

The migratory behaviour of yolk-sack larvae of cod, *Gadus morhua*

Uwe Waller & Harald Rosenthal
Institut für Meereskunde an der
Christian-Albrechts-Universität Kiel¹

Abstract

An experimental system was used to observe horizontal and vertical swimming behaviour of yolk-sack larvae of cod in order to assess the importance of migratory behaviour of early larval stages in oxygen depleted water masses, as they frequently occur on Baltic spawning grounds. Two to three day old yolk-sack larvae were placed in a funnel-shaped glass cylinder filled with filtrated seawater (T: 6 °C, S: 10 - 16). The behaviour was recorded with a VHS video system. At the different salinity levels swimming direction and swimming speed during sinking of inactive larvae and during active swimming was calculated from subsequent video frames. The vertical distribution of larvae within the experimental cylinder was registered. The results emphasize an upward-directed migratory behaviour of yolk-sack larvae, whereby salinity may support this behaviour by increasing the buoyancy of larvae.

Introduction

Numerous studies with marine fish larvae had shown that environmental temperature, salinity, and dissolved oxygen level may have significant effects on survival. Examples are summarized by ROSENTHAL & ALDERDICE (1976). For Baltic cod, the low environmental oxygen level appears to be a major problem affecting recruitment at a very early life history stage: Field observations around Bornholm Island revealed that cod eggs are distributed in a depth range with low dissolved oxygen levels (WIELAND 1988) and experimental investigations showed that mortality rates during egg development increases at low oxygen levels (WIELAND, WALLER & SCHNACK 1994). Therefore, survival of cod eggs may have been poor and inadequate in this area for many years.

Even after hatch low environmental oxygen may affect cod larvae. WIELAND & ZUZARTE (1991) found older cod larvae distributed close to the surface indicating an upward movement after hatch. Because swimming activity requires a sufficient oxygen supply a reduced oxygen level in the environment may hinder yolk-sack larvae to approach their feeding areas near to the surface.

This experimental study was set up to begin with a description of migratory behaviour and swimming activity of Baltic cod larvae shortly after hatch.

Material & Methods

Egg and sperm of cod were obtained by stripping fish caught around Bornholm Island, Baltic Sea. The eggs were incubated at salinities between 13.0 and 13.5 and 6 °C temperature.

After hatch the yolk sack larvae were kept in a small recirculating system (40 L) at 13.0 - 13.5 salinity and 6 °C temperature. The water was processed with a mechanical filter, treated with ozone and passed through activated carbon before it was fed back into the holding container. Every day 10 % of the water was replaced.

For the experiments 2 - 3 day old yolk-sack larvae were used which presented typical activity pattern. At the time when the experiments were started the larvae had have an average length of 4.5 ± 0.2 mm.

The experimental apparatus was set up in a temperature controlled laboratory (6 °C). During experiments the larvae were kept in a glass cylinder of 10 cm in height and 6 cm in diameter which was divided into five vertical segments by engraved marks. The cylinder was illuminated from the top through an incandescent lamp. Light intensity at the water surface was set to around 2000 Lux. The behaviour of larvae was observed with a video camera (PAL, 50 frames/s) which was fixed horizontally at the side of the glass cylinder. The video camera was connected to an VHS video cassette recorder and a monitor placed in a separate room so that behaviour of larvae could be observed without disturbance.

The behaviour of larvae was investigated at 10.4, 12.4, 14.0, 14.3, and 15.6 salinity. Prior to the experiments the larvae had adapted to the different salinities for one hour. The larvae were then placed into the experimental chamber and after 15 minutes the behaviour was recorded for a one hour period. The oxygen level during experiments was always close to saturation.

¹Düsternbrooker Weg 20, 24105 Kiel, Germany

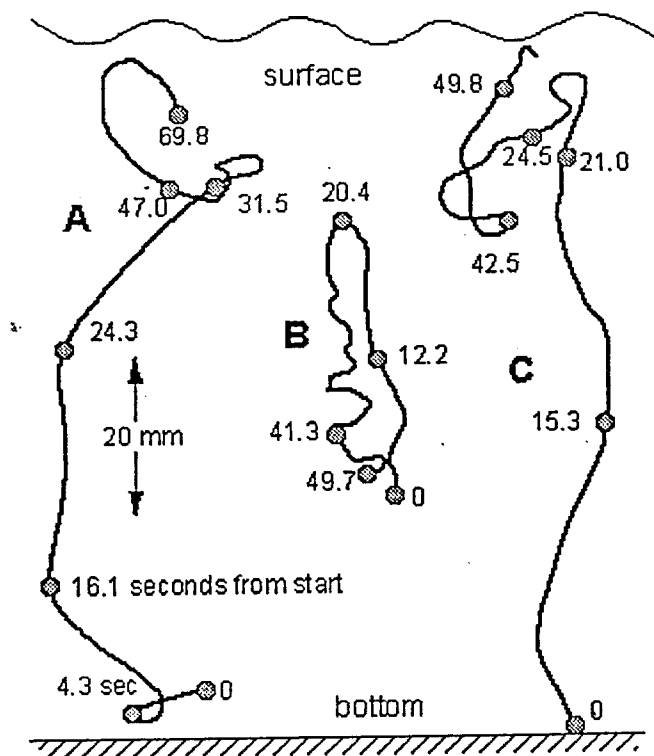


Figure 1: Tracks of individual yolk-sack larvae of cod at 12.5 to 15.6 salinity.

From randomly taken video sequences the number of larvae found in the five different segments of the glass cylinder was counted. The position of larvae on successive screen images was transferred from the screen on transparency film which was used to quantify swimming angle and swimming speed using the time code inserted at the bottom of each video frame. The swimming speed was determined for time intervals of 3 - 6 s. Tracks of individual larvae were obtained by drawing a polygon through positions recorded at different times.

Results

In all experiments yolk-sack larvae were swimming with quick tailbeats towards the surface, whereby periods of activity were followed by periods of rest. The polygons in Figure 1 show characteristic patterns of individual larvae. After short outbursts of swimming activity, which typically lasted less than 30 sec, the larvae were observed to be inactive and slowly sinking towards the bottom indicating that the specific gravity of larvae exceeded that of the ambient water, i.e. of brackish water (≤ 15.6). In some cases the larvae reached the surface (Fig. 1, track A and C), while others were sinking down again to the starting

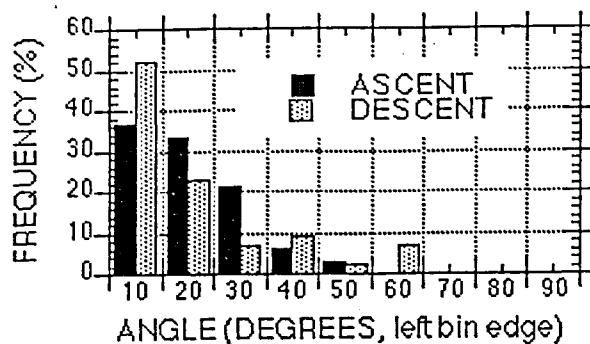


Figure 2: Swimming angle of yolk-sack larvae of cod during inactive sinking (descent) and during active swimming (ascent): $0^\circ \rightarrow$ body axis horizontal, $90^\circ \rightarrow$ body axis vertical.

point (Fig. 1, track B). The upward movement of yolk-sack larvae was always the result of swimming activity and sinking during inactivity.

During ascent one third of the observed larvae was swimming almost perpendicular, i.e. the angle between body axis and the vertical axis was less than 20° (Fig. 2). The rest of the larvae were swimming diagonally. No larvae swimming in an angle less than 60° , that is in a nearly horizontal orientation, were observed. The head of larvae was always orientated towards the surface.

During sinking more than 50 % of the observed larvae were orientated head first and nearly parallel to the vertical axis (angle between body axis and vertical axis $< 20^\circ$, Fig. 2). The rest of the larvae were in a diagonal orientation which may reduce the sinking speed due to a higher hydrodynamic resistance. However, no larvae were observed in an almost horizontal position. Thus, the results provide no hints that larvae attempted to increase their hydrodynamic resistance by tilting the body axis in a more horizontal position. Whether the pectoral fins were used to reduce sinking speed could not be observed with the available optical equipment.

The sinking speed of larvae was depending on the experimental salinity. At a salinity of 10.4 the larvae were sinking at 1.5 - 2.6 mm/sec or 0.3 - 0.6 bodylength/sec². The average speed amounted to 2.2 mm/sec or 0.5 bl/sec. At the highest salinity tested (15.6) the sinking speed decreased to 0 - 1.2 mm/s and the average speed amounted to 0.6 mm/sec or roughly 0.1 bl/sec. The relationship between salinity and sinking speed of yolk-sack larvae can be described with a linear function (Fig. 3):

²bodylength/sec=bl/sec

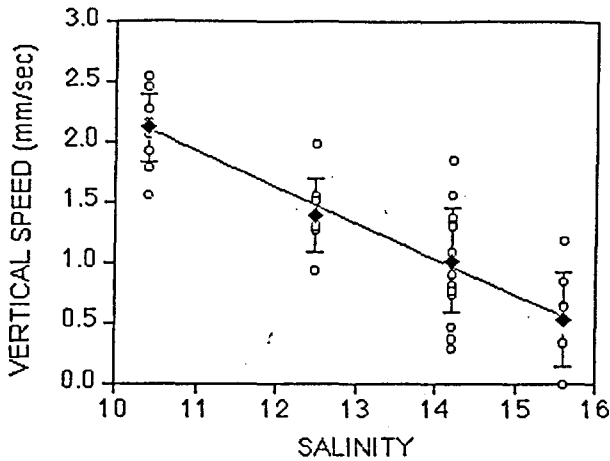


Figure 3: Sinking speed of inactive yolk-sack larvae of cod.

$$Y = -0.295 X + 5.166, n = 44, r^2 = 0.713, p < 0.05$$

From the linear regression the salinity at which yolk-sack larvae achieve neutral buoyancy could be estimated: by rearranging the equation and solving it for a sinking speed = 0 it results a salinity of 17.5. However, this is a rough estimation for yolk-sack larvae which had adapted to the test salinities only for a one hour period.

The swimming speed (vertical and horizontal vector) ranged between 1.5 and 6.7 mm/seconds in all experimental salinities clearly exceeding the sinking speed. The average speed at salinities between 10.4 and 15.6 amounted to 4.3 mm/s (± 1.3 mm/s) or 0.9 bl/sec which was nearly double the sinking speed. The vertical speed was 4.0 (± 1.2 mm/s) on the average. No significant differences could be found for the swimming speed at the different experimental salinities (H-test, $p = 0.05$).

The vertical distribution of larvae was depending on the salinity. At the lowest salinity level (10.4) roughly 60 % of the larvae were observed at the bottom compared to 18-24 % at the highest salinity levels (14.2 and 15.6, Fig. 4). Only 30 % of the larvae were swimming at the surface at 10.4 salinity compared to 53-63 % at 14.2 and 15.6 salinity. At 12.5 salinity 47 and 42 % of the larvae were found at the bottom and at the surface, respectively. All this implies that a higher ambient salinity may support the upward migration of yolk-sack larvae. However, the salinity for a neutral buoyancy of yolk-sack larvae was estimated around 17.5 salinity so that in this experiment inactive larvae were sinking, even at the highest salinity levels (15.6). Thus, the swimming performance of larvae mainly determined the migratory success in these experiments.

POSITION

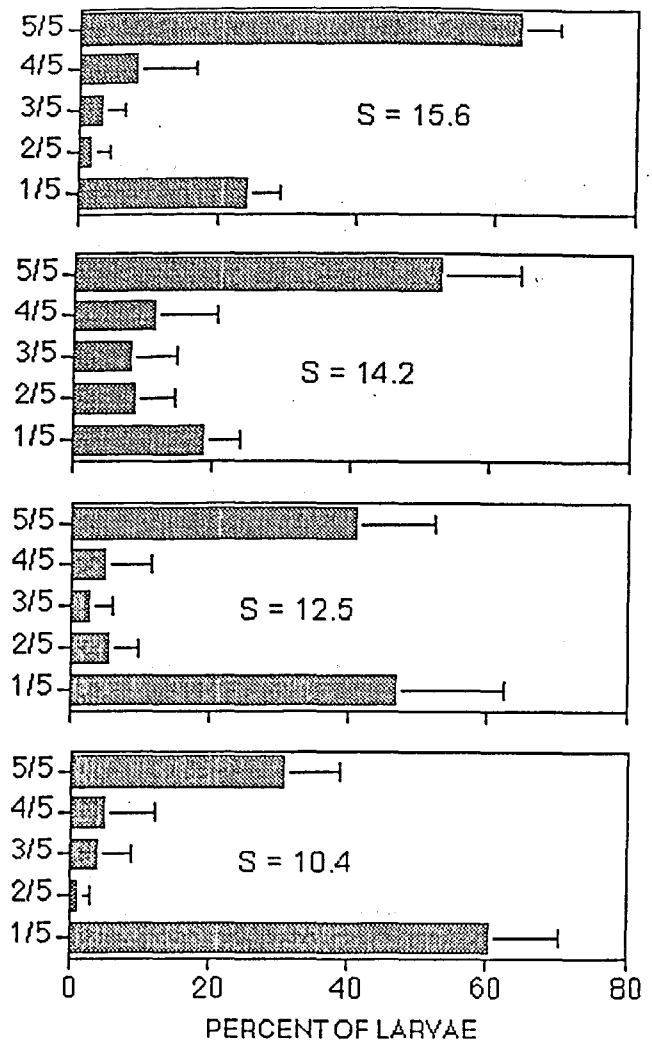


Figure 4: Vertical distribution of cod larvae at different salinities. The experimental chamber was divided into five segments. 5/5: larvae observed at the surface, 1/1: larvae observed at the bottom.

Discussion

The typical swimming behaviour of yolk-sack larvae of cod was characterized by a change of activity and inactivity which is in agreement with the results of SKIFTESVIK (1992). This behavioural pattern seems to be wide spread in fish larvae and it is described for *Clupea harengus* (ROSENTHAL 1968) and *Hippoglossus hippoglossus* (PITTMAN, SKIFTESVIK & BERG 1990).

Resting larvae were never observed in an almost horizontal position which would reduce sinking speed and therefore support the upward directed swimming behaviour. They always were completely inactive so that their orientation in space appeared to be de-

terminated only by external forces. Thus, it is to expect that larvae will turn in a position determined by their center of gravity, if they remain inactive for longer periods. Because the height of the experimental chamber did not allow to observe larvae for longer times, these experiments are preliminary and need to be redone in a larger experimental set-up.

The average swimming speed found in these experiments (4.3 mm/s or 0.9 bl/s) compares well to the swimming speed of cod larvae (1 bl/s) reported by (SKIFTESVIK 1992). It is lower than the highest mean cruising speed for cod larvae (1.7 bl/s) measured by YIN & BLAXTER (1989). The maximum cruising speed (5.7 bl/s) and the escape speed (7 and 15 bl/s) reported by YIN & BLAXTER (1987) for cod larvae was never reached in this study. It can be assumed that the measured swimming speed (1.2 – 6.8 mm/s or 0.3 – 1.5 bl/s) reflect well the routine speed of 2-3 day old yolk-sack larvae.

The sinking speed of inactive yolk-sack larvae ranged between 0 and 0.6 bl/s. At high ambient salinities the larvae were sinking slowly, while at lower salinities the sinking speed was high. The swimming speed did not change at the different experimental salinities and was always in the range between 0.3 and 1.5 bl/s clearly exceeding the measured sinking speed. Therefore, yolk-sack larvae could approach the surface, even if they were resting for certain periods of time. A high salinity of the water may have supported the upward movement by reducing the sinking speed.

Because salinity on the Bornholm spawning ground is typically below 17, i.e. below the salinity required by yolk-sack larvae to achieve neutral buoyancy, and decreases towards the surface, yolk-sack larvae must actively swim to the surface. But, the swimming activity of Baltic cod larvae may be affected by low environmental oxygen levels on the spawning ground. Swimming generally requires a sufficient oxygen supply. Further, the relationship between energy demand and swimming speed of fish larvae follows a power-function (KAUFMANN 1990) implying that the oxygen uptake is steeply increasing at higher swimming speeds. Even if it is yet unknown in which way reduced oxygen levels affect swimming activity of cod larvae, investigations with other fish larvae showed that swimming activity of larvae decreases at low ambient oxygen levels (KAUFMANN & WIESER 1992). NISSLING (1993) observed cod larvae to be mostly inactive and moribund at reduced dissolved oxygen levels, so that larvae may not be able to swim at all. Thus, it is unlikely that cod larvae are able

to approach the feeding areas in oxygen depleted water masses, as they frequently occur on the Bornholm spawning ground (WIELAND 1988, WIELAND, WALLER & SCHNACK 1994).

However, migratory behaviour of cod larvae in their natural environment is almost unknown. Future experimental studies as well as field studies should focus on distribution, migratory patterns, and energetics of yolk-sack larvae under simulated low oxygen conditions.

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