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The Propagation of Cod *Gadus morhua* L.

A CASE STUDY ON THE DISTRIBUTION OF COD LARVAE AND AVAILABILITY OF PREY ORGANISMS IN RELATION TO PHYSICAL PROCESSES IN LOFOTEN

B. Ellertsen, P. Fossum, P. Solemdal, S. Sundby
and S. Tilseth*

Institute of Marine Research, P.O.Box 1870,
N-5011 NORDNES Norway

ABSTRACT

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The distribution of cod larvae and copepod nauplii off the Lofoten islands was studied in the years 1979-82. The highest concentrations of cod larvae and copepod nauplii were found in the Austnesfjord, Hølla-Henningsvær and the Vesterålsfjord area.

The feeding condition of cod larvae was studied in relation to prey abundance, and a direct proportionality was seen between gut content and prey abundance in the larvae at the end of the first feeding period.

Vertical migration of cod larvae was observed at a diurnal station in the Vesterålsfjord under calm weather conditions. The feeding condition of the cod larvae were bad under the prevalent prey density (<10 prey org. per l) at this station.

At a diurnal station in the Austnesfjord, the onset of turbulent mixing lowered the prey and cod larval densities and created a homogeneous vertical distribution of cod larvae

*Authorship equal

and prey animals. This was reflected in the gut content analysis when the percentage of cod larvae with gut contents, and the number of prey organisms per larval gut and the percentage of newly taken prey organisms fell to a critical level.

INTRODUCTION

It is generally accepted that the variations in stock sizes of various fishes are determined early in their life history, and that the survival of the broods depends to a certain extent on the quantity of food available for the larvae in the plankton.

G.O. Sars (1879) considered wave action and the drifting ashore of eggs and larvae as the main mortality factor in North-east Atlantic cod (*Gadus morhua* L.). The later hypothesis by Hjort (1914) on a "critical period" in the early life of fish larvae, suggesting a lack of available food organisms at the time of yolk absorption as the predominant factor causing high mortality, has been the subject of several investigations. May (1974) on the basis of 11 investigations reported in the literature, concluded that no conclusions could be drawn about the existence of a critical period in fish larvae due to inadequate sampling methods. Sampling methods have been improved and it is now possible to collect larvae and their food organisms from the same water masses at discrete depths (Ellertsen et al., 1981a; Lough, 1984; Fridgeirsson, 1984; Solemdal and Ellertsen, 1984).

Investigations on cod larvae and their food organisms have been carried out in the field by Wiborg (1948), Marak (1960), Bainbridge and McKay (1968), Ellertsen et al. (1977), Last (1978), and others, providing information on prey type selection, prey size, etc.

Apart from lack of food several other factors which lead to a high mortality during a "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), an effect of freshwater outflow in

the coastal current has been suggested by Gran (1923; 1930), Sund (1924) and Skreslet (1976).

The physical environment may cause distributions of eggs, larvae and prey organisms which are not optimal for the feeding of fish larvae. During moderate weather conditions cod larvae are found in the upper 20 m and their main prey items, copepod nauplii (Wiborg, 1948), have a vertical distribution with a clear maximum at depths of 5-15 m in daytime and the upper 10 m at night (Ellertsen et al., 1981a), and the nauplii concentrations may be high enough to provide sufficient food for growth and survival of the larvae. The horizontal distribution of eggs and larvae is affected by the weather conditions (Ellertsen et al., 1981b; Rae, 1957); the effect of wind on the vertical distribution of eggs is shown by Solemdal and Sundby (1981). To what extent the wind conditions influence feeding in cod larvae is the subject of the present investigation, which is designed to provide information on the feeding conditions of cod larvae sampled in areas differing physically with regard to wind and wave exposure.

MATERIALS AND METHODS

The distribution of cod larvae in the Lofoten area was studied in the three first weeks of May in 1979-1982. Cod larvae were sampled with Juday nets (0.5 m² opening and 375 µm mesh size) and modified conical nets (0.75 m², 1 m² and 2 m² opening and 375 µm mesh size) in 50-0 m vertical hauls at 200 stations off the Lofoten archipelago. The largest nets were used in areas where the abundance of cod larvae was low. The vertical distribution of cod larvae was investigated by the submersible electric pumps described by Solemdal and Ellertsen 1984. Samples were taken at 5, 10, 15, 20, 25, 30 and 35 m depth. Fifteen m³ of sea water were sampled at each depth. The diel vertical distribution of cod

larvae was investigated both in the sheltered Austnesfjord (in 1980) and the open bay of the Vesterålsfjord (in 1982).

The larvae were preserved in 4% formalin in 10⁰/∞ sea-water for morphometric measurements and gut content analysis. After dissection, the rest of the gut and liver were removed. The larvae were rinsed in fresh water, dried to constant weight (min. 24 h) and weighed on a Cahn electrobalance to the nearest µg. The use of formalin preserved larvae to estimate dry weight has some disadvantages as indicated by Theilacker and Dorsey (1980). Loss of fat can reduce the weight up to 30%. In spite of this we have used formalin preserved larvae. The reason is that we tried to see some trends in the weight distribution in relation to prey abundance. The same age groups of larvae are compared, the same preservation procedure followed, and the most fat containing organ, the liver, is removed together with the gut during dissection.

The vertical distribution of microzooplankton was investigated by using a small submersible electric pump (Flygt 2051, 250 l/min). Samples were pumped on deck through a 50 m long and 5 cm in diameter hose. Samples were taken from following depths: 0, 2.5, 5, 7.5, 10, 12.5, 15, 20, 25, 30 and 40 m. The samples were collected in calibrated tanks (23.7 l), filtered through 90 µm mesh size nylon gauze and the zooplankton preserved in 4% formalin. The whole zooplankton sample was counted and identified under a binocular microscope. In 1981 and during the diurnal station in 1980 the abundance of microzooplankton was estimated with the "in situ" particle counter system described by Tilseth and Ellertsen (1983). Zooplankton samples were taken in connection with cod larval sampling at every second station on each transect of stations, and every second hour through the 24 h period at diurnal stations (the Austnesfjord and the Vesterålsfjord).

Salinity and temperature data were collected by a CTD-sonde. The static stability of water masses is expressed by the squared Brunt-Vaisälä frequency (Phillips, 1977) and

computed for every 5 m intervals for the diurnal stations. The vertical mixing of the upper layer is largely a function of the energy input by the action of wind (proportional to the squared mean wind speed), and the stratification of the water column. In 1980 a Wolfe wind recorder was used to read the mean wind speed per h. In 1982, the wind speed was manually measured every 30 min.

A study of the vertical migration of cod larvae and their prey organisms was carried out at two diurnal stations in Austnesfjord (1980) and Vesterålsfjord (1982). Vertical migration of planktonic organisms is influenced by the buoyancy of the organisms and the vertical movement of the water masses. The most important cause of vertical movement of the water masses is vertical turbulence which is a function of the wind mixing and stratification of the water masses. In the diurnal station, the effect of energy impact from wind stress (given as the squared wind speed) on the static stability of the water masses, expressed as the squared Brunt-Vaisälä frequency, was studied.

The spawning activity of the North-east Atlantic cod was studied for the period 1975-1983. The maximum and 50% spawning were correlated to the mean sea temperature to estimate the correct time of the "first feeding period" of the larvae. In recent years, maximum spawning occurred at the end of March or the first days of April (Pedersen, 1984). First feeding of cod larvae occurred in the first two weeks of May.

The resorption of the epithelial cells surrounding the yolk sac was used as an index of larval age. The yolk sac staging system described by Ellertsen et al. (1980) was extended with three more stages (Fig. 1).

In stage 8 the epithelial cells which surrounded the yolk sac are reduced to a string under the stomach. In stage 9 this string is broken up and in stage 10 the epithelial cells are absent. The duration of stages 8 + 9 is about 2 weeks and independent of larval growth. A comparison of larvae in the same stage will therefore be a comparison of larvae in

the same age groups within the temperature range experienced in different parts of the Lofoten area at this time of the year.

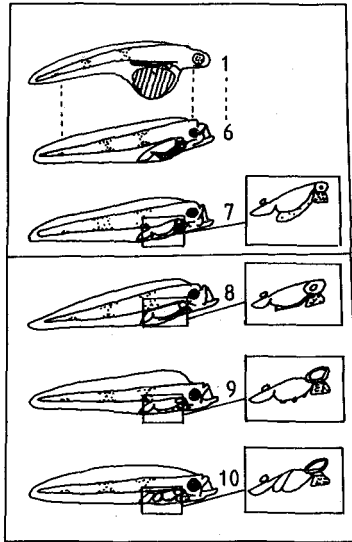


Fig. 1. A staging system of cod larvae which focus on the resorption of the yolk sac content and development of gut, liver and jaw apparatus, st. 1-7 (Ellertsen *et al.*, 1980). The larvae in stage 8-10 are staged on the resorption rate of epithelial cells surrounding the yolk sac (see text).

This was verified by comparing two groups of cod larvae. One was fed a maintenance ration in the laboratory and did not grow at all ($t=6^{\circ}\text{C}$); the other was a fast growing group in a concrete enclosure experiment ($t=7-8^{\circ}\text{C}$) (Ellertsen *et al.*, 1981c). No significant difference in the resorption of the epithelial cells surrounding the yolk sac was seen. However, more experiments at different feeding and temperature regimes must be carried out to verify this.

In the gut content analysis the same stages were compared. The yolk sac stages representing cod larvae in the first exogenous feeding stages (5 and 6) were pooled, as were the

larvae expected to be in the most critical stages (7, 8 and 9). Samples were analysed from several time periods from the different areas. Means are given with \pm SD.

RESULTS

Distribution of cod larvae and copepod nauplii

The distribution of cod larvae in the Lofoten area during the first weeks of May is dependent on the time and location of spawning, and the physical condition and velocity of the water masses in the drift route of the eggs. The North-east Atlantic cod spawn mainly in the eastern part of Lofoten as shown in Fig. 2. The drift route is shown in Fig. 2, and a vertical section on the western side of the Lofoten islands is presented in Fig. 3. The eggs float in the upper 50 m in the near land zone (Sundby, 1983), in 1982 this was in water with a temperature of 5.0°C and a salinity below $34.0^{\circ}/\text{oo}$. The velocity of this drift depends on the formation of eddies, the bottom topography and the wind stress.

Since the incubation time, and therefore the length of the drift, depends on the water temperature, the whole area from the inner parts of Lofoten to Langøy (Fig. 2) must be surveyed to ensure that the main hatching and first feeding areas are covered. The distributions of cod larvae in 1979 and 1982 are shown in Fig. 4. In 1979, most of the eggs hatched in the Vesterålsfjord-Langøy area and in 1982, most eggs hatched on the eastern side of the Lofoten islands. The occurrence of cod larvae during the same period in 1980 and 1981 was low and larvae were only observed in a few Juday net hauls. Characteristic of 1979 and 1982 was a similar pattern of distribution in the coastal current close to the shore, with the highest concentration of cod larvae in the Austnesfjord, Henningsvær-Hølla area and the Vesterålsfjord area. The density of cod larvae in the Austnesfjord was high in all four years.

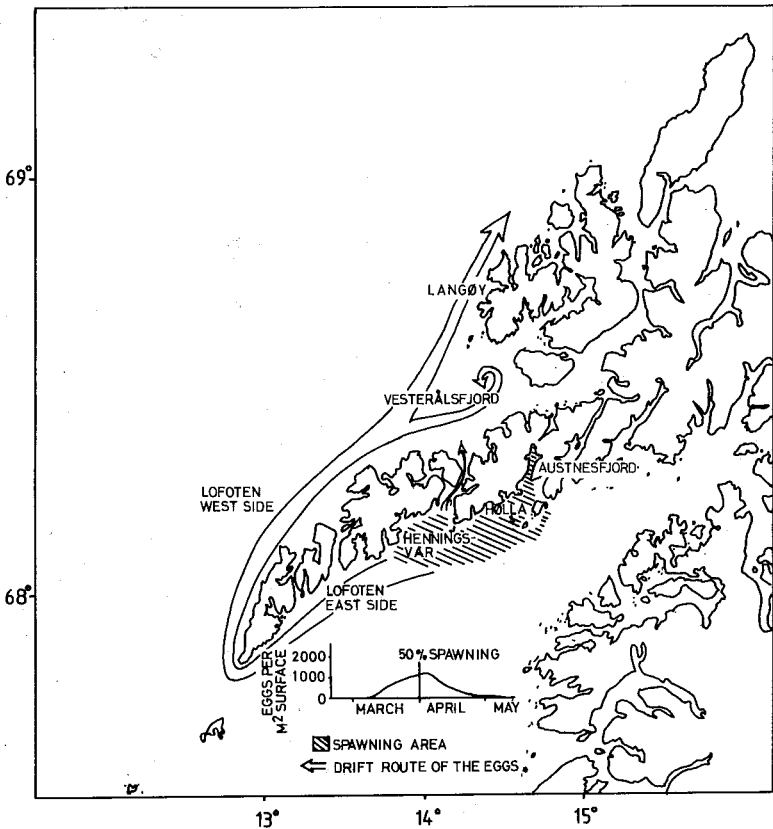


Fig. 2. The spawning area in Lofoten, the mean spawning curve (for the period 1976-82) and the drift route of the eggs of the North-east Atlantic cod.

The distribution of copepod nauplii, mainly *Calanus finmarchicus*, in the Lofoten area was investigated in the years 1980, 1981 and 1982. The results are presented in Fig. 5 as the mean density of nauplii per l in the upper 40 meters of the water column. The abundance of copepod nauplii varied from year to year; ≤ 10 nauplii per l in 1980, ~ 40 nauplii per l in 1981 and ≤ 20 nauplii per l in 1982. The distribution was similar to that of cod larvae, with highest densities of nauplii occurring in the Austnesfjord, Hølla-Henningsvær and Vesterålsfjord areas.

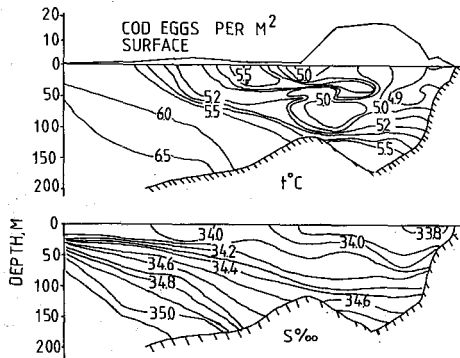


Fig. 3. Distribution of cod eggs, temperature and salinity on a section of the western side of the Lofoten islands, 17 May 1982.

Relation between feeding rates and naupliar abundance

In 1982, gut content analyses were made on larvae from four localities having different stresses of wind and currents and abundances of prey organisms (Fig. 5); the sheltered Austnesfjord had 21.0 nauplii per l, with a range of 17-24 nauplii per l ($N=2$) the ocean bay of Vesterålsfjord 5.8 ± 4.4 nauplii per l with a range of 0-23 nauplii per l ($N=23$) and the eastern and western parts of Lofoten had 5.6 ± 2.3 with a range of 2-11 ($N=11$) and 4.3 ± 3.0 with a range of 1-10 ($N=22$) nauplii per l respectively. Larvae from these areas were compared with regard to their dry weight and gut fullness.

The results are presented in Fig. 6. as the cod larval feeding incidence (percentage of larvae with gut content) and feeding ratio (number of food items per larva) (Tilseth and Ellertsen, 1983). In the Austnesfjord the cod larval feeding incidence was $89 \pm 6\%$ for stage 7, 8 and 9 larvae. The youngest larvae (stage 5 and 6) showed a feeding incidence of $43 \pm 4\%$. The feeding incidence of the oldest larvae (stage 7, 8, 9) from the Vesterålsfjord was $89 \pm 7\%$. The feeding inci-

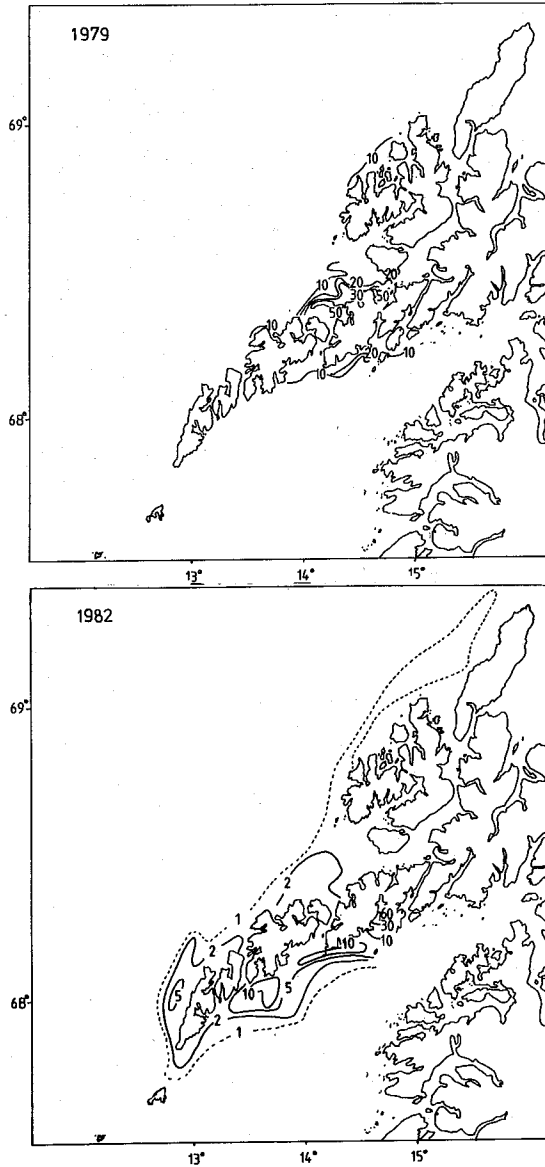


Fig. 4. The horizontal distribution of cod larvae, N/m² surface, in May 1979 and May 1982.

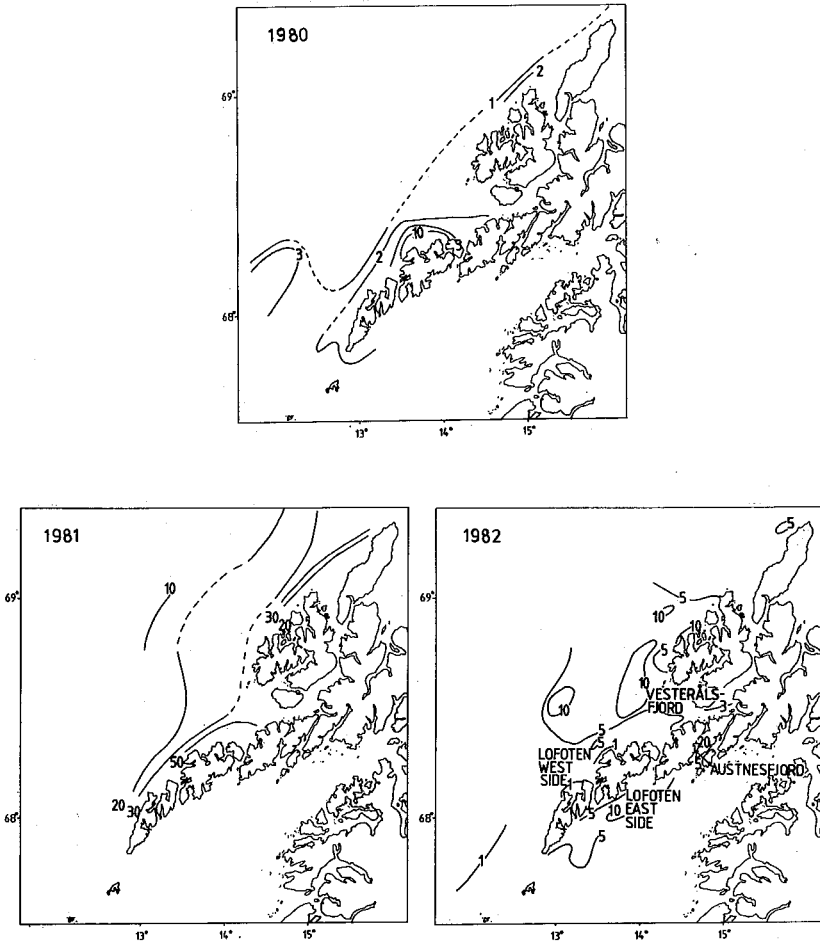


Fig. 5. The horizontal distribution of copepod nauplii (N/l) in May 1980, May 1981 and May 1982.

dence of the youngest larvae (5 and 6) was, however, only $21 \pm 21\%$. The feeding incidence of the oldest larvae (stage 7, 8 and 9) from the east side of the Lofoten islands was $79 \pm 13\%$, the feeding incidence of the youngest larvae (stage

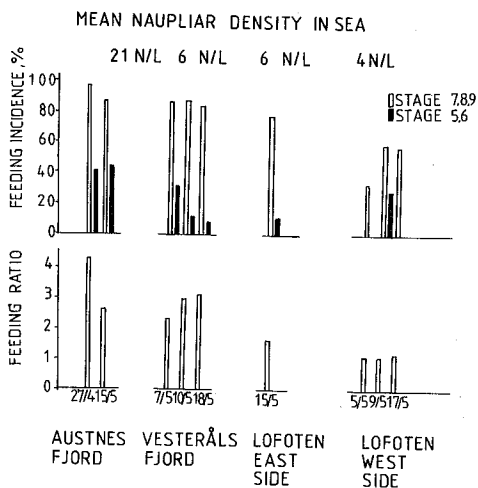


Fig. 6. The feeding incidence (percentage of larvae with gut content, FI%), and feeding ratio (food items per larva, FR) in cod larvae from four selected areas.

5, 6) was $15 \pm 10\%$ in this area. The feeding incidence in stage 7, 8 and 9 larvae from the west side of the Lofoten islands was $59 \pm 4\%$. The youngest larvae (stage 5 and 6) in these samples had not been able to capture nauplii at all, except for larvae in one sample on 9 May when 22% of the youngest larvae were found with gut contents. The cod larval feeding ratio has been calculated only for the oldest larvae from the different areas. The results are presented in Fig. 6, showing a cod larval feeding ratio of 3.2 ± 1.0 nauplii/larval gut in samples from the Austnesfjord, 2.7 ± 0.3 nauplii/larval gut in the Vesterålsfjord and 1.7 ± 0.7 nauplii/larval gut in samples from Lofoten east side and 1.2 ± 0.1 nauplii/larval gut in samples from the west side of the Lofoten islands.

The dry weights of cod larvae stages 6, 7 and 8 from the four different areas are compared in Fig. 7. Too few larvae in stage 9 were found in the Austnesfjord and Lofoten east side to be presented in this figure. The mean dry weights of

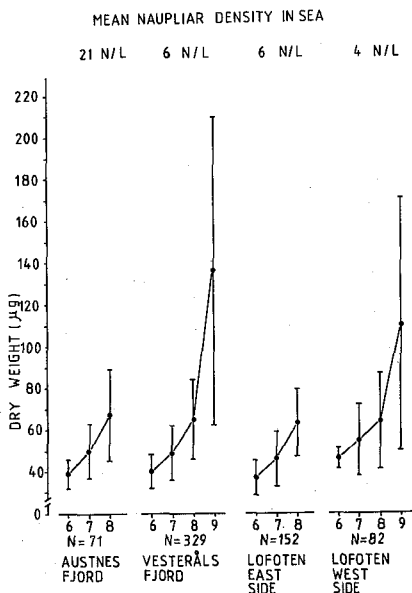


Fig. 7. The dry weight of cod larvae in stage 6, 7 and 8 in four selected areas.

stage 8 larvae was the same in all areas. The larvae in stage 6 were heavier in the most exposed area, the western side of Lofoten, having mean weights of 46 μg . The larvae in stage 6 weighed 39 μg in the Austnesfjord, 37 μg in the eastern part of Lofoten and 40 μg in the Vesterålsfjord.

Effects of mixing

Vertical processes were related to the vertical distribution of copepod nauplii and cod larvae at the two diurnal stations in Austnesfjord on 12-15 May 1980 and Vesterålsfjord on 12-13 May 1982. The physical situation in the Austnesfjord after a period of calm weather conditions, typical for this sheltered location, was one of high stratification (Fig. 8). Three different water masses were present in the fjord,

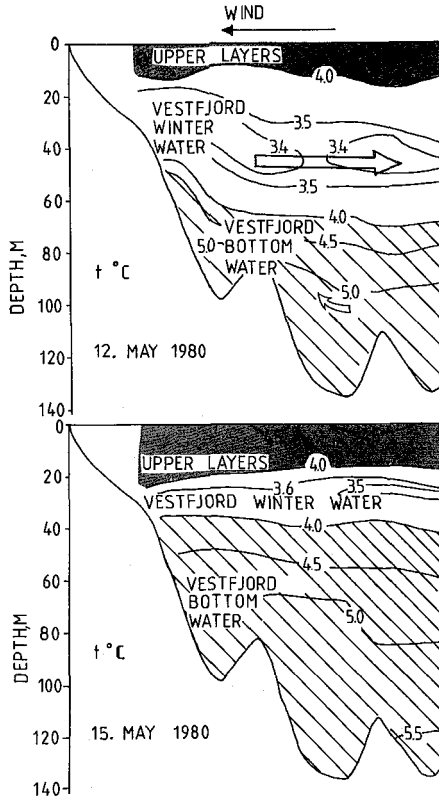


Fig. 8. The vertical structure of temperature and salinity in Austnesfjord at the onset of turbulent mixing 12 May and after two days with turbulent mixing 15 May 1980.

Vestfjord winter water was found between an upper layer and Vestfjord bottom water. There was a high abundance of copepod nauplii and cod larvae, and the planktonic organisms were patchily distributed in the water masses. Then a heavy impact of energy, from strong winds blowing against the head of the fjord, created turbulent mixing, and the Vestfjord winter water was pressed out of the system between the bottom water and the upper layers. As a result there was a trans-

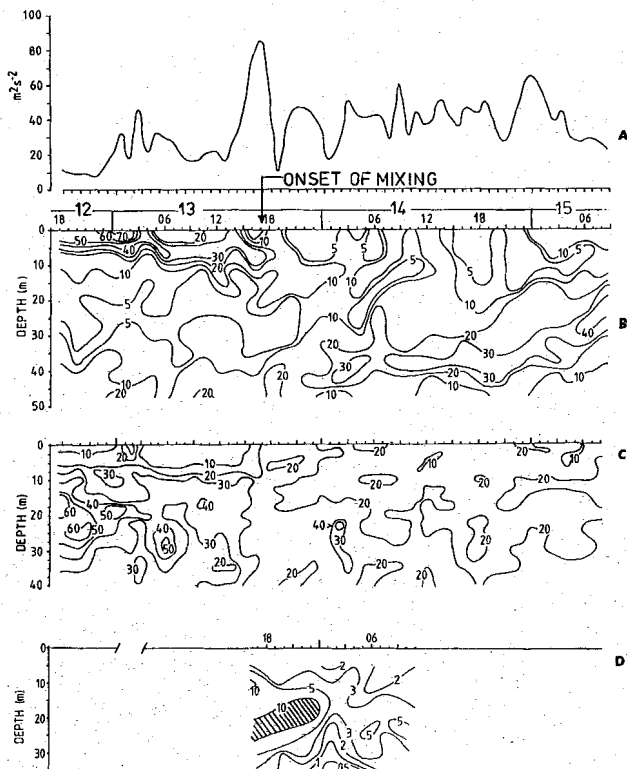


Fig. 9. The squared wind speed (A), the squared Brunt-Vaisälä frequency (B), the density of microzooplankton given as particles per liter (C) and density of cod larvae as larvae per m^3 (D) in the diurnal station in the Austnesfjord 12-15 May 1980.

port of nauplii and larvae out of the system and patches in the upper water masses were broken up and the distribution of organisms became more homogeneous. Fig. 9B shows the stratification of the water masses given as the Brunt-Vaisälä frequency, and the wind situation (Fig. 9A). There were very stable water masses at the beginning of the sampling period, represented by a high Brunt-Vaisälä frequency. After the wind started to blow the stability was broken down.

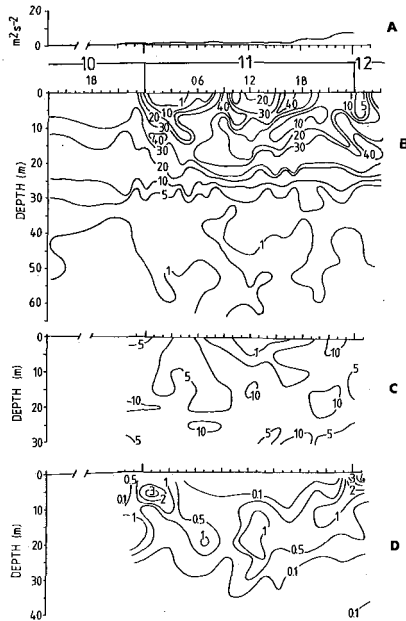


Fig. 10. The squared wind speed (A), the squared Brunt-Vaisälä frequency (B), the density of microzooplankton given as nauplii per liter (C) and density of cod larvae as larvae per m^3 (D) in the diurnal station in the Vesterålsfjord 10-12 May 1982.

High concentrations of copepod nauplii were found in the transition layers between the upper water and the Vestfjord winter water at the beginning of the sampling period. A high energy impact at about 1700 h created a lot of turbulent mixing and this is seen as a decrease of the Brunt-Vaisälä frequency. There was a falling concentration of copepod nauplii and cod larvae throughout (Fig. 9C, D) and the upward migration of cod larvae was hindered by the turbulent mixing.

At the diurnal station in Vesterålsfjord there was high stratification of the upper water masses (Fig. 10B) with very little impact of energy from wind stress (Fig. 10A) and significant vertical migrations towards the surface of the cod larvae and copepod nauplii were seen in the middle of the night (Fig. 10D).

TABLE 1.

The feeding incidence (percentage of larvae with gut content) (FI) and the percentage of larvae with newly captured nauplii (NC) in the gut, at two diurnal stations; Austnesfjord (1980) and Vesterålsfjord (1982).

Date	Hours	Year	NC	FI	Number of larvae
13/5	1610	1980	24	100	22
"	1650	"	23	95	21
"	1940	"	17	91	22
"	2000	"	20	91	22
"	2230	"	9	95	22
14/5	0100	"	16	50	21
"	0120	"	5	45	22
"	0430	"	6	70	20
"	0725	"	5	95	22
"	1010	"	5	86	22
10/5	2240	1982	18	59	17
11/5	0050	"	0	61	31
"	0230	"	0	35	31
"	0700	"	0	35	26
"	1200	"	20	47	15
"	2020	"	23	59	22
12/5	0045	"	0	42	36

The data from 1980 is from Tilseth and Ellertsen (1983).

This was found in one sample from 25 m depth at 1000 h. The highest cod larval feeding ratios were found in samples from 20-30 m depths.

The gut content analyses of cod larvae from the diurnal station in the Vesterålsfjord are also presented in Fig. 11. The densities of cod larvae were much lower than in the Austnesfjord and numbers sufficient for gut content analyses ($N \geq 20$) were not found in samples from all depths. The cod

larval feeding incidence varied between 35% and 61% ($48 \pm 11\%$). The highest larval feeding incidence (60%) was found in samples from 20 m depth at 2300 h and 10 m depth at 1230 h. The cod larval feeding ratio varied between 0 prey/larval gut to 1.5 prey/larval gut with a mean of 0.8 ± 0.4 . Larvae with empty guts were found in one sample from 20 m depth at 0130 h, and the highest feeding ratio was found in larvae from 10 m depth at 1230 h. The percentage of larvae with newly captured nauplii in the gut are presented in Table 1. $18.6 \pm 6\%$ of the gut content was newly taken nauplii in larvae from Austnesfjord before the turbulence had broken down the stability of the water masses. Later the percentage fell to $7 \pm 5\%$ throughout the diurnal station. In Vesterålsfjord, gut contents contained $9 \pm 11\%$ newly captured prey organisms, in 4 samples, there were no newly captured nauplii, while about 20% newly captured nauplii were found the first evening and in two samples the next day.

The light situation in Lofoten this time of the year is described in Gjøsæter and Tilseth (1982).

DISCUSSION

The egg size and the dry weight of the newly hatched cod larvae is variable due to intraspecific and spawning time effects on the egg size (Solemdal, 1970; Solemdal and Sundby, 1981). The mean weight of a sample of larvae in stage 6 (beginning of the first feeding period) is expected to be equal in different first feeding areas in Lofoten. In the Austnesfjord, the east side of Lofoten and in the Vesterålsfjord, however, the weight of stage 6 larvae was lower than on the western side of Lofoten. The larvae in stage 8 were of equal weights in the four areas.

An explanation for the variable dry weight of stage 6 larvae could be that the smallest larvae are lost from the population in the area most exposed to wind and current. Owing to vertical turbulence, the prey organisms in this

area are often evenly distributed, and in such an area, a large larva with a large search volume would have a great advantage. Smaller larvae will easily be runts and may more easily be predated out of the population while a yolk sac reserve remains. The effects of time and the egg size provide another possible explanation for the variation in dry weight. The biggest eggs are spawned at the beginning of the spawning season (Solemdal 1970). At hatching these eggs will have the most northern distribution, and the larvae will be found in the exposed areas on the western side of the Lofoten islands.

The dry weight of the larvae is a conservative parameter which reflects the egg size and the feeding history of the larvae during the last few days, while the gut content reflects the feeding history of the larvae in the hours prior to the catch, and can be correlated with the corresponding abundance of microzooplankton. Tilseth and Ellertsen (1984) gave some indications of criteria of gut contents of larvae in good feeding condition. A feeding incidence $>90\%$, a feeding ratio >3.0 and a percentage of newly ingested nauplii above 10%, indicate a good availability of food to first feeding cod larvae. In the lab the larvae start to feed in stage 5 or 6 (6-7 days old), but will not be in a critical stage deprived of food until until they reach stage 8.

In the surveys feeding incidences (FI%) and ratios (FR) indicating a good availability of food organisms were only found in the Austnesfjord and in 2 out of 3 surveys in the Vesterålsfjord, and this variable feeding response in the larvae reflects the abundance of prey in the four different areas.

At the two diurnal stations in the Austnesfjord and Vesterålsfjord, good feeding conditions were seen in the Austnesfjord before the onset of turbulent mixing. More than 60 copepod nauplii per l occurred in pump samples from the transition layer between the upper layers and the Vestfjord winter water. Micropatches with even higher prey densities

were probably present in this layer. The turbulent mixing lowered food availability and this was clearly reflected in the gut content analyses, both the FI%, the FR and the percentage of newly taken prey organisms decreased.

The critical prey density for first feeding cod larvae has been found to be between 20 and 190 nauplii per l, depending on the swimming speed and feeding success (Solberg and Tilsteth, 1984). This corresponds well with the findings in the Austnesfjord with cod larvae in good feeding condition at the prey densities present.

The Vesterålsfjord diurnal station shows that a prey density <10 nauplii per l is insufficient for adequate feeding of cod larvae. A fifty percent feeding incidence, 1.0 copepod nauplii per gut and a variable percentage of newly taken prey organisms, indicate that most of the larvae were starving. This was seen in spite of calm weather where stratification and the creation of patches should be maximized.

This contrasts with the pelagic prey densities observed in pond and concrete enclosure experiments. Øiestad and Moksness (1981) and Kvenseth and Øiestad (1984) report high feeding incidences of herring larvae in an enclosure and of cod larvae in a pond at similarly low prey densities of <10 per litre.

An explanation of these discrepancies could be that in ponds and enclosures higher concentrations of prey develop near the bottom or the walls, or that undetectable micro patches develop in the water mass because of the special physical conditions. Øiestad and Moksness (1981) report that prey densities increased near the bottom of enclosures.

When the static stability of the water masses is high, a maximum layer of microzooplankton with dense patches of copepod nauplii will migrate vertically in response to diel changes in light intensity, as described by Tilsteth and Ellertsen (1983). The cod larvae may tend to stay in this layer by altering their searching behaviour in response to the prey density, as described for anchovy larvae (Hunter and

Tomas, 1974). Vertical migration was seen in Vesterålsfjord giving distinct maxima in the surface layer during night time. The highest concentrations of copepod nauplii were also found near the surface during night time. However, turbulent mixing will hinder this migration and distribute the larvae and the prey organisms evenly in the water masses, like the situation during the diurnal station in the Austnesfjord.

Our observations support the hypothesis of Vlymen (1977) that survival of fish larvae in the open sea depends on the existence of small scale patchiness of forage. Only in two samples from Vesterålsfjord were larvae found in good feeding conditions when the prey density was low. At such low prey densities, some larvae will always find sufficient prey for survival, but most of the larvae will be runts that starve to death or are eaten by predators. Successful first-feeding of cod larvae, the first and perhaps the most important step towards creating a good year class, appears to be dependent on both biological and physical factors affecting the abundance and availability of microzooplankton. These factors must be considered on a population wide basis and include the timing of reproduction of cod and *Calanus*, weather conditions, and the stability of the water column.

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