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The Propagation of Cod *Gadus morhua* L.

GROWTH, ENERGY CONSUMPTION AND PREY DENSITY REQUIREMENTS IN FIRST FEEDING LARVAE OF COD (*Gadus morhua* L.)

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ABSTRACT

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Growth, oxygen uptake, swimming activity, feeding ability and energy content were investigated in cod larvae from several groups under different experimental conditions.

At yolk absorption the larvae consumed 0.090-0.120 µl O_2/larva/hour depending on the larval group examined. The larval energy consumption either measured as oxygen uptake or calculated from larval weight decrement, was of the same magnitude. The oxygen uptake was 20-30% higher under 100 lux illumination than in darkness, a difference which was of the same magnitude (20%) as the difference in weight decrement between larvae held at a constant 500 lux and larvae held in constant darkness. Light-adapted larvae showed a 6-10 times higher swimming frequency (bursts of swimming per min) than dark-adapted ones.

The overall utilization of yolk for somatic growth varied between 65 and 70% depending on the larval group examined. The utilization seemed independant of temperature and light intensity when these parameters were kept within the natural range observed during hatching in the Lofoten area.

The specific energy content of eggs and larvae showed a steady decrease through the experimental period from 5.8 cal/mg ash free dry weight in newly fertilized eggs to 4.8 cal/mg ash free dry weight in larvae 12 days after hatching.

The larvae showed maximum swimming speeds at days 5, 6 and 7 post-hatching (10-20 cm/min). There was a significant correlation between mean swimming speed (cm/min) and mean

swimming frequency (number of swimming bursts/min) throughout the experimental period.

The larvae showed maximum feeding success (22%) at day 7 post-hatching.

The results are discussed in relation to larval prey density requirements at the onset of feeding.

INTRODUCTION

The objective of the present study was to determine the energy demand and food requirements in first-feeding larvae of cod (*Gadus morhua* L.) held in the laboratory. The parameters investigated were growth, oxygen uptake, feeding ability and swimming ability. The behaviour/energetics approach has been employed in several larval species in order to elucidate the question of larval survival potentials through the first-feeding stage (Lasker, 1963; Rosenthal and Hempel, 1970; Blaxter and Staines, 1971; Hunter, 1972; Laurence, 1978; Hunter and Kimbrell, 1980; Houde and Schekter, 1980, 1983). Calculated values of larval food density requirements at first-feeding vary among the species examined but generally tend to be higher than the average concentrations present in the sea. In a review, Theilacker and Dorsey (1980) question the extrapolation of experiments under laboratory conditions to events in the open sea. In the present investigation some of the parameters tested were measured under different experimental conditions, in order to evaluate some of the effects of different laboratory conditions on larval behaviour and energy demand.

MATERIALS AND METHODS

Biological material

Eggs and sperm were stripped from ripe cod, caught off the western coast of Norway. The eggs were artificially fertilized in the laboratory and incubated in 10 l aquaria at 5°C,

as described by Tilseth and Ellertsen (1984). The light intensity was adjusted to 100 lux by neutral filters in a 12/12 h light/dark cycle, measurements being made at the water surface (Tektronix J 16 photometer, illuminance probe J.6511, optimum sensitivity 550 nm). Food was not added to the rearing aquaria.

Altogether 16 groups from different female fish were used designated A to P). In one group the eggs and larvae were reared at three different temperatures (3, 5 and 7^{o}C) and in two different light regimes (500 lux constant illumination and constant darkness). The larvae studied during feeding success and swimming speed experiments were handled throughout the hatching period by the methods of Tilseth and Ellertsen (1984), so that all larvae studied were of the same age.

Growth

The dry weight of eggs, larvae and larvae with dissected yolk sacs was determined in several groups. Eggs and larvae were quickly rinsed in distilled water, dried to constant weights at 102^{o}C, and individually weighed on a Cahn electro balance. During the egg stage the embryonic tissue, which is very fragile, was stabilized for 1 h in 4% formalin in 10^{o}/oo sea water before removing the chorion and yolk sac. Cod larvae preserved in formalin for more than one month lose approximately 20% of their dry weight (Solberg, 1980). However, one h preservation of eggs and larvae did not lead to any significant weight reduction.

Oxygen uptake

The oxygen consumption was measured manometrically by means of a Warburg respirometer (Towsen and Mercer Ser. II) following standard manometric techniques (Umbreit et al., 1964). The flask volumes were approximately 25 ml and the temperature was kept at 5.0^{o}C. Ten to twenty larvae were transferred from the rearing aquaria to each Warburg flask in

5 ml sea water. After a 1 h acclimation the flasks were closed and the experiment started. Each experiment lasted 15-20 h and the light intensity was adjusted to 100 lux at the surface of the water bath throughout the experiment. The influence of light on larval oxygen consumption was tested by covering some of the flasks with black plastic.

Energy content

The specific energy content of eggs, chorions and larvae was determined in one group by a Phillipson microbomb calorimeter according to the method of Paine (1971) and Preus (1975). The chorions were removed from the eggs by squeezing the eggs on a filter paper and washing with distilled water. The eggs, chorions and larvae were freeze-dried to constant weight (20 h), ground in a mortar and pressed to a pill of 3-5 mg dry weight. The specific energy content is given as calories/mg ash free dry weight. The ash content was found by burning known amounts of eggs, chorions and larvae at 600^{o}C in a furnace.

Feeding success, perceptive field

The experiments were performed with larvae from one group in a feeding aquarium with a temperature of 5^{o}C and the light intensity adjusted to 100 lux at the water surface. The feeding success was defined as the percentage of successful captures of prey organism to the total number of observed attacks.

Five larvae were simultaneously transferred to the aquarium. The first larva that started to attack prey was observed for 15 min. The remaining four were disregarded. The number of attacks were recorded and the larva preserved in 4% formalin in 10^{o}/oo sea water for gut content analysis. During each attack the larval reactive perceptive distance was estimated visually relative to the larval standard length which was measured immediately after the 15 min observation

period. The reactive perceptive distance was defined as the distance from the larval eye to the prey organism at the moment when the larva altered its swimming pattern to chase its prey.

Swimming speed

The larval swimming speed was measured in two groups. Twenty larvae were simultaneously transferred from the incubator to a circular aquarium of 30 cm diameter and 5 cm deep. The temperature was 5°C and the light intensity adjusted to approximately 100 lux at the water surface. The light source was placed at a 45° angle to the water surface (Fig. 1), which made it possible to evaluate the position of the larvae relative to the bottom and surface by observing the distance between the larvae and their shadows. Larvae staying at the bottom or surface were neglected. The swimming activity was recorded on video tape by a TV camera for 15 min. An adaptation period of 30 min was allowed after transfer. The swimming speed of each larva was calculated by measuring the swimming distance on the TV-monitor screen after playback of the video tape. The swimming distance was calibrated to a centimetre marker placed in the aquarium. The swimming activity was also observed in darkness by a infrared sensitive TV-camera, using a Kodak Wratten gelatin filter no 87 (>700 nm) between the light source and the swimming aquarium (light intensity 0.1 lux).

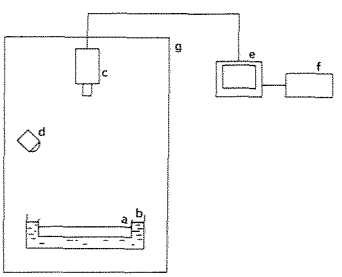

Fig. 1. Outline of the observation system for recording of cod larval swimming speed a= swimming aquarium, b= thermostat controlled water bath, c= TV camera, d= light source, e= monitor, f= video recorder, g= light proof box.

Cod larvae show locomotory activity in brief intense bursts of swimming (Ellertsen et al., 1980). The frequency of these bursts was calculated during the swimming speed recordings.

Both larval standard length and myotome height were measured daily in 20 larvae. The height of the myotome was measured just behind the anus.

RESULTS

Growth and yolk utilization efficiency

Fig. 2 shows the dry weights of eggs, chorions and larvae of group A and B reared at 5°C in a 12/12 h light (100 lux)/dark cycle. Although the eggs from the two groups at fertilization and hatching were of the same weight, they gave rise to larvae of different maximum weight and length. The overall conversion efficiency of yolk into somatic tissues was 64 and 71% in groups A and B, respectively, while the efficiency at hatching was 74% in both groups.

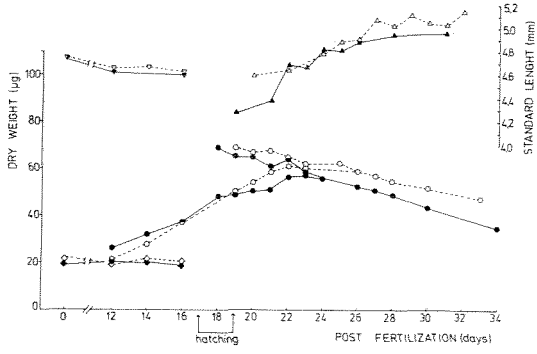

Fig. 2. Standard length (▲Δ), dry weight of eggs (▼▽) chorions (◆◇), whole larvae (●○), and larvae with dissected yolk sacs (●○) of group A (—▲▼●◆—) and B (--Δ▽○◇--). SD=±2-3% of values. t=5°C. Light intensity 100 lux in a 12/12 hour light/dark cycle.

Fig. 3 shows the dry weights of larvae from group C reared at three different temperatures (3°, 5° and 7°C) and two different light regimes at each temperature (constant darkness and constant 500 lux illumination).

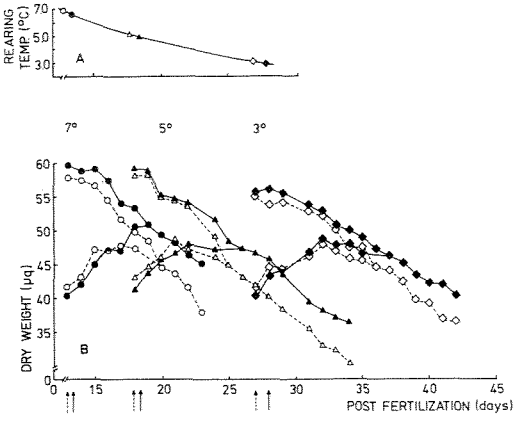

Fig. 3. A: Time of hatching against rearing temperature and B: Dry weight of whole larvae and larvae with dissected yolk sacs of group C reared at 7°C (●○), 5°C (▲△) and 3°C (◆◇). —●▲◆— larvae reared at constant darkness, --○△◇-- larvae reared at constant 500 lux illumination. Arrows indicate time of 50% hatching in light- (↑) and dark- (↑) adapted eggs. (SD=±2-3% of values).

The overall conversion efficiency of yolk mass into somatic tissues was higher in dark-adapted larvae reared at 7°C (74%) than in the other rearing categories (68-69%).

The weight data of whole larvae from group C were fitted by the linear regressions given in Table 1.

At all rearing temperatures the data indicate an approximately 20% higher weight reduction rate (curve slope) in light-adapted larvae compared to dark-adapted ones. The differences were statistically significant at all three temperatures (t-test).

TABLE 1

The table shows the regression lines fitting the data of total larval dry weight of group C given in Fig. 3. Data for the three first days after hatching are omitted in all calculations.

temp.	light regime	regression	r
7°C	darkness	y= 83.1 - 1.76x	0.99
	500 lux	y= 90.4 - 2.26x	0.99
5°C	darkness	y= 87.5 - 1.53x	0.99
	500 lux	y= 92.3 - 1.84x	0.99
3°C	darkness	y= 91.3 - 1.22x	1.00
	500 lux	y=100.0 - 1.53x	0.99

The temperatures of the rearing aquaria are given in Table 2. Due to the energy from the light, the surface temperatures of the light exposed aquaria were constantly 0.2-0.3°C higher than in the corresponding dark exposed aquaria. After hatching, the larvae moved into the water column where the temperatures of corresponding light and dark exposed aquaria were similar.

The peak hatching (50%) occurred earlier in light adapted eggs than in dark-adapted ones. The data of rearing temperature (y) versus days from fertilization to peak hatching (x) fits the exponential function $y=268 \cdot e^{-5.76 \cdot x}$ with an r^2 of 1.00. The hatching success was better than 95% in light-adapted eggs at all temperatures. In dark-adapted eggs the hatching success was better than 95% at 7°C, 85-90% at 5°C and 75-80% at 3°C.

TABLE 2

Rearing temperatures (^{o}C) in light (500 lux) and dark exposed aquaria during the egg and larval stages of group L.

Thermostat set temperature	3°		5°		7°	
developmental stage	egg	larval	egg	larval	egg	larval
500 lux	3.1±0.2	2.9±0.2	5.2±0.2	5.0±0.2	6.9±0.3	6.9±0.3
darkness	2.9±0.2	2.9±0.2	5.0±0.2	5.0±0.2	6.7±0.3	6.9±0.3

Oxygen consumption

Fig. 4 shows the oxygen uptake in larvae from groups D, E and F.

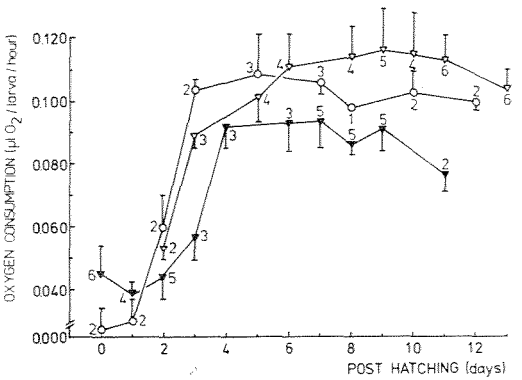

Fig. 4. Oxygen uptake (STPD) in larvae of group D (o), E (▽) and F (▼) at 5.0°C and 100 lux light intensity. Number of measurements is marked at each point. Bars are SD.

After an initial rise, the uptake stabilized at a constant level between 0.090 and 0.120 $\mu l O_2$/larva/h. By the end of the yolk sac stage (6-7 days post-hatching), the larvae reached their maximum tissue weight, 51.2 ± 1.3 µg, 56.4 ± 2.0 µg and 58.2 ± 1.6 µg dry weight/larva in groups D, E and F, respectively, giving a weight specific uptake of 1.8, 1.9 and 2.0 $\mu l O_2$/mg dry weight/h.

Fig. 5 shows the oxygen uptake of larvae from groups G and H in constant darkness and in constant 100 lux illumination, and Fig. 6 the activity of larvae from groups K, L, M and N in 100 lux illumination and 0.1 lux red light. Five and six days post-hatching the light-adapted larvae consumed 20-30% more oxygen than dark-adapted ones, while the difference in swimming frequency (bursts of swimming per min) was 6-10 fold between light-(100 lux) and dark-adapted (0.1 lux red light) larvae.

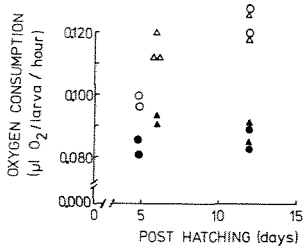

Fig. 5. Oxygen uptake in larvae of group G(●○) and H(▲△) at constant darkness (●△) and constant 100 lux illumination (○△)

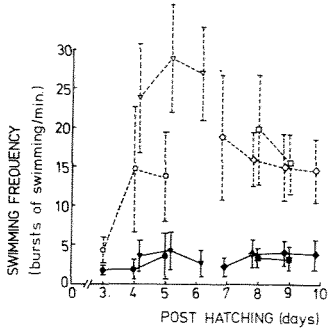

Fig. 6. Swimming activity in larvae of group K(●○), L(▲△), M(◆◇) and N(■□) at constant darkness (●▲◆■) (0.1 lux red light) and constant 100 lux illumination (○△◇□).

Feeding success, perceptive field

Table 3 gives the feeding success of larvae from group J.

TABLE 3

The variation in cod larval feeding success from the onset of exogenous feeding at age 5 days after hatching, to the end of yolk absorption at age 8 days after hatching. (X: mean percent feeding success, SD; standard deviation, SL; mean larval standard length (mm). N; number of larvae examined.

Age	Feeding success		SL	N
	$\bar{X}$	SD	mm	
5	11.2	1.4	4.48	7
6	13.5	5.1	4.52	10
7	22.2	6.5	4.60	8
8	14.0	4.4	4.64	9

The larvae obtained their maximum feeding success at day 7 post-hatching. The prey organisms were made up of copepod nauplii (74% of total) and bivalve veligers (26% of total). The average size of all prey ingested was 193±39µm.

The reactive perceptive distance varied from 0.5 to 1 SL (standard length). No correlation was found between reactive perceptive distance and size of the prey. The larvae did, however, react to prey both above and below the horizontal axis of the larval body.

Swimming speed

Fig. 7 gives the standard length, myotome height, swimming speed and swimming frequency in larvae of group O and P.

In both groups the myotome height and swimming speed reached their maximum 1-2 days before yolk absorption. The growth in length, however, did not cease until, or even after, yolk absorption. Correlation of corresponding mean values of swimming speed and swimming frequency, given in Fig. 6, showed a level of significance better than 99.9% in both groups (t-test), which means that distance travelled per burst of swimming did not differ much between larvae of different age.

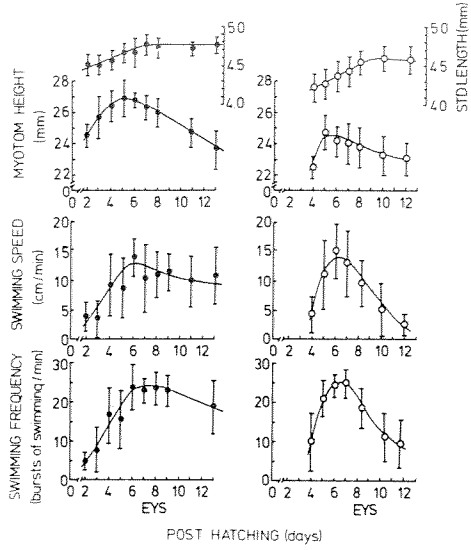

Fig. 7. Standard length, myotome height, swimming frequency and swimming speed in group O(●) and P(o) larvae. EYS = end of yolk sac. Curves fit by eye.

Energy content and energy balance

Table 4 gives the energy content/mg ash free dry weight in eggs, chorions, yolk mass and larvae of group B at different developmental stages. The ash content in newly-fertilized eggs was 8.9%, and in yolk sac larvae 8.3%.

Fig. 8 shows the balance between yolk energy reserves and catabolic energy demand in larvae of group B.

At day 5 post hatching the energy reserves of the yolk sac were less than the larval daily catabolic energy demand, and the larvae entered a state of negative energy balance.

TABLE 4

Specific energy content of whole eggs, chorions, yolk mass and larvae from group B (cal/mg ash free dry weight). Energy content of yolk is calculated from values of whole eggs and chorions at day 1.

	Whole eggs		Chorions		Yolk	Larvae	
Age, days post-fertilization	1	12	1	12	1	20	30
Energy content	5.8	5.6	5.5	5.5	5.9	5.2	4.8

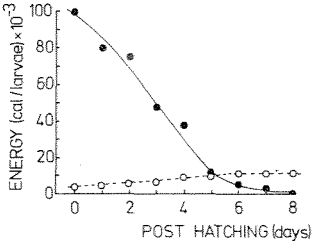

Fig. 8. Energy content of yolk mass (●) and daily energy consumption (o) in larvae of group B reared at 5°C.

DISCUSSION

Biological material

Larval groups from different female fish were studied separately. The data showed significant differences both in larval metabolic rate and growth, even between groups of eggs with similar weights. The egg groups seem therefore to reflect different growth and energetic potentials depending

on parental background. Accordingly, a mixing of groups would have increased the variance of the measured parameters and masked small daily changes within each group.

Hatching success

The lowered hatching success found in the dark-adapted eggs of group C at 3 and 5°C might result from reduced muscular activity in these embryos. The light-adapted eggs hatched somewhat earlier than corresponding dark-adapted ones. The difference, however, might be fully explained by the slight deviation in rearing temperature between light and dark aquaria.

Growth and yolk utilization

The overall utilization of yolk for growth of somatic tissues varied between 65 and 74% depending in the larval group examined. The utilization in light-adapted larvae of group C seemed independent of rearing temperature. As discussed by Howell (1980), several larval species show temperature dependent yolk utilization. These include Atlantic salmon (*Salmo salar*) (Hayes and Pelluet, 1945), herring (*Clupea harengus*) (Blaxter and Hempel, 1966), plaice (*Pleuronectes platessa*) (Ryland and Nichols, 1967), tautog (*Tautoga onitis*) (Laurence, 1973) and yellowtail flounder (*Limanda ferruginea*) (Howell, 1980). Some of the authors, however, reported temperature independence over a specific interval of the temperature range tested (Hayes and Pelluet, 1945; Blaxter and Hempel, 1966; Laurence 1973).

The temperature of the surface layers in the Lofoten spawning area during April to mid-May varies between 3 and 6°C (Midttun, 1975). The 68-69% yolk utilization registered both in light- and dark-reared larvae of group C at 3 and 5°C therefore might be an optimized adaptation within the natural temperature range, while the 74% utilization registered in dark-reared larvae at 7°C, is probably a reaction to an

unnaturally high rearing temperature. Ware (1975) assumed that natural selection would favour organisms maximizing their growth. The present observed deviation, however, is not necessarily a benefit to the larvae as the yolk volume available for swimming performance is reduced.

Oxygen uptake

Manometric methods are frequently used when measuring oxygen consumption in fish larvae (Holliday et al., 1964; Lawrence, 1969, 1978; Hunter and Kimbrell, 1979; Cetta and Capuzzo, 1982), but are not considered as particularly satisfactory with these animals (Hunter and Kimbrell, 1979, Theilacker and Dorsey, 1980).

The uptake at yolk absorption, however, showed a good correlation with the catabolic energy production calculated from the larval daily weight decrement. This is to be expected provided the only source of energy is of endogenous origin. A similar correpondence was reported in larvae of Pacific sardine (*Sardinops caerulea*) (Lasker, 1962) and largemouth bass (*Micropterus salmoides*) (Laurence, 1969). The weight-specific oxygen uptake at yolk absorption also showed a good correlation with the uptake registered in larvae of the Arcto-Norwegian cod at the same developmental stage (1.9-2.0µl O_2/mg dry weight) measured by means of oxygen electrodes (Davenport and Lønning, 1980).

The increasing oxygen uptake measured during the first couple of days after hatching was probably related to growth of somatic tissues and increased swimming activity.

The 20-40% difference in oxygen consumption measured between light- and dark-adapted larvae was moderate compared with the 6-10 fold difference in swimming frequency (bursts of swimming/min) registered under similar light conditions. The impact of activity on oxygen consumption in cod larvae thus seemed low compared with the 3.5 fold difference registered between active and inactive larvae of Pacific sardine (Lasker and Theilacker, 1962) and the 9-10 fold difference

registered between active and inactive larvae of herring (Holliday et al., 1964). As discussed by Hunter and Kimbrell (1979) and Theilacker and Dorsey (1980), the larval activity might have been depressed in the Warburg flasks, thus leading to an underestimation of the impact of activity on oxygen consumption. The difference in weight reduction rate, however, between light- and dark-adapted larvae, was no more than 20%, thus confirming the relatively low contribution of activity to routine metabolism in larvae of cod.

Swimming activity

Maximum swimming activity occurred simultaneously with maximum somatic tissue weight. The swimming speed was probably somewhat underestimated as the measurements were only made in the horizontal plane. The deviation, however, is probably minor, as cod larvae examined at similar ages tended to maintain their depth when the light was kept constant at intensities normally experienced at sea (Tilseth and Strømme, 1976). Hunter and Kimbrell (1979) and Weihs (1980) proposed that the intermittent swimming pattern of fish larvae has a respiratory function, each burst of swimming being triggered by a fall in oxygen tension around the larvae. In cod larvae this seems unlikely since the swimming speed dropped to nearly zero during darkness.

Feeding success

The 11-22% feeding success found at yolk absorption was higher than in most other larval species examined, such as herring (Blaxter and Staines, 1971; Rosenthal and Hempel, 1970), anchovy (*Engraulis mordax*) (Hunter, 1972) and coregonid larvae (Braum, 1967). The feeding ability was more in accordance with the 32% feeding success registered in first-feeding larvae of plaice (Blaxter and Staines, 1971) which was attributed to their greater manoeuvring ability compared

with herring. The same ability was registered in larvae of cod (Ellertsen et al., 1980).

Energy content and energy balance

The decrease in specific energy content of eggs and larvae measured during the experimental period was probably due to conversion of yolk rich in energy into larval somatic tissues of lower specific energy content.

As shown in Fig. 8, the larvae after day 5 entered a state of negative energy balance. At this stage the larval somatic tissue weight and swimming activity was at its maximum, as also was the larval feeding incidence (Ellertsen et al., 1980). The physiological condition of the larvae therefore seems optimized for survival during this period.

Food density requirements

One of the objectives of the present study was to determine the larval energy and food density requirements at the onset of feeding. The density might theoretically be calculated from the following equation:

$$N = \frac{ER}{EC \cdot SV \cdot FS}$$

N = number of prey organisms/l
ER = energy requirement in first-feeding larvae
EC = energy content of prey organism
SV = larval search volume
FS = feeding success

The main prey organism of first feeding cod larvae are nauplii of *Calanus finmarchicus* with mean carapace length 250µm (Wiborg, 1948; Ellertsen et al., 1976). As far as is known data of weight and energy content of copepod nauplii are unavailable. Volumetric considerations, combined with data of specific weight (Gross and Raymond, 1942), and water

content (Tande, 1979), indicate a dry weight of a 250µm nauplii of 0.3µg. This is close to the 0.29µg average weight of copepod nauplii offered first feeding larvae of three subtropic marine fishes by Houde and Schekter (1980). The specific energy content was taken as 5.5 cal/mg dry weight, a mean of the values used by Lasker (1962) and Houde and Schekter (1983), giving an energy content of a 250 µm nauplii of 1.7×10^{-3} cal. At yolk absorption the larvae consumed oxygen equivalent to 0.010-0.013 cal/larva/day (4.6 cal/ml O_2, Brett and Groves, 1979). This, however, only accounts for the catabolic energy. When exogenous food is offered, some of it will be used for growth. During the yolk sac stage the larval daily growth rate was 5-7% (dry weight). If this also applies to first-feeding larvae, the anabolic requirement will correspond to 0.03-0.04 cal/day. The utilization of exogenous food for growth and metabolism is not known in cod larvae, but is probably less than 50%, as found in several other species of marine fish larvae (Cetta and Capuzzo, 1982; Houde and Schekter, 1983). In the present calculations it is taken as 40%. The data compiled thus indicates a total larval demand for exogenous food at the onset of feeding corresponding to 0.09-0.13 cal/larva/day. In May, the light intensity in the Lofoten area is sufficient for feeding 24 h/day (Gjøsæther and Tilseth, 1982). The calculated food density requirements are given in Fig. 9.

The calculated minimum values are higher than the average densities (<20/l) obtained by a in situ particle counter and pump in the Lofoten area in April-May (Tilseth and Ellertsen, 1984a). Similar estimates of critical prey densities in first-feeding fish larvae based on laboratory examination of larval food, searching potential and energy demand, tend to give higher values than generally observed at sea (Rosenthal and Hempel, 1970, 1971; Hunter 1972; Houde and Schekter, 1983). As pointed out by Houde and Schekter (1983), the calculated values are based on average performances. The possibility therefore exist that only exceptionally fit larvae are able to survive under the normally observed

marginal food densities, and that large scale survival is dependent on patchy food distribution, as proposed for larvae of northern anchovy by Vlymen (1977) and Lasker and Zweifel (1978). Using an in situ particle counter Tilseth and Ellertsen (1984a) observed patchy distribution of copepod nauplii in the Lofoten area at densities of 100-300/l.

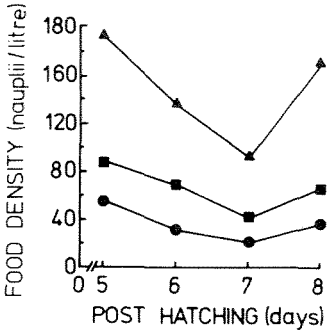

Fig. 9. Food density requirements in first feeding larvae of cod from the onset of exogenous feeding (day 5), to yolk absorption (day 8). The curves are based on maximum (●—●), mean (■—■) and minimum (▲—▲) values of swimming speed, feeding success and catabolic energy demand.

As pointed out, however, by Blaxter and Staines (1971), Rosenthal and Hempel (1970) and discussed by Houde and Schekter (1980), major errors may occur in calculated larval search volumes which are very sensitive to deviations in the observed perceptive distances. Likewise, the swimming speed of cod larvae in a 5 cm deep laboratory aquarium containing filtered sea water is not necessarily the same as in the open sea. Von Westernhagen and Rosenthal (1979) reported lower swimming speeds in laboratory-reared herring larvae compared with "wild" ones, and Hunter and Thomas (1974) reported a change in the swimming pattern of the larvae of Pacific mackerel (*Scomber japonicus*) when offered food. Accordingly the present calculated values should be regarded as preliminary estimates.

ACKNOWLEDGEMENTS

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