity of the larvae increased from the second day to the fourth day after hatching when more than 90 per cent of the larvae showed intermittent swimming associated with feeding behaviour. Swimming activity was high throughout the period of yolk resorption until the eleventh day after hatching. On the thirteenth day a marked reduction in activity occurred and the first three larvae were observed in the "head down" position (described by Blaxter & Ehrlich, 1974). Four days later all 50 larvae were dead.

Discussion

The exact determination of the "point of no return" presupposes a successful rearing of the larvae through the critical first feeding stages. This has not yet been accomplished for cod larvae. However, changes observed in the cod larval activity and neutral buoyancy during starvation could indicate the PNR as observed for herring and plaice larvae by Blaxter and Ehrlich, (1974). The changes in neutral buoyancy of cod larvae living on their yolk reserves are very similar to those of plaice larvae observed by Blaxter & Ehrlich (1974). During starvation there was a decrease in the specific gravity of the cod larvae probably due to an increase in water content and protein catabolism. This change in specific gravity increased significantly from the ninth day after hatching, reaching a minimum on the thirteenth to fourteenth day.

The change in activity, i.e. the larval ability to respond to changes in light intensity, decreased from the eleventh day and dropped to less than 50 per cent from the thirteenth to the fourteenth day. At this stage the larvae were truly moribund because from the thirteenth to fourteenth day onwards the specific gravity increased again and the fish larvae in the "head down" position were observed. Marine fish larvae are known to be hypotonic to the surrounding sea water (Blaxter, 1969). The increase in specific gravity at this stage was probably due to breakdown in osmoregulation and the following increase of salt in the body fluid leading to osmotic equiliribrim with the surrounding sea water. At this stage the cod larvae had most probably passed the PNR and had obviously reached a state of irreversible starvation, because three days later all larvae were dead.

If no food becomes available the cod larvae must presumably reach the PNR eight to twelve days after hatching (at 5°C). The PNR is probably close to the twelfth day after hatching, because there was a significant drop in swimming activity associated with feeding behaviour from about 60 per cent on the eleventh day to about 40 per cent on the twelfth day.

SUMMARY

1. Cod larvae living on their yolk reserves showed a steady increase in specific gravity towards the end of the yolk-sac stage. During incipient starvation there was a progressive decrease when the larvae became truly moribund and sank to the bottom. A few days later all larvae were dead.

2. The change in activity was closely related to the changes in specific gravity.

3. Cod larvae responded to changes in light intensity one to two days after hatching. During the period of high activity the larvae did not show active vertical migration towards the surface when light decreased after adaption to 10 hours light. There was a reduction in activity in darkness and the position of the larvae in the water column was dependent upon their buoyancy.

4. The time to reach the PNR was assessed from the changes in buoyancy and activity and was determined to occur close to the eleventh day after hatching or three days after yolk resorption (at 5°C).

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