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FEEDING AND VERTICAL DISTRIBUTION OF COD LARVAE IN RELATION TO AVAILABILITY OF PREY ORGANISMS.

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ABSTRACT

The project "First feeding in cod larvae" investigates the biology and distribution of cod larvae and their food organisms. The investigation seeks to increase our knowledge about the growth and mortality of cod larvae.

Field investigations in the Lofoten area, carried out since 1975, have studied interrelations between cod larvae and their prey organisms (mainly copepod nauplii) such as vertical distribution, feeding condition in relation to nauplii density, the size of food selected, etc.

A fish pump (capsulpump, capacity 10 m^3/min) has been introduced for sampling cod larvae from discrete depths. A plankton pump (200 l/min) was used for sampling food organisms. Patchy distribution of plankton organisms was studied by use of an in situ particle rate meter. A larval bioassay, using laboratory-reared larvae, was performed in order to test the feeding incidence of larvae in water masses of different food densities.

The highest concentrations of cod larvae were observed at depths of 5-15 m. The overall concentrations observed ranged from 0-15 larvae/m^3. Few larvae were observed in the surface meter.

Diurnal vertical migration was observed in copepod nauplii. The highest daytime densities were found at 5-15 m, and at night at a depth of 0-10 m. Nauplii concentrations up to 600/l were observed close to the surface. A decrease in mean nauplii size with increasing depth was observed.

A preference for nauplii as larval food was observed, close to 100% of the organisms found in the larval guts were nauplii, while other organisms of suitable food size were only sporadically taken by the larvae, i.e. bivalve larvae, gastropod veligers, copepod eggs, etc.

Cod larvae produced by artificially fertilized eggs have been used to detect larval fish food in the Lofoten area.

The bioassay experiments showed a clear relationship between the increase in larval gut contents with increasing prey densities. The number of nauplii in the gut of first feeding cod larvae sampled at discrete depths corresponded to the density profile of nauplii.

The value of larval feeding incidence as a parameter in evaluating the relationship between cod larval feeding conditions and prey density, based on the bioassay experiments is discussed.

INTRODUCTION

The mean annual production of the Arcto-Norwegian cod stock is about 800 000 - 1000 000 tons. The annual average catch of this stock in Norway is about 300 000 tons (1965-1976), and is of great importance to the Norwegian fisheries. The stock is distributed in the Barents Sea and the adult population migrate to the Norwegian coast for spawning.

The year-class strength of this cod stock varies on an annual basis by a factor of about 20:1.

The year-class strength is established at the 0-group stage (about ½ year old cod). Since the number of eggs spawned is exceedingly higher than the number of 0-group cod, there must be an enormous mortality during the first half year.

Several factors leading to this high mortality and fluctuations in the fisheries have been suggested, and numerous investigations have taken place in Norwegain waters to test different hypotheses.

During the years 1864-70 G.O. Sars carried out the first investigations on eggs and larvae from Arcto-Norwegian cod spawning in Lofoten (SARS 1879). His observations covered most of the fields still in focus; spawning period and areas (also those outside Lofoten), description of egg and early larval development, vertical distribution of the larvae and the patchy distribution of fish larvae and their prey organisms. He considered wave action and the drifting ashore of eggs and larvae as the main mortality factor, and proposed artificial hatching to improve fishery during periods of low stock size.

In the century following Sars's pioneer study the investigations on cod eggs and larvae in Lofoten have focused on the causes of the fluctuations in the fisheries. To explain this phenomenon Hjort put forward the hypothesis of a "critical period" in the early life of fish larvae, suggesting that lack of available food organisms at the time of yolk sac absorption was the predominant factor causing high mortality (HJORT 1914).

Investigations on cod larvae and their food organisms have been carried out by Dannevig (1919) and Wiborg (1948 a, 1957) and others, and several investigations have been undertaken in different countries to test Hjort's hypothesis of the "critical period". May (1974) concluded, on the basis of 11 investigations reported in literature, that due to improper sampling methods no conclusions could be drawn about the existence of a critical period.

Several other factors leading to high mortality besides the "critical period" have been suggested. A correlation between SW winds and the subsequent year-class of Arcto-Norwegian cod has been indicated by Rollefsen (1930, 1932). Though his conclusions are debatable, his combined laboratory/field approach has proved very fruitful.

The effects of freshwater outflow in the coastal current on primary production, the effect of varying outflow due to meteorological conditions (GRAN 1923, 1930), and the effect of artificial outflow due to hydroelectric power production have been suggested by Skreslet (1976). Sund (1924) suggested an indirect effect of the yearly varying freshwater outflow on the varying transport of eggs and larvae offshore.

Effects of long-term climatic change have been indicated by Otterstad (1942). Besides his hypothesis of the critical period, Hjort (1914) also suggested that the transport of larvae from Lofoten to the Barents Sea is influenced by the meteorological conditions.

An understanding of this high mortality is still incomplete. The aim of the present project is to test Hjort's hypothesis and to increase our knowledge about the growth and survival of cod larvae. Besides, the drift and dispersal of cod larvae from the spawning area in Lofoten to nursery grounds in the Barents Sea is being studied in order to link the larval investigations to the international 0-group investigations in the Barents Sea.

Laboratory and enclosure experiments on some biological aspects of cod larvae have been carried out to aid our understanding of larvae sampled at sea. Consequently the project is divided into three parts:

1, Laboratory experiments to establish feeding behaviour, activity in relation to light intensity and food density, time for first feeding, point of no return (PNR), effects of starvation, etc. (See ELLERTSEN et al. 1979 b).

2, Enclosure experiments, rearing of cod larvae of known age and quantity, in a 4400 m^3 basin, to obtain data on first feeding, feeding incidence, growth rate, mortality rate, etc. (See ELLERTSEN et al. 1979 d).

3, Field investigations, mainly in the Lofoten area. The present paper deals with investigations in the field. (See also ELLERTSEN et al. 1979 a).

Investigation areas.

Borgundfjorden.

Borgundfjorden is located on the western coast of Norway (Fig. 1), and is traditionally a spawning area of cod. A few observations have been carried out in the area, especially on the vertical distribution of cod larvae and copepod nauplii.

Lofoten.

The main area of investigation is Vestfjorden in north-western Norway (Fig. 2a). A close description of the area is given in ELLERTSEN et al. 1979 a.

Special attention has been paid to Austnesfjorden, an important spawning area in the Lofoten archipelago (Fig. 2b).

METHODS

Field investigations have been carried out from the following research vessels:

1975: "Peder Rønnestad", "Asterias"
1976: "Peder Rønnestad", "Asterias", "H.U. Sverdrup"
1977: "H.U. Sverdrup", "Johan Ruud".

Sampling of cod larvae.

In 1976 the greater portion of the larvae was collected using a 500 µm mesh-sized Juday net, with a mouth area of 0.1 or 0.5 m^2 depending on weather conditions, larval concentrations, etc. The plankton buckets were equipped with 300 µm nylon gauze. Vertical hauls were carried out at a depth of 30-0 m, broken hauls were occasionally made at 30-20, 20-10, and 10-0 m.

Occasionally, a 500 µm mesh-sized, two-chambered net with rectangular mouths, 40 x 60 cm each, were used. Collecting depths were identical with depths using the Juday net.

In 1977 these methods could not fulfill our requirements for samples of cod larvae from discrete depths. In addition to a Bongo-60 net (375 µm mesh size) without a closing device and a Juday net (375 µm, 0.5 m^2 mouth area), a commercial fish pump (U 230) was used for sampling from discrete depths: 1, 2, 5, 10, 15, and 20 m. The fish pump had a theoretical capacity of about 10 tons per minute, with a lifting height of 3.5 m above sea level. The rotor was worked hydraulically, the water being pumped through a 8" soft rubber hose. The length of the hose was 30 m. With a longer hose the pump could be operated at greater depths.

The hose was fitted to one end of a U-shaped metal pipe, with a plastic pipe connected, via a short flexible hose, to the other end (Fig. 3). Initially, filtering was carried out using a Juday net, 0.5 m^2, 375 µm, kept just above surface level along the side of the ship. The plastic pipe was lowered into the net and

the pump was started. To record water volume a simple flowmetre (a nautical log) was installed inside the U-shaped pipe (Fig. 3).

This way of handling this apparatus proved unsatisfactory, mostly due to an unstable flowmetre which resulted in incorrect estimations of the volumes filtered.

Later the filtration was performed on deck by filtering through a Juday net (180 µm, 0.1 m^2) placed inside a 400 litre plastic jar (Fig. 4). At certain intervals the water flow was tested by filling the jar. The most stable flow was obtained at about 2000 l/min.

While testing the pump, it was found that a mesh size of 375 µm in the Juday net was too big. A large number of larvae got stuck between the meshes, resulting in damaged individuals (loss of tail, head, eyes, etc.). On using a 180 µm mesh-sized Juday net the number of larvae with damages proved minimal.

The use of the fish pump was a success for the project purposes, even though filtering such large volumes proved laborious. Technically, the method can be considerably improved, especially the regulation of water flow and the measuring of water volumes. Further testing of a larger fish pump will be done in 1979.

Samples of larvae were preserved in 4% buffered (hexamine) formalin solution using 10 °/oo salinity sea water, a solution which in our laboratory tests was found to give minimal shrinkage of the fish larvae. Counting of larvae was occasionally done at sea, further examination of samples was usually carried out at the Institute of Marine Research in Bergen. Several aspects of the larvae were examined, such as standard length, functional jaw, yolk sac stages, development of swimbladder, gut content, etc. (See ELLERTSEN et al. 1979 b, d).

The larvae were dissected and the gut contents analysed. The degree of digestion of the nauplii eaten by the cod larvae was assessed according to the following criteria: 1) no visible

digestion, 2) a transparent zone between carapax and interior of the nauplii, and 3) the interior of the nauplii completely dissolved.

Zooplankton sampling.

During preliminary investigations in 1975, and occasionally in 1976, zooplankton catches were made using a 90 µm, 0.1 m^2 Juday net and a Clarke-Bumpus net (90 µm mesh-size).

Because of the need for more detailed information with regard to vertical distribution of copepod nauplii, depth of maximum concentrations, etc. a transference to the use of plankton pumps as our main zooplankton collecting gear became necessary.

Plankton organisms were collected by pumping 100 or 20 litres (1976 and 1977, respectively) from each of the following depths: 0, 2, 5, 10, 15, 20, 25, and 30 m. Occasionally additional samples were taken from 1, 7.5, 12.5, 35, 30, 45, and 50 m. We used a monopump with a capacity of 200 l/min. The samples were filtered through a 90 or 40 µm mesh nylon gauze.

All samples were preserved in a 4% buffered formalin solution. The samples were partly examined at sea when immediate estimates of nauplii densities, distributions, etc. were necessary for further decisions concerning the localization of 24-hour stations, etc. The rest of the examination was done in Bergen.

In nauplii size determinations microscopes with 20-50x magnification were used to measure the carapax length (Fig. 5). Owing to the large number of scrutinized nauplii in the cod larvae guts this measure was found to be most exact. While the carapax were intact and suitable for measuring the naupliar abdomens were usually broken apart, especially in completely digested nauplii where only the exoskeleton remained.

Other parametres.

Salinity and temperature were registered using a CTD-sonde or Nansen water bottles.

Wind data were kindly supplied by the Norwegian Institute of Meteorology, the weather station located at Skrova (See ELLERTSEN et al. 1979 a). In 1977 a wind log was also placed onboard the ship.

Field hatchery

An incubator system for pelagic fish eggs, described by Tilseth and Strømme (1976), was installed on land at Austnesfjorden, Lofoten. Seawater was pumped from 20 m depth and filtered through 50 and 10 µm Fulflo filters before entering the system.

Bioassay experiments

The experiments were conducted according to the method described by LASKER (1975). First feeding cod larvae were sorted out from the field hatchery and transferred to a thermostat controlled room at 5°C on board R/V "Johan Ruud". Cod larvae at yolk sac stage 5 and 6 are considered as first feeding larvae (ELLERTSEN et al. 1979 b). Samples of seawater were brought on deck via the hose of a "particle rate meter" pump (see below). Samples of seawater containing different particle concentrations were collected. Twelve liter were collected in black plastic jars to test whether the samples of seawater contained suitable food particles for cod larvae. A 2 l subsample was taken from each jar for nauplii counting. The remaining 10 l were transferred to the thermostat controlled room for larval bioassay experiments. Thirty cod larvae in the first feeding stage were gently added to each jar. The jars were covered with two 20% neutral filters, in order to reduce the light intensity (Ellertsen et al. 1979 b). A suitable cultured food organism was not available to run control experiments to determine if the particular batch of cod larvae was in good condition and would feed. As a control experiment the number of nauplii in one jar was concentrated.

The larvae were permitted to feed for 5 hours, then MS 222 (1 : 200 000) was added to the seawater and they were collected after 2 minutes. The larvae were preserved in 4% formalin in 10 °/oo seawater for later examinations.

The particle rate meter

Essential for the application of the larval bioassay method is the detection and sampling of food particles edible for first feeding cod larvae. This consists mainly of copepod nauplii. An instrument suitable for this purpose has been developed by Dr. Edward Scura at the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla Laboratory, USA. The instrument works on the Coulter Counter principle. The sensor with an aperture of 1 mm is mounted in the mouthpiece of a 30 m submersible hose which is connected to a membrane pump on deck. The time from detection of a patch until sampling on deck is 60 seconds.

RESULTS

Distribution of copepod nauplii.

Only small numbers of copepod eggs were observed in most samples, in concentrations ranging from 0 to 2 eggs per litre. The ratio of copepod eggs to copepod nauplii grew rapidly with increasing depth, as exemplified in the following table (st. 238, 1976):

	eggs / nauplii
0 m	0.01
15 "	0.03
30 "	0.13
35 "	0.30
40 "	0.36
45 "	0.39
50 "	0.74

Most samples revealed that few eggs were distributed close to the surface, a fact that is supposed to be connected to the sinking of copepod eggs.

The predominating copepod nauplii in the Lofoten area were found to belong to Calanus finmarchicus (Gunnerus).

Austnesfjorden (Fig. 2) formed an important basis in our investigations. Even in this restricted area large changes in nauplii concentrations were observed from one day to the next. In Austnesfjorden st. 237-239 were investigated 30 April - 1 May 1976. Zooplankton were sampled from several depths down to 30 m. The concentrations ranged from 6.8 to 86.0 nauplii per litre within single samples (mean concentrations 40.6, 36.4, and 22.4 nauplii per litre, st. 237, 238, and 239, respectively). Next day, 2 May, another 24-hour station (st. 266-277), located about 700 m distance from the previous stations, was investigated. Here the nauplii concentrations ranged from 1.0 to 9.2 nauplii per litre (mean concentration 6.0 nauplii per litre all stations and depths pooled).

Vertical distribution of nauplii - naupliar size

Where their size is concerned the vertical distribution of nauplii does not seem to be homogeneous. Measuring the carapax length of nauplii from several stations, it was found that mean nauplii sizes decreased with increasing depth (Fig. 6).

However, this phenomenon was not totally consistent. At one 24-hour station in 1977 nauplii sizes were found to increase at 30 m and below (Fig. 7). Nevertheless, the total impression is that of a tendency towards reduced size with increasing depth.

Diurnal changes in nauplii concentrations.

Several 24-hour stations have been made during the period 1975-1977. Fig. 8-13 and 16-17 show profiles of nauplii concentrations from some 24-hours stations.

Austnesfjorden 6-8 May 1975. St. 39-58.

Samples were taken close to the surface with a Clarke-Bumpus net, mesh size 90 µm. The concentrations were found to decrease

in the morning until early afternoon, followed by an increase in the evening. Concentrations varied between about 200 to 5200 nauplii per m^3 (Fig. 8).

Borgundfjorden 15-16 April 1975. St. 57-69.

Samples were taken at 0 and 9 m with a Clarke-Bumpus net, 90 µm. Nauplii concentrations were reduced close to the surface in the morning, followed by an increase towards the afternoon (Fig. 9). The reverse was observed at 9 m with an increase in the middle of the day. Concentrations at 0 m varied between 200 ind per m^3 at 12 p.m. to about 2100 per m^3 in the evening.

Borgundfjorden 17-18 April 1975. St. 79-87.

Zooplankton was collected with a Clarke-Bumpus, 90 µm. Fig. 10 shows the diurnal concentrations at 0 m. The curve shows a decrease in the middle of the day, while at 8 m an increase was observed in the daytime. Echo depth at the station is about 30 m.

Borgundfjorden 24-25 April 1975. St. 117-122.

Samples were collected from depths of 3, 8, and 14 m. In Fig. 11 all depths are grouped together showing an increase from about 3500 ind per m^3 in late afternoon to about 5500 ind per m^3 at 0300, followed by a decrease to about 3500 ind per m^3 at 1100 next morning. At all depths throughout the period a similar trend was observed in the variation of nauplii concentrations.

From 1976 on, pump sampling made it possible to obtain information of the vertical distribution of nauplii at exact discrete depths.

6-7 May a 24-hour station was made in Austnesfjorden (st. 330-341). Fig. 12 shows the nauplii profiles. Maximum concentrations varied within 1-10 m depth. A sudden increase close to the surface at st. 335 may be due to an influx of new water masses. No hydrographic parametres were recorded at this time.

As shown in Fig. 21, regardless of size not all copepod nauplii can be regarded as cod larvae food. First feeding cod larvae seem to omit eating nauplii smaller than approximately 120 µm and larger than 380 µm (carapax length). This implies that nauplii concentrations alone, all nauplii grouped together, do not give a proper impression of the food supply to the larvae.

The nauplii material from some 24-hours stations has been split into size-groups: $\leq$ 100 µm, 120-200 µm, 220-300 µm, and $\geq$ 320 µm. Fig. 13 shows nauplii profiles throughout a 24-hour period 10-11 May 1977. Concentrations at different depths were found to change during the period, especially in the upper 15 m. Minimal changes were found within the smallest nauplii ($\leq$ 100 m).

Current measurements with moored Aanderaa current metres in 6 m and 50 m depths were made at the mouth of Austnesfjorden during the period 21 April - 13 May 1977. The semidiurnal tidal component dominates the water movements giving maximum velocities of about 20 cm/s. The residual current seems to be dominated by wind currents giving maximum velocities of about 15 cm/s in 6 m depth. Fig. 14 shows a 25 hour running mean of the current vectors in Austnesfjorden and wind velocity vectors at the meteorological station "Skrova" outside the mouth. The wind current in the upper layer is compensated by a flow in the opposite direction in deep water.

At the time of the 24-hour station 10-11 May 1977 (st. 893-912), a very weak stratification was established in the uppermost 10 m. Fig. 15 shows isoplets of temperature, salinity, and σ_t during the 24-hour station. The overall Brunt-Vaisälaä frequency $N^2 = \frac{g}{\rho_o} \frac{\partial \rho}{\partial z}$ was ranging between 4-6 x 10^{-5} sek^{-1} in the upper 10 m. Below, the value of N^2 was an order of magnitude smaller. The tidal current was in the nip phase with maximum velocities of 4 cm/s. Assuming a linear decrease in the tidal velocities towards the head of the fjord and a linear proportionality with the cross section area of the fjord give a maximum tidal current of about 3 cm/s at the 24-hour station.

The wind was weak and variable (1 m/s) during the first 12 hours. During the next 12 hours wind direction was from north and the speed was increasing to 7 m/s. However, the current velocity is not more than 2 cm/s in 6 m depth at the mouth. The total transport length of the water masses past the station during the 24 hour period is estimated to 1200-1600 m. Thus the effect of advecting nauplii from other regimes should be limited. The forced vertical mixing of nauplii by the action of the wind should be neglected during the first 12 hours, while in the last 12 hours mixing may have had a limited effect. (For general information on meteorological effects upon the hydrological situation in the Vestfjorden area, see ELLERTSEN et al. 1979 a).

Fig. 16 shows nauplii profiles from diurnal station 1027-1033 18-19 May 1977. Changing distribution patterns throughout the period were observed within the different size groups.

Fig. 17 shows the relationship between diurnal nauplii profiles and the sampling hours of a 24-hour period arrived at by pooling the results of 6 separate 24-hour stations. The abscissa gives the relative occurrence of nauplii at separate depths, expressed as mean percentages for the six 24-hour stations where 100% equals the whole water column (7 sampling depths).

The weather conditions during some of these 24-hour stations are shown in the following table:

	wind strength Beaufort	state of sea
st. 237- 239 1976	2	0
st. 266- 277 "	0-4	0-2
st. 330- 341 "	1-5	1-2
st. 893- 912 1977	0-4	0-2
st. 1027-1033 "	0-2	0

Bioassay experiments.

Twenty cod larval bioassay experiments were performed with an average of 28 larvae per test. In twelve of these tests the larvae were in yolk sac stage 5; in the remaining eight only about 50% were in yolk sac stage 5, while 50% were in yolk sac stage 6.

The relationship between the estimated nauplii density in the test aquaria and the mean number of nauplii eaten by cod larvae is presented in Fig. 19. (The mean number of nauplii eaten by the larvae is based on the number of larvae with nauplii present in the gut.) There seems to be a rapid increase in the mean number of nauplii eaten by cod larvae in relation to nauplii densities. The figure indicates that the mean maximum gut content of cod larvae (yolk sac stage 5-6) is about three nauplii (220 µm mean carapax length), and that this value is reached at nauplii density > 0.1 nauplii/ml.

Table 1 shows the number of nauplii in different degrees of digestion present in cod larval guts (sum of 20 bioassay experiments). Only about 1% of the nauplii present in the guts of cod larvae were newly eaten (degree 1, see page 7), about 20% in digestion degree 2 and about 80% of the total number of nauplii were completely digested (degree 3).

Table 1. The frequency of nauplii in the three degrees of digestion in the cod larval guts. The figures are totals from 20 bioassay experiments.

	Degree of digestion of nauplii		
	1	2	3
No. of nauplii	7	102	412
% of total	1.3	19.6	79.1

The data from the bioassay experiment with mean nauplii density 0.02/ml (0.01-0.04 nauplii/ml) are compared with the data from seven bioassay experiments with mean nauplii density 0.32/ml (0.1-0.6 nauplii/ml). These results are shown in Tables 2 and 3.

Table 2. The frequency of nauplii in three degrees of digestion in cod larval guts, from seven bioassay experiments. Nauplii densities; 0.01-0.04 nauplii/ml. (Total of 190 cod larvae).

Mean naup. density	Degree of digestion of nauplii			Larvae with naup. in gut	Naup./ larvae
	1	2	3		
0.02/ml	1	5	78	54	1.55
%	1.2	5.9	92.9		

Table 3. The frequency of nauplii in three degrees of digestion in cod larval guts, from seven bioassay experiments. Nauplii densities; 0.1-0.6 nauplii/ml. (Total of 197 cod larvae).

Mean naup. density	Degree of digestion of nauplii			Larvae with naup. in gut	Naup./ larvae
	1	2	3		
0.32/ml	3	77	193	90	3.03
%	1.1	28.2	70.7		

The percentage of nauplii eaten by cod larvae in digestion degree 1 was similar for the two groups of experiments. However, there was a substantial difference in the percentage of nauplii in digestion degrees 2 and 3. At the lowest nauplii densities the percentage of nauplii in digestion degree 2 was only 5.9%, compared to 28.2% in digestion degree 2 at the highest nauplii densities.

In the experiments where the nauplii densities were low, 92.9% of the nauplii were completely digested, while only 70.7% of the nauplii were completely digested at the highest nauplii densities.

Table 4. The feeding incidence and mean number of nauplii in the guts of yolk sac stages 5 and 6 cod larvae. The figures are the mean values of four bioassay experiments.

YOLK SAC 5					YOLK SAC 6				
Naup. gut	% f.i.	$\overline{SL}$	SD	n	Naup. gut	% f.i.	$\overline{SL}$	SD	n
2.3	43	4.86	±0.18	44	3.0	66	4.87	±0.15	65

Table 4 shows the feeding incidence and the mean number of nauplii present in the guts of cod larvae in yolk sac stages 5 and 6. The results are the mean values of four bioassay experiments with yolk sac stages 5 and 6 larvae present at the same time. The density of nauplii varied between 0.1-0.6 nauplii/ml. Yolk sac stage 6 larvae were able to capture more prey organisms in all four experiments than larvae at yolk sac stage 5. The maximum feeding incidence was 77% in yolk sac stage 6 larvae, and only 50% in those of yolk sac stage 5. There was no difference in standard length between larvae of the two yolk sac stages.

Larvae were observed with green food remains in 16 of 20 bioassay experiments. In five of these experiments the green food remains were identified as copepod fecal pellets, and in one experiment as much as 43% of the cod larvae had eaten these pellets. The density of the pellets was estimated to be 0.02 pellets/ml. The pellets had probably been eaten at the bottom of the experimental aquaria.

In all bioassay experiments the armoured dinoflagellate Peridinium sp. was present; however, it was only found in cod larval gut contents in six of 20 experiments. The highest cod larval feeding incidence on Peridinium sp. was 10.4%. The flagellate density

during that experiment was 0.32 cells/ml and the density of nauplii 0.28 nauplii/ml. The cod larval feeding incidence on nauplii in the same experiment was 55%.

Feeding of cod larvae in the sea.

The mean number of nauplii in guts of first feeding cod larvae was found to increase with increasing larval length (Fig. 20). Fig. 21 shows the size distribution of nauplii in larval guts in relation to the size of first feeding cod larvae from the 24-hour station 10-11 May 1977. All sizes of first feeding cod larvae were found to eat nauplii of the same size.

Comparisons between nauplii sizes found in the sea and in larval guts show a slight selection; the smallest and largest nauplii seem to be omitted by the larvae (Fig. 22).

Most nauplii in larval guts were found to be in degree of digestion 3 (about 80%), while newly eaten nauplii (degree 1) constituted only about 5% of the nauplii observed. A slight change in this ratio was observed during the first 24-hour period in May (Fig. 23). Fig. 24 shows the vertical density of nauplii and cod larvae from the 24-hour station 18-19 May 1977 in Austnesfjorden (st. 1026-1034). The cod larvae were collected by fish pump. The maximum concentrations of larvae in single profiles varied between about 4 to 13 per m^3. At st. 1032 a Bongo 60 was used for sampling larvae, resulting in 1-3 larvae/-m^3 (Fig. 24).

A comparison has been made on first feeding larvae in yolk sac stage 5 (ELLERTSEN et al. 1979 b), separating those with empty guts from the others. Fig. 25 shows that larvae with and without food could be distinguished with respect to size, the empty larvae being smaller. Fig. 25 also shows density of nauplii, number of nauplii in gut, and feeding incidence.

DISCUSSION

Methods.

In most previous investigations fish larvae have been collected in different types of nets, such as Juday, Gulf, Hai, Bongo net, etc. Similar equipment, and to a larger degree plankton pumps, have been used for collecting larval food organisms.

On investigating the feeding in cod larvae in relation to food organisms, we believed that using nets for sampling the larvae would give inaccurate data, since the net could be hauled through different regimes of larval densities during a single haul. Using nets in vertical hauls in 5 m intervals down to 20 m as in this investigation would also be laborious.

Accepting the theory of a patchy distribution of plankton organisms brought about the need for sampling larvae and food organisms from restricted water masses. The use of a fish pump for sampling the cod larvae has proved successful for our purposes.

As with other sampling apparatus, pumps are subject to the avoidance by some planktonic organisms. Using a high capacity pump for filtering rather small volumes of water in short pump series may reduce this avoidance.

The particle rate meter was well suited for detecting the patchy distribution and density of plankton organisms.

Nauplii distribution.

Investigations on the vertical distribution of copepod nauplii are scarce, and little information on the distribution of nauplii was available from literature at the onset of this investigation. This might be partly due to difficulties in adequate sampling.

The predominant copepod nauplii in the Lofoten area were those of Calanus finmarchicus, as also stated by Sømme (1934) and Wiborg (1948 b).

Spawning of C. finmarchicus takes place close to the surface at night (Harding, Marshall and Orr 1951). The sinking velocity of eggs (Marshall and Orr 1955, Salzen 1956) and time from spawning to hatching (Marshall and Orr 1955) in the temperatures experience in the Lofoten area, should give a hatching depth of 50 m or below. The fact that most nauplii are found within the upper 30 m is supposed to be a function of the sinking of eggs and a migration towards the surface among the nauplii. Dynamic turbulences in the water masses may reduce the net sinking velocity of Calanus eggs. Marshall and Orr (1955) report that most C. finmarchicus nauplii are found in the upper 50 m in northern Norway.

The decreasing nauplii size with increasing depth is also supposed to be a function of the hatching of nauplii at greater depths, giving increasing percentages of the youngest and smallest nauplii stages with depth. A similar increasing ratio of younger nauplii stages of C. finmarchicus with depth was observed in IBP investigations in April 1969 in western Norway (Bjørke, pers. comm.).

Nauplii concentrations in our investigations were generally within the density range 5-60 nauplii/l, occasionally higher (up to 600/l) (Fig. 18). Previous investigations in Austnesfjorden revealed nauplii concentrations within the range 1-22/l (Wiborg 1948 b). These lower values may be due to use of another sampling gear (Clarke-Bumpus), but most probably to larger mesh size, 145 µm.

The concentration range of nauplii observed in Lofoten was generally within the ranges found in other investigations. Allen (1939) observed 10-30 nauplii/l off California, Beers and Stewart (1971) found a mean concentration of nauplii in the eastern tropical Pacific to be 27/l, Mel'nikov (1976) reports a concen-

tration range of 5-28 microzooplankton nauplii per litre in the tropical south-eastern Pacific, similar concentration ranges were observed in other investigations (Hargrave and Geen 1970, a.o.). (For a review see Houde 1978.)

These concentrations are small compared to 2800 nauplii of Eurytemora affinis/l as observed by Heinle and Flemer (1975) in USA and 1440 E. affinis nauplii/l in Schlei Fjord as observed by Schnack (1972). Up to 635 nauplii of Calanipeda sp./l is reported by Malovitskaya and Zhuraleva (1962, ref. in Duka 1969).

Vertical distribution of nauplii has been the subject of very few investigations, especially the distribution in intervals over a few metres. Wiborg (1948 b) made horizontal hauls in five depths down to 100 m, maximum concentrations were observed within the upper 30 m, and few nauplii were found below 50 m.

Kraefft (1910) observed maximum concentrations in the upper 10 m in the Baltic and Kattegat. Broken hauls using an Apstein net were taken at several depths down to about 100 m. Arthur (1955) observed an almost logarithmic decrease in nauplii numbers from the surface down to 50 m off California. The investigations mentioned above are in concordance with our findings, the highest densities in our investigation were found within the upper 20 m.

Diurnal vertical migration.

Most plankton organisms perform diurnal vertical migration. With respect to copepod nauplii little information is available on vertical migration. Barnes & Marshall (1951) say that (p. 255) "..nauplius stages...are not known to show diurnal migration". In the chapter dealing with diurnal vertical migration Marshall & Orr (1955) say about C. finmarchicus that "..nauplii and eggs are found mainly near the surface". As shown in the present paper the depth of maximum density of copepod nauplii changes during a 24-hour period, from 5-15 m during daytime to 0-10 m at night. This is not necessarily connected to an overall increase in nauplii numbers in the 0-30 m water column.

This phenomenon seems to be very consistent, and is believed to be due to a diurnal vertical migration among the nauplii. This migration takes place over a span of few metres, and is probably to some extent dependent upon the size of the nauplii. The smallest nauplii were not found to perform such a diurnal migration. This may be due to their lower swimming abilities. The first stages of C. finmarchicus nauplii do not depend on phytoplankton for feeding and their distribution does not have to follow that of phytoplankton.

Weather conditions were found to be an important factor in the distribution pattern of nauplii. During low wind intensities and calm sea nauplii profiles were obtained showing distinct layering with respect to nauplii concentrations.

Prevailing high wind intensities were found to influence the vertical distribution of cod eggs by the increased turbulence in the water masses, and may also affect the vertical distribution of nauplii. This is a subject for our future research.

Bioassay experiments.

The cod larval bioassay experiment was performed according to Lasker (1975). However, in contrast to Lasker's (1975) information about the survival of the northern anchovy (Engraulis mordax) at different prey densities, our information about the survival of cod larvae at different densities was limited. However, the method itself, performed with first feeding cod larvae in seawater pumped on deck from depths containing prey organisms at different densities, would give additional information when comparing the results with those of cod larvae sampled at the specific depths. The bioassay experiments, however, were performed in stagnant seawater, and there is no reason to believe that the prey density was homogenous during each experiment. The density was only determined at the start of each experiment. The data were therefore pooled in two groups; low density 0.01-0.04 nauplii/ml and high density 0.1-0.6 nauplii/ml, when considering larval feeding incidence and the degrees of digestion of the gut content.

The results from the bioassay experiments showed that first feeding cod larvae were able to capture nauplii even at very low prey densities. However, feeding incidence never exceeded 80% at the highest prey densities (0.5-0.6 nauplii/ml) even in the most developed larvae (yolk sac stage 6). The results also showed that yolk sac stage 6 larvae of the same population, age and standard length as yolk sac stage 5 larvae were able to catch more nauplii (Table 4). This indicates that not only larval standard length (See ELLERTSEN et al., 1979 b, Fig. 6), but also larval development stages at first feeding have to be considered in relation to larval feeding conditions.

The bioassay experiments were run for 5 hours; this test period is probably too long. This is indicated in Tables 1, 2, and 3, which shows that only about 1% of the nauplii in the gut of cod larvae were newly eaten. The effect of prey density is shown in Tables 2 and 3. At the lowest prey density, more than 90% of the cod larval gut contents were completely digested, and only about 6% half digested; while at the highest prey densities about 30% of the nauplii were half-digested and about 70% completely digested. Recent investigations have shown that cod larval digestion rate is very fast, in the order of about 30 minutes for complete digestion even at low temperatures, and the gut clearence rate varied between 3 to 5 hours (TILSETH pers.comm.).

The mean feeding incidence at the highest and lowest prey densities was of about the same order, i.e. 50-60%. This is probably close to the maximum feeding incidence in cod larvae at the very onset of exogenous feeding (yolk sac stage 5). The feeding incidence of yolk sac stage 6 and 7 larvae sampled at sea was in all instances, regardless of prey density, close to 100%. Due to the slow gut clearance rate feeding incidence is not thought to be a good parameter in evaluating larval feeding conditions. The condition of prey organisms in different degrees of digestion and the gut content must also be considered. Further investigations on cod larval digestion rate, gut clearance rate at different temperatures and prey densities are needed. The influence of these factors on the survival of cod larvae is further discussed in ELLERTSEN et al. (1979 e).

Feeding of fish larvae in the sea.

The correlation between fish larvae and their prey organisms, in relation to distribution, species composition and density has been the topic of numerous investigations (Wiborg 1948 a, Shelbourne 1957, Lasker 1975, Arthur 1977, Bjørke 1978, Last 1978).

The difficulties involved by using conventional plankton equipment for mortality studies as a result of starvation is discussed by May (1974) and Dekhnik and Sinyukova (1976).

The significance of the patchy distribution of prey organisms for feeding of fish larvae was shown by Lasker (1975). In relation to methods for patchiness studies, Hunter (1976) states: "Dispersion of patches can best be studied by changes in the distribution of the organisms and not by measuring the continuous characteristics of physical and chemical factors of seawater". The methods introduced in this paper are an attempt to carry out sampling of fish larvae and prey organisms concurrently with, hopefully, the same degree of accuracy.

The main objective of this investigation has been to demonstrate from vertical profiles, the effects of nauplii density on the feeding condition of first feeding cod larvae.

First, some problems concerning the size relationship between cod larvae and prey organisms and speed of digestion have to be considered.

The prey organisms in Lofoten consisted almost exclusively of copepod nauplii, mainly those of Calanus finmarchicus. During the investigations in the period: end of April - beginning of May, in the years 1975-77, the proportion of copepod eggs in the sea was very low, and the proportion in the guts negligible. Similar results were found from the same area by Sysoeva & Degtereva (1965). Sysoeva (1972) showed variation of the proportion of copepod eggs in guts from year to year, depending on the onset of spawning of Calanus finmarchicus.

Compared to the more complex prey species composition in other areas Last (1978), cod larvae in Lofoten have a very homogenous prey composition. The tendency for longer first feeding larvae to contain more nauplii seems to be a general phenomenon, described also from the laboratory and enclosure experiments (Ellertsen et al. 1979, b, d).

The size range of nauplii eaten by cod larvae is seemingly uncorrected to first feeding larval length (Fig. 21). The larvae seemed to avoid the smallest sized particles, and were possibly not able to eat the largest particles (Fig. 22). This was also observed in the bioassay experiments where larvae selected the larger sized particles even when smaller particles were present at higher densities at the same time. First feeding cod larvae seem to select sizes within the nauplii size range 120-360 µm, as demonstrated in Fig. 22.

Digestion

The gut contents of larvae sampled at sea showed a higher frequency of newly eaten and half digested nauplii at lower prey densities (Fig. 23), compared with the results from the bioassay experiments (Tables 2 and 3). This could partly be due to the lower temperature in the sea i.e. slower digestion rate. The difference, however, is too big to be only caused by the temperature. The prey organisms must have been more accessible in the sea due to the higher observed frequencies of newly eaten and half digested nauplii in the guts of the larvae. The discrepancy between the prey densities estimated in the bioassay experiments and in the sea, could be explained by the possible presence of micropatches not discovered in the sea, or that the prey density was overestimated in the experimental aquaria. The last is more likely, because the bioassay experiments were performed in stagnant seawater, the prey density was estimated at the start of the experiments, and the nauplii could have sunk to the bottom of the aquaria during the experiments.

Vertical distribution.

The majority of first feeding cod larvae in Austnesfjorden were distributed in the upper 20 m during the calm weather conditions described. This is in agreement with Wiborg (1948 b), who investigated the same area.

A closer look at the vertical profiles shows maximal densities of larvae at 5-15 m, 0-15 m for the nauplii. Concentration maxima for fish larvae and nauplii corresponded fairly well during daytime. No indication of a diurnal vertical migration of cod larvae was found, in contrast to older larvae (Ellertsen et al, 1979 d).

Within yolk sac stage 5, which is the smallest first feeders, the largest specimens were found at 5-10 m, the strata of maximum nauplii density. Also the density of the yolk sac stage 5 larvae and the number of nauplii in the guts corresponded well to the nauplii density. However, it is interesting to note that the mean maximum gut content of first feeding cod larvae from the bioassay experiments at the highest nauplii densities (Table 3, Fig. 19), was equivalent to the mean maximum gut content of first feeding cod larvae sampled at the depth containing highest nauplii density at sea (Fig. 25).

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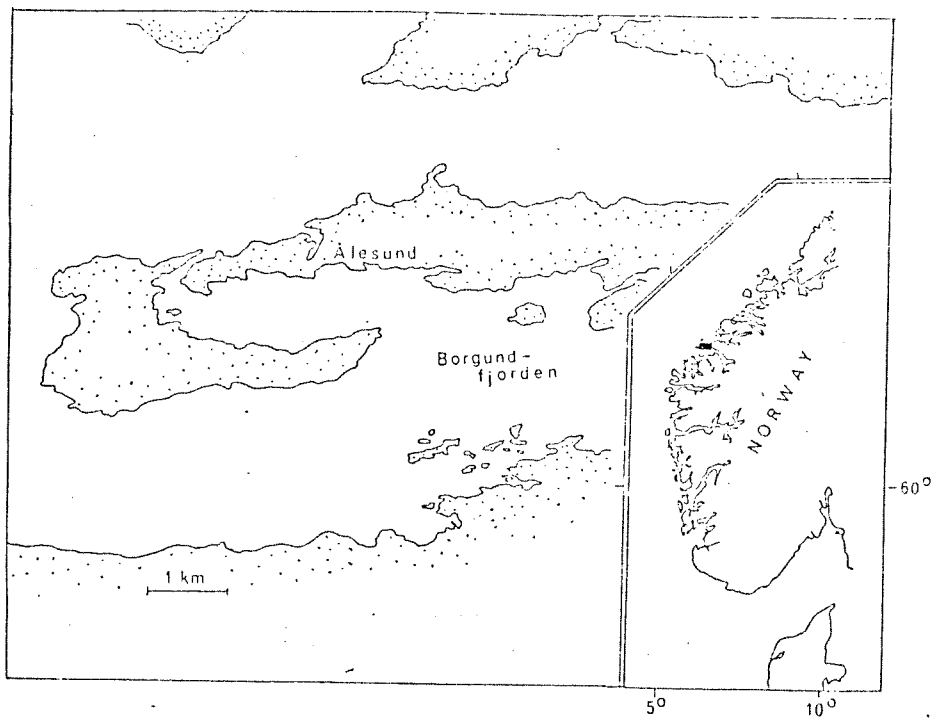


Fig. 1. Borgundfjorden in western Norway.

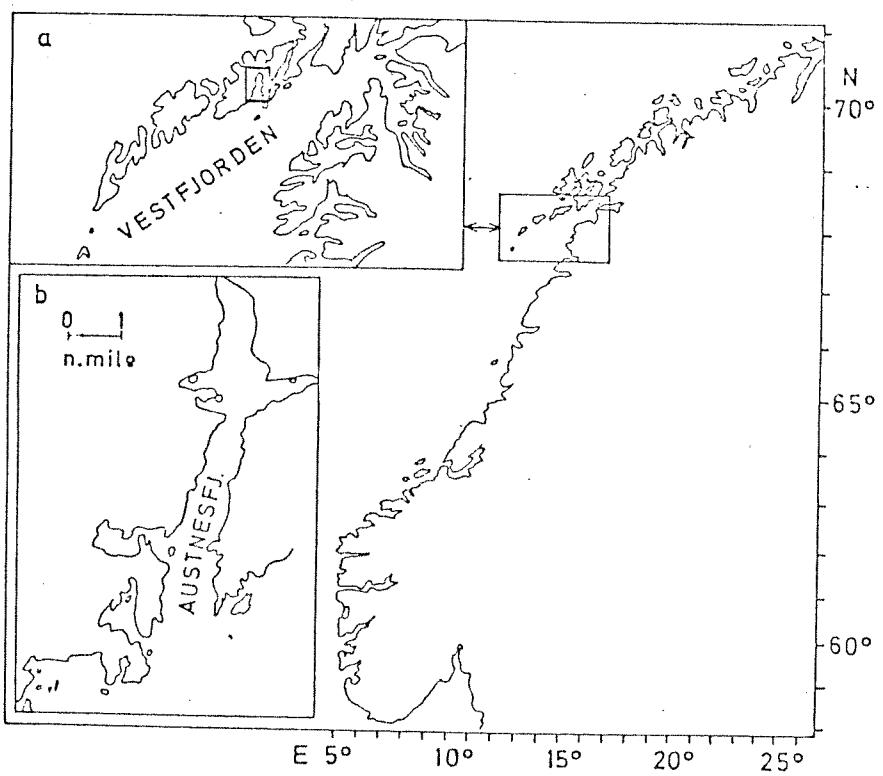


Fig. 2. Investigation area in northwestern Norway, a, Vestfjorden, and b, Austnesfjorden.

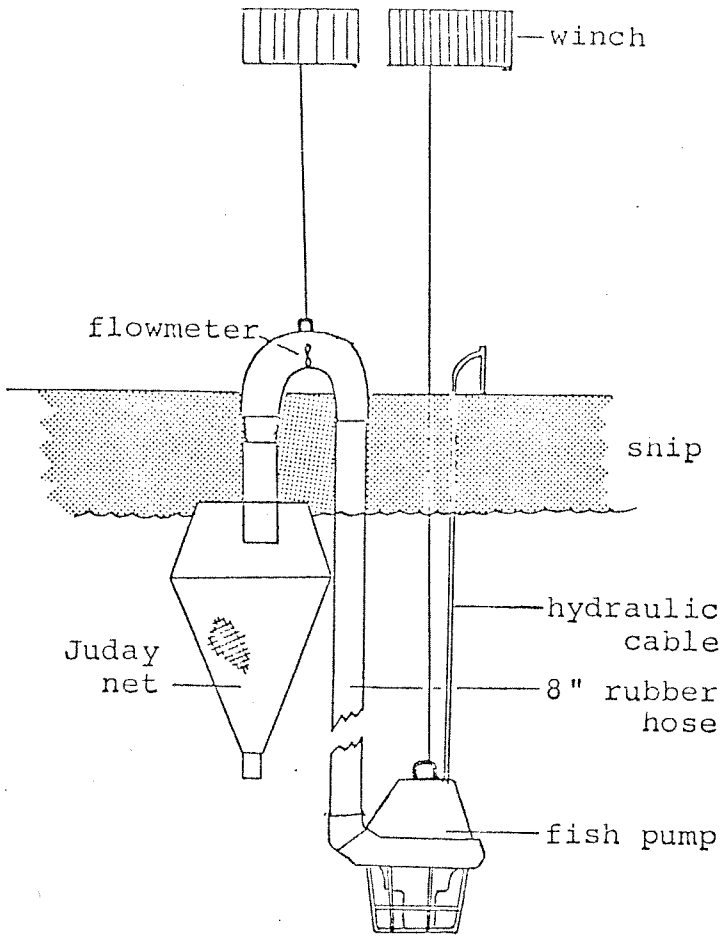


Fig. 3. Filtering carried out by keeping a Juday net along the side of the ship.

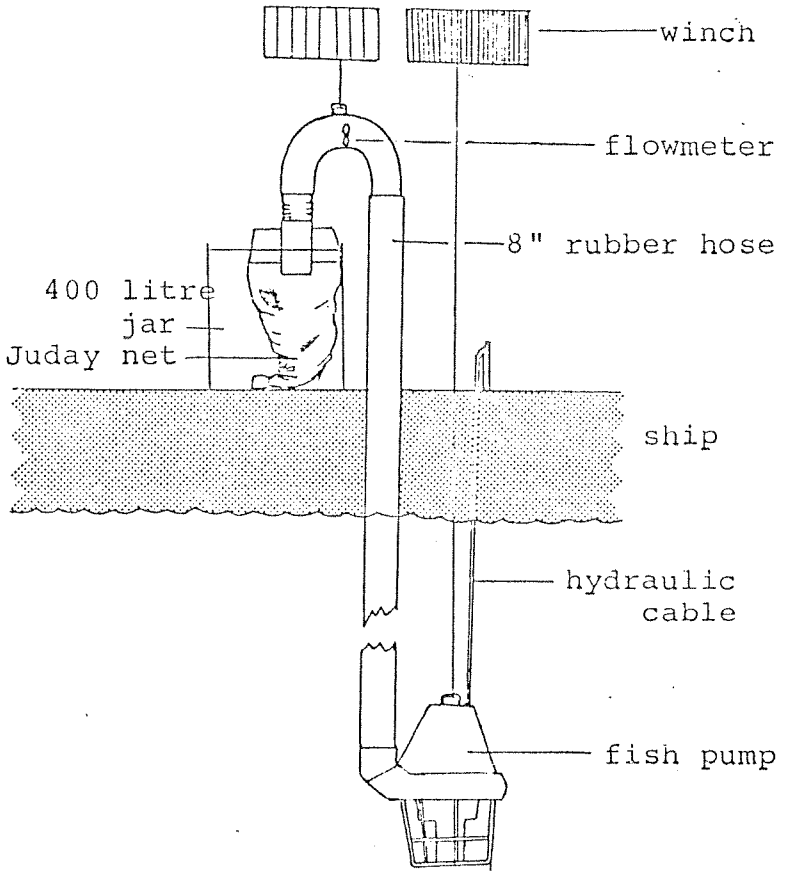


Fig. 4. Filtering performed on deck.

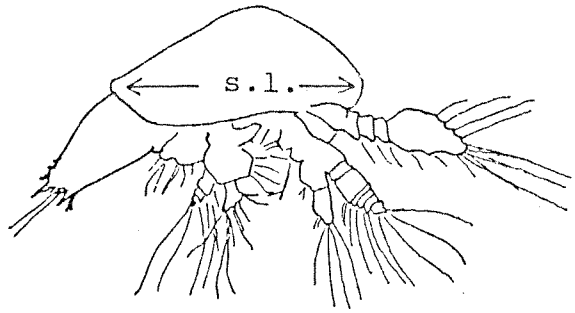


Fig. 5. Standard carapax length.

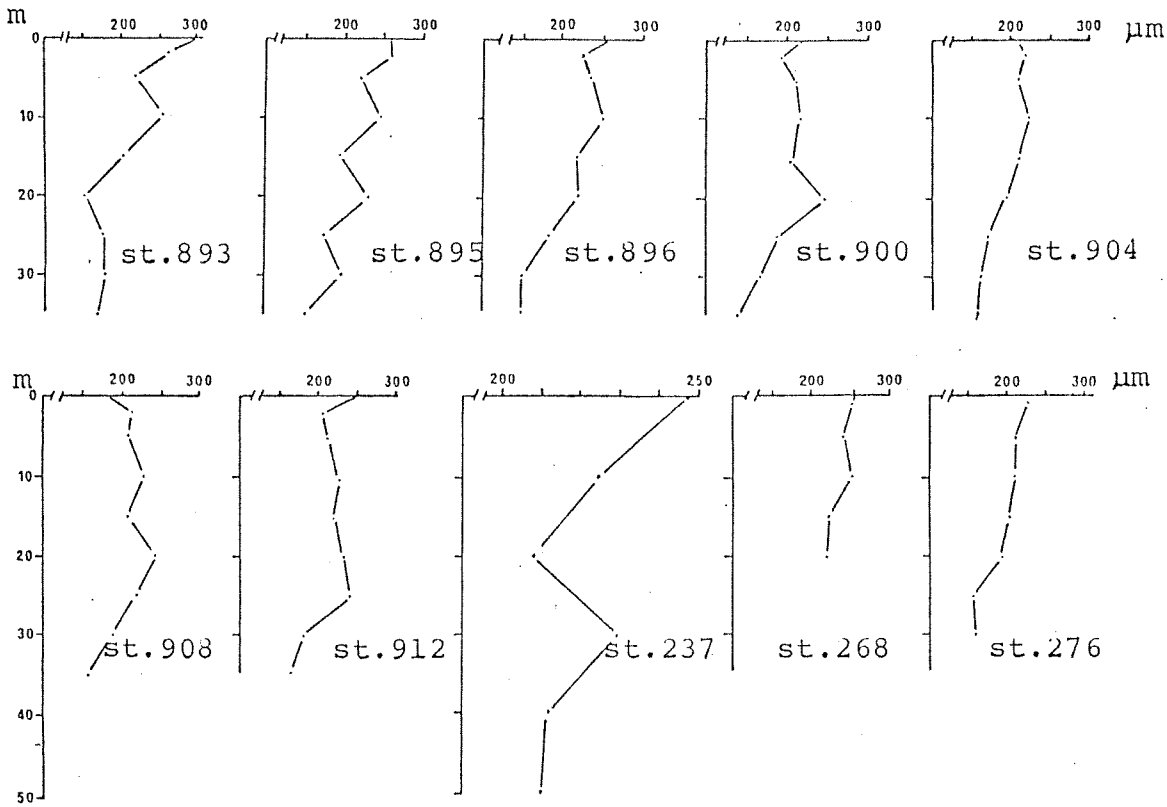


Fig. 6. Mean nauplii sizes (carapax length) in relation to depth at different zooplankton stations.

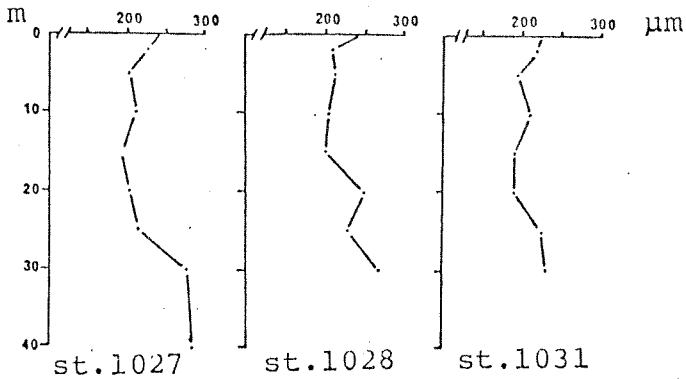


Fig. 7. Mean nauplii size in relation to depth at diurnal station 1027-1031.

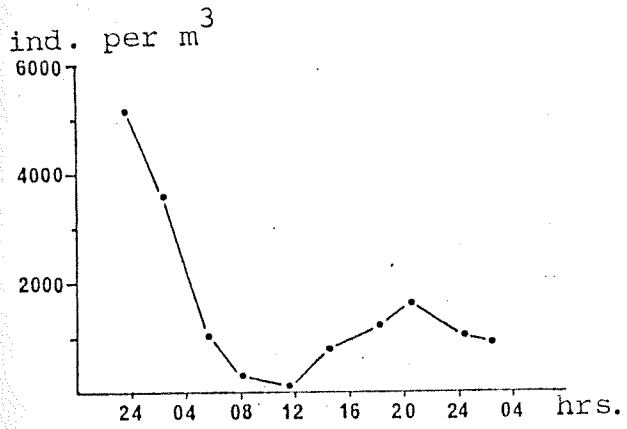


Fig.8. Nauplii concentrations at 0 m, st.39-58.

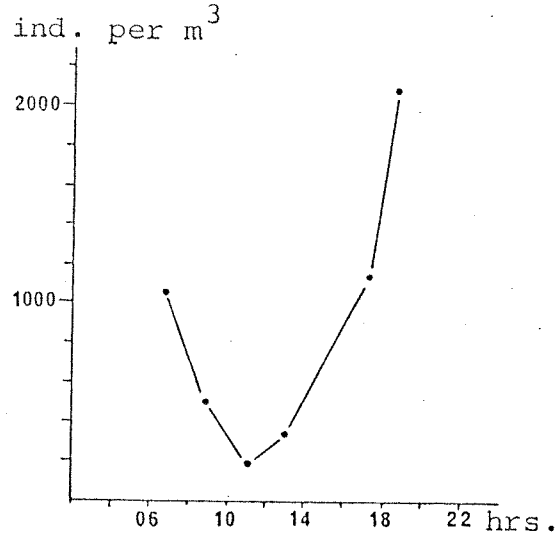


Fig.9. Nauplii concentrations at 0 m, st. 57-69.

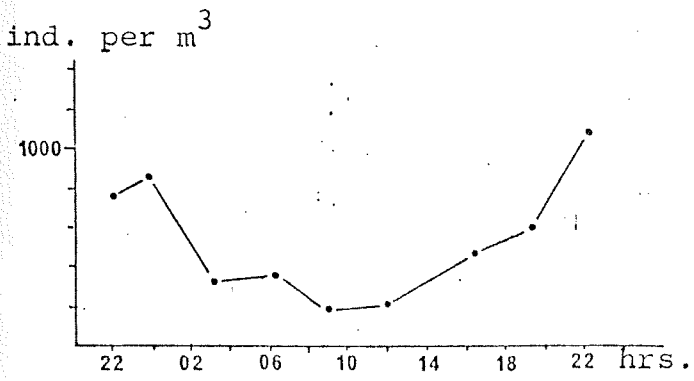


Fig.10a. Nauplii concentrations 0 m, st.79-87.

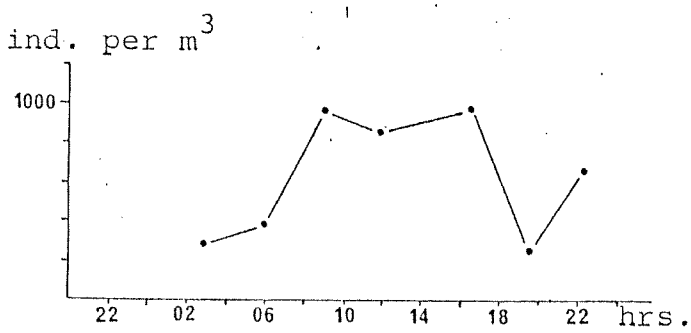


Fig.10b. Nauplii concentrations 8 m, st.79-87.

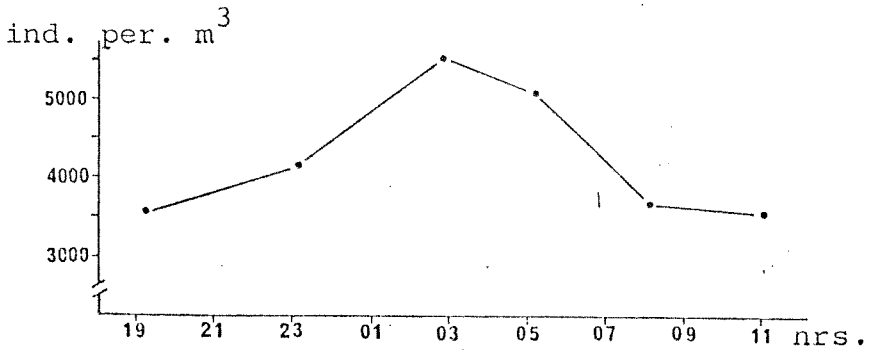


Fig.11. 24-hour station 117-122. Total number of nauplii in 3, 8 and 14 m depth.

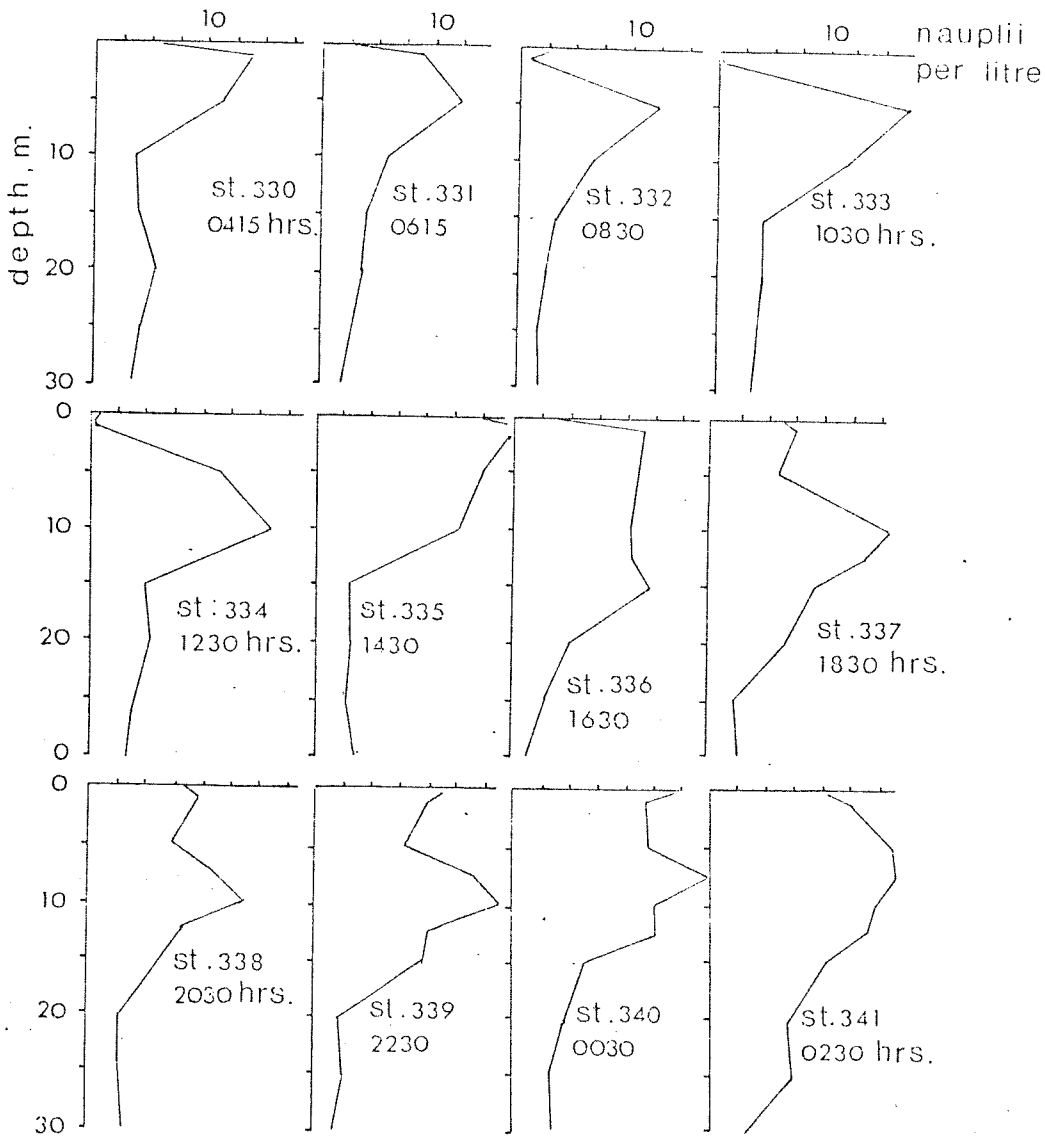


Fig. 12. Nauplii profiles 24-h. station 330-341
6 - 7 May 1976.

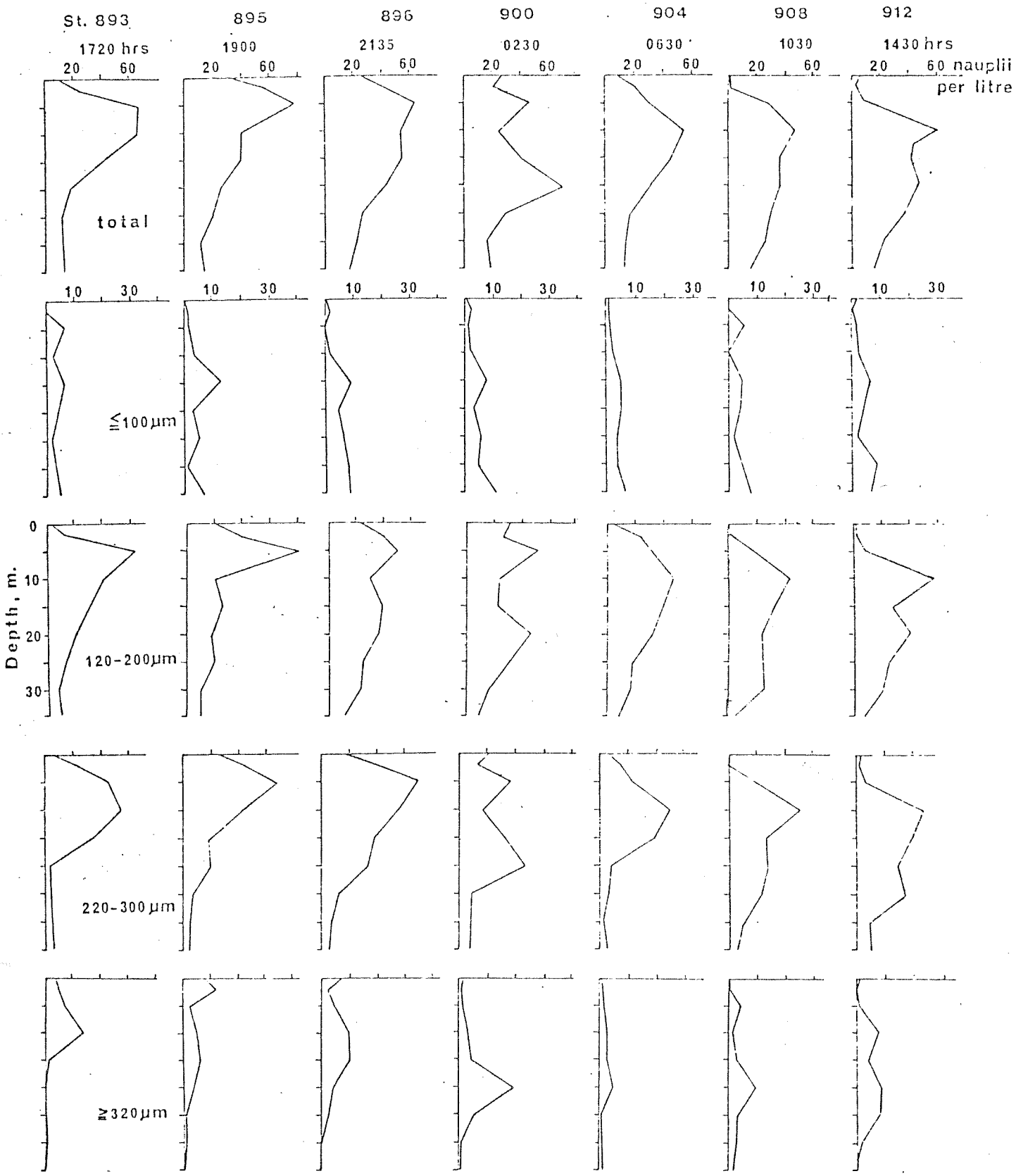


Fig.13. 24-h. station 893-912 10-11 May 1977.

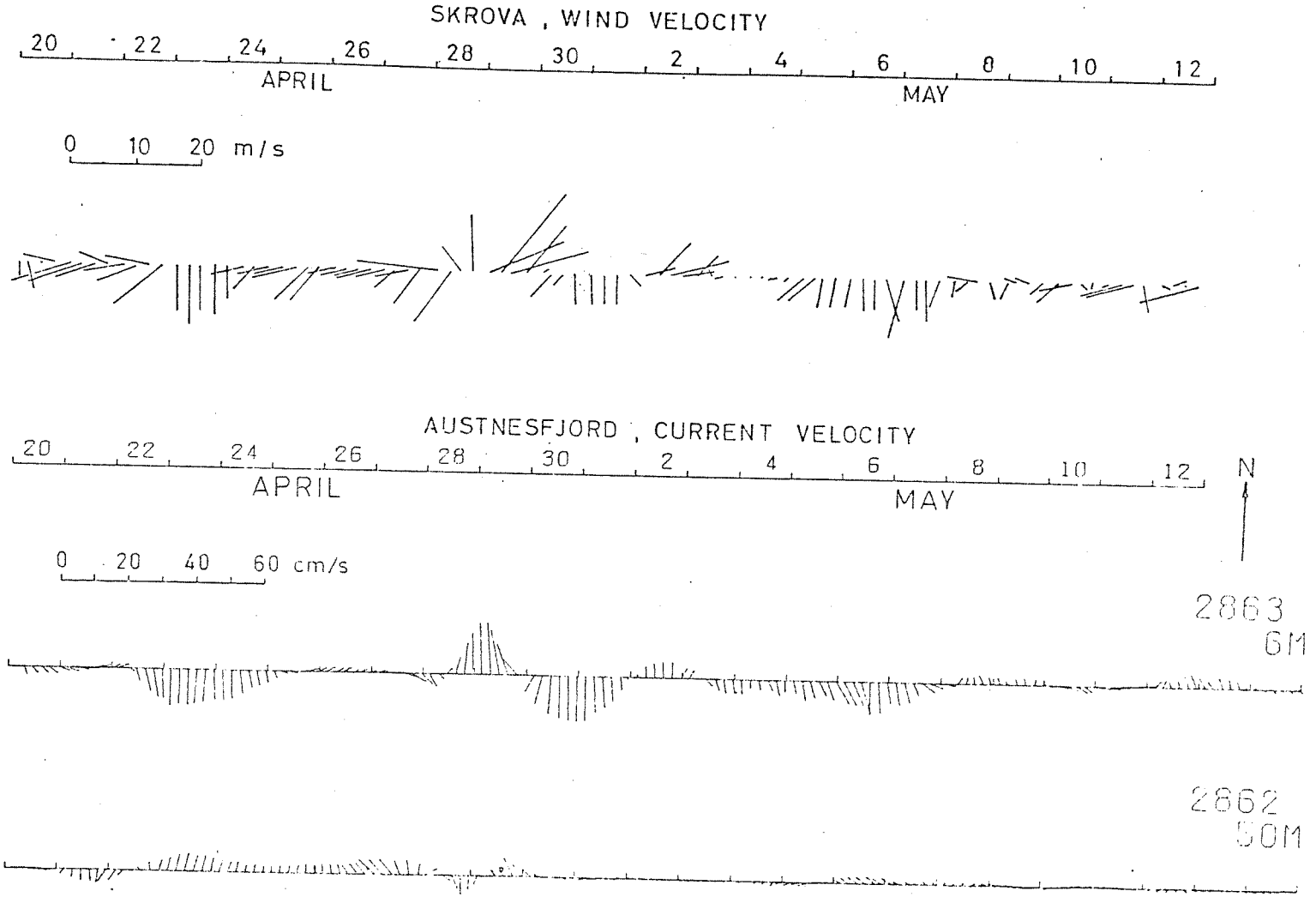
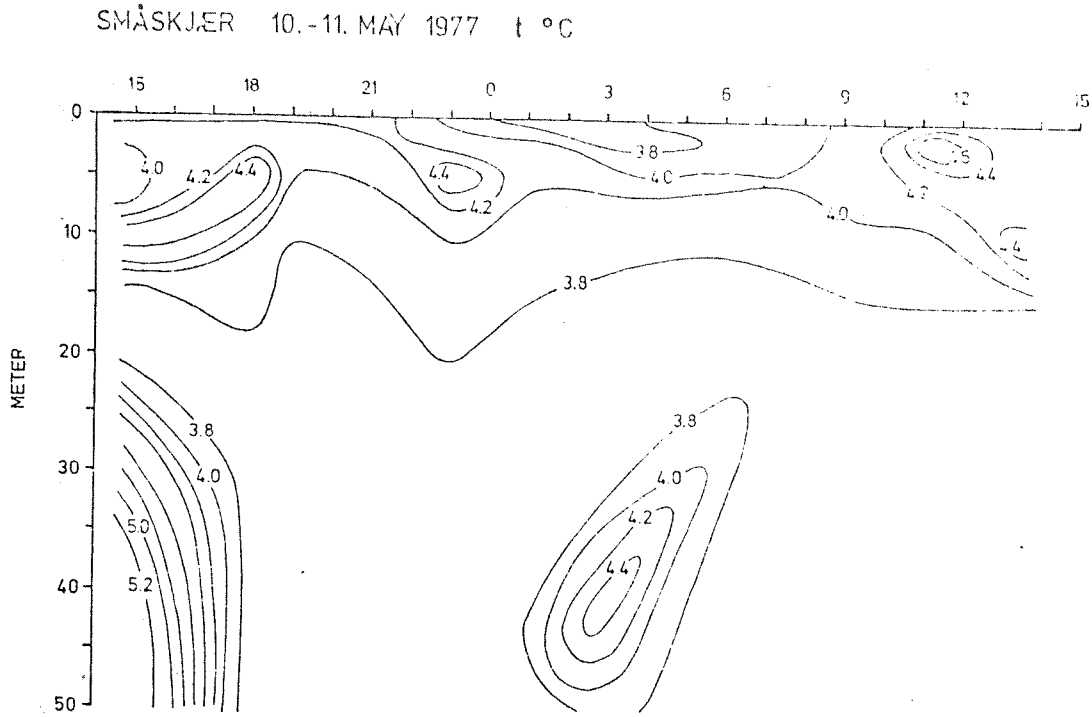
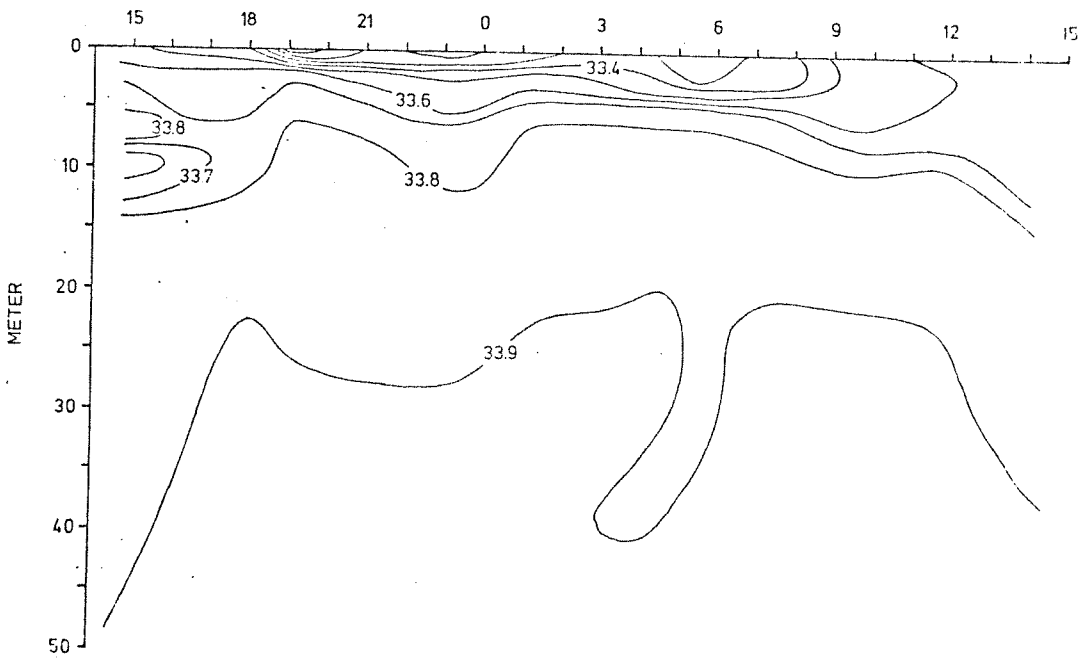


Fig. 14. Wind vectors at meteorological station Skrova and current vectors in 6 m and 50 m depth at the mouth of Austnesfjorden April-May 1977.





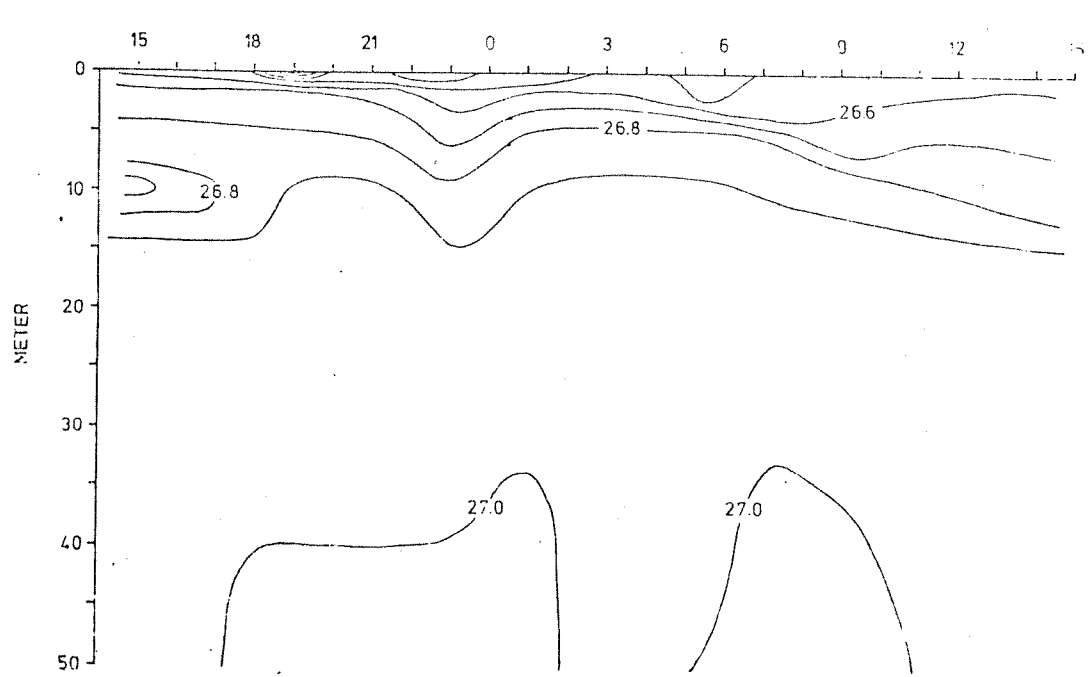


Fig. 15. Isopletes of temperature, saltinity and density at 24 hours station 10-11 May 1977.

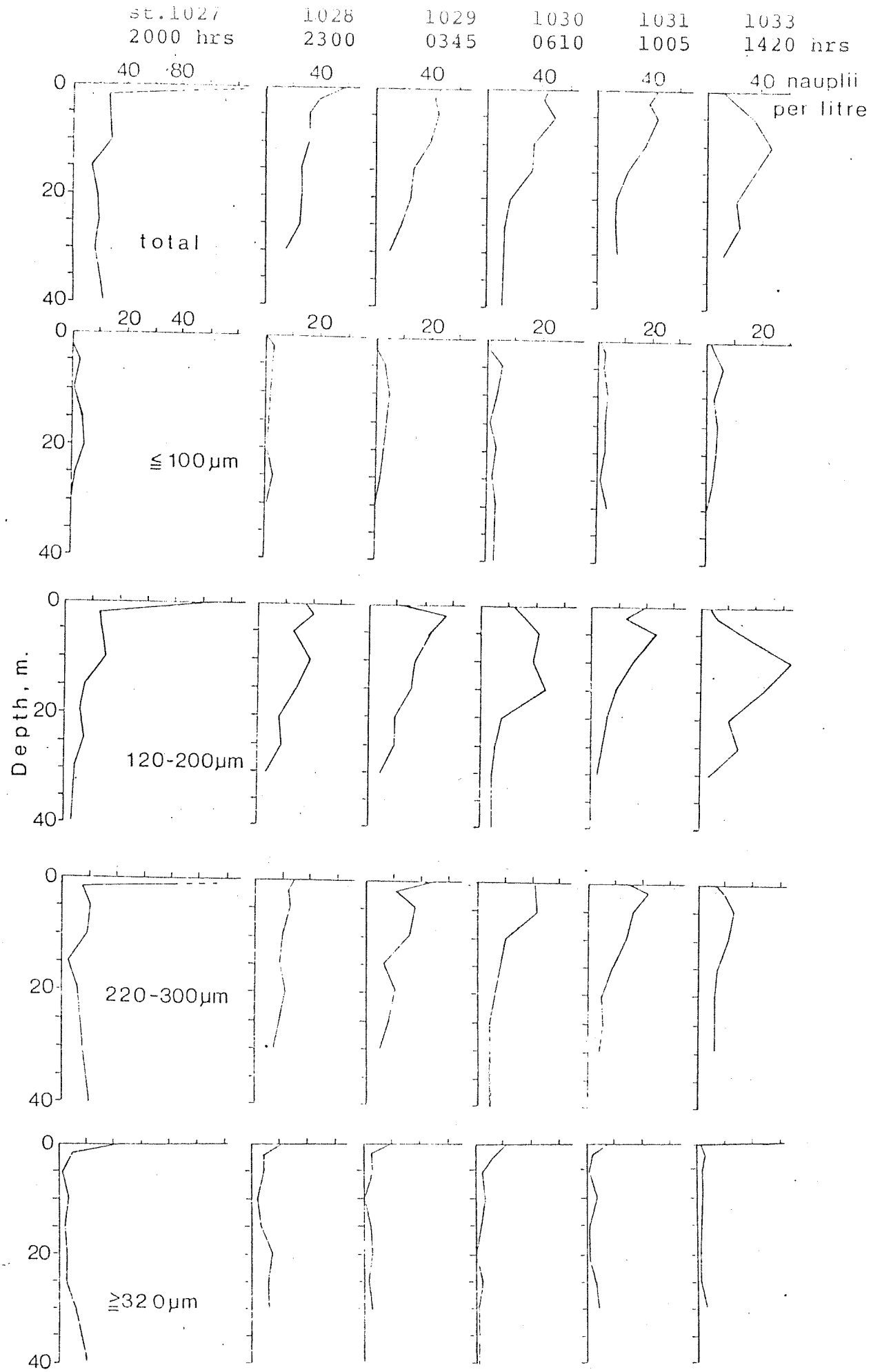


Fig. 16. 24-h. station 1027-1033 18-19 May 1977.

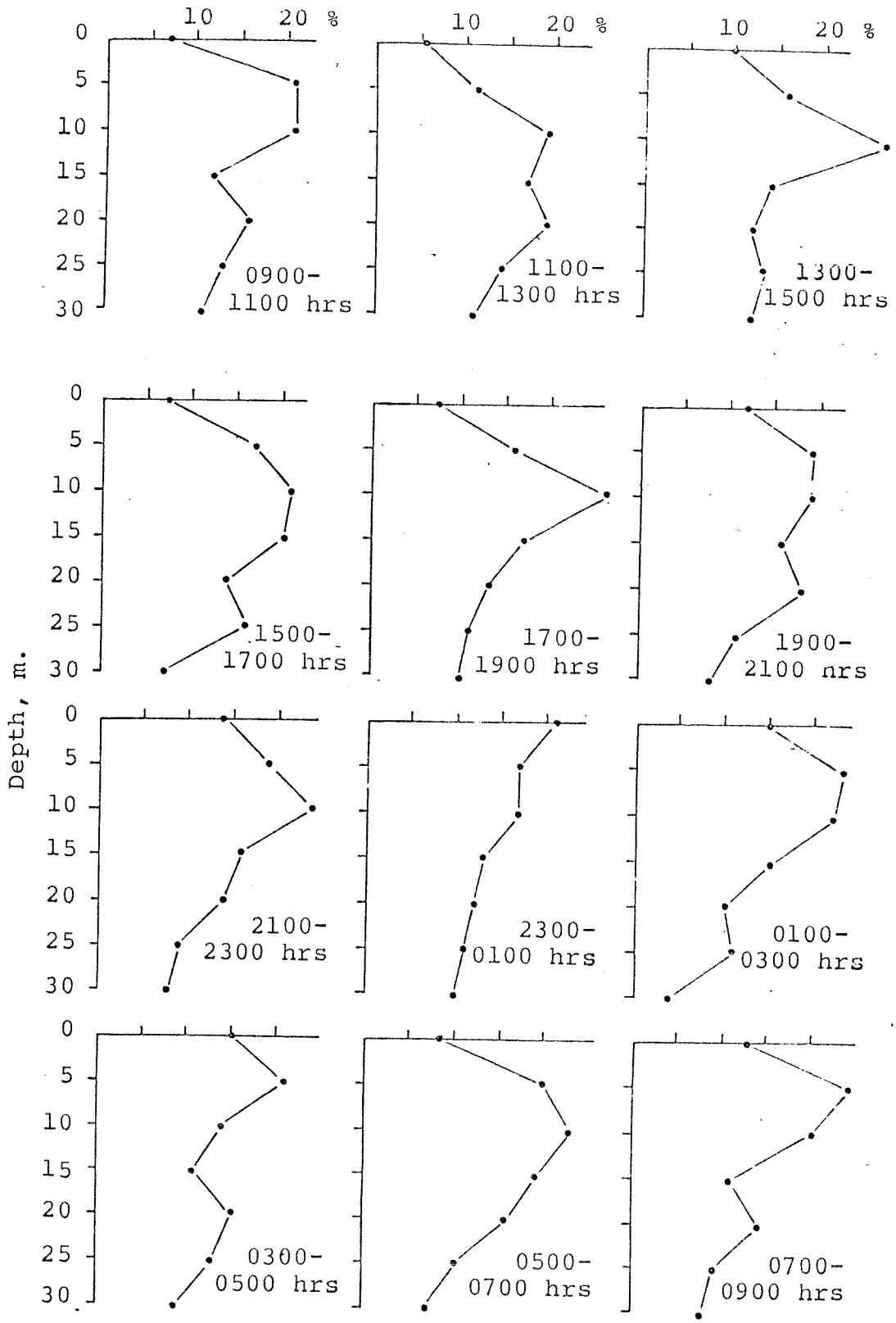
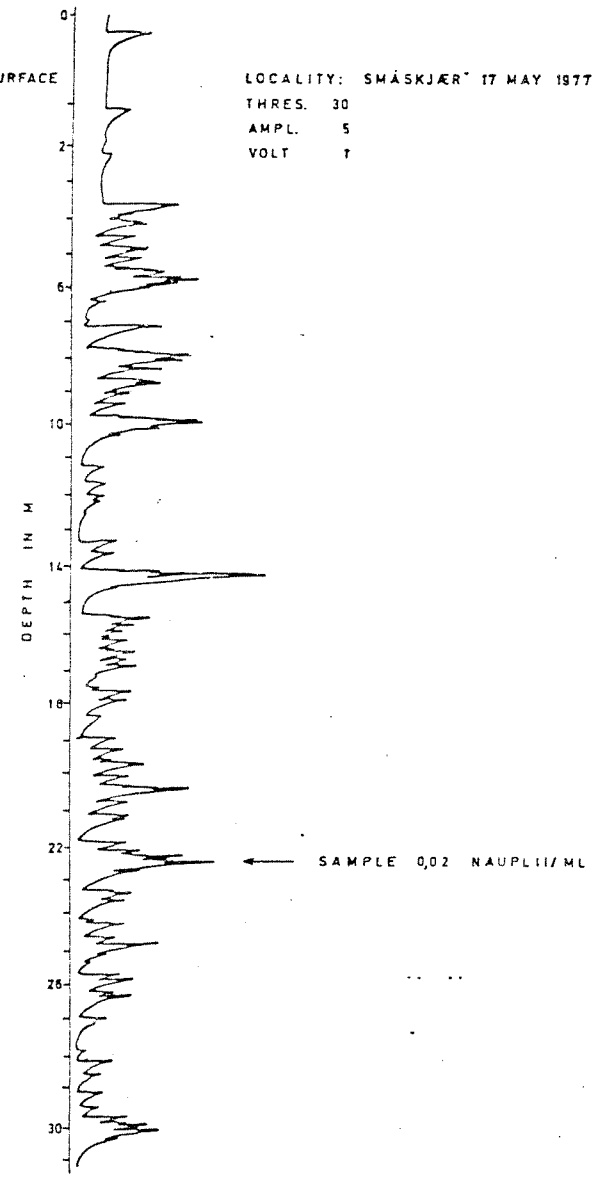


Fig. 17 . Relationship between diurnal nauplii profiles and sampling hours of a 24-h. period. (For furtner explanation see text).



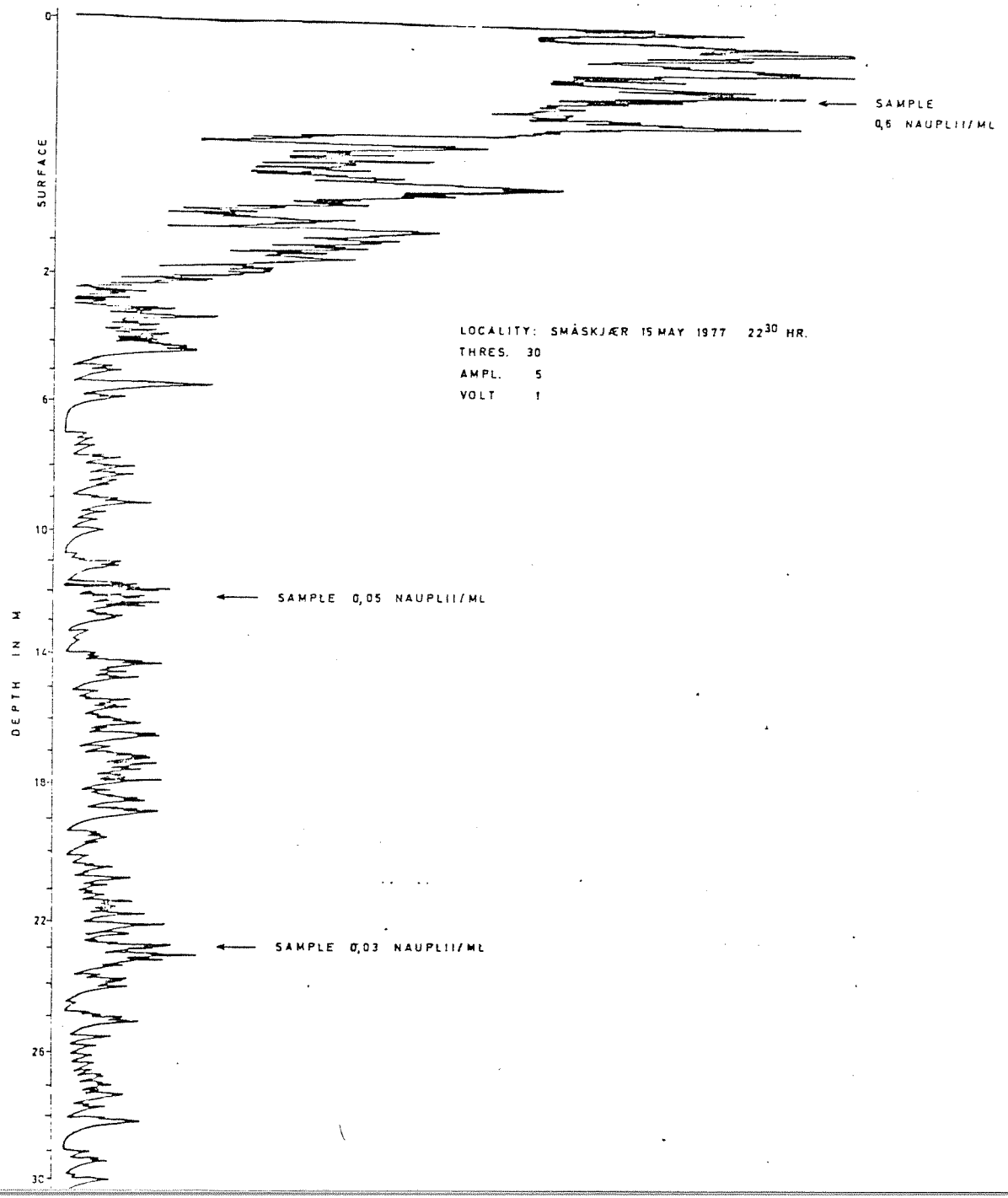


Fig. 18. Particle rate meter profiles.

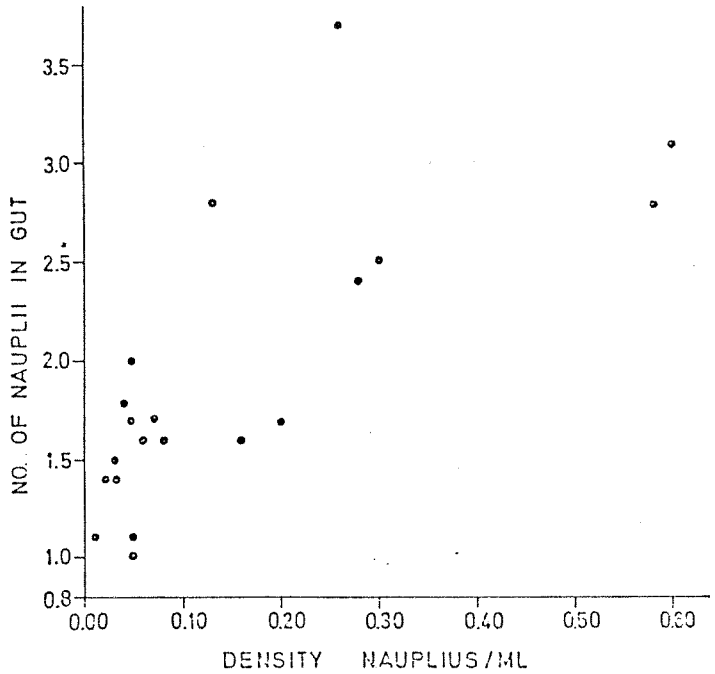


Fig. 19 .The relationship between the mean number of nauplii in the gut of cod larvae and the density of nauplii in the experimental aquaria.

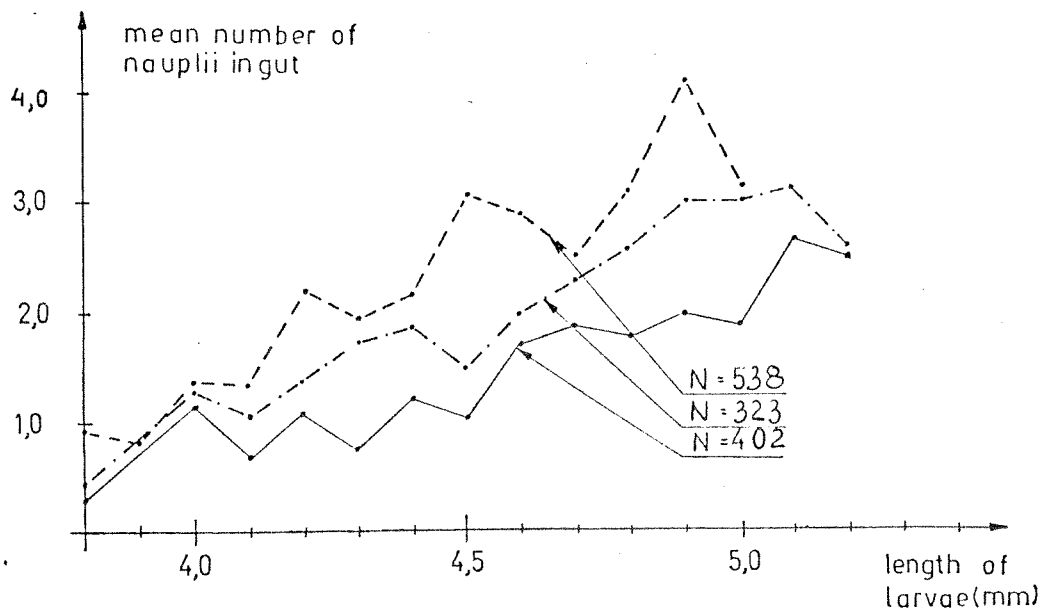


Fig.20. The mean number of nauplii in gut of larvae at three 24-hour stations: 3 May 1976 (———), 10-11 May 1977 (- - - - -) and 18-19 May 1977 (—·—·).

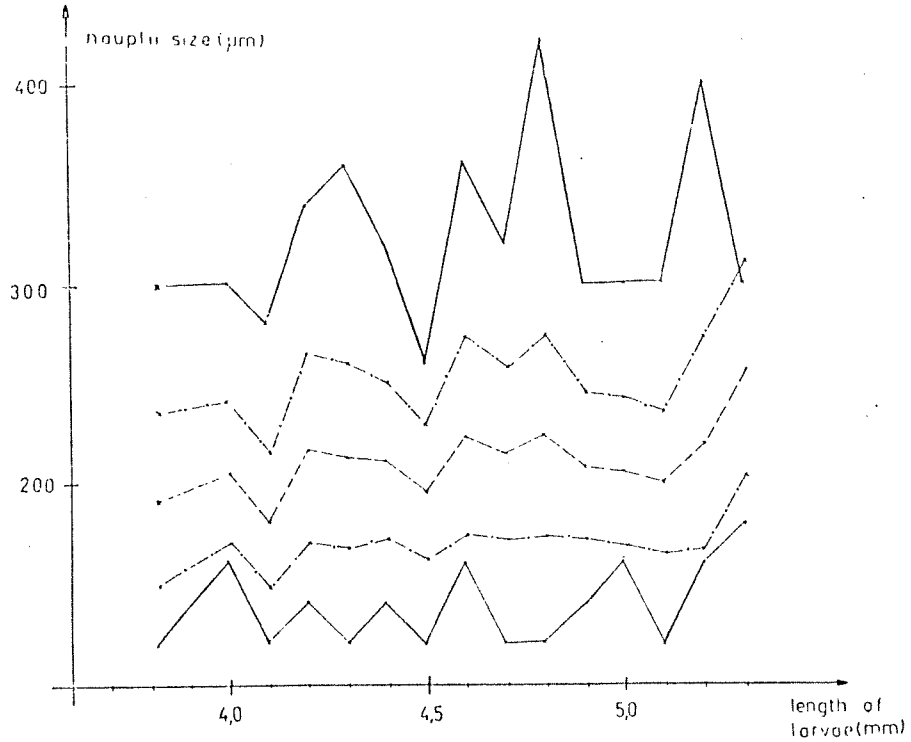


Fig.21. Mean (– – – –), upper and lower standard deviation (–·–·–·–), and smallest and biggest nauplii size (———), observed in gut of larvae at different length. The larvae were caught at 15 m depth 10-11 May 1977.

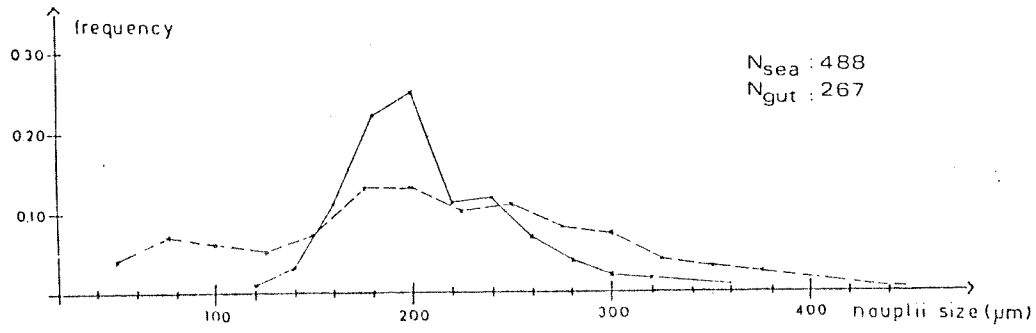


Fig.22. Carapax-length distribution of copepod nauplii observed in the sea (– – –) and gut of larvae (———) at a 24-hour station in the Lofoten area 18-19 May 1977.

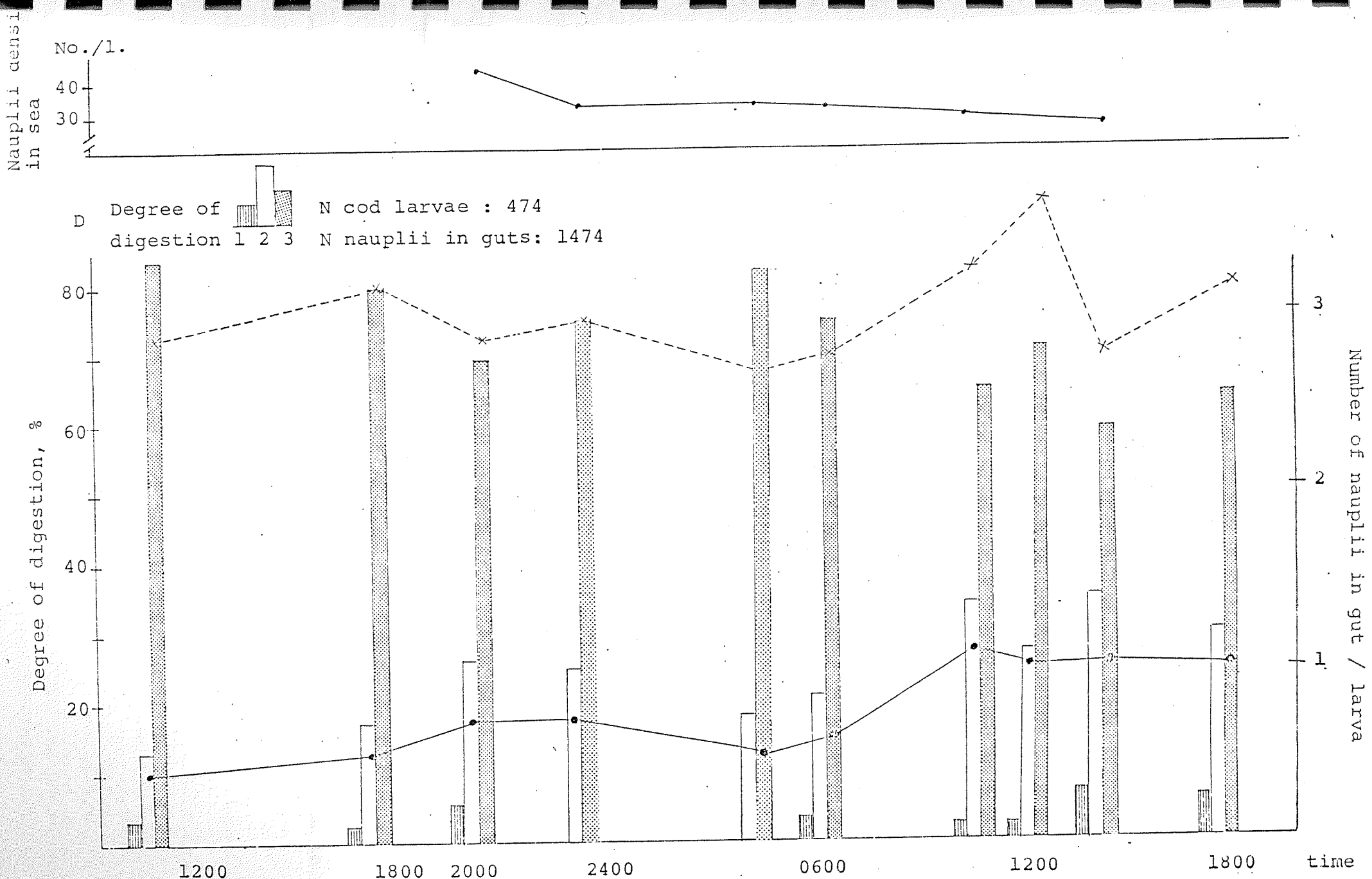


Fig. 23. Degrees of digestion of nauplii in the guts of first feeding cod larvae throughout a 24-hour station, 18-19 May 1977. Degrees of digestion: 1 - No visible digestion, 2 - A transparent zone between carapax and the interior of the nauplii, 3 - the interior of the nauplii completely dissolved. × - total number of nauplii in the guts of the cod larvae, ● - number of nauplii at degree of digestion 3. The upper curve shows the mean nauplii density in the upper 20 m during the 24-hour station.

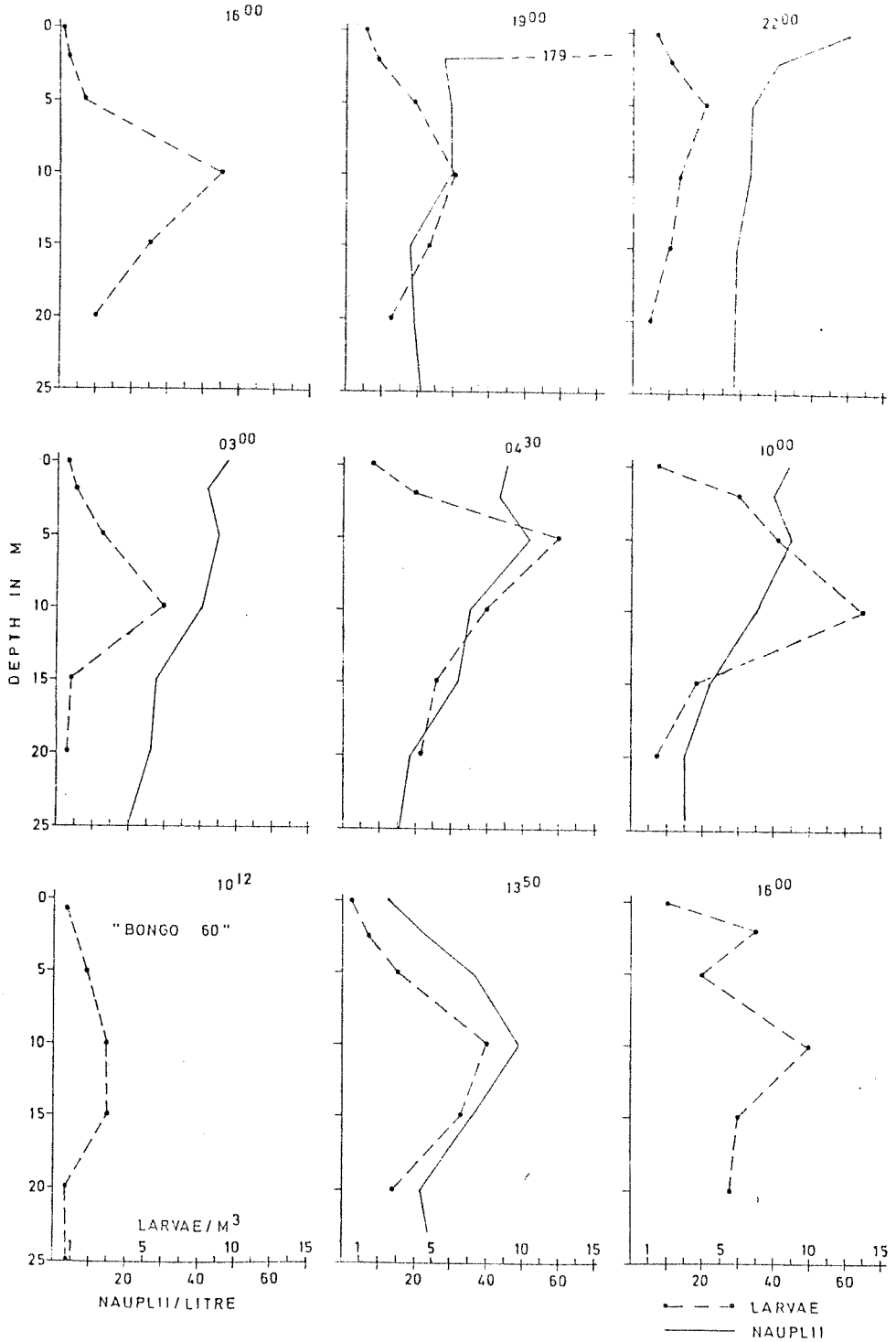


Fig.24. Distribution of copepod nauplii and cod larvae in relation to depth, 18-19 May 1977.

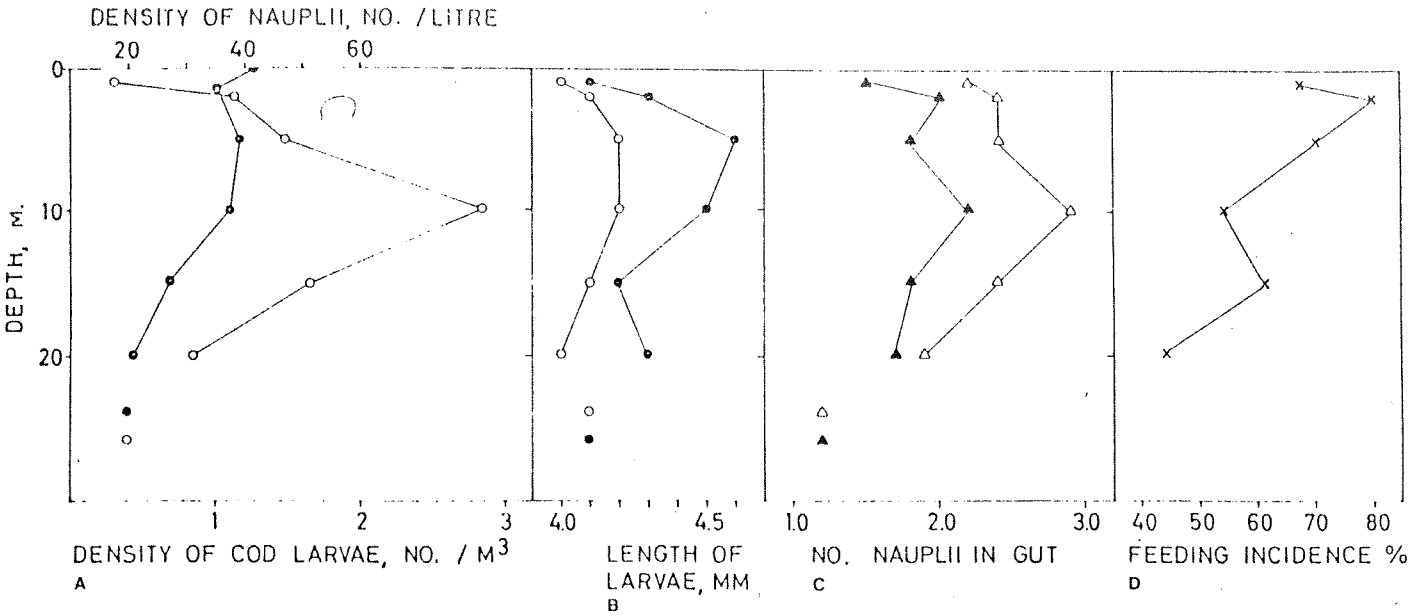


Fig.25. Cod larvae, yolk sac stage 5, from 24-hour station 18-19 May 1977, all stations pooled.

a, Density of nauplii, no/l(●), and cod larvae, no/m^3 (o),

b, Standard length of larvae, mm, with gut contents (●), and without gut contents (o),

c, Number of nauplii in the guts of the cod larvae. Total number, △ , and number with degree of digestion 3, ▲ ,

d, Feeding incidence, %.