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Impact of physical environment on the behaviour of cod larvae

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The behavioural development of unfed cod larvae from hatching until death due to starvation and the behaviour of fed cod larvae beyond metamorphosis were studied by means of a PC-aided video system. The development of activity, mean swimming speed, and swimming speed in active periods were found to be closely related to the different stages of morphological development. Cod larvae kept in a natural light regime showed a diel rhythm in activity. Experiments with cod larvae kept at different levels of light intensity from hatching to death by starvation showed that light level strongly influenced both the spatial distribution and the longevity of larvae.

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Introduction

Morphological and behavioural development of larvae are, to a large extent, adaptations to the habitat they occupy. The habitat preference of fish larvae is a compromise between risk of starvation and risk of predation (Aksnes and Giske, 1990). Vertical migration can be understood as a diel habitat shift resulting from changes in both the costs (predation risk) and benefits (food availability) (Dill, 1987).

In Lofoten waters, the majority of first-feeding cod larvae are distributed in the upper 30 m (Ellertsen *et al.*, 1990), and their maximum concentration has been found between 10 and 25 m depth (Gjøseter and Tilseth, 1982). Ellertsen *et al.* (1984) found that cod larvae carry out diel vertical migration during calm weather conditions.

In order to respond to changes in the risk of predation, an animal needs to collect information regarding the risk. If, however, such information is prohibitively costly to obtain (e.g., entails a high probability of being preyed on), evolution will favour fixed behaviours (Sih, 1987). Given the sighting distance of a half to one body length (Solberg and Tilseth, 1984), we can assume that fish larvae in early stages will not obtain information about the predator density. They will thus react in a fixed manner towards factors that can change the relations between themselves and their predators. Light is the physical factor generally believed to be of greatest importance in the determination of behaviour and spatial distribution of fish larvae with respect to prey and predators (Woodhead, 1966; Blaxter, 1975; Batty, 1987).

The objectives of this study are to describe the behavioural development of starved and fed cod larvae, and to show how the diel change in light intensity influences the activity of the larvae. The results are discussed with a view to observations from the natural environment.

Materials and methods

For all experiments naturally spawned eggs from the cod broodstock at Austevoll Aquaculture Research Station were collected (according to Huse and Jensen, 1983) and incubated in 250-l incubators at temperatures between 3 and 5°C. Day 0 was defined as the point at which 50% hatching had occurred.

Experiment 1: Behavioural development

The eggs were transferred to 70-l observation chambers one day prior to estimated hatching. One group of 1500 larvae was starved and died out by day 15. The other group of 1500 fed larvae was studied to day 68. At that time, cannibalism had made an impact on mortality, but 98 larvae were still alive when the experiment was terminated.

The fed group of larvae was given cultivated rotifers (*Brachionus plicatilis*) and *Tisbe* sp. nauplii during days 4–35 and zooplankton collected from the sea thereafter. The temperature was maintained at 5°C and at salinity 34. Approximately 15% of the water was renewed daily. The light intensity was 300 lux at the surface.

Two categories of behaviour were defined: swimming and resting. Activity was defined as the percentage of

time spent swimming during the total observation time. Swimming speed during activity periods was defined as the average speed from commencement of activity to its cessation and was measured in millimetres per second. Measurements were obtained from 10 randomly chosen larvae during each observation period.

Behavioural studies were conducted using a computer-aided video system, allowing three-dimensional measurement of the position of the larvae in 70-l observation chambers (for a more detailed description, see Huse and Skiftesvik, 1985, 1990). Each of 10 randomly chosen larvae was tracked for 5 min and their position and behaviour logged each second.

Experiment 2: Mortality and distribution in relation to light intensity

In experiment 2, 400 larvae were transferred to each of the two parallels kept at the following levels of light intensity: 1250 lux, 250 lux, 2.5 lux, and darkness. The larvae were transferred to the 10-l experimental units at day 1 after hatching. Dead larvae were siphoned out and counted every day throughout the experiment. The larvae were not fed. The temperature was between 4.5 and 5°C, and the salinity was 34.

Experiment 3: Growth in relation to light intensity

In experiment 3, 400 larvae were transferred to each of the five parallels kept at the following levels of light intensity: 1000 lux, 100 lux, 10 lux, and darkness. The larvae were transferred to the 10-l experimental units at day 1 after hatching. The temperature was about 5°C, and the salinity was 34. The larvae were not fed. At days 3, 6, 9, 11, 13, 16, 18, and 20, or to the time when the group died, 24 randomly chosen larvae from each group were sampled for morphometric measurements. Notochord length and myotomal height were measured on live larvae, and thereafter the larvae were washed in distilled water and frozen. After being freeze-dried, the total larval dry weight was measured on a Metler M 3 electrobalance.

Experiment 4: Measuring the larval activity through day and night

In this experiment, 25 larvae were transferred at day 1 to a 100 ml unit with seawater of salinity 34 for activity registration by use of linear array ultrasonographic equipment. The equipment presents the echoes reflected from larvae at a 1 mm wide cross-section. Activity was defined as the number of larvae penetrating the cross-section per unit time. The 100 ml unit was held in a water bath with running water of 8.5°C (Fig. 1). The water bath was placed outdoors in the shade, and the weather was cloudy during the experiment. The light intensity did not exceed 2000 lux. Registration of larval activity lasted 5 days and started at day 2. The larvae were not fed, and no larvae died during the experimental period. The experiment was carried out at the Austevoll Aquaculture Research Station, which is situated at 60°6′N 5°14′E, during the period 10–14 April 1992.

Results

Behavioural development

Activity was below 10% in the first three days after hatching, but rose to above 30% on day 4 in the fed group when the prey was introduced (Fig. 2A, B). The unfed group rose to about 30% on days 6–7. Thereafter, the activity decreased gradually to approximately 2% on day 14, the day before mass mortality (Fig. 2B). The fed group showed an increase in activity to a level of about

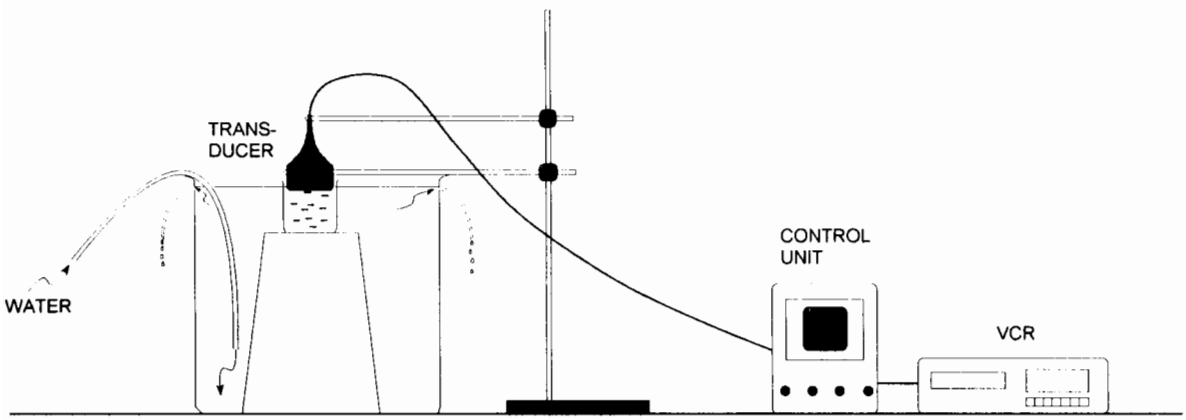

Figure 1. Layout of the experiment system used in Experiment 4 for ultrasonographic registration of larval activity.

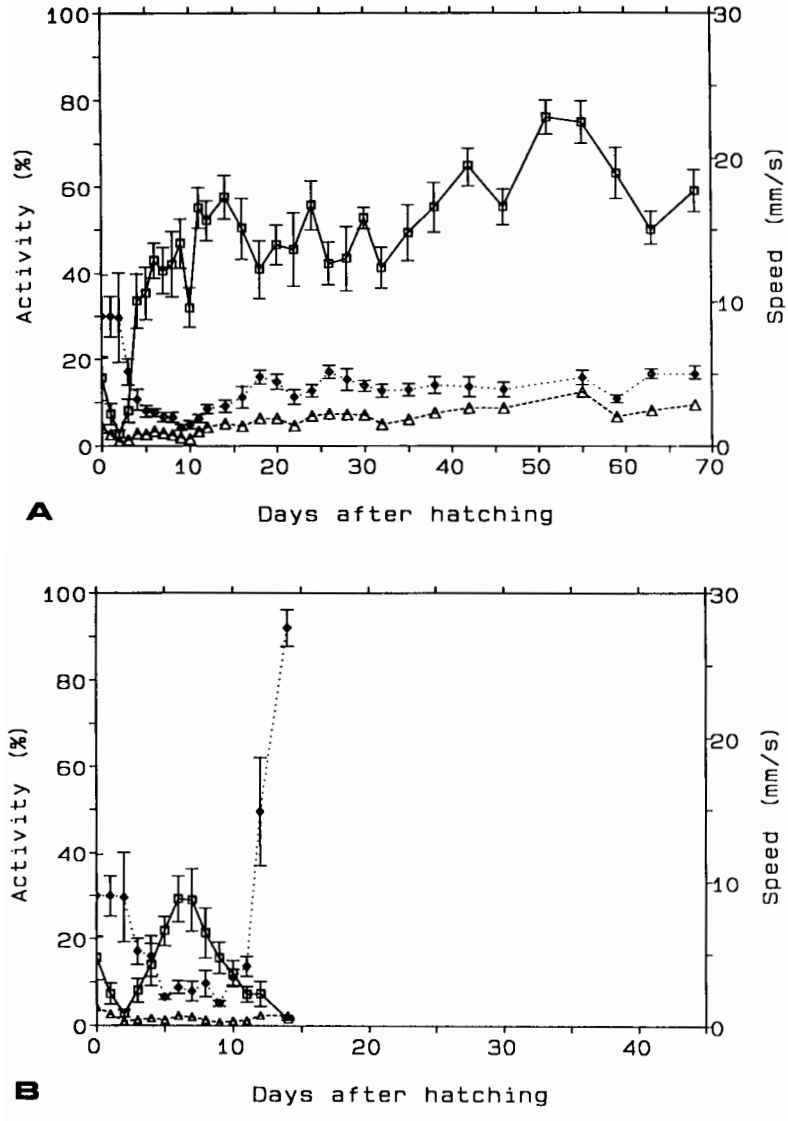

Figure 2. A. Development of activity measured as the percentage of time the larvae were swimming (solid line), swimming speed in active periods (dotted line), and mean swimming speed (dashed line) of fed cod larvae. Each point is the mean and standard error of 10 larvae. B. Development of activity measured as the percentage of time the larvae were swimming (solid line), swimming speed in active periods (dotted line), and mean swimming speed (dashed line) of starved cod larvae. Each point is the mean and standard error of 10 larvae.

40%, and remained at this level until day 35, with a slight increase thereafter (Fig. 2A).

Swimming speed during the active periods decreased from about 9 mm s^{-1} during the first few days to about 5 mm s^{-1} on day 4 (Fig. 2A, B). In the fed group, swimming speed during the active periods decreased further, and was steady at around 2 mm s^{-1} until day 11. After day 11, swimming speed during active periods increased gradually to just below 5 mm s^{-1}, and remained there for the rest of the experimental period. In the unfed group, swimming speed during the active period increased to more than 25 mm s^{-1} at day 14. The mean swimming speed (swimming distance × $time^{-1}$) showed a gradual increase throughout the experimental period (Fig. 2A, B).

Based on the observations made, there was no indication that actively swimming cod reacted to prey. They reacted to prey items when they had a stop in their active swimming, sometimes even while occasionally still moving. When a prey item was located, and the prey was in the right position, the cod larvae could suck it into the mouth. If the prey was in an unfavourable position, the cod larva could manoeuvre itself to another position in relation to the prey.

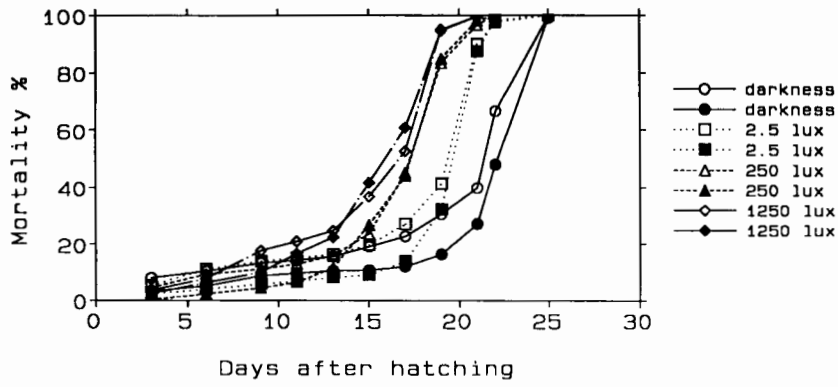

Figure 3. Mortality (%) of cod larvae in relation to light intensity during incubation.

Effect of light intensity on longevity of starving cod

Mortality rate of cod at different levels of light intensity

Mortality was low throughout the first two weeks, but increased thereafter (Fig. 3). It rose first in the groups exposed to the highest level of light, followed by the 250 lux groups, the 2.5 lux groups, and, finally, the darkness groups.

Larval distribution in different levels of light intensity

Larvae from different light intensity groups did not show similar vertical distribution. An increase in light intensity caused the larvae to move down in the water column, as they were observed at the bottom (Fig. 4). The number of larvae in the water column and the length of time they were spread in the water were dependent on the light intensity.

Growth at different levels of light intensity

Length varied significantly in accordance with treatment, with the exception of day 6 (ANOVA one-way, $p < 0.05$). The larvae kept in darkness were longer than the others. Development of larval length of unfed larvae kept at different levels of light intensity is shown in Figure 5A. At day 3, the larvae from the darkness group were significantly longer than those kept at 10 and 1000 lux, and the larvae of the 100 lux group were significantly longer than those at 1000 lux. There were no differences between the groups at day 6. At day 9, larvae in the 100 lux group were shorter than those kept at 10 lux and darkness. At day 11 there was only one significant difference, between 100 lux and darkness. At day 13, larvae from the darkness group were significantly longer than the groups kept at 10 and 100 lux. Three days later, the larvae of the darkness group were significantly longer than those of all other groups, and the 100 lux

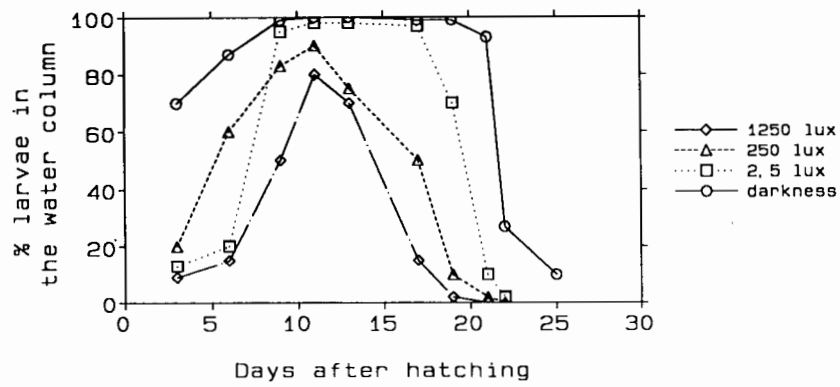

Figure 4. Percentage of cod larvae in the water column in relation to light intensity during incubation.

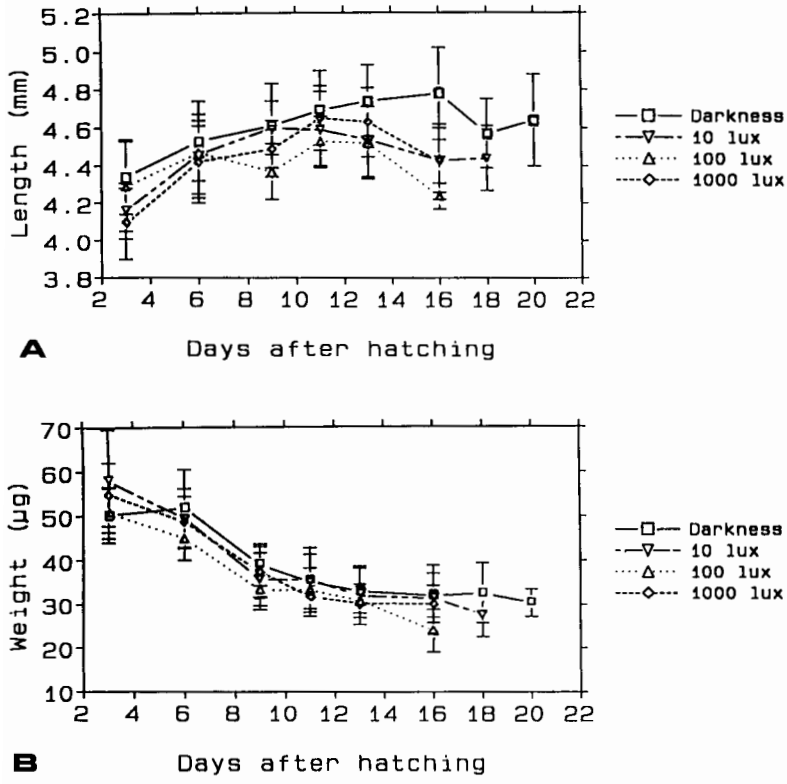

Figure 5. A. Body length of unfed cod larvae in relation to light intensity during incubation. B. Dry weight of unfed cod larvae in relation to light intensity during incubation.

group was significantly shorter than the others. The 100 and 1000 lux groups died before the next measure. At day 18, the darkness group was still longer than the 10 lux group. At day 20, only the darkness group was alive.

Myotomal height varied significantly in accordance with treatment, with the exception of day 9 (ANOVA one-way, $p < 0.05$). At day 3, the larvae of the darkness group were significantly higher than those of the group 1000 lux, and also higher than the 100 lux group at day 6. No differences between groups were found at day 9. Larvae from the darkness group were significantly higher than those from the 100 lux group at days 11 and 13. At day 16, the larvae of the darkness group were significantly higher than those of all the other groups.

Dry weight of the larvae varied significantly in accordance with treatment, with the exception of days 11 and 13 (ANOVA one-way, $p < 0.05$). The larval dry weight is shown in Figure 5B. At day 3, larvae from the 10 lux group had a significantly higher weight than those kept in darkness. The larvae in the darkness group were significantly heavier than those in the 100 lux group at days 6 and 9. No differences were found between the groups at days 11 and 13. At day 16, the larvae from the 100 lux group had a significantly lower weight than larvae from the other groups.

Diel activity of cod larvae

The larvae did not respond to changes in light intensity in the first few days after hatching. From day 3, they had more activity at day than at night (Fig. 6).

Discussion

The development of larval activity, swimming speed, and thereby swimming distance are determined in nature through a selection process and reflect the demand of the larva for food and the requirement of protection against predators. Starvation and predation are the main agents of larval mortality in nature (Hunter, 1976). A laboratory situation may be different in many respects from the natural environment. However, behavioural studies indicate that behaviour in early larval stages is a set of fixed responses triggered by given factors. In addition, to survey the environment for predators would be difficult for a larva with a visual distance of only about 5 mm.

Changes in the behaviour of the larvae may also indicate a change in their demands. The change of swimming mode found at time of start-feeding (Skiftesvik, 1992), as can also be seen in Figure 2, reflects the

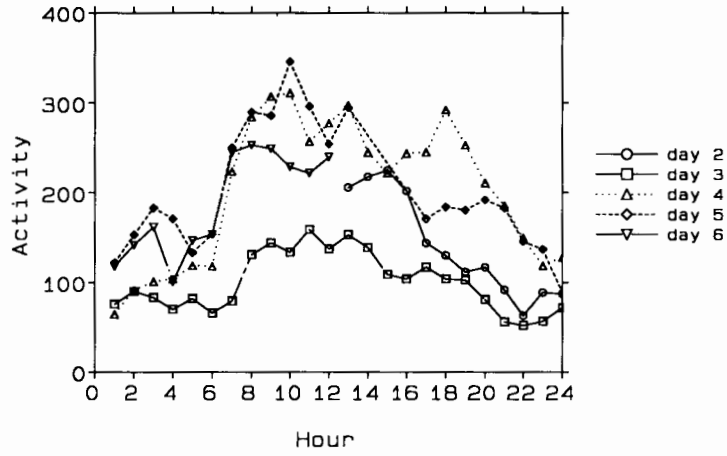

Figure 6. Diurnal activity of cod larvae on days 2–6 after hatching. Activity is measured as the number of times larvae were swimming through an ultrasonic plane.

need for exogenous food. When the larvae start to look for prey, they decrease swimming speed and increase activity. An increase in activity presumably renders the larvae more visible to predators. Moving prey can be detected more easily than motionless prey (Kislalioglu and Gibson, 1976). In studies cited by Sih (1987), reduced activity was a typical antipredator response. Therefore, when the larvae start to search for food, they expose themselves to greater risk of predation.

When cod larvae are ready to start-feed, they increase activity and decrease swimming speed. If they do not find any prey, they reduce their activity. Reduced swimming activity of unfed cod larvae was also found by Ellertsen *et al.* (1980). Low activity implies reduced consumption of energy; thus, reduced activity may delay the point-of-no-return. The change in neutral buoyancy of cod larvae was registered by Ellertsen *et al.* (1980), and the period when the cod larvae were heaviest corresponds with the time the unfed cod larvae reduce their activity. It may be that starving larvae will separate from the fed ones in their natural environment.

Like most marine fish larvae, cod larvae are visual feeders (Ellertsen *et al.*, 1980) and active feeding occurs only above a certain light intensity (Blaxter, 1966). The visual abilities of fishes varies interspecifically (Nicol, 1989) and during development (Blaxter, 1986). Ellertsen *et al.* (1976, 1980) found that cod larvae were able to capture *Artemia salina* nauplii at 0.4 lux, but not at 0.1 lux. So the cod larvae in experiments 2 and 3 would be able to feed in all the light intensities used except darkness. Registration of light intensity from the surface to 40 m depth during 24 h in May in Lofoten was carried out by Gjøsæter and Tilseth (1982). Light intensities below 0.4 lux were observed only at night and only in the deepest part of the registration area. However, a reduced feeding intensity at night is reported by Tilseth and Ellertsen (1984).

The level of light intensity influences larval activity, and can also influence their distribution in the water. In Lofoten, Ellertsen *et al.* (1984) found that cod larvae show diel migration only during calm conditions. When they migrated vertically, they were in the lower part of their distribution field during the day and in the upper part at night, as is the case with many other vertically migrating aquatic organisms (Clark and Levy, 1988). The larvae kept in darkness in experiment 2 were, for most of the experimental period, distributed throughout the water column. In the other groups, the larvae within the water column were fewer, and they were there for a shorter period of the experiment. The number of freely swimming larvae in the water column decreased with increasing light level. As reported by Ellertsen *et al.* (1980), this observation indicates a negative phototaxis.

Larvae kept at different levels of light intensity had different body shapes. Those kept in darkness were significantly longer than those of the other groups and they were also among the highest. Dry weight, however, was not different from the others after day 11, except from the 100 lux group at day 16. It can be assumed that increased swimming activity will give the larvae more muscles and thereby a broader body shape. Zeutzius and Rahmann (1984) found that dark-reared larvae of Tilapia had a different body shape from the control fish; they had an increased body depth.

The shortening of lifetime of the larvae with increased light intensities in experiments 2 and 3 indicates a higher energy consumption when light intensity increases. On the basis of the results from experiment 4, diel activity of the larvae, the shorter lifetime of the larvae in light conditions is probably a result of increased activity. This

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