

C.M. 1976/F:34

International Council for the
Exploration of the SeaDemersal Fish (Northern)
Committee

Ref.: Plankton Committee

The influence of light and food density on the feeding success in
larvae of cod (Gadus morhua L.); field and laboratory observations

by

B. Ellertsen ^{*)}, E. Moksness ^{**)}, P. Solemdal ^{*)},
T. Strømme ^{**)}, S. Tilseth ^{*)} and V. Øiestad ^{*)}

INTRODUCTION

Reviewing investigations on larval mortality and the critical period concept for fish larvae, MAY (1974) concluded: "However, it should simply be stated that with present sampling techniques such collections are generally not precise or accurate enough to disclose whether or not larval mortality is concentrated at the end of the yolk-sac stage".

The critical period concept has been the aim of several laboratory investigations, working on feeding behaviour and food demands of the fish larvae under different environmental conditions (BLAXTER & HEMPEL 1963, LASKER et al. 1970, HUNTER 1972).

On the basis of detailed knowledge of anchovy larvae obtained in the laboratory, LASKER (1974) performed a larvae bioassay in the field. This is a new approach to test the hypothesis of the critical period concept of fish larvae, put forward by HJORT (1914). The present investigation is the first step in developing a larvae bioassay on cod larvae and is divided into three parts:

*) Institute of Marine Research
Directorate of Fisheries
5011 Nordnes, Norway

***) Department of Fisheries
Biology,
University of Bergen
Norway

- 1) Laboratory experiments to establish feeding success in relation to light intensity and food density.
- 2) Rearing of cod larvae in a large basin (ELLERTSEN et al. 1975) to obtain data on first feeding, feeding success, growth and mortality.
- 3) Field investigations on the relation between feeding success and food density.

MATERIALS AND METHODS

Laboratory experiments

Artificially fertilized eggs of Arcto-Norwegian cod were obtained in March from the Lofoten area. Eggs from different females were kept separately and were sent by air to the Institute of Marine Research, Bergen, the day after fertilization. The incubation of eggs and larvae at the laboratory are described in another paper being presented at this meeting (TILSETH & STRØMME 1976).

Cod larvae were placed in a 10 x 10 x 1 cm perspex chamber in a thermostate at 5°C, and their feeding behaviour observed through a dissecting microscope.

Upon hatching one group of cod larvae, all from the same female were isolated. This larval population was not fed. Thirty larvae were transferred daily from this population to each of three incubator cylinders together with newly hatched Artemia salina nauplii. The nauplii densities were: 0.1, 1.0 and 10 nauplii/ml., respectively. Each cylinder contained 3 litres of stagnant sea water (see Fig.2 in TILSETH & STRØMME 1976). An "airlift" kept the density of food organisms homogenous without disturbing the larvae. The experiments lasted for 6 hours, then the larvae were anaesthetized in 1 : 20000 MS 222 and the stomach contents investigated. The experiments was repeated with new larvae and nauplii daily from hatching to death from starvation of the larval cod population. The light intensity was 1000 lux. at the surface of the cylinders. The cylinders were placed in a thermostat at 5°C.

The very same method was used to study the feeding activity of cod larvae on phytoplankton. Two different species of different sizes were selected, and the feeding activity was observed at the following densities:

1. Dunaliella sp., mean diameter 7.5 μ , 1000, 10 000, and 100 000 flagellates /ml.
2. Peridinium trochoidum mean diameter 25 μ , 10 50 100 and 1000 flagellates /ml.

Light intensity

The cod larval feeding activity on Artemia nauplii (1/ml) was observed at the following light intensities, 1000, 10, 8.4, 4.2, 1.4, 0.4 and 0.1 lux. The feeding activity on the flagellate P. trochoidum (1000/ml) was observed at 1000, 10, and 0 lux. The incubator cylinders were placed in a light proof box in a thermostat at 5°C. The light intensity was adjusted with neutral filters. The experiment started five days after hatching and lasted until the thirteenth day after hatching, following the procedure described above.

Basin experiments

The cod eggs were collected from a spawning pond on March 9 and 10. The eggs from March 9 were incubated at the laboratory at about 7°C, while the eggs from March 10 were incubated at a somewhat higher temperature in order to obtain simultaneous hatching. The hatching started for both groups on March 19 and the age is calculated from March 21, the day of 50% hatching. Consequently, the cod larvae can be regarded as a homogenous group. About 200.000 of them were transferred on March 25 to a 1.700 m² large basin situated on land and with a maximum depth of 4½ m. Daily sampling of larvae with plankton nets gave information on larval growth and diet and on stomach filling and feeding success. Point sampling every week pelagically, near the bottom and at the bottom by

means of a centrifugal pump gave information on density and composition of the plankton community from which the cod larvae took their food. Siphon sampling was carried out weekly at different depth to measure temperature, salinity, concentration of nutrient salts, oxygen saturation, chlorophyll a and densities of different phytoplankton species.

Field investigations

The spawning intensity was investigated from March 17 to April 10 1976 with R/V "Asterias". Egg samples were taken at 48 hour intervals at 3 localities, number of eggs younger than 48 hours used for computing the spawning curve, Fig.1. The spawning curve maximum, about April 1 1976, is approximately 10 days earlier compared to 1975.

On the basis of the spawning maximum and temperature condition in the Vestfjord the larval survey with R/V "H.U.Sverdrup" was carried out from April 23 to May 10.

In the Borgundfjord, Western Norway, a cod larvae survey was carried out in the first part of April 1976 with R/V "Peder Rønnestad". Larval distribution in the Lofoten area was obtained by Juday-nets (0.5 or 0.1 m² opening) with mesh size 500 μ and the net in the plankton - cup was 300 μ .

The distribution of food organisms was obtained by pumping 100 litres (monopump, 200 l/min) from each of the following depths: 0, 2, 10, 15, 20, 25 and 30 meters. Occasionally the 1, 7.5, 12.5, 35, 40, 45 and 50 meter depths were sampled. The samples were filtered through a 90 μ - net, and counted on board. On the basis of the concentrations of cod larvae and food organisms 4 localities were investigated during a 24 hour period, except the stations 236-239 in Austnesfjord, see Fig. 2, which was sampled for 12 hours. Profiles of food organisms and cod larvae in the upper 30 meters were sampled every second hour.

Length (from the mouth to the end of the notochord), yolk-sac stage, number and size of nauplii in stomach of the cod larvae was partly worked up on board, to determine the further progress of the survey.

Samples were preserved in 4 % buffered formalin, and examined at the Institute of Marine Research, Bergen. The yolk sac stages were divided into the following categories:

1. Large yolk sac, (more or less spherical)
2. Medium yolk sac (pear - shaped).
3. Small yolk sac (string - shaped).
4. No yolk sac.

RESULTS

Laboratory experiments

First feeding and feeding behaviour

The cod larvae started active feeding on Artemia nauplii five days after hatching (Fig. 3). Observations on the larval feeding behaviour, and examination with a microscope, showed that the active feeding coincided with the development of a functional jaw. The larvae manoeuvred carefully up to the prey organism with the pelvic fins, opened the mouth suddenly and expanded the oral cavity and the nauplius was sucked into the mouth.

Starved cod larvae exhibited feeding behaviour until the day before mass mortality of the larval population which occurred at 18 days after hatching (Fig. 3).

Feeding success influenced by food concentrations

The period of highest feeding activity on Artemia nauplii was from the seventh to the twelfth day after hatching. The highest percentage of cod larvae with nauplii in the gut was found at a density of

1:000 nauplii/litre. This seemed to be the optimum density, because the feeding success was lower at densities of both 10 000 and 100 nauplii/litre (Fig. 3). Observations on the feeding behaviour at the highest density of nauplii, showed that the cod larvae avoided dense concentrations and this consequently disturbed the feeding activity.

The cod larval feeding activity on small flagellates (Dunaliella sp.) was passive. The experiment started the day after hatching. At the highest concentration, more than 80 percent of the cod larvae had flagellates in the gut (Fig. 4). Examination of the cod larvae through microscope showed that the flagellates were concentrated on the gill arches before entering the gut.

A significant reduction in the percentage of larvae with flagellates in the gut occurred on the fourth to the fifth day after hatching. The reduction was due to the development of a functional mouth apparatus, and as the gill arches were covered the flagellates were spit out. At the end of the yolk sac stage and beyond the percentage increased again. This could be due to the larvae at this stage actually feeding on the flagellates, or more probably, that the larvae were enfeebled and too weak to avoid clogging of the gill arches. At the end of the experiment this was quite likely what happened, on the twelfth day all larvae died 2 hours after being transferred to the incubator containing 100.000 flagellates/ml.

The feeding activity of cod larvae on the larger flagellate (25 μ) Peridinium trochoidum densities is shown in Fig. 5. Initial feeding was observed five days after hatching (see Fig. 6), which again coincided with the development of a functional mouth apparatus. The most active period was at the end of yolk resorption (EYS). On the average 60 flagellates were found in the larval gut (Fig. 5), and more than 90 per cent of the larvae were found to have been feeding on the flagellates (Fig. 6).

Feeding success influenced by light intensity.

The larval cod feeding activity on Artemia nauplii (1000 nauplii/litre) at different light intensities is shown in Figs. 7 and 8. Again the

first feeding larvae were observed five days after hatching. The amount of larvae with nauplii in the gut increased to more than 80 per cent at the time of yolk resorption. The maximum was obtained at a light intensity of 1,4 lux. Not more than 50 per cent of the larval population was feeding on nauplii at 10 and 1000 lux (Fig. 7). The number of nauplii found in the gut of feeding larvae at different light intensities is shown in Fig. 8. The amount of ingested nauplii increased to about 2.5 - 3 nauplii/larvae on the eighth day after hatching at 1.4 - 4.2 and 8.4 lux. From this day on the experiment was continued at the light intensities 1.4 and 1000 lux and in addition at 0.4 lux. The ingestion of nauplii was found to be decreasing. The most active period was between seven and ten days after hatching. Observations on the feeding activity of cod larvae at 1000 lux showed that about 50 per cent of the larvae tried to "escape" this light intensity by swimming deeper. This obviously disturbed the feeding activity. No larvae were found feeding on Artemia nauplii at 0.1 lux.

Cod larval feeding success on P. trochoidum (1000/ml) at 1000, 10 and 0 lux is shown in Fig. 6. The highest percentage of larvae with flagellates in the gut was found at 1000 lux., with a feeding success of more than 90 percent at EYS. However, at this density of flagellates, 1000/ml, a considerable part of the ingested cells probably taken incidentally. In the most active feeding period, it was found that 20 to 45 percent of the larvae in complete darkness had ingested flagellates (Fig. 6).

Field observations

First feeding

Basin

The cod larvae were transferred to the basin on March 25. Both on this day and the next day when about 60% of the larvae had either medium yolk sacs or yolk-sac remains no larvae were observed with nauplii in the gut (Table 1). On March 28, seven days after hatching, when 10% still had remains of yolk - sacs, about 80% had started to eat nauplii. During the following days the larvae continued to have a feeding success of between 60-100%, usually highest in the evening as shown in Table 1.

Lofoten area

275 larvae with large yolk-sac, stages 1 and 2 were all without food organisms in the gut. Of the 308 larvae with yolk sac stage 3, 53 larvae or 17% had food organisms in the gut. The feeding success of these first feeders varied according to density of nauplii, as shown in Fig.9. Numbers and mean length of the different groups of yolk-sac 3 larvae are given in Table 2.

Diurnal feeding success

Basin

As earlier demonstrated, a higher percentage of the cod larvae had food in the gut in the evening than in the morning (Table 1). The number of food organisms in the gut also increased during the day as seen from Table 3. The day and night sampling on April 5 and 6 indicated that this was to some extent a result of an accumulation of food in the gut. As will be seen from Fig.10 the larvae seemed to eat intensively from 03 00 to 06 00 and from 13 00 to 17 00. A close study of Fig.10 seems to indicate a feeding time of 12-15 hours in early April and a digestion time of about 10 hours. Consequently, a summation of the gut contents at 09.00 and 19.00 should give an idea of the daily food intake, as illustrated in the last column in Table 3.

Lofoten area

Fig. 11 shows the feeding success of cod larvae (all size groups) during a 24 hour period. The material is from the 24-hour stations 119-130, 330-343 and 360-371 (see Table 2). Data on the larval concentration are also given.

Feeding success influenced by food concentration

Basin

The reduction in catch of cod larvae during the first months is illustrated in Fig.12. The reduction seems to be particularly severe during the first week of April, when the larvae are about two weeks old. The mean larval length increased from 3.8 mm

at hatching to 5.3 mm 20 days later.

The increase since initial feeding on March 28 was 0.7 mm (from 4.6 mm to 5.3 mm).

The larvae taken for investigation of gut contents were divided into three length groups, as can be seen from Table 4. It is obvious that the largest larvae at any time had the best feeding success, while the smallest larvae seemed to stagnate in their daily food intake at below five organisms as demonstrated for the two periods March 28 to April 1 and April 7 to 9.

From this background of heavy mortality, moderate mean length growth and large differences in daily food intake, it is of interest to look at the density of nauplii in the basin at the time when the larvae started to eat on March 28 and the feeding conditions the following two weeks. As seen from Fig. 13 the mean density at that time was one nauplius per litre water. However the vertical point sampling indicated a concentration maximum of nauplii at a depth of about 2-3 meters as seen from Table 5. At that depth a density of four nauplii per litre water was observed. The density decreased rapidly in early April (Fig. 13), and the larvae had to hunt for food in concentrations of 0.1 - 1.0 nauplii per litre as seen from Table 6. During the day and night sampling the highest observed density was 1.6 nauplii per litre water.

Nevertheless, the largest larvae increased their daily consumption from about 13 nauplii at the end of March to about 23 at the end of the first ten days in April (Table 4). The small larvae were only able to increase the daily intake by one organism, from 4 to 5.

Lofoten area

Data on concentrations of nauplii as a mean for each 24-hour station together with number and mean length of the three size groups of cod larvae are given in table 2.

Nauplii profiles from stations with high and medium concentrations are given in Fig. 14.

Fig. 15 shows feeding success of cod larvae (larvae with food in the gut), number of nauplii in the gut and number of cod larvae per m³ for the four 24-hour stations.

In Fig. 9 the same larvae are split into 3 length groups and the feeding success for each group shown.

The stomach contents were completely dominated by nauplii. Only two larvae contained copepod eggs. The amount of copepod eggs in the water was always low, ranging from 0 to 1.8 per liter.

DISCUSSION

First feeding and feeding behaviour

In contrast to the darting and snapping behaviour described on herring larvae by ROSENTHAL & HEMPEL (1971) and also observed on plaice (ROLLEFSEN 1946) and anchovy larvae (HUNTER 1972), cod larvae swim close to the prey organism and suck it into the mouth as earlier observed by BROWN (1969).

Initial feeding by cod larvae with the remains of yolk-sac was earlier observed by WIBORG (1948). The laboratory experiments showed an increased feeding success with a maximum at the end of the yolk-sac stage (Fig. 3).

Large phytoplankton species have been observed in the guts of cod larvae by BAINBRIDGE & MCKAY (1968) and by NORDENG & BRATLAND (1971), but seem to play a more important role for anchovy (LASKER 1974) and plaice (SHELBOURNE 1957).

Feeding success influenced by light intensity

The observed light threshold for feeding success at 0.1 lux is in agreement with the value observed by BLAXTER (1965) for herring larvae. Based on this threshold BLAXTER (1966) calculated a feeding period of 16 hours for herring larvae in Southern Norway, coinciding with the present observations in the basin (Fig. 10).

The cod larvae seem to have two main feeding periods (Fig. 10 and 11) with a leveling out in the amount of food in the gut during the middle of the day (Fig. 10, Table 3), as earlier observed for herring larvae by HENTSCHEL (1950). The laboratory results (Fig. 8) indicate inhibiting effect resulting from the high light intensity at the middle of the day, leading to reduced feeding activity.

Feeding success influenced by food concentration

Food concentrations are widely different in the laboratory experiments, in the basin and in the field. In the laboratory experiments the concentration range was 100-10,000 nauplii per litre and was chosen from LAURENCE (1974), working on haddock larvae. Laurence observed a threshold for survival at 500 nauplii per litre, a concentration seldom found in nature.

The relevant data on feeding success and food concentrations for the basin and field are given below. In spite of a considerably lower density of food organisms in the basin, the feeding success was much higher compared to feeding success in the field at all food concentrations.

	Basin	Borgund and Lofoten area			
Nauplii/litre	1.0	4.7	8.5	9.1	24.0
Feeding success, %	95	15	36	38	67
Mean larval length	4.6	4.5	4.8	4.8	4.6

The same high feeding success was found for herring larvae in the basin at food concentration of 0.1-1.0 nauplius per litre (ELLERTSEN et.al. 1975), in contrast to a field threshold concentration above 10 nauplii per litre found by LISIVNENKO (1961) working on Baltic herring larvae. Thus there must be environmental conditions other than food concentration in the basin resulting in higher feeding success than in the field.

Although high feeding success in the basin (Table 1), a large number of larvae had a low daily intake (Table 3). The high death rate in early April (Fig. 12), may indicate that these larvae did not get

sufficient food to survive. Consequently, a seemingly high feeding success may hide marginal feeding conditions. The time of mass mortality in the basin coincides with that observed in the laboratory for starved larvae. Actually, a mean daily intake of only three organisms might be the same as no food intake and result in death of starvation as pointed out by LASKER (1974) for Engraulis mordax.

The large and medium sized larvae increased their food intake during the deterioration in feeding conditions in early April (Table 3 and Fig. 13). This was probably due to an increase in search potential and hunting success, resulting in a higher survival rate.

The concentration of nauplii throughout a 24-hour period in the field, seems to be constant. The vertical profile shows a maximum in the upper 20 metres, varying somewhat according to time. The great reduction in the concentration of nauplii from May 1 to May 6 in the Austnesfjord clearly illustrates the different feeding conditions for cod larvae hatched on the same place, but at different time. Both the feeding success and the amount of food in the gut for the three length groups of larvae are strongly influenced by the density of nauplii in the field (Fig. 9). Similar results have been found for other species (BAINBRIDGE & FORSYTH 1971, LISIVNENKO 1961, ZAIKA & OSTROVSKAYA 1972).

SUMMARY

1. Studies on cod larvae have been carried out in the laboratory, in a large basin and in the Borgund fjord and Lofoten area.
2. Observations from the Borgund fjord and the Lofoten area indicated that feeding success was dependent upon concentration of nauplii, particularly the initial feeding.
3. In the basin most of the larvae started to feed, but the daily intake was very different for different size groups indicating marginal feeding conditions.
4. The high mortality in the basin during the third week corresponded with mass mortality of starved larvae in the laboratory. This was another indication on marginal feeding conditions in the basin.

5. Light threshold for feeding success was about 0.1 lux.
6. Large phytoplankton was partly actively grazed.
7. Small phytoplankton was taken passively.
8. Feeding activity started five days after hatching, corresponding to the development of a functional jaw.

REFERENCES

- BAINBRIDGE, V. & FORSYTH, D.C.T. 1971. The feeding of herring larvae in the Clyde. Rapp.P.-v.Réun.Cons.perm.int. Explor.Mer., 160: 104-113.
- BAINBRIDGE, V. & MCKAY, B.J. 1968. The feeding of cod and redfish larvae. Spec.Publ.int.Comm.Northw.Atlant.Fish., 7: 187-217.
- BLAXTER, J.H.S. 1965. The feeding of herring larvae and their ecology in relation to feeding. Calif.Coop.Oceanic. Fish.Inv., 10: 79-88.
- BLAXTER, J.H.S. 1966. The effect of light intensity on the feeding ecology of herring. Pp393-409. In "Light as an ecological factor", edited by R. Bainbridge, G.C. Evans & O. Rackham, Blackwell Sc.Publ. Oxford, 452 pp.
- BLAXTER, J.H.S. & HEMPEL, G. 1963. The influence of egg size on herring larvae. J.Cons.perm.int.Explor.Mer., 28(2):211-240.
- BROWN, M.V. 1969. Feeding behaviour of cod (Gadus morhua). J.Fish.Res.Board.Can., 26: 583-596.
- ELLERTSEN, B., SOLEMDAL, P., TILSETH, S. & ØIESTAD, V. 1975. A study on survival and growth of fish larvae in a large basin, related to feeding conditions. A preliminary study on herring larvae (Clupea harengus L.) and fry. Coun.Meet.int.Coun.Explor.Sea, 1975(E:44): 19 pp. (mimeo).
- HENTSCHEL, E. 1950. Die Nahrung der Herringslarven. Helgoland Wiss.Meeresunters., 3:59-81.

- HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapport Process Verbeaux Reunions Conseil Perm.Intern. Exploration Mer, 20: 1-228.
- HUNTER, J.R. 1972. Swimming and feeding behaviour of larval anchovy Engraulis mordax. Fish.Bull., 70(3): 821-838.
- LASKER, R. 1974. A link between food chain studies and fisheries research: a larval fish bioassay. Coun.Meet.int.Coun. Explor.Sea, 1974(H:10): 29 pp, 5 fig. (mimeo).
- LASKER, R., FEDER, H.M., THEILACKER, G.H. & MAY, R.C. 1970. Feeding, growth and survival of Engraulis mordax larvae reared in the laboratory. Mar.Biol. 5: 345-353.
- LAURENCE, G.C. 1974. Growth and survival of haddock (Melanogrammus aeglefinus) larvae in relation to planktonic prey concentration. J.Fish.Res.Board.Can., 31:1415-1419.
- LISIVNENKO, L.N. 1961. Plankton and the food of larval Baltic herring in the Gulf of Riga. Trud.Nauch.-Issled.Inst. Ryb.Khox, Tatvian SSR 3, 105-138. Fish.Res.Board.Can. Transl.Ser. No. 444. 34 pp.
- MAY, R.C. 1974. Larval mortality in marine fishes and the critical period concept. pp 3-19. In, The early life history of fish, edited by J.H.S. Blaxter, Springer-Verlag, New York; 765 pp.
- NORDENG, H. & BRATLAND P. 1971. Feeding of plaice (Pleuronectes platessa L.) and cod (Gadus morhua L.). J.Cons.int. Explor.Mer., 34(1); 51-57.

- ROLLEFSEN, G. 1946. Kunstig oppdrett av flyndreyngel. pp 91-113. In, Forskning og framsteg, edited by C.L.Godske, J.W. Eides Forlag, Bergen. 89 pp.
- ROSENTHAL, H. & HEMPEL, G. 1971. Experimental estimates of minimum food density for herring larvae. Rapp.P.-v.Réun.Cons.perm.int.Explor.Mer., 160:125-127.
- SHELBOURNE, J.E. 1957. The feeding and condition of plaice larvae in good and bad plankton patches. J.mar.biol. Ass.U.K. 36: 539-552.
- TILSETH, S. & STRØMME, T. Changes in buoyancy and activity during starvation of cod larvae (Gadus morhua L.). Coun.Meet.int.Coun.Explor.Sea, 1976(F:33) 12 pp. (mimeo).
- WIBORG, K.F. 1948. Investigations on cod larvae in the coastal waters of northern Norway. FiskDir.Skr.Ser.HavUnders. 9 (3), 27 pp.
- ZAIKA, V.Y. & OSTROVSKAYA, N.A. 1972. Indicators of the availability of food to fish larvae. 1. The presence of food in the intestines as an indicator of feeding conditions. J. Ichthyol., 12: 94-103.

Table 1a. Percentage of larvae with food organisms in the gut. Each estimate based upon 20 - 50 larvae.

Date	09	15	19	Percentage with yolk sac
March 25	-	0	-	60
March 26	-	0	-	60
March 27	-	25 ^x	-	-
March 28	-	-	85	10
March 29	95	-	96	0
March 30	77	80	79	
March 31	72	95	100	
April 1	62	88	98	
April 2	84	97	85	
April 3	80	84	-	
April 5	84	84	91	
April 7	85	-	80	
April 9	80	90	100	

^x only four larvae

Table 1b. Percentage of larvae with food organisms in the gut. Diurnal sampling on April 5 and 6.

Hour	03	06	09	13	17	19	21	24
Percentage	70	68	84	84	100	91	90	100

Locations	Aspevågen, Alesund	Austnesfjord, Lofoten	Austnesfjord, Lofoten	Austnesfjord, Lofoten
Stations	119 - 130	330 - 343	360 - 371	236 - 239
Time	8 - 9 April 1976	6 - 7 May 1976	8 - 9 May 1976	30 April-1 May 1976
Gear	Zaitzev net, 0 and 30m Clarke Bumpus, 90 μ	Juday net, 30-0m Plankton pump, 200 $\frac{1}{min}$	Juday net, 30-0m Plankton pump, 200 $\frac{1}{min}$	Juday net, 30-0m Plankton pump, 200 $\frac{1}{min}$
Mean number of nauplii/liter (extremes in paranthesis)	4.7 (0.9 - 7.6)	8.5 (1.7 - 18.7)	9.1 (1.2 - 22.7)	24 (1.3 - 85.5)
Kind of larvae	Number	Length, mm	Number	Length, mm
Yolk sac stage 3				
1. Without food	71	4.0	45	4.2
2. Containing food	2	4.7	8	4.3
Without yolk sac				
a) < 4.9 mm				
1. Without food	115	4.2	19	4.3
2. Containing food	26	4.3	17	4.6
b) > 4.9 mm				
1. Without food	18	5.3	2	5.1
2. Containing food	9	5.2	13	5.5
Not measured				
1. Without food	23	-	17	-
2. Containing food	3	-	12	-
Sum:				Sum
1. Without food	227	4.2	161	4.4
2. Containing food	40	4.5	88	4.8
			50	4.6
			137	4.3
			68	5.4
			5	4.3
			45	4.6
			137	315
			854	854

Table 2. Number and length of cod larvae from the four 24-hour stations, given for three length groups with and without food in the stomach.

Table 3. Mean number of food organisms in the gut per larvae. Daily intake estimated as the sum of gut content at 09 and 19.

Date	09 Mean per larvae with food (mplf)	15 mplf	19 mplf	Total of 09 and 19 hrs.
March 28	-	-	5.3	-
March 29	2.7	-	3.4	6.1
March 30	3.4	4.1	7.0	10.4
March 31	3.1	3.3	6.4	9.5
April 1	2.5	2.7	4.1	6.6
April 2	3.3	2.9	4.3	7.6
April 3	3.1	2.6	-	-
April 5	3.6	4.2	9.2	12.8
April 7	4.4	-	8.1	12.5
April 9	6.8	6.3	11.0	17.8
Mean for the period	3.7	3.7	6.5	10.2

Table 4. Mean number of food organisms per larvae; larvae separated into three length groups.
 Daily intake estimated as the sum of gut content at 09 and 19.

Time	09		15		19		Daily intake					
Size groups	L ¹	M ²	S ³	L	M	S	L	M	S			
No. of food organisms/ larva from March 29 - April 1	3.4	1.8	1.5	4.3	3.5	2.2	9.4	4.5	2.3	12.8	6.3	3.8
Mean length in mm										4.9	4.6	4.3
No. of larva investigated										27	32	27
No. of food organisms/ larva from April 7 - April 9	8.5	4.6	2.5	5.3	6.3	2.0	14.9	8.9	2.4	23.4	13.3	4.9
Increase in food intake since first period										10.6	7.0	1.1
Mean length in mm										5.7	5.3	4.8
Length increase since first period										0.8	0.7	0.5
No. of larva investigated										30	37	36

1 = Large, 2 = medium, 3 = small

Table 5. Vertical densities of nauplii per litre on March 29 and 30. Sampled by a plankton pump.

Depth	Station 1 (March 29)	Station 2 (March 29)	Station 2 (March 30)
0m	0.3	0.0	0.5
$\frac{1}{2}$ m	0.4	0.5	0.5
1m	0.3	0.9	0.4
$1\frac{1}{2}$ m	1.6	1.1	0.7
2m	2.9	1.5	0.8
$2\frac{1}{2}$ m	<u>4.1</u>	3.3	<u>1.5</u>
3m	1.6	<u>3.6</u>	1.4
3.2m	1.4	3.0	0.4
3.4m	0.4	1.9	0.2
Over the bottom	0.3	0.0	0.1
Bottom	2.2	1.6	0.8
Mean no.	1.4	1.6	0.7

Table 6. Vertical densities of nauplii per litre throughout 24 hours on April 5 and 6.

Hour	03	06	09	13	17	21	24
Depth							
0 m	0.8	0.1	0.4	0.1	0.0	0.5	0.0
$\frac{1}{2}$ m	0.7	0.1	0.7	0.0	0.1	0.8	0.1
1 m	0.8	0.4	0.8	0.1	0.4	1.2	0.1
2 m	0.8	0.4	1.0	0.1	0.4	1.1	0.2
3 m	0.3	1.1	1.6	0.3	0.2	1.5	0.6
Over the bottom	0.8	0.3	1.3	0.1	0.4	0.1	0.2
Bottom	0.0	1.6	1.2	0.0	0.0	0.8	0.4
Mean no.	0.6	0.6	1.0	0.1	0.2	0.9	0.2

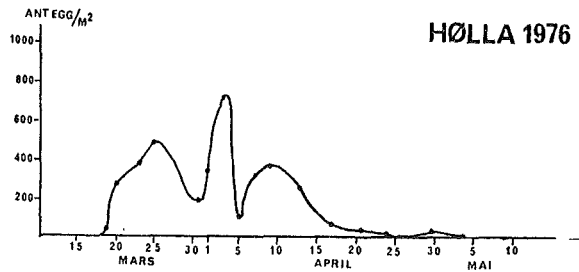
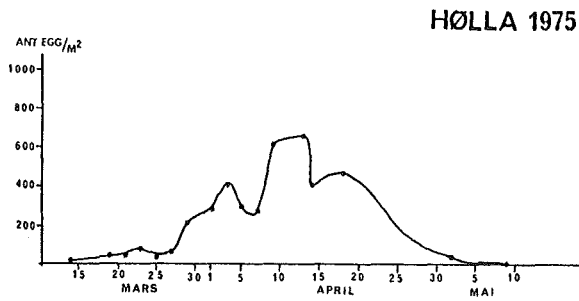


Fig. 1. Spawning at Hølla, Lofoten, in 1975 and 1976. Each data point based on three Juday net stations, sampled from 100-0 m in 1975, and 100-30^m in 1976. Number/m² includes newly fertilized to 48 hr old eggs.

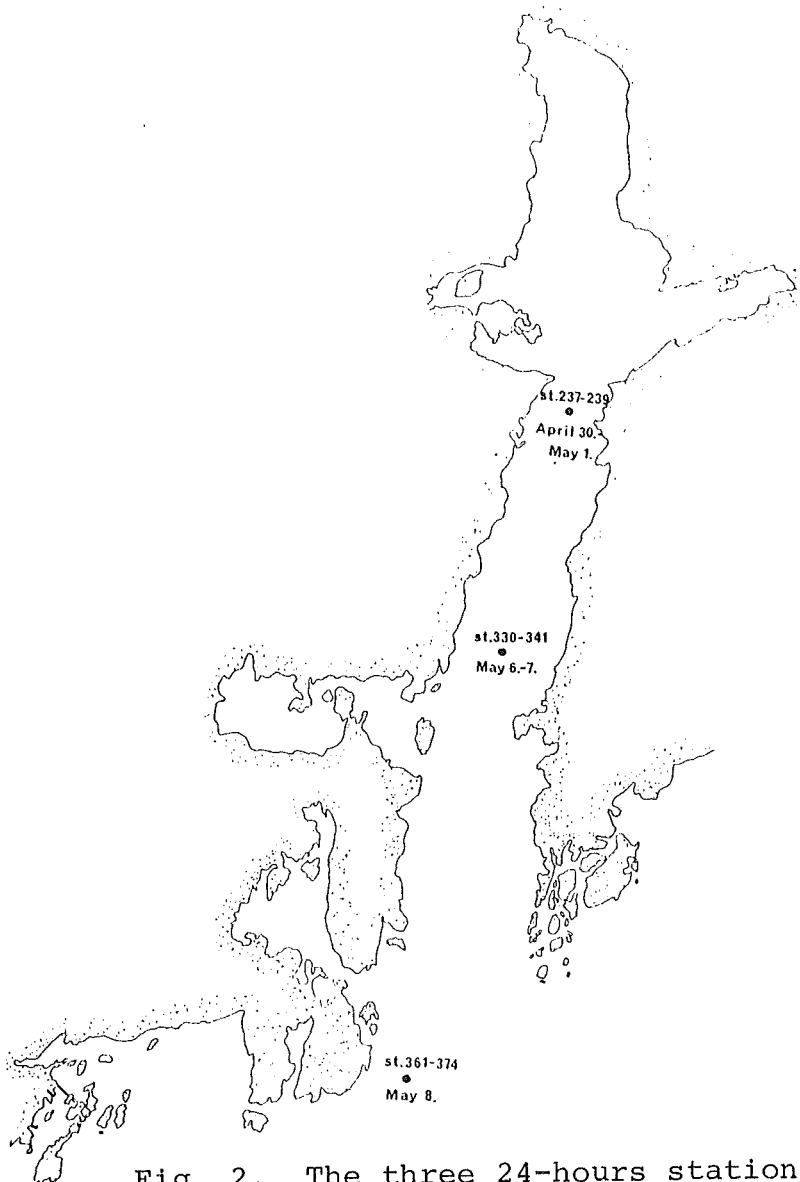


Fig. 2. The three 24-hours stations in Austnesfjord, Lofoten, with station numbers and sampling dates.

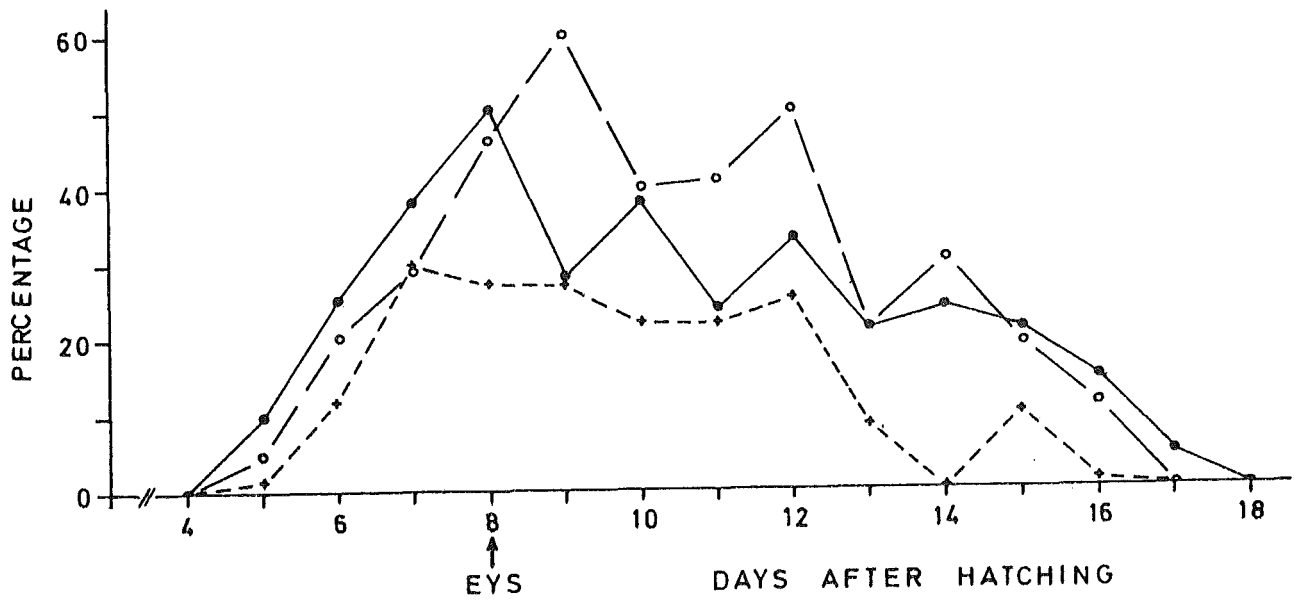


Fig. 3. Feeding success of a starved cod larvae population on Artemia nauplii, from hatching to mass mortality. Each data point represents 30 larvae, feeding on 10000 nauplii/l (●—●), 1000 nauplii/l (○—○) and 100 nauplii/l (+ --- +), respectively, for six hours.

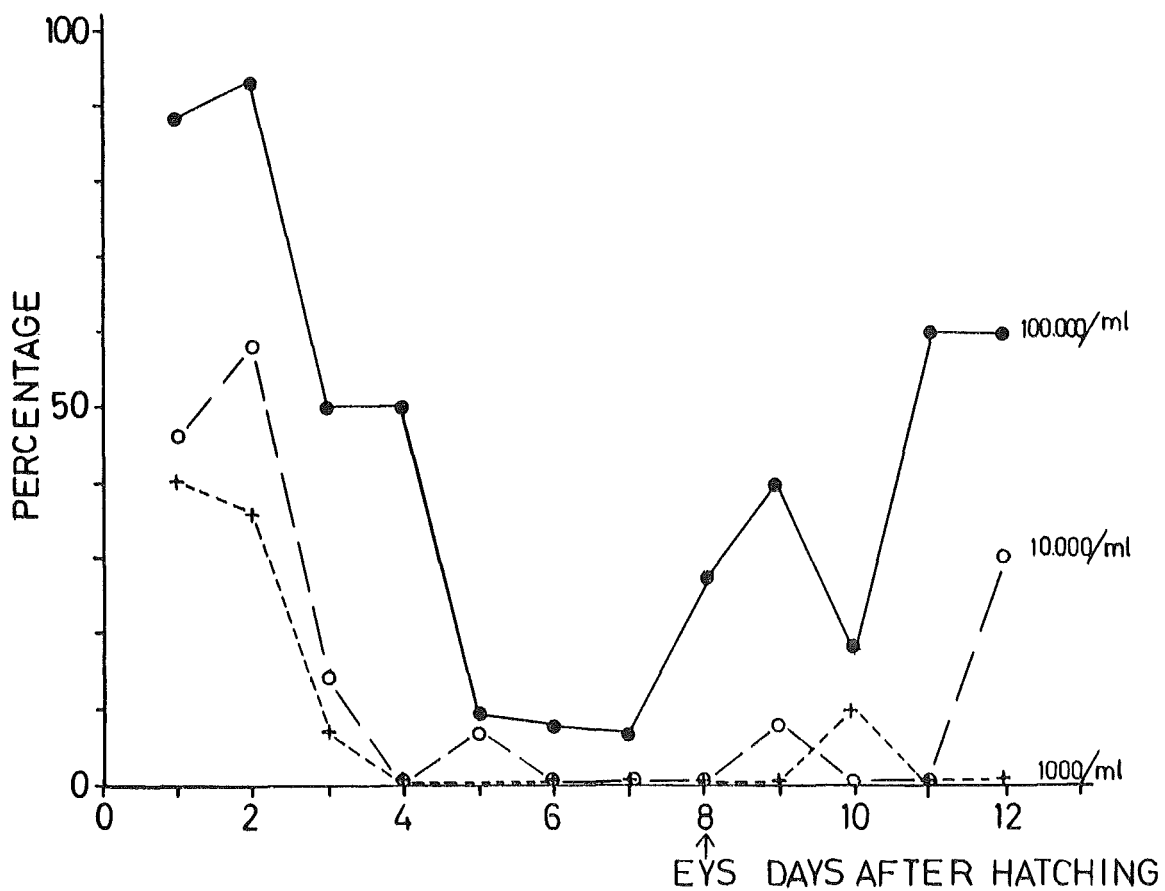


Fig. 4. Feeding success of a starved population of cod larvae on different concentrations of Dunaliella sp. Each data point represents 30 larvae.

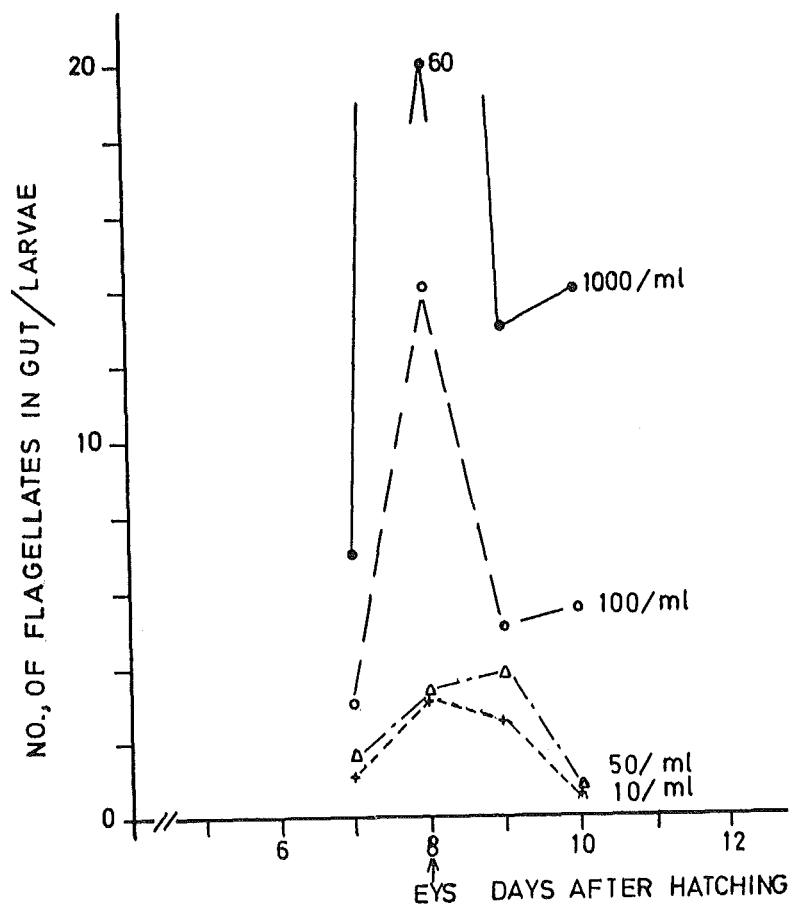


Fig. 5. The mean number of flagellates in the guts of four groups of cod larvae (30 starved larvae per group) fed on different concentrations of Peridinium trochooidum. The experiments were conducted six hours per day, from the seventh to the tenth day after hatching.

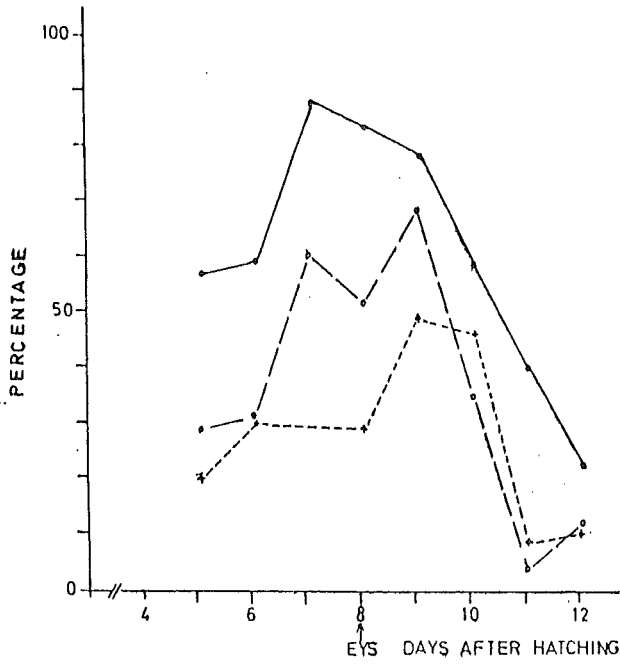


Fig. 6. Feeding success of cod larvae sampled without replacement from a starved population on Peridinium trochoidum (1000/ml) at the following light intensities: 1000 lux (● — ●), 10 lux (○ — ○), and 0 lux (+ — +). The experiments lasted six hours per day.

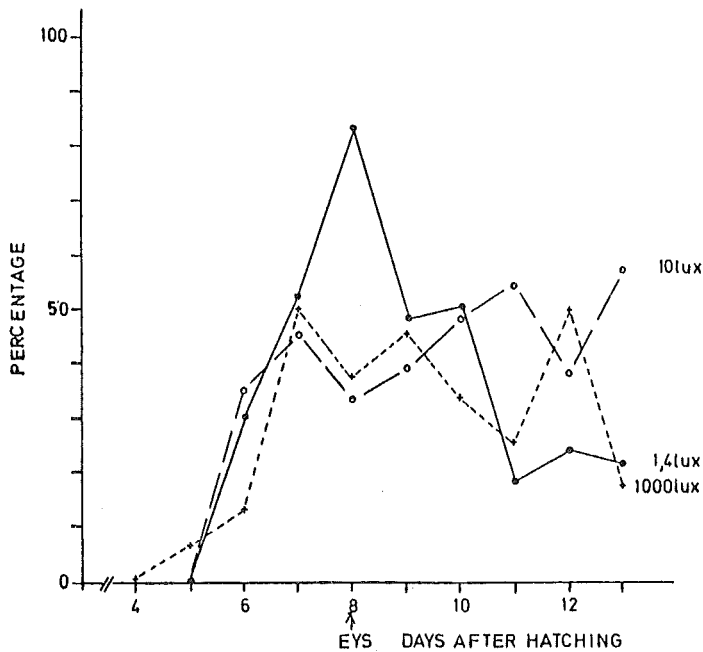


Fig. 7 The feeding success of a starved population of cod on a concentration of 1 Artemia nauplii/ml at different light intensities. Each data point represents 30 larvae. The experiments ran six hours.

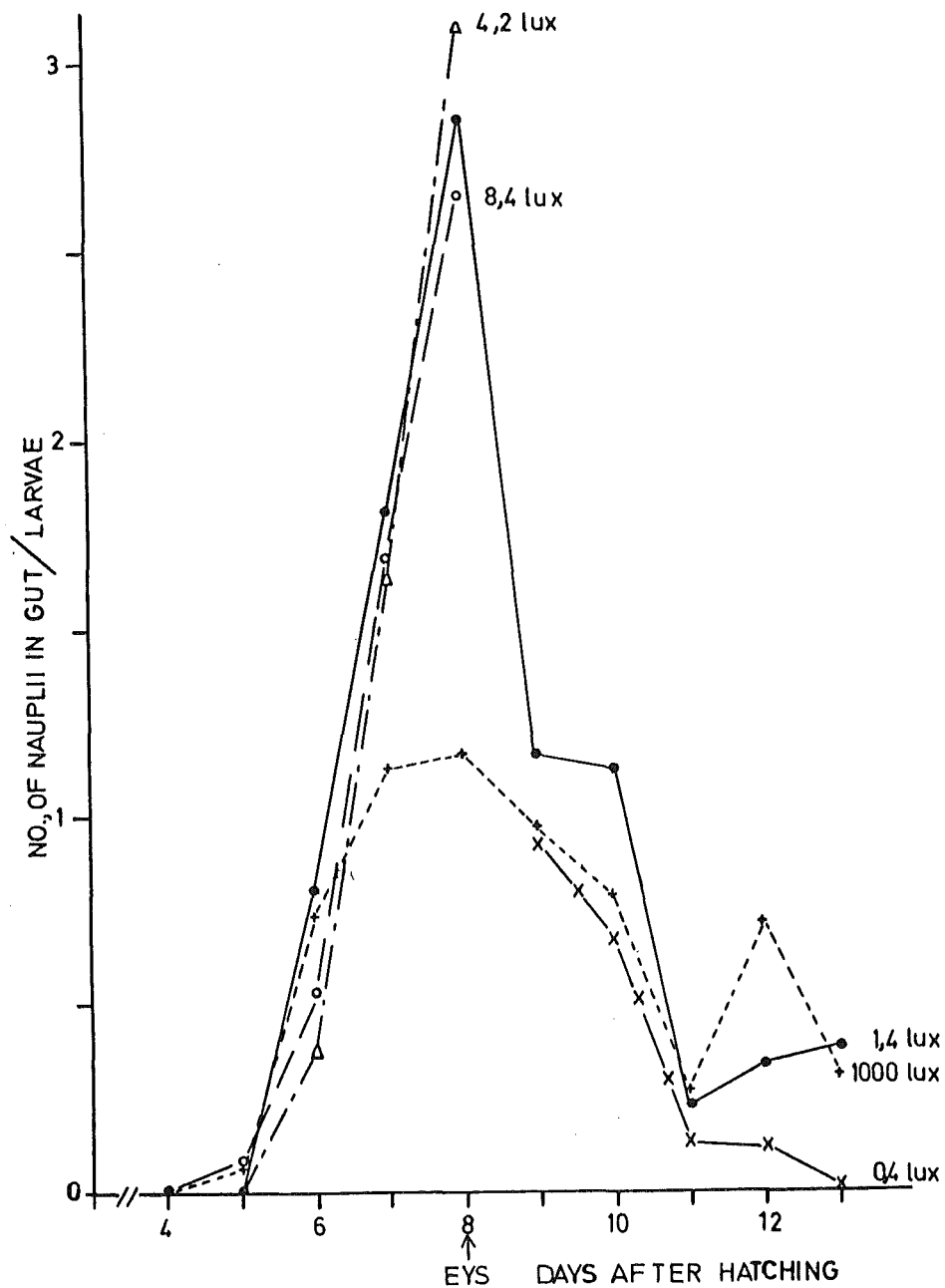


Fig. 8. Mean number of *Artemia* nauplii (1 nauplius/ml) in the guts of five groups of cod larvae kept at different light intensities (A group in composed of 30 larvae, taken without replacement from a population starved from hatching). The experiments ran six hours per day, daily from hatching to day 13.

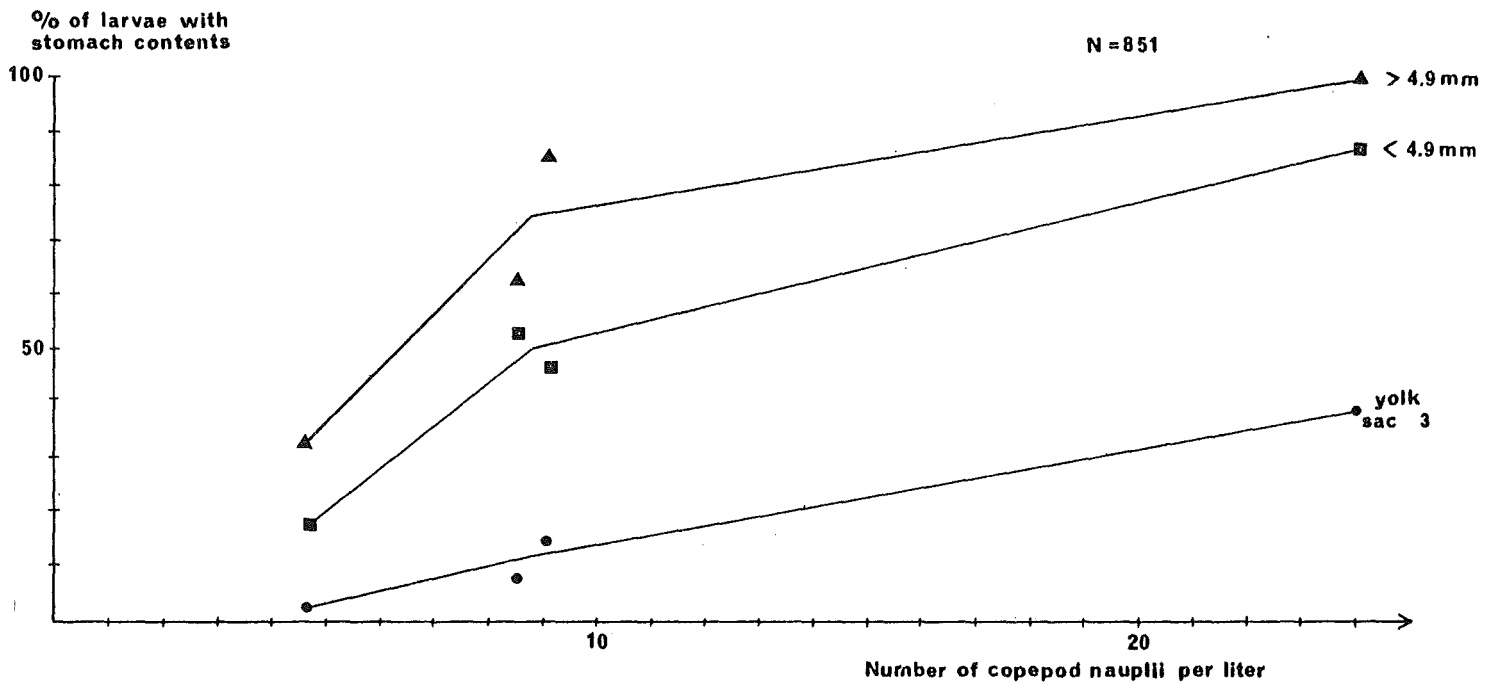


Fig. 9 Feeding success of three size groups of cod larvae from the four 24-hour stations.

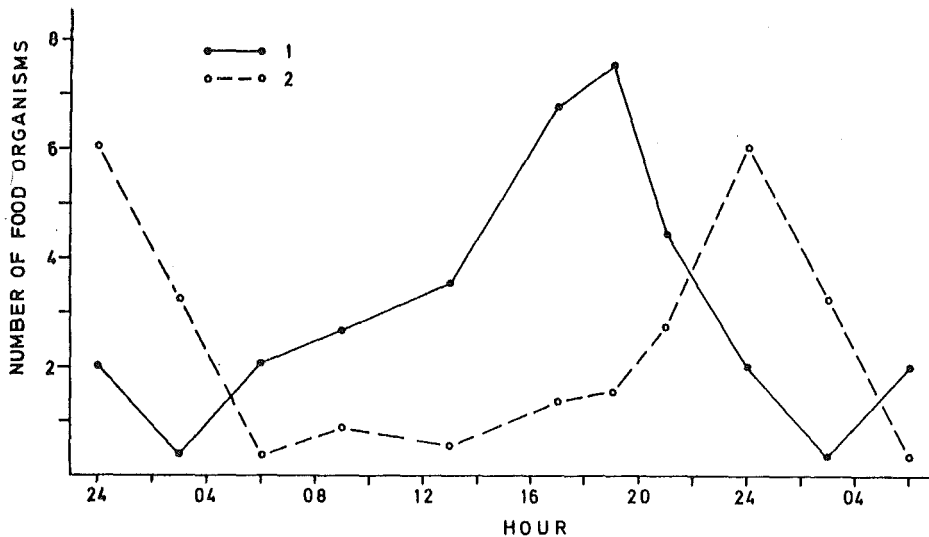


Fig. 10 Mean number of food organisms in the guts of cod larvae during a day and night sampling on April 5 to 6. Number of newly eaten and half digested organisms (1) is given separately from fully organisms (2).

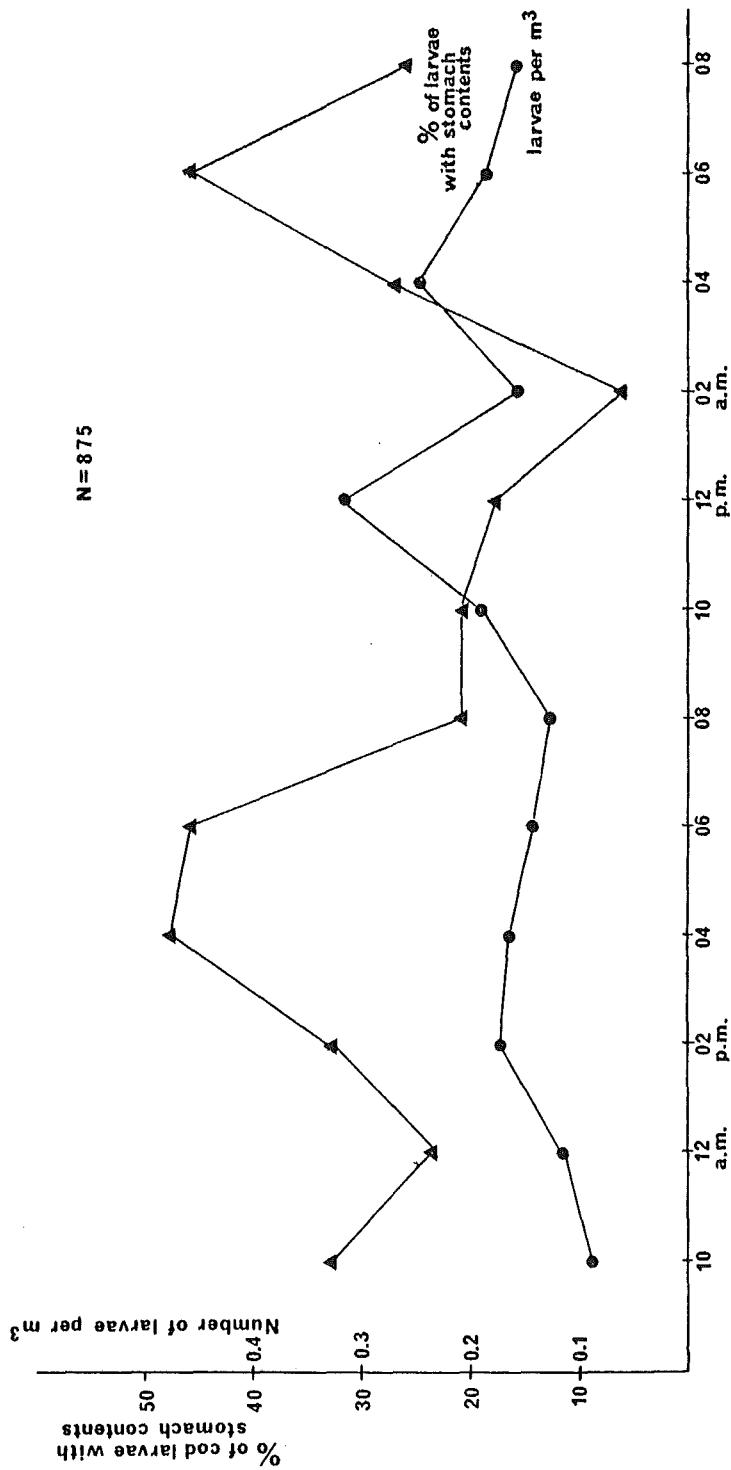


Fig. 11. Feeding success (% cod larvae with stomach contents) and concentration (larvae/m³) during a 24-hour cycle. Material from three 24-hour stations (119-130, 330-341 and 360-374) are pooled.

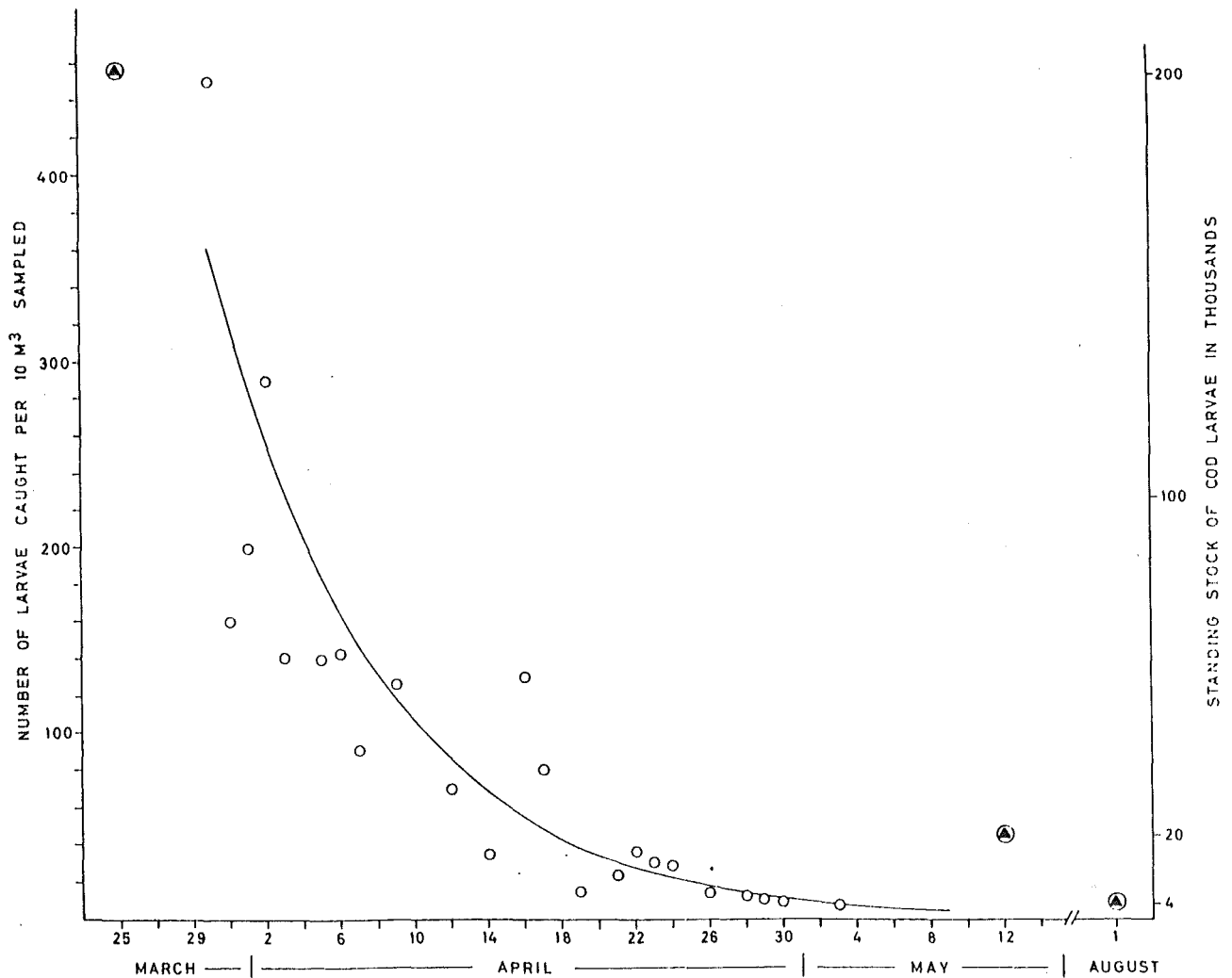


Fig. 12. Catches of cod larvae at 0900 hrs. from March 30 until May 3.

number of larvae sampled by a 0.1 m^2 Juday net, sampling volume 10 m^3 (1:440 of the total volume of the basin).

Start population (March 25), estimate (May 12) after sampling 15 m^3 at each of three depths at 2400 hrs. with a bongo-like net, and the surviving cod fry (August 1) collected after draining the basin.

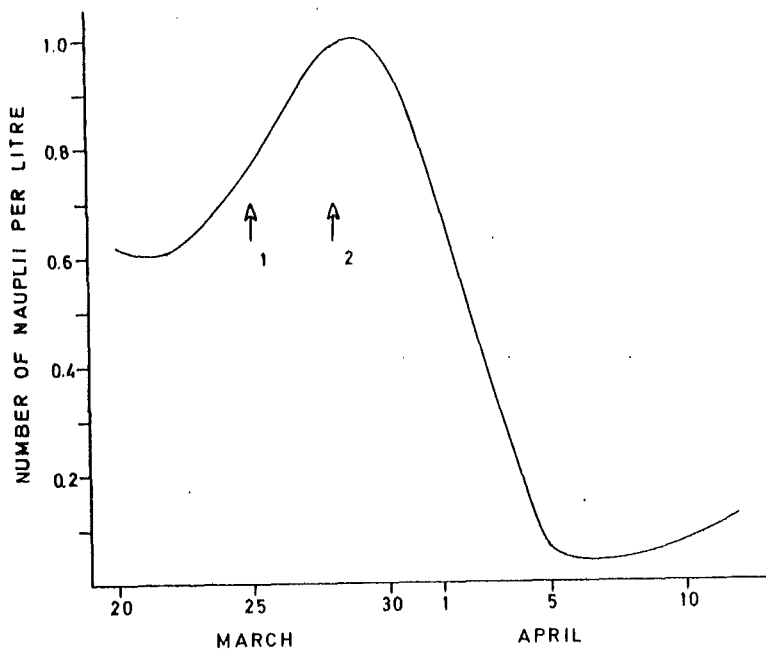


Fig. 13. Estimated standing stock of nauplii per litre in the basin from March 22 to April 12 based on daytime pump samples. The date of transfer of the larvae from the laboratory to the basin (March 25) and the day of initial feeding (March 28) are indicated with arrows (1) and (2).

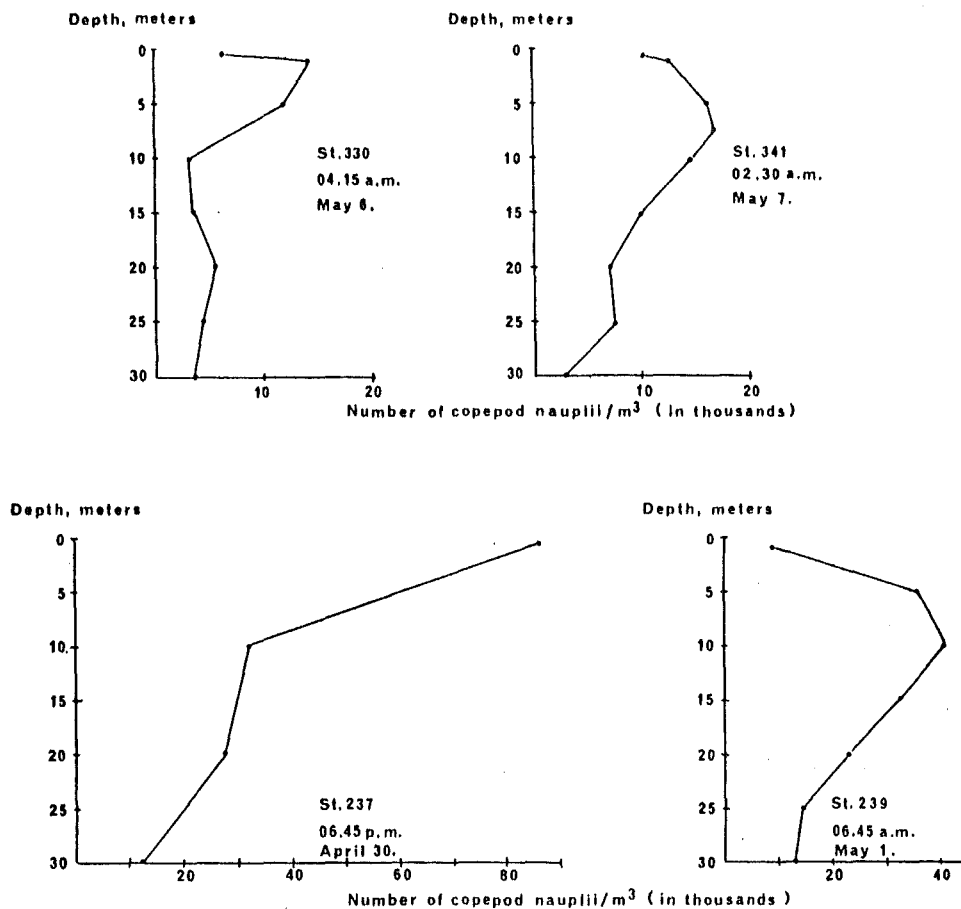


Fig. 14. Examples of nauplii profiles from the 24-hour stations 330-341 and 236-239 in Austnesfjord.

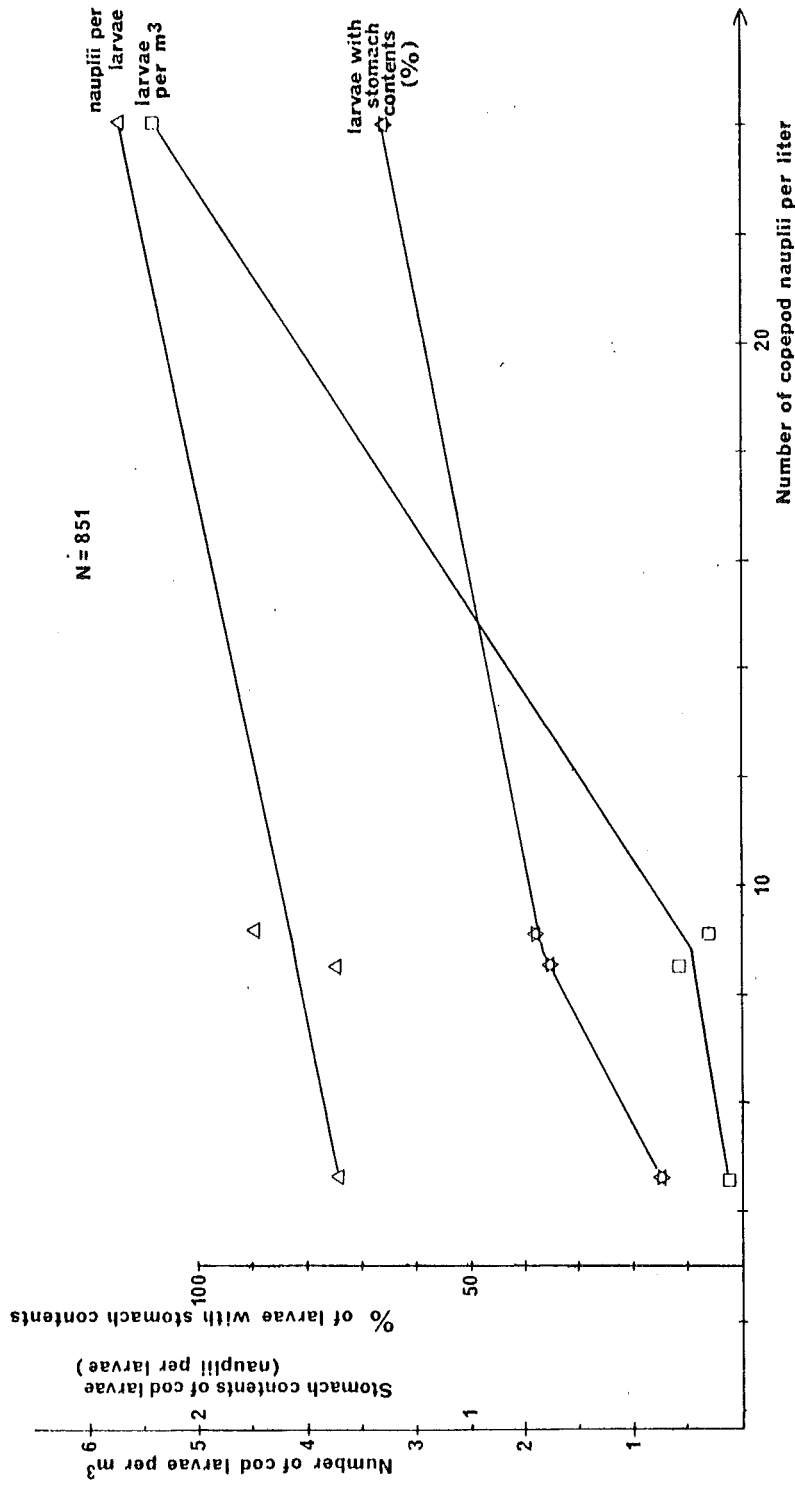


Fig. 15. Feeding success (% cod larvae with stomach contents), number of nauplii per larvae, and concentration of cod larvae (larvae/m³) at the four 24-hour stations.