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Effects of light on the development, activity and mortality of halibut (Hippoglossus hippoglossus L.) yolk sac larvae.

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ABSTRACT

Halibut yolk sac larvae were kept at different light intensities from Day 1 posthatch. Measurements of activity and swimming speed showed that larvae that were kept in darkness were more active, but had lower swimming speed than those kept in light. Larvae kept at 1000 lux had lower yolk sac utilization than larvae kept at lower light intensities, probably due to stress caused by light. Larvae kept at 1 and 10 lux had higher body dry weight when the experiment was terminated. Differences in pigmentation were found. An autecological model is discussed, suggesting that halibut yolk sac larvae are distributed in relatively shallow waters during the first week posthatch, thereafter sink into deeper waters, and rise again when the time of first feeding approaches.

INTRODUCTION

Different species of fish larvae occupy different depths (Russell 1976, Kinne 1982) and their distribution may change as development proceeds (Brewer and Kleppel 1986). Some species show vertical migration, others do not. Some species are

stationary at some stages but migrate at other stages of development (Kuwahara and Suzuki 1984, Castonguay and McCleave 1987, Gartner et al. 1987). Avoidance of predators and searching for food are the most important factors determining different strategies (Dawkins 1976), also for fish larvae (Hunter 1981).

Some physical factors may determine larval behaviour. The factor which is generally believed to be of greatest importance is light, with its variations in intensity, wavelength, polarization, diurnal and seasonal variation and contrast (Woodhead 1966, Blaxter 1975, Batty 1987). In aquaculture, the larvae often have no opportunity to select a light intensity by changing their distribution, and their activity levels may be directly related to the characteristics of the light (Batty 1987). This in turn affects yolk utilization and growth efficiency.

The purpose of this study was to investigate the effects of different light intensities on halibut larvae throughout the yolk sac stage. Larval growth, behaviour and pigmentation was studied. Mortality and bacterial numbers in the incubators was monitored throughout the experiment. Results are discussed in relation to larval autecology and aquaculture.

MATERIALS AND METHODS

Husbandry

Eggs from one female were fertilized with sperm from two males of the halibut broodstock at Austevoll Aquaculture Research station. The eggs were reared in incubators as described by Jelmert and Rabben (1987) at 6-7°C until just before hatching. Then the eggs were transferred to 10 l plastic buckets. The buckets were filled with seawater piped from 55 m and filtered through a sand filter, UV radiated and a 0.2 um microfilter. There were five groups, each of which had 6 incubators. Group A was kept in darkness, whereas the other groups were exposed to light of the following intensities: 1 lux (B), 10 lux (C), 100 lux (D) and 1000 lux (E). All groups were kept in a room cooled to 5°C. Approximately 50 larvae were transferred to each incubator at Day 1 after hatching. Day 0 was defined as when 50% of the eggs had hatched. The water in the buckets was changed once a week.

Sampling

Samples were taken once a week for behavioural studies, measurements of dry weight, myotomal height, length, pigmentation and enumeration of bacteria. One

to two incubators in each group were terminated in each successive week of treatment, for complete analyses of the environmental status. Mortalities were removed at Days 4, 11, 16, 18, and 23.

Statistical testing

Testing for statistical significance was done with Student's t-test.

Enumeration of bacteria

Samples for total counts of free-living bacteria were taken from each incubator once a week at the same time as the other samplings. Water samples were fixated in glutaraldehyde to final concentration of 2.5%, and stored until further processing. The fixed samples were stained with 4'6-diamidino-2-phenylindole (DAPI) (Porter and Feig 1980), filtrated on 0.2 um Nuclepore filters and counted in a Nikon epifluorescence microscope, operated at 600x.

Behaviour

Behavioural studies of larvae were conducted using a computer-aided video system, allowing three-dimensional registration of the larvae in 19 l observation chamber (system decribed in Huse and Skiftesvik 1990). Temperature was maintained at 5-6° C. From each light intensity group, 25-30 larvae were sampled at day 8, 15 and 22, and transferred as a group to the observation chamber holding the same light level. The larvae were acclimated one hour before the observation started. Each of ten randomly chosen larvae in a group were observed for five minutes during an observation period. Measurements of activity levels (percent of swimming time during the observation time where 100 % is equal to continuous swimming) were taken, as well as mean swimming speed of total time and mean swimming speed of active time.

Morphometric measurement

From each light intensity group, 24 larvae were taken for morphometric measurement. Notochord length and myotomal height were measured on live larvae, then the larvae were washed in distilled water and frozen. The yolk sac and larval body were separated after being freeze-dried, and weight were measured on a Metler M 3 electrobalance weight.

Pigmentation and stage of development was recorded from ten live larvae from each group, using a Wild Heerbrug dissecting microscope. Larvae were then fixed in cacodylate-buffered glutaraldehyde for later mapping of pigment patterns.

RESULTS

Behaviour

Level of activity for all groups is shown in Figure 1. At Day 8, larvae of Group A (darkness) showed significantly higher activity than all other groups ($p<0.05$). Larvae of Group E showed significantly lower activity than larvae of Groups C and D. ($p<0.05$). By Day 15 after hatching, the larvae of Group A showed significantly higher level of activity than larvae of Groups C and E. ($p<0.05$). By Day 22, there were found no significant differences among the groups with respect to activity.

Mean swimming speed in periods of activity is shown in Figure 2. By Day 8 and Day 22, no significant differences among the groups were found. By Day 15, mean swimming speed during active periods was significantly lower in Group A compared to Group D ($p<0.05$).

Mean swimming speed is shown in Figure 3. By Day 8, Group A showed significantly higher mean swimming speed, compared to Group E ($p<0.05$). By Day 15, the larvae of Group D had significantly higher mean swimming speed compared to all other groups ($p<0.05$). At Day 22, the larvae of Group A had significantly lower mean swimming speed than the larvae of Group B ($p<0.05$)

Growth

The mean dry weight (N = 24 larvae) of larval body, yolk sac and total weight are shown in Figure 4.

Day 8 after hatching only the weight of larval body in group D was significantly higher than the larvae in group A and E ($p< 0.1$). Day 15 after hatching the dry weight of the larvae of group B was significantly higher than the larvae of group A, D and E, and the larvae of group D had significantly higher dry weight than the larvae in group A ($p<0.1$). By Day 22, the dry weight of larvae in group B and C were significantly higher than for the larvae in group E ($p<0.1$).

On Day 8 after hatching, the mean dry weight of the yolk sac in group D was lower than the dry weight of the larvae of group A, B, C and E ($p<0.1$). The yolk sacs of the larvae in group E were significantly higher than in group B, C and D. On Day 15 after hatching, the yolk sac dry weight of the larvae of group D were significantly lower than the dry weight of the yolk in group A, B and E ($p<0.1$). The larvae of Group A had a significantly higher dry weight of the yolk sac than

Groups C, D and E. The yolk sac dry weight was significantly higher in Group B than Group C and E, and the yolk sac dry weight of Group C was higher than in Group E ($p<0.1$). On Day 22, the yolk sac dry weight of the larvae of Group A was significantly higher than in all other groups, and B had a higher yolk sac dry weight than Groups D and E ($p<0.1$).

Total dry weight

On Day 8 after hatching, the total dry weight of Group E is highest, however, there were no significant differences in total dry weight among the different groups ($p<0.05$). Seven days later, the larvae of Group E had significantly lower total dry weight than all the other groups. On Day 22 after hatching, the larvae of Group E had significantly lower dry weight than Groups A and B ($p<0.05$).

Bacteria

Mean numbers of total counts of bacteria for each group is shown in Figure 5. There were found no significant differences among the groups at any time. Variation within groups was large, as is shown in Table 1.

Mortality

Cumulative mortality of all groups throughout the experiment is shown in Figure 6. Mortality was negligible before Day 11. Between Days 11 and 16, however, mortalities begin to increase in Groups B, D and E. This is due to one outlier within each of the groups, as the only groups which did not include one incubator with high mortality were Groups A and C.

At Day 19, however, all groups were found to include 1-2 additional incubators with high mortality, this resulting in the increased mean mortality which is shown in Figure 6. When the experiment was terminated, at Day 23, the mortalities were highest in the group kept in darkness, followed by the group kept at 1000 lux. The highest survival (60%) was in Group D (100 lux).

Pigmentation

There were differences in intensity and pattern of pigmentation already eight days after hatching. At 1000 lux, the larvae were transparent with the exception of a light band of pigment spots following a transverse line across the retina, both anterior and posterior to the lens, almost perpendicular to the fetal eye gap. At fifteen days posthatch, the eye pigmentation in this group was still incomplete, with the transitionally unpigmented bar posterodorsal to the lens being almost clearly delineated. There were also pigment spots along the tail margin which, although following along the dorsal and anal finfold, came short of the actual caudal fin,

such that to the naked eye the caudal end seemed about one third shorter. There were also 7-8 stellate melanophores near the anus. By 20 days after hatching, the eyes had silvery blue reflections but it was still possible to discern the unpigmneted bar. The body pigmentation became broader along the finfolds and caudal end, and included larger melanophores adjacent to the anus.

At 100 lux, the light band of pigment across the eye was also evident at day 8. By day 15 the eye was still incompletely pigmented and, when viewed from above, much of the interior of the retina remained transparent. The transitional unpigmented bar was indistinctly delineated. On some larvae the caudal half of the band of tail pigment was thicker than that which followed the dorsal and anal finfolds. There were occasional melanophores adjacent to the anus. On the last day of sampling the pigmentation was slighlty less advanced than under 1000 lux, but the general pattern was the same.

The group held at 10 lux only showed a band of pigment posterior to the lens, while the spreading shape of melanocytes could just be discerned at day 8. By day 15, the eye and tail pigmentation was lighter than in the above groups although the unpigmented bar could be identified. There were small melanophores near the anus.

At 1 lux, the pigment band posterior to the lens was slightly visible but there was no indication of tail pigmentation. One week later, there seemed to be little difference between this group and 10 lux.

The group held in darkness also had a light band of pigmentation posterior to the lens, but no tail pigmentation. However, seven days later the eyes were still weakly pigmented with a slight scattering of pigment over the retina and no distinguishable unpigmented bar. There was also a thin band of pigment along the caudal end, where the melanophores were visible as thin streaks, and no pigment near the anus. This relatively slow rate of pigmentation persisted until the end of the experiment.

DISCUSSION

Behaviour and growth

The overall mean swimming speed gives an indication of the energy consumption, while activity levels and swimming speed during active periods indicate what way

the energy was used.

On Day 8 the larvae had large yolk reserves but are still lacking pectoral fins and eye pigmentation (Pittman et. al. 1990b), which thus limits the speed they can maintain in the water. The swimming speed in active periods in the different light intensities was not significantly different between groups nor from previous measurements (Skiftesvik et al. 1990).

However there are differences in activity levels between the groups on Day 8. Larvae kept in darkness were active about twice as long periods as those kept in light. The larvae kept at 100 lux had a significantly higher dry weights than the larvae kept in darkness and at 1000 lux on Day 8 after hatching. However the yolk sac dry weight was significantly lower in Group D than the yolk sac dry weight of all the other groups. Level of activity was significantly higher in Group D than in Group E. This indicates that the larval body growth was most efficient in Group D, however, a large part of the energy of the yolk sac had been used in activity. Activity was significantly less in the lighted groups ($p < 0.05$) and least at 1000 lux. Activity levels below 1.0 - 100 lux were comparable to previous measurements made at 300 lux (Skiftesvik et al.1990). Since the light sensitive organ at this stage is probably the pineal, which suppresses activity in the presence of light (Guthrie 1986), the data suggest that this may be the active mechanism in regulating halibut larval activity during this early stage. The yolk sac of the larvae kept at 1000 lux had significantly lower dry weight than the larvae kept at 1, 10 100 lux. We may then hypothesize that energy would be conserved if halibut were kept in lighted conditions during the first week the optimum of light level the first week might be between 100 and 1000 lux.

On Day 15, many differences appeared, the most remarkable one being the elevated energy consumption at 100 lux. At this stage, eye pigmentation was advancing in the lighted groups. In this case, the speed was slightly higher at 100 lux than in other light groups and significantly higher than in darkness ($p < 0.005$). Activity levels, however, was not significantly different at 100 lux, nor from previous measurements (Skiftesvik et al. 1990).

In darkness, activity was significantly higher than at 10 and 1000 lux, but no other significant differences in behaviour were found. The raw data notes that both these groups were in poor condition and swam weakley, so the differences may be an artifact of general form rather than a result of light level. The larvae of Group A were significantly lower in dry weight than the larvae in Groups B, C and E. The

yolk sac dry weight of the larvae in Group A was significantly higher than the yolk sac dry weight in Groups C, D and E.

There appear to be two possible explanations for the special behaviour at 100 lux. Since only the speed had been affected, the most probable cause is a stressful stimulus, in this case light levels. On Day 15 the dry weight of the larvae in Group D was significantly lower than that of the larvae in Groups B and C, and the yolk sac dry weight of the larvae in Group D (100 lux) was significantly lower than that of the larvae in Groups A, B and E. This indicates that the larvae of Group D had a poor utilization of the yolk, probably due to stress (see Opstad and Bergh 1990) Speed increased from darkness to to 100 lux (in this experiment) and further to more than 8 mm/s under 300 lux (Skiftesvik et al. 1990). The deviating results with respect to behaviour at higher light levels may be due to an elevated bacterial population in the incubators and consequently poor larval condition. However, larvae of Group E had the lowest total dry weight of all groups.

Thus it seems that by Day 15 energy will be conserved by keeping the larvae in relatively dark conditions, in contrast to the first week after hatching.

On Day 22, the larvae kept at 1 and 10 lux (Groups B and C) still had the highest larval dry weight. These two groups had significantly higher larval dry weights than Group E (1000 lux). The yolk sac dry weights of the larvae kept in darkness were significantly higher than that of all other groups, showing a low energy consumption of larvae kept in darkness from Day 8 to Day 22.

The larvae in Group A also had significantly lower mean swimming speed than the larvae of Group B, showing that larvae kept in darkness during this period used low amounts of energy on activity. On Day 22 after hatching, the total dry weight of Group E was now lower than Groups A and B only, indicating a shift in light optimum.

Pigmentation

There are two aspects which are of interest - the pattern of pigmentation and the timing of pigmentation. The general pattern of eye and body pigmentation was the same in all groups. Pigmentation in the retina proceeded from a thin band running anterior and posterior to the lens, almost perpendicular to the fetal eye gap. This gradually expanded over the retina but was concentrated at the circumference. An area of lighter pigmentation could be seen near the fetal eye gap and a distinctly unpigmented bar appeared posterodorsal to the lens, prior to full eye pigmentation.

This has been found in previous investigations (Pittman et al. 1990 a,b) and can be used as a marker of developmental stage. Suggestions for the function and ecological significance of this form of development are discussed in Helvik and Pittman (1990).

Expansion of melanophores along the body was concentrated along the dorsal and anal finfolds, the caudal end and the anus. The pigment band followed the edge of the finfolds but curved before the caudal fin and gave the larva a foreshortened appearance. Thus, even when the caudal fin was expanding and the caudal skeleton becoming more complex, the dark silhouette suggested a smaller and less developed animal. This "reduced" profile has been seen to persist beyond full yolk absorption (Pittman unpubl. data) and suggests a strategy for reducing predation by breaking up or confusing the outline of the halibut larva. Melanophores are also concentrated around the anus two weeks after hatching and may be quite large ten days later, suggesting a possible camouflage of consumed food.

The effect of light intensity on the timing of early pigmentation was most apparent when comparing the group held in darkness to the lighted groups. Pigmentation on both the body and the eye was delayed in darkness, concurring with Grun (1979) that dark-rearing of fishes which normally receive light results in a delay or interruption of the visual development processes. Pigmentation rate under white light was also positively correlated with light intensity, concurring with Grun (1979) but contrasting to the results obtained from halibut larvae kept under various intensities of blue light (Helvik and Pittman 1990). Comparison of the results from different intensities of blue and white light is only in its preliminary stages and will not be discussed here.

Bacteria

Total counts of bacteria are higher than what has been found in our previous experiments, which were done with continuous flow incubators (Opstad and Bergh 1990, Pittman et al. 1990a). Mean concentration of bacteria quickly rises above 10^6, and this takes place before the mortality increases. This is in agreement with the statement by Opstad and Bergh (1990), that in stagnant (or, as in this case, semi-stagnant) incubators, rapid accumulation of bacteria takes place before large numbers of larvae die. In contrast, continuous flow causes a delay in the increase in bacterial concentrations. The high variation within the groups is of importance when interpreting the other results of this experiment as it is probably a major source of noise in the data.

Vertical distribution

The change of optimum light level might be interpreted as a consequence of an adaption to the natural environment of the larvae. Helvik and Pittman (1990) have shown that halibut eggs are unable to hatch in the presence of light, thus hatching probably takes place at large depths. The hatching process quickly separates the larvae from the eggshell and the larvae tend to rise, whereas the eggshell sinks (Helvik 1988). During the first week of the yolk sac stage, the larvae seem to have a requirement for light. Somewhere around our first day of sampling (Day 8), a shift in the light optimum occurs, thus the larvae are probably adapted to larger depths compared to the early yolk sac stage. Towards the end of the experiment, the optimum level of light again becomes higher, this lead us to believe that the larvae are adapted to rise again. These observations are in agreement with the findings of Pittman et al. (1990b), who studied passive rising and sinking of halibut yolk sac larvae which were kept at the same temperature as in this experiment. They found that the larvae tended to rise during the first 2-3 days of the yolk sac stage. After a period of neutral buoyancy, they gradually began to sink. Just before Day 30, they tended to rise again.

Being in an endogen phase of development, the yolk sac larvae are maximally adapted to avoidance of predators (Bailey and Houde 1989, Skiftesvik et al. 1990). During the first week of development, the larvae are almost unpigmented, thus they are well adapted to not being located by visual predators. At this stage, the larvae are relatively unmotile, partly due to the huge size of the yolk sac (Pittman et al. 1990b). The first observation of eye pigmentation was done at Day 8, thus eye development seems to be correlated with the pattern of rising and sinking. The eye becoming pigmented is a costly development in an ecological sense, as the larvae then become more vulnerable to visual predators. If it is true that the larvae at this stage migrates to deeper waters, this should be due to the need to avoid visual predators. At this stage of development, the larvae's swimming speed increases (Pittman et al. 1990b), thus the larvae are better adapted to avoid tactile predators. The most abundant tactile predators are copepods, which are probably unable to catch the halibut larva at this stage of development (Lillelund and Lasker 1971, Yen 1987). According to Kinne (1982), tactile predators are mainly distrubuted at deeper waters. Thus, staying at shallower depths could be an adaption caused by the need to reduce predation by tactile predators.

The next shift in vertical distribution occurs just before Day 30 at 5°C. (Pittman et al. 1990b). This is correlated with the opening of the window of first feeding (Skiftesvik et al. 1990), and is thus probably due to the larvae starting searching

for food. At this stage, the larvae develop a more predator-like behaviour: The larvae are actively searching for food, at the expence of exposing themselves more to predators. The rising to shallower waters thus seems to be the ecological prize to pay for feeding themselves.

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Table 1. Total counts of bacteria in the incubators (in multiples of 10^6 * ml^{-1})

Incubator/Day	8	15	22	28
A1	1.44			
A2	-	0.769		
A3	1.21	-	1.12	
A4	1.94	0.584		
A5	1.25	0.601	2.41	
A6	0.596	1.38	1.98	
B1	1.59			
B2	1.16	0.71		
B3	0.69	1.27	1.36	
B4	1.18	0.430	1.09	
B5	-	0.929	0.604	1.40
B6	1.28	-	1.38	
C1	1.41			
C2	0.94	0.879		
C3	0.572	1.44	0.879	
C4	1.89	0.575	3.12	
C5	0.746	-	1.32	
C6	0.609	1.06	1.88	1.71
D1	0.975			
D2	0.706	0.851		
D3	0.663	-		
D4	0.817	0.586		
D5	0.592	0.773	1.30	0.681
D6	0.389	1.12	0.688	2.18
E1	2.19			
E2		1.51		
E3	0.798	1.09	2.36	
E4	1.23	0.720		
E5	1.72	1.36	1.25	
E6	0.541	1.25		

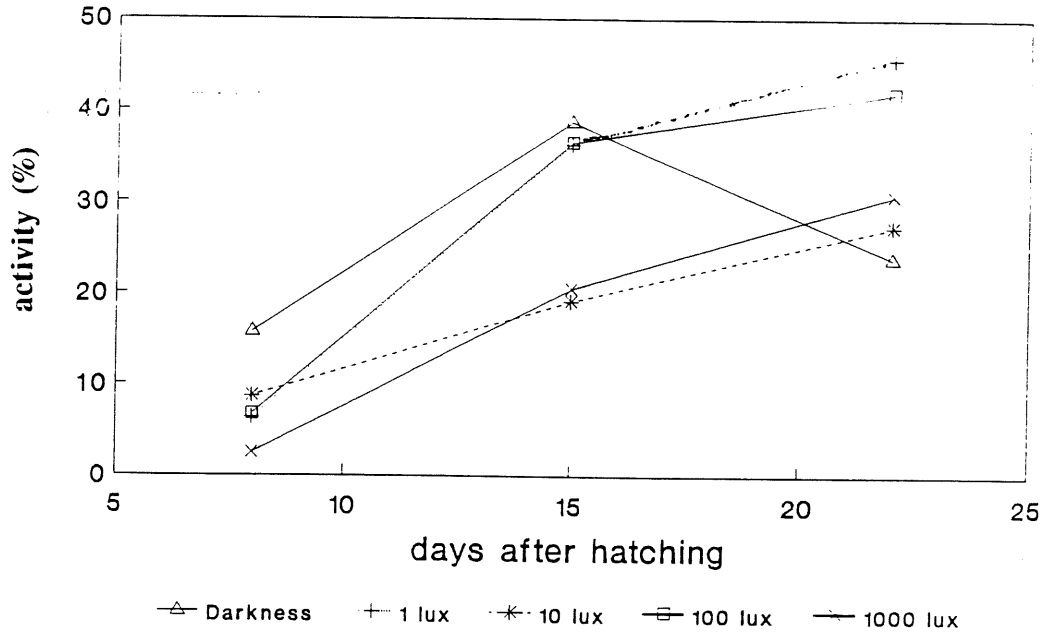

Figure 1. Activity level (percentage of time in active swimming) of halibut larvae at different levels of light.

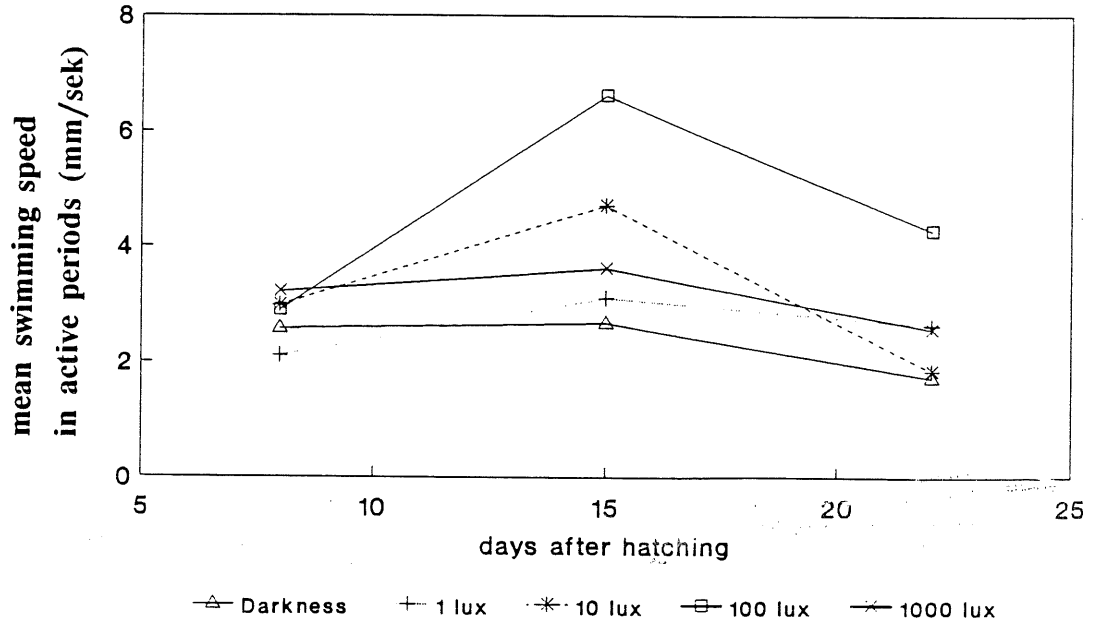

Figure 2. Mean swimming speed in periods of activity of halibut larvae at different levels of light.

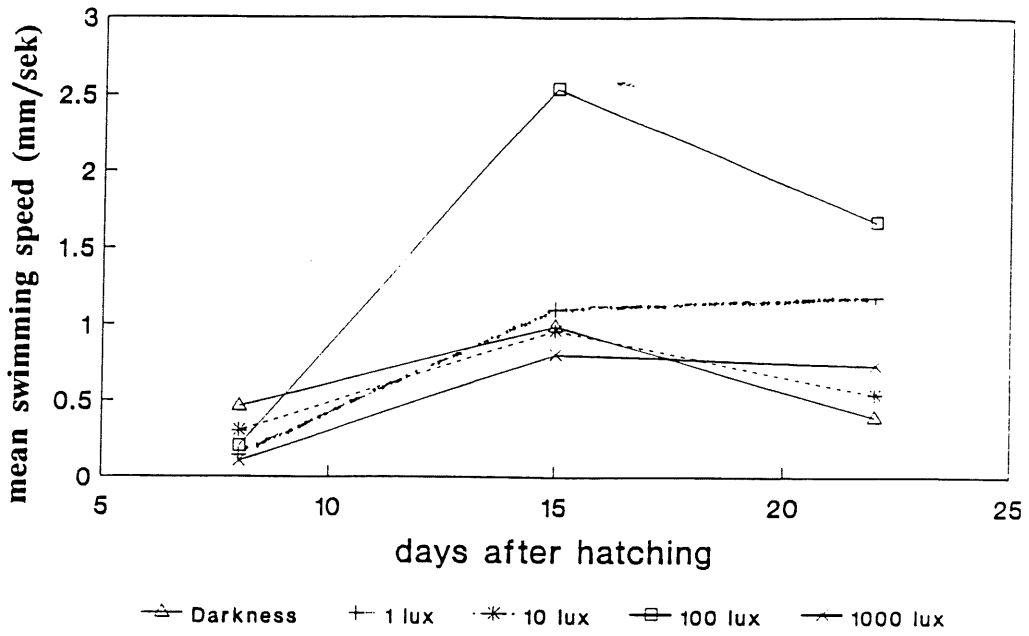

Figure 3. Mean swimming speed of halibut larvae at different levels of light.

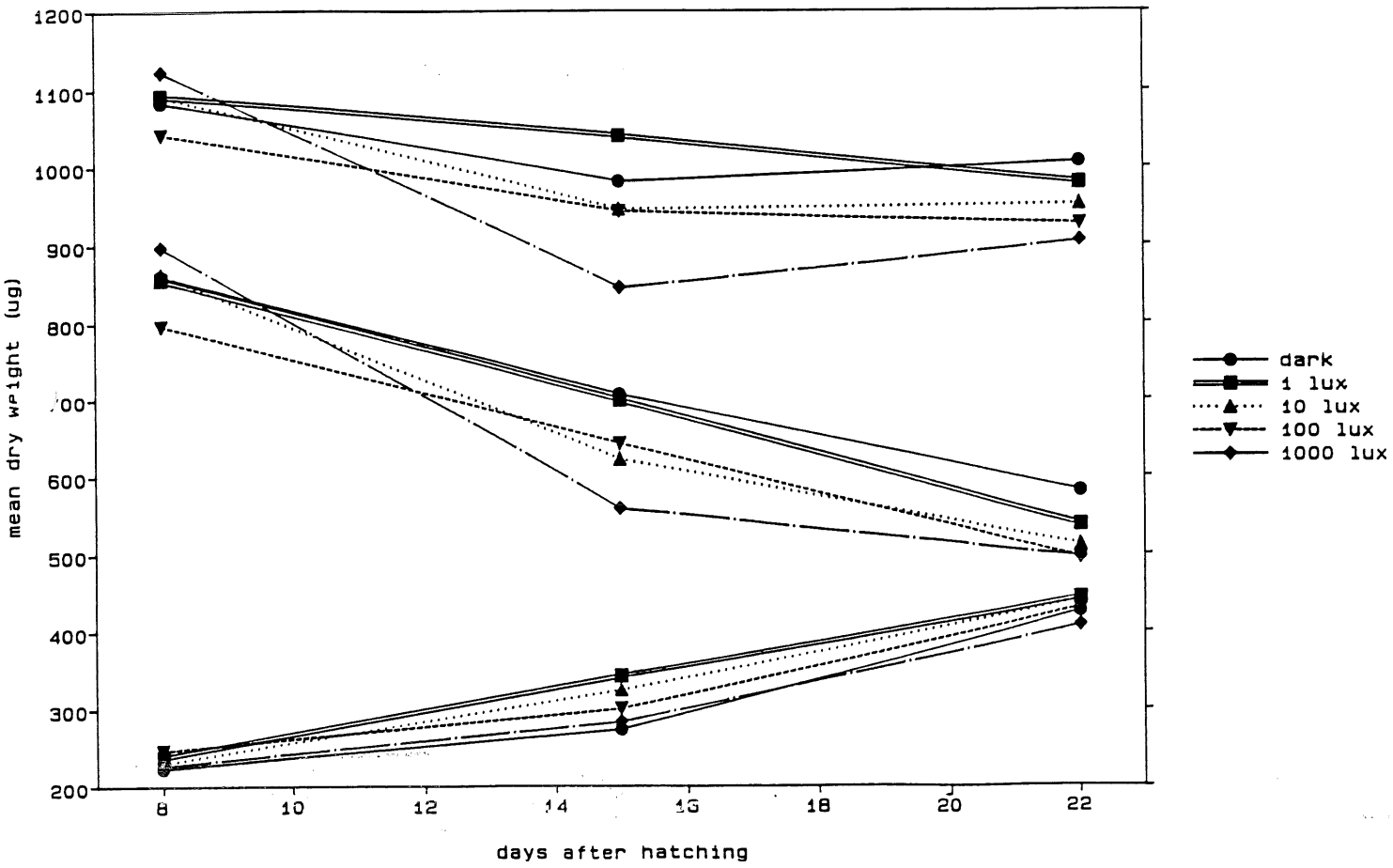

Figure 4. Dry weight of a) whole larvae, b) yolk sac and c) larval body at different levels of light.

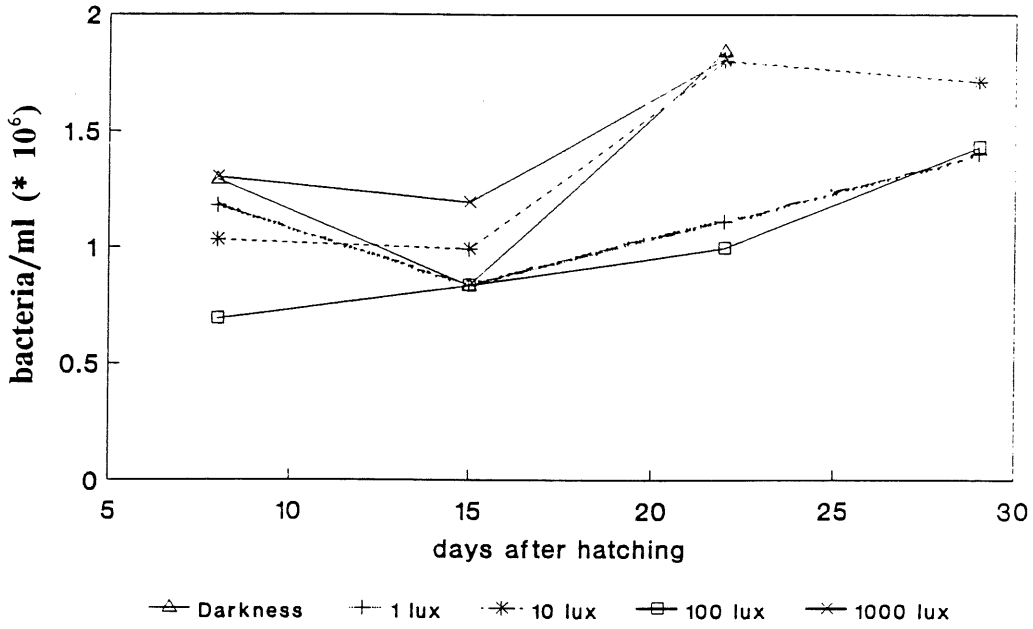

Figure 5. Mean numbers of total counts of bacteria in the incubators of different levels of light.

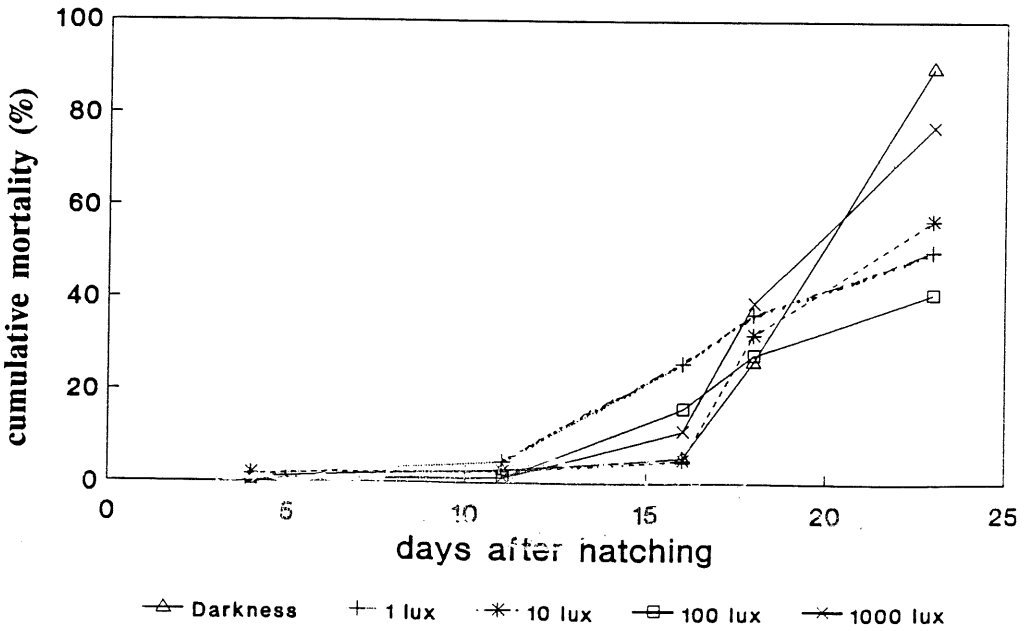

Figure 6. Mean cumulative mortality of Groups A, B, C, D and E. throughout the period of the experiment.

FIN