THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
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THE EFFECT OF BIOLOGICAL AND PHYSICAL FACTORS ON THE SURVIVAL OF ARCTO-NORWEGIAN COD AND THE INFLUENCE ON RECRUITMENT VARIABILITY

By

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ABSTRACT

Data from egg and larval field investigations in the Lofoten area are used together with long time series of data on temperature and zooplankton in Lofoten and abundance indices of Arcto-Norwegian cod. The importance of environmental factors at the spawning grounds on the year class strength is discussed.

High temperature is a necessary, but not sufficient condition for the production of strong year classes. Spawning of <u>Calanus finmarchicus</u> in Lofoten is strongly influenced by the temperature in the upper layer, causing large variations in the time of nauplii production.

The peak spawning of the Arcto-Norwegian cod is fixed within a period of one week in late March/early April and is very stable between years. The incubation period is influenced by the temperature of the coastal watermasses which vary between 0.5 and 4.5°C, causing a maximum difference in peak hatching of more than two weeks.

Young larvae are found to have the center of their distribution close to the spawning ground, where the best feeding conditions for the larvae also are found. However, the distribution of subsequent stages of eggs shows both spreading and transport. Only the most advanced larvae seem to be able to survive the drift through "poorer" feeding areas on their way from the "retention" area to the Barents Sea.

Gut analyses of larvae subjected to different prey densities indicate that the critical prey density for successful feeding must be on the order of 5-10 plankters per liter.

Length/dry weight plot of larvae from 1982-1985 indicate the best growth conditions in 1983 followed by -84, -82, and -85. In 1983, 1984 and 1985 outstanding year classes of Arcto-Norwegian cod were produced, while the year class was of medium size in 1982.

INTRODUCTION

The Arcto-Norwegian cod, (Gadus morhua L.) is a boreal species, migrating between its feeding area in the Barents Sea and its spawning grounds in Norwegian coastal waters, mainly the Lofoten area. The Arcto-Norwegian cod stock is situated close to the limits of its environmental range (GARROD and COLEBROOK 1978). Annual temperature variations, as shown by SÆTERSDAL and LOENG (1984), influence the distribution area of cod significantly. These authors put forward the following hypothesis: "....through evolutionary processes the reproduction of the Arctic cod is adjusted to the variations in the feeding area caused by climatic fluctuations". The coastal current in Lofoten and adjacent waters, where eggs and larvae are found, also shows annual variation in temperature. The temperatures in the Barents Sea and along the coast of northern Norway are to a certain degree correlated because most of the variations are large scaled (BLINDHEIM, LOENG and SÆTRE 1981).

The year class strength is mainly determined during the first year (HJORT 1914). Recent results indicate that there is good correlation between the number of postlarvae present in the sea in June-July and the year class strength at age 0.5 year (BJØRKE and SUNDBY 1986). Thus there is reason to believe that the year class strength is established during the early stages. Many attempts have been made to identify the factors responsible for yearly variations in year class strength. The starvation hypothesis first put forward by HJORT (1914) as "the critical period concept", was further analysed by WIBORG (1957), KISLYAKOV (1961), SYSOEVA and DEGTEREVA (1964), BARANENKOVA (1965), ELLERTSEN et al. (1976, 1977, 1979, 1980, 1981). The role of predation upon fish eggs and larvae has been investigated by MURPHY (1961), HUNTER (1984), and MELLE and ELLERTSEN (1984). Physical factors acting directly on the egg and larval populations are shown to influence the mortality significantly (GARROD and COLEBROOK 1978, KOSLOW 1984, SINCLAIR, TREMBLAY and BERNAL 1985). An effect of the age distribution on year class strength is suggested by PONOMARENKO (1973).

In the present paper the year class variations will be related to biological and physical factors, with special reference to the effects of temperature.

MATERIAL AND METHODS

Time series of temperature in the upper 30 m in March-April at a fixed hydrographical station Skrova in Vestfjorden, Fig. 1, were analysed for the period 1947-1985. The data were compared to the year class strength of three year old cod based on Virtual Population Analysis (ANON 1985).

The occurrence of C. finmarchicus from the Skrova fixed station in Lofoten, was analysed for the period 1960-84. Zooplankton was sampled weekly by a 36 cm Juday net with 180 µm mesh size from 300-0 meters. The frequencies of the different developmental stages were determined by identifying to stage the first 100 C. finmarchicus observed in a counting chamber.

The vertical distribution of microzooplankton was investigated in connection with the cod larval surveys. Samples were usually taken using small submersible electric pumps (200 l/min) from the following depths: 0, 2.5, 5, 7.5, 10, 15, 20, 25, 30 and 40 m. The samples were collected in calibrated

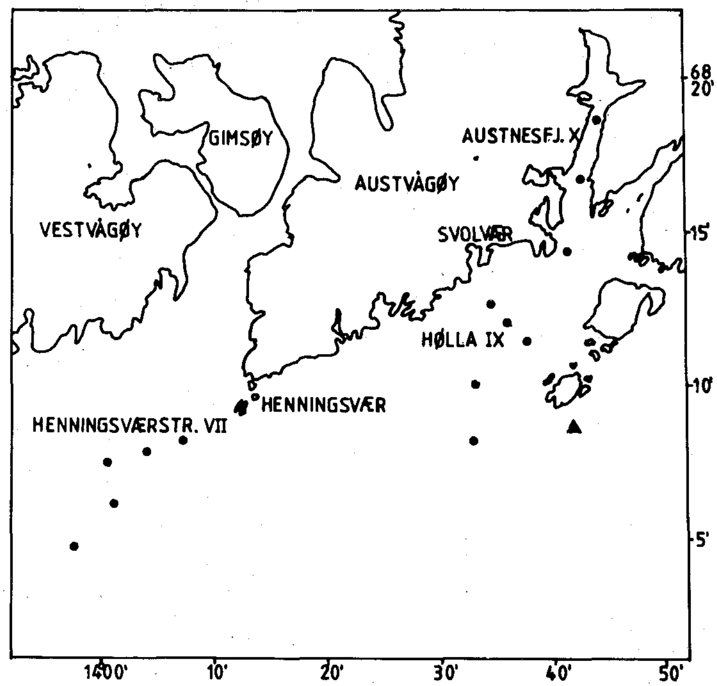


Fig. 1. The main traditional spawning area of Arcto-Norwegian cod in Lofoten. Sampling stations for vertical net hauls are shown (●) and the fixed station Skrova (▲).

tanks (23.7 l), filtered through 90 µm mesh size nylon gauze and the zooplankton preserved in 4% formaldehyde. The entire sample was counted and identified under a binocular microscope.

The zooplankton data were compared with sea temperature and time of appearance of the different developmental stages of C. finmarchicus.

Cod eggs were sampled from 13 localities on the spawning grounds in the Lofoten area in March-May (Fig. 1) with vertical net hauls (diameter 80 cm, mesh size 375 µm) from 100-0 meters, to calculate the spawning intensity curves. These curves were based on abundance estimates of eggs from fertilization to 2 days of development.

Cod egg surveys were performed in the northern Norway in March-April 1983-85 (SUNDBY and SOLEMDAL 1984, SUNDBY and BRATLAND 1987). The eggs were sampled with vertical net hauls (diameter 56 or 80 cm, mesh size 375 µm) from 50-0 meters to calculate the egg production of the different spawning areas of the Arcto-Norwegian cod. The egg production was calculated from abundance estimates of eggs from fertilization to 7 days of development.

Cod larvae were sampled during the first fifteen days of May with vertical net hauls (diameter 80 cm, mesh size 375 µm) from 50-0 meters and with large submersible electrical pumps (SOLEMDAL and ELLERTSEN 1984). The larvae were preserved in 4% formaldehyde in 10°/oo sea water.

One of the main objectives of our investigations was to show the possible correlation between the number of food organisms in the larval gut and the prey density in the sea. The larvae most suitable for such studies are the larvae that have just resorbed their yolksac, stage 7 larvae (see FOSSUM 1986, for a description of the different stages). These larvae are fully developed and able to fill their gut at optimum feeding conditions (TILSETH and ELLERTSEN 1984a), and would therefore better reflect the feeding conditions for first feeding larvae in the sea than older or younger larvae.

Survival of eggs and larvae was calculated in 1983 and 1984. The number of 7-15 and 15-20 day old eggs and cod larvae in age groups 1-4, 4-8, 8-16 and 16-24 days post hatching was calculated from the horizontal distribution found at different surveys. The calculation was made according to the method described in SUNDBY and SOLEMDAL (1984). The number of eggs and larvae in different age groups was compared with the estimated number of eggs spawned 1-5 weeks earlier calculated from the egg surveys described in SUNDBY and BRATLAND (1987). In this way different independent estimates of the survival can be calculated. The total number of larvae found in early May was also calculated according to the method described in SUNDBY and SOLEMDAL (1984), based on the horizontal distribution of the larvae.

RESULTS

Spawning and transport of eggs

The spawning period in Lofoten for the years 1976-1983 is shown in Fig. 2. Data for 50% spawning are given in Table 1, showing a high degree of stability between years, with the mean peak spawning occurring the 31 March.

The distribution of cod eggs, both horizontal and vertical, is described elsewhere (ELLERTSEN et al. 1981, SOLEMDAL and SUNDBY 1981, SUNDBY 1983).

The temperature in the coastal water varies considerably from year to year. The mean temperature in the upper 30 meters at Skrova each year for the period 1980-83 is shown in Fig. 3. The relation between temperature and incubation time of cod eggs is shown in Fig. 4.

The years 1981 and 1983 represent extreme cold and warm years. Hatching curves for 1981 and 1983 are calculated on the basis of the spawning curve and temperature. Adding 1 week to the hatching curve, one gets the date of first feeding. The results are shown in Fig. 5.

About 40% of the eggs of the Arcto-Norwegian cod are produced in the Lofoten area. Within the Lofoten spawning area 50-80% of the eggs are spawned in a small area around Henningsværstraumen (SUNDBY and BRATLAND 1987). Fig. 6 shows the characteristic distribution of newly spawned eggs (0-2 days old), which are concentrated along the Lofoten archipelago. Fig. 7 shows the distribution of the same eggs, 5-7 days later. They have been spread out due to the horizontal turbulent diffusion. During the 5 days period the area of their distribution has increased approximately 2.5 times, and the average peak concentration (at Henningsværstraumen) decreased to 1:2.1. The advection of the eggs during the 5 day period has been relatively small in Vestfjorden, but on the west side of Lofoten a tongue of the eggfield has rapidly run out in an offshore direction. Fig. 8 shows the distribution of the same spawning products 30 days later as first feeding larvae. In spite of the transport and diffusion indicated by the younger egg stages, the distribution of first feeding larvae show no large changes from the newly spawned eggs, but as the figure indicate there has been a considerable reduction in abundance.

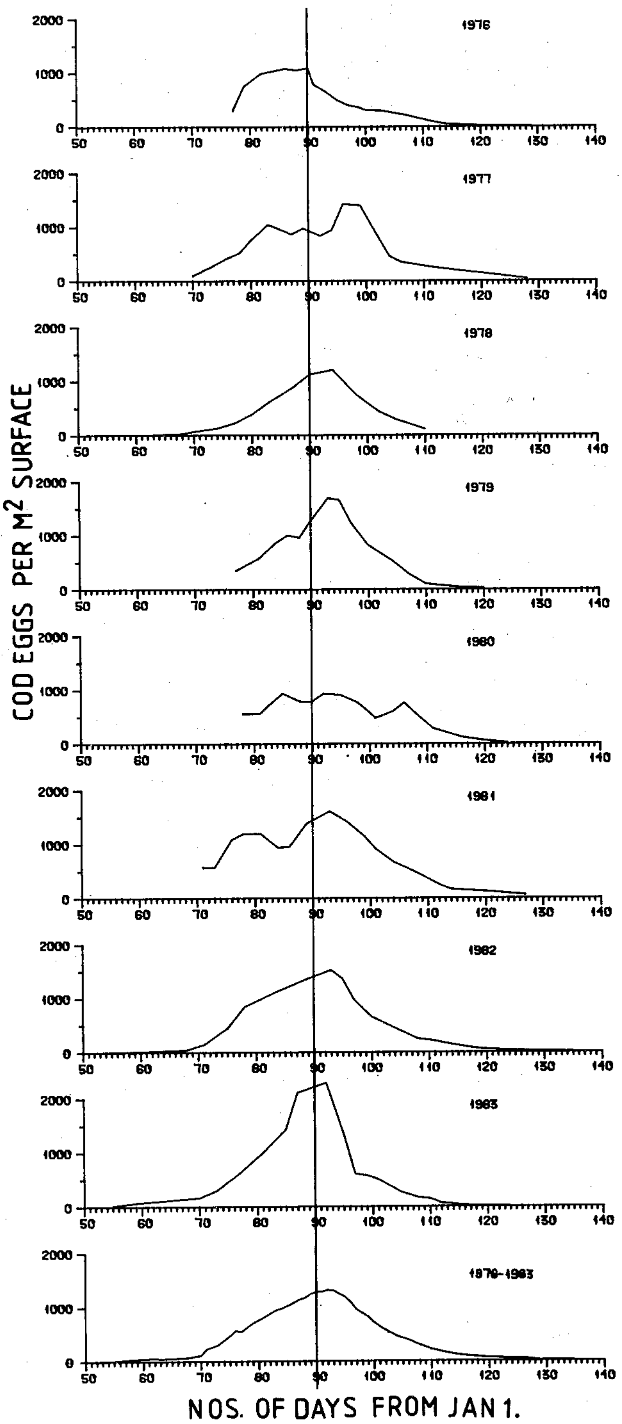


Fig. 2. Spawning intensity curves from Lofoten for the years 1976-83 and the mean spawning curve. Vertical bar represent mean date of 50% spawning for the period 1976-83.

Table 1. Day of 50% spawning in Lofoten during the years 1976-83. Ma=March, Apr=April.

Year	1976	1977	1978	1979	1980	1981	1982	1983	1976/83
Day	28 Ma	2 Apr	31 Ma	2 Apr	3 Apr	31 Ma	30 Ma	29 Ma	31 Ma

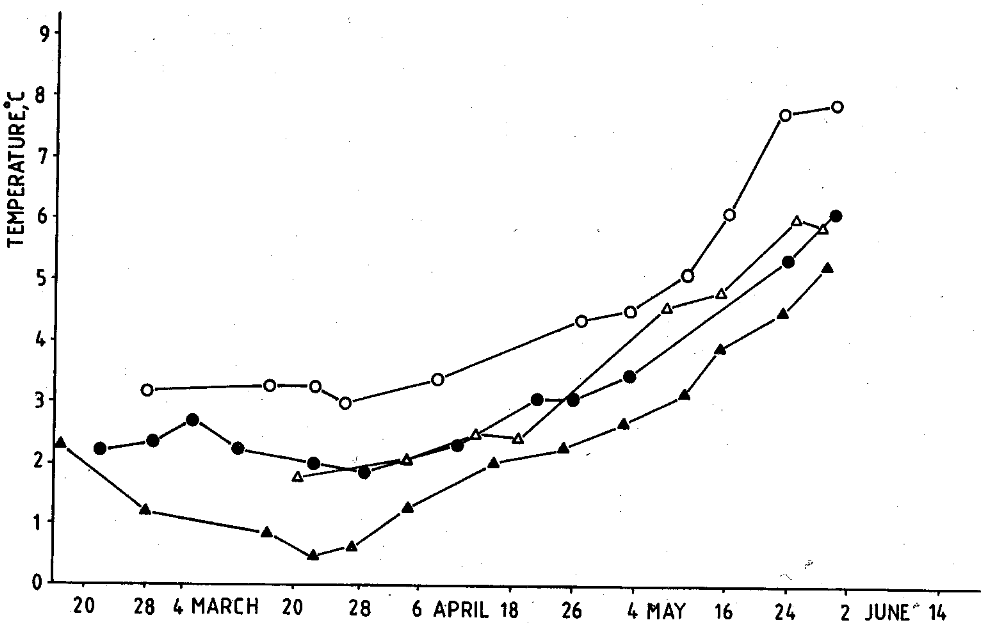


Fig. 3. Mean temperature in the upper 30 meters at the fixed station Skrova (see Fig. 1), (●) 1980, (▲) 1981, (Δ) 1982, (o) 1983.

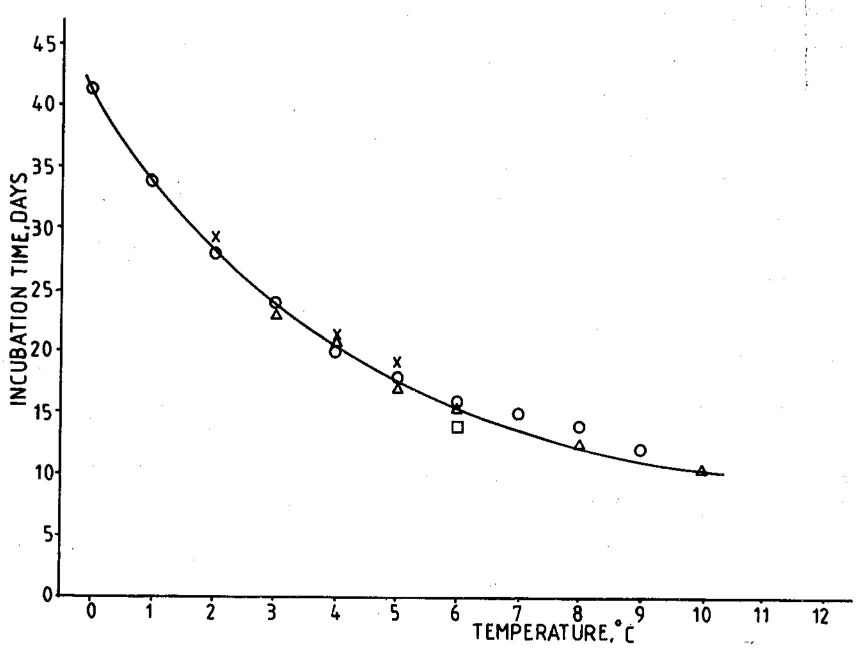


Fig. 4. Incubation period of cod eggs in different temperatures according to APSTEIN (1909) (o), DANIELSSSEN and IVERSEN (1974) (□), DANNEVIG (1895) (Δ) and STRØMME (1977) (x).

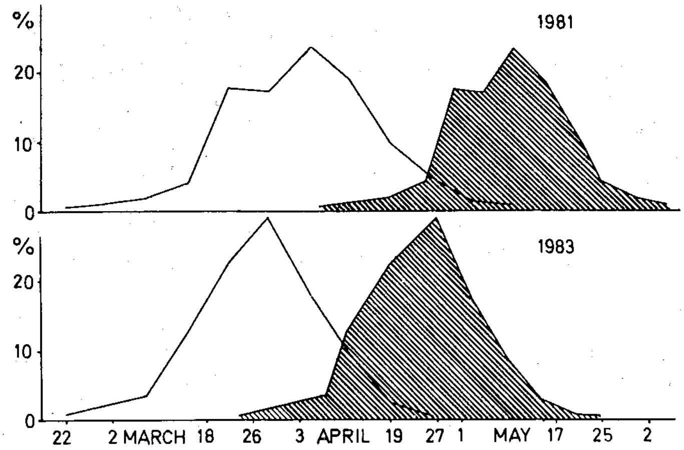


Fig. 5. Spawning curves (open) and first feeding curves (hatched) from the years 1981 and 1983.

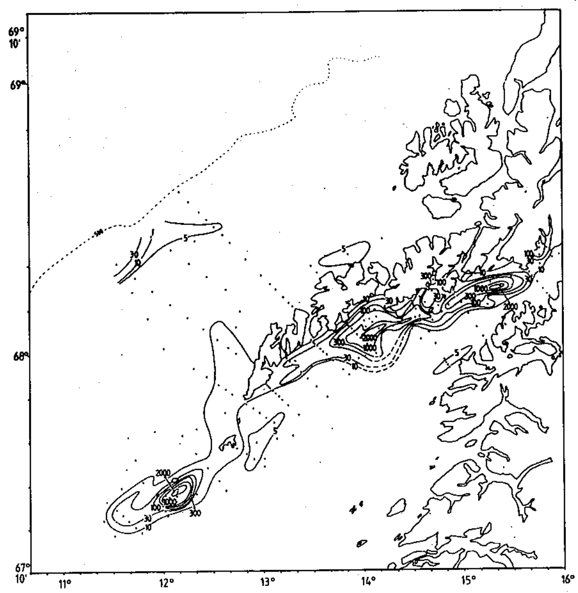


Fig. 6. Distribution and abundance of stage 1 eggs, 0-2 days old, number$\cdot$m^{-2}.

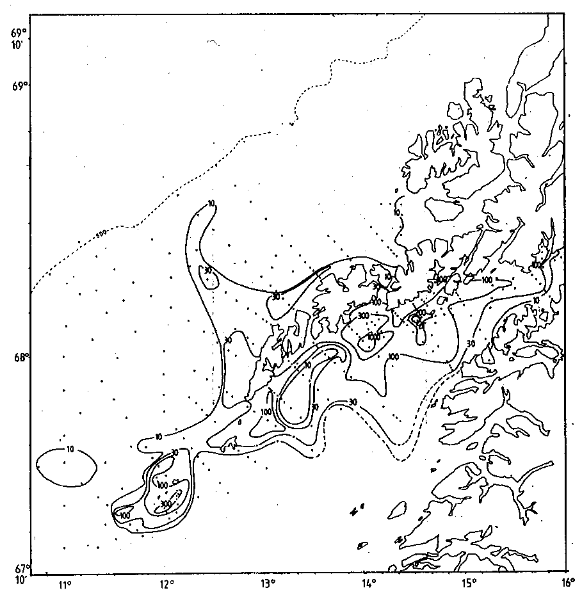


Fig. 7. Distribution and abundance of stage 3 eggs, 5-7 days old, number$\cdot$m^{-2}.

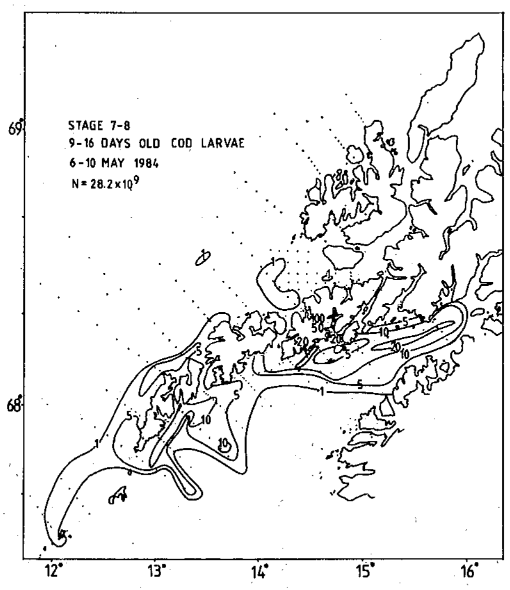


Fig. 8. Distribution and abundance of first feeding larvae, 9-16 days post hatching, number$\cdot$m^{-2}.

Calanus finmarchicus spawning and naupliar distribution

The time of spawning of Calanus finmarchicus is important for the cod larvae, as they mainly feed upon C. finmarchicus nauplii (Ellertsen et al. 1977).

The C. finmarchicus samples consist 60-90% of adult females at the end of March, but only 4-5% a month later when the copepodit stages I (CI) and II (CII) dominate.

When comparing the dates for maximum occurrence of C. finmarchicus CI with the sea temperatures in April (Fig. 9), a linear regression analysis gives

$$y = 7.62 - 0.037X \quad (R^2 = 0.85)$$

A more rapid development from eggs to nauplii to CI at higher temperatures contributes slightly to the correlation. However, the temperature difference of about 2.5°C from a "cold" (1981, 1.9°C) to a "warm" (1960, 4.4°C) year would result in only a few days difference in development time, not a month or more as shown in Fig. 9. The figure therefore expresses temperature dependent spawning in C. finmarchicus.

The distribution of nauplii for the years 1980-85 is shown in Fig. 10. These maps, together with a series of previously published (ELLERTSEN et al. 1984, TILSETH and ELLERTSEN 1984b) data give an impression of the Lofoten as a variable area with regard to naupliar distribution.

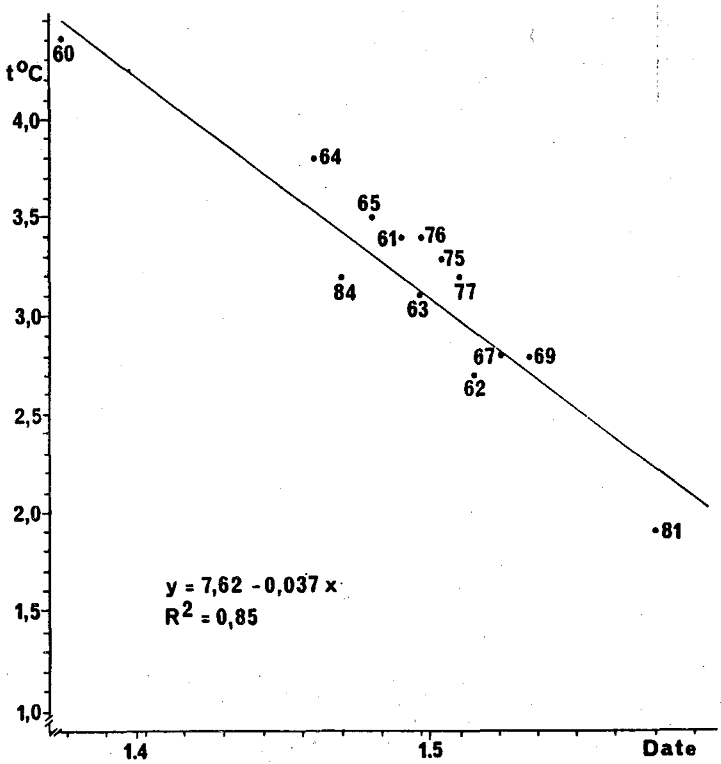


Fig. 9. Time of maximum occurrence of Calanus finmarchicus copepodite stage I versus temperature.

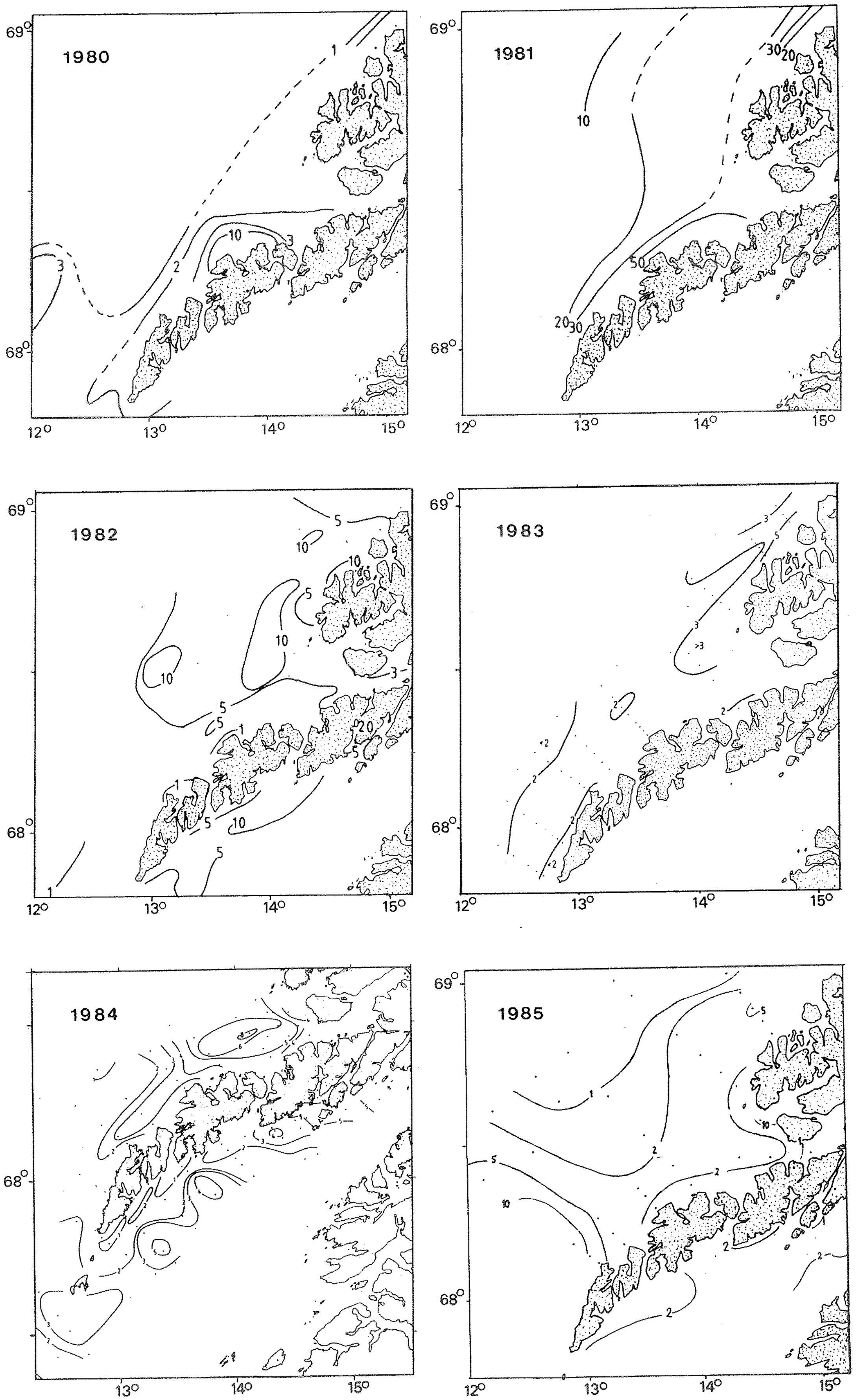


Fig. 10. Distribution and abundance of copepod nauplii 1980-85, number·l^{-1}.

In the years 1980-82 the horizontal distribution of nauplii (Fig. 10) and cod larvae (Fig. 15) was covered at the same time, while there was a time lag of one week between the coverages in 1983 and -84 (the horizontal distribution of cod larvae was found first). In 1985, however, the horizontal distribution of nauplii was covered 3 weeks in advance of the cod larval investigation.

The sheltered Austnesfjord usually has the highest densities, 10-20 up to 600 nauplii per liter, followed by the less sheltered Vesterålsfjord (1-20 n/l), the Lofoten east side (1-10 n/l) and the west side of Lofoten, usually 1-5 n/l. Numbers given in Fig. 10 are based upon integrating all pump samples (10) in the water column at each station. The actual density at a given depth might deviate considerably from the integrated value (TILSETH and ELLERTSEN 1984b).

The relation between yearclass strength and temperature

Fig. 11 shows the relation between the year class strength represented by estimates of 3 year old cod by VPA and the mean temperature in March and April for the upper 30 meters in Lofoten. RANDA (1984) showed that the VPA of the year classes at age 3 is well correlated with the 0-group estimates. The figure shows that in cold years good year classes never occur, while in warm years good year classes may be produced. The four years 1963, 1969, 1973 and 1975 are excluded since they all appear to be inconsistent with the other independant estimates (NAKKEN, pers. comm.).

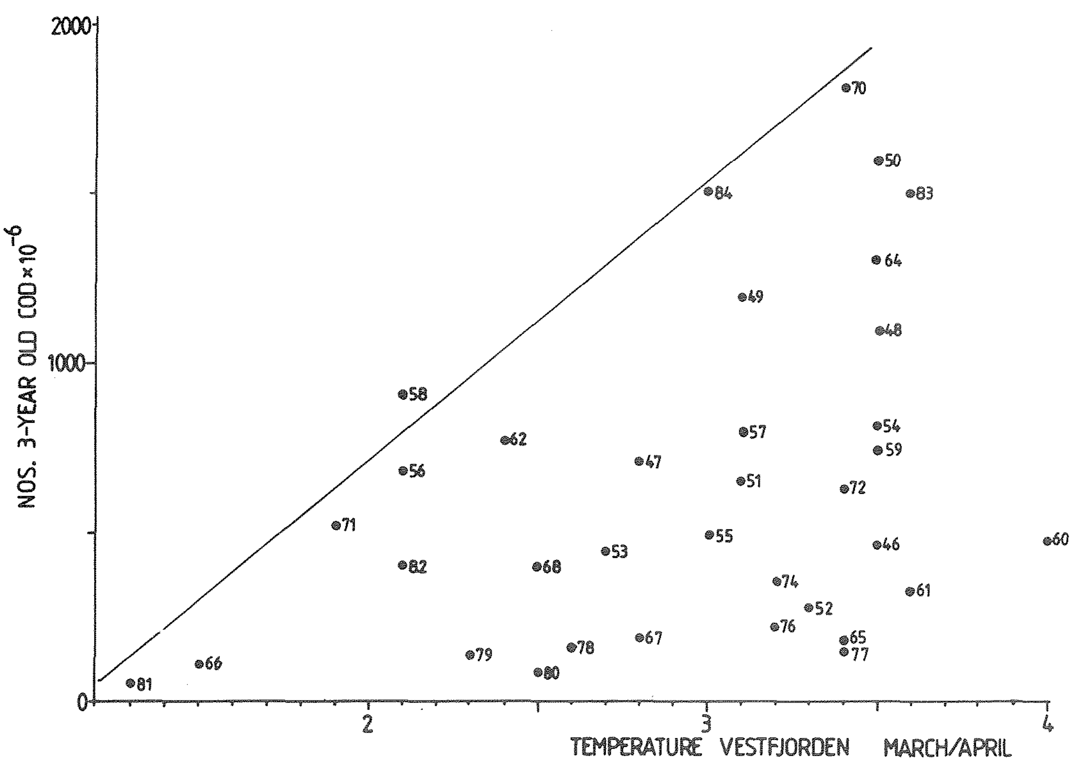


Fig. 11. The relation between the yearclass strength and the mean temperature in March-April in Lofoten.

Density dependent food uptake

Table 2 shows the results of larval cod (stage 7) gut content analyses and the integrated density of nauplii in the water volumn at different stations in the Lofoten area. Only samples made at daytime are included. A plot of larval feeding ratio against integrated naupliar density is given in Fig. 12.

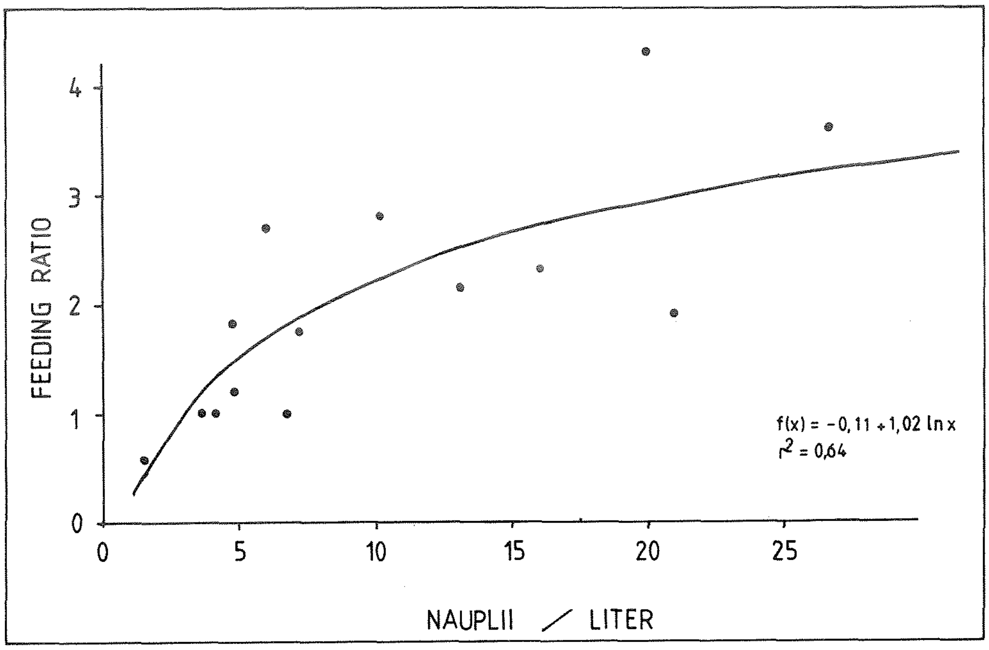


Fig. 12. Feeding ratio in cod larvae in relation to food density.

Table 2. Feeding incidence, % of larvae with gut content, and feeding ratio, number of prey organisms per larval gut, of stage 7 larvae, from surveys and diurnal stations in the period 1976-84. The abundance of copepod nauplii is estimated from plankton pump samples.

Area		Abundance of copepod nauplii, n/L	Number of cod larvae	Feeding ratio	Feeding incidence
Austnesfjorden	(84)	31.5	26	3.5	96
Austnesfjorden	(77)	26.7	67	3.6	94
Austnesfjorden	(82)	21.0	8	1.9	88
Austnesfjorden	(82)	20.0	15	4.3	93
Austnesfjorden	(83)	16.0	26	2.3	81
Vesterålsfjorden	(82)	13.1	24	1.9	79
Austnesfjorden	(84)	10.3	20	2.8	90
Henningsvær	(82)	7.2	12	1.8	75
Vesterålsfjorden	(82)	6.7	91	1.0	55
Vesterålsfjorden	(82)	6.0	8	2.7	88
Ballstad	(82)	4.8	5	1.2	80
Austnesfjorden	(76)	4.7	88	1.8	86
Sørvågen	(82)	4.1	11	1.0	45
Høllа	(82)	3.6	12	1.0	58
Lofotodden	(83)	1.5	9	0.6	44

A statistically significant correlation is found between the gut content of the cod larvae and the density of copepod nauplii ($p<<0.05$, $r^2=0.64$, N=14, logaritmic correlation). The figure indicates that the critical density for successful feeding must be in the order of 5-10 nauplii per liter.

The carapace length of the nauplii in the gut of the larvae is shown in Fig. 13. The mean carapace length increases along the drift route of the larvae. The area of investigation is divided into 6 subareas shown in Fig. 14.

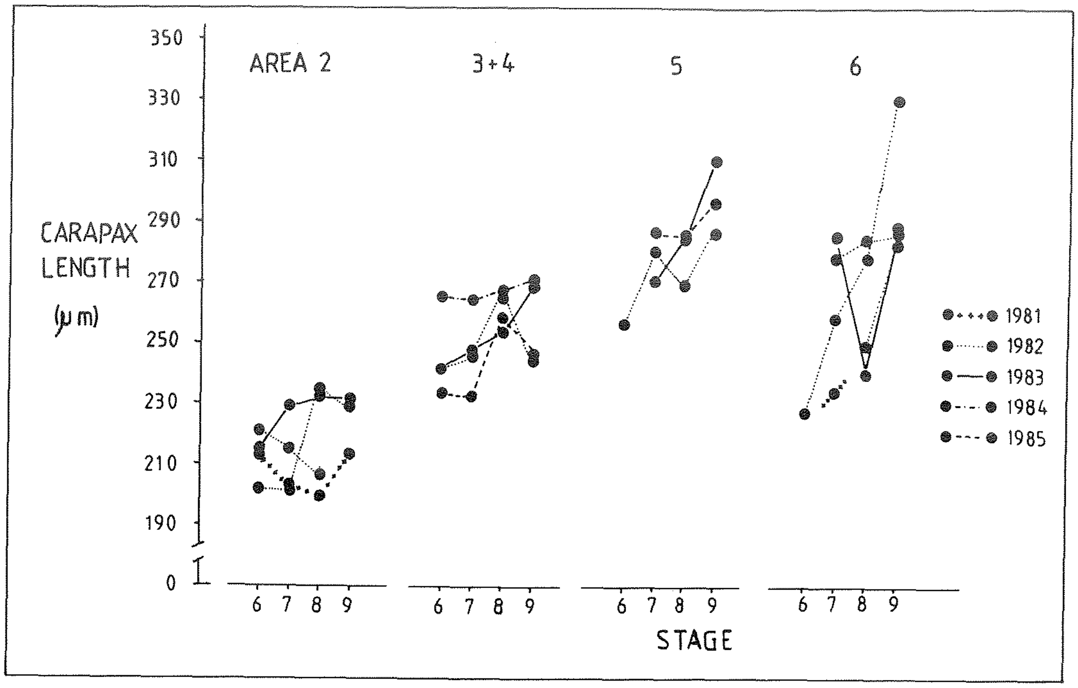


Fig. 13. Naupliar carapax length in stomach content of cod larvae in relation to area and cod larval stage.

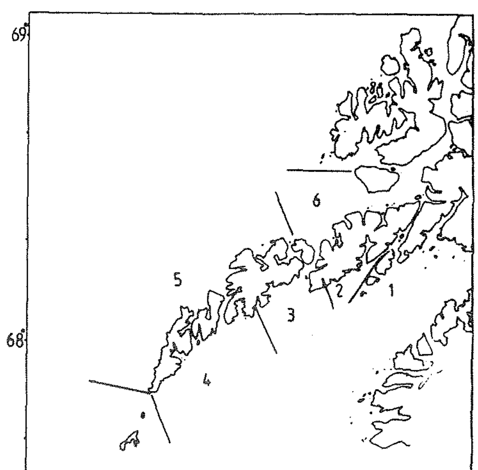


Fig. 14. Lofoten subareas 1-6.

"Good" and "bad" areas

The distribution and abundance of larvae in early May for the period 1979-1985 is shown in Fig. 15. Large numbers of larvae were found in the period 1983-1985, and the center of their distribution was the Vestfjord (for distribution of first feeding larvae see Fig. 8). The number of larvae estimated from the horizontal distribution is shown in Table 3. The number of cod larvae varies by approximately two orders of magnitude from 2×10^9 larvae in 1980 to 125×10^9 in 1985.

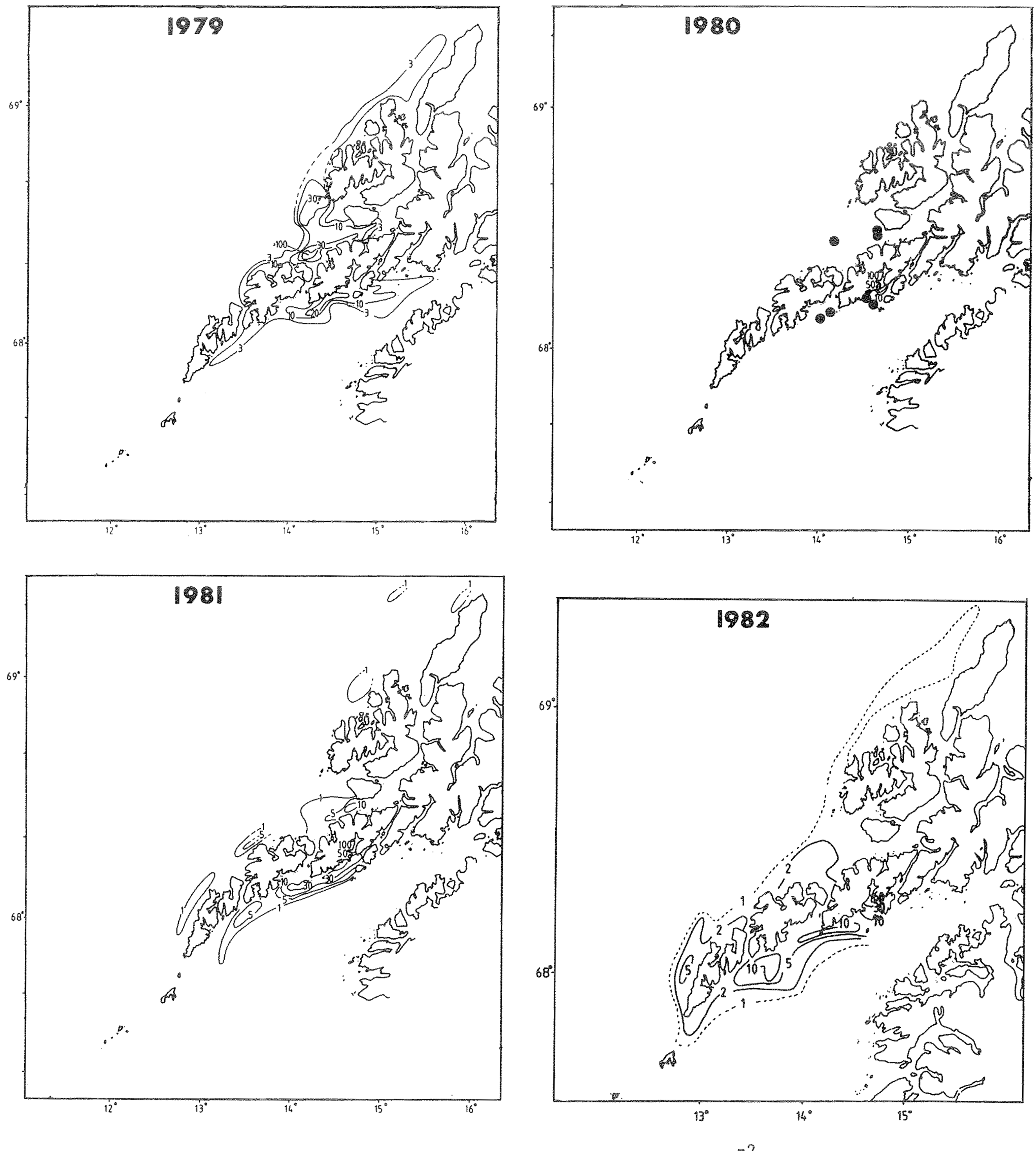


Fig. 15. Distribution and abundance of cod larvae 1979-85, number·m^{-2}.

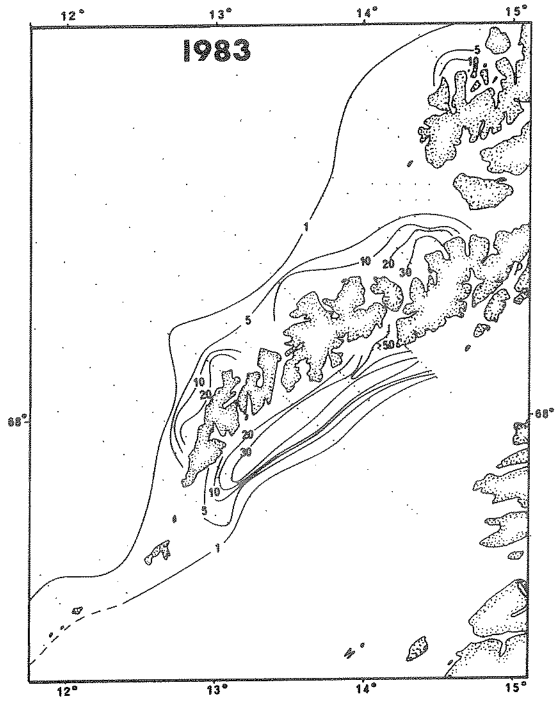
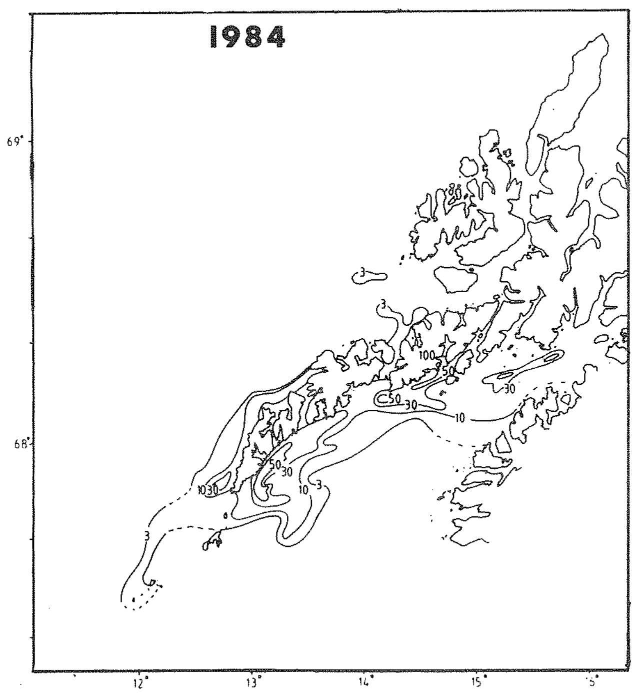
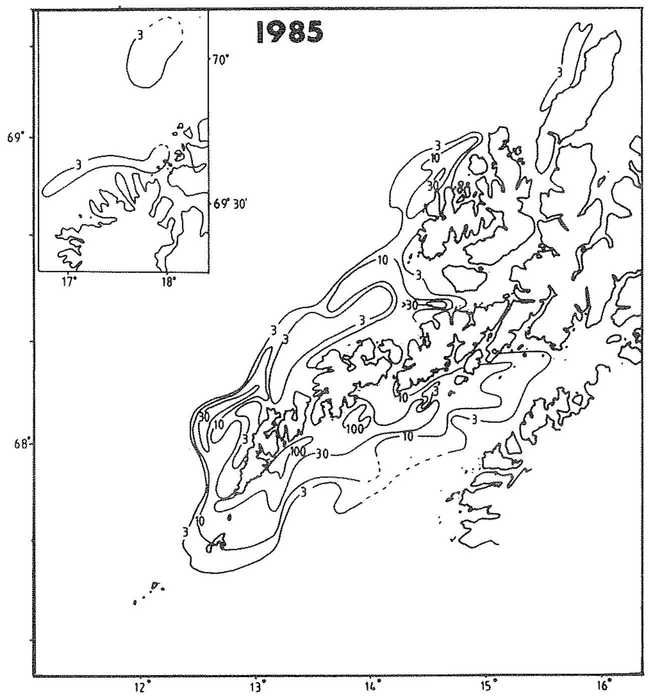


Fig. 15. Continued.





The feeding incidence and feeding ratio of the cod larvae from the different subareas are presented in Tables 4 and 5.

The feeding incidence and ratio are indicators of the food availability in the sea the last hours before the larvae were caught. The feeding ratio and incidence show that the best feeding conditions are found on the inner side of Lofoten, subareas 2-3, and in the Vesterålsfjord, subarea 6, while the conditions on the outer side of Lofoten seems to be more marginal. Subarea 4 in the outermost part of Vestfjord shows larvae in an intermediate feeding condition.

Table 3. Nos. of cod larvae (N) in the Lofoten area for the period 1979-85 (N_1=Nx10^{-9}).

Year	1979	1980	1981	1982	1983	1984	1985
N_1	30	2	15	13	89	89	125

Table 4. Feeding incidence, % of larvae with gut content, in different larval stages from different subareas during the years 1982-85. A.1= Area 1, etc.

Stage	6				7				8				9			
Year	82	83	84	85	82	83	84	85	82	83	84	85	82	83	84	85
A.1	-	-	26	-	-	-	66	-	-	-	91	-	-	-	89	-
A.2	34	70	51	22	75	98	83	82	90	100	96	-	100	100	100	-
A.3	15	28	-	63	67	83	-	92	88	95	-	-	100	100	-	-
A.4	11	35	30	37	99	94	86	81	-	100	90	80	-	-	94	100
A.5	29	13	44	67	69	59	82	87	75	77	-	91	100	91	-	-
A.6	36	25	-	-	88	74	-	-	88	87	-	-	100	94	100	-

Table 5. Feeding ratio, prey organisms per larval gut, in different larval stages, in the different subareas, during the years 1982-85.

Stage	6				7				8				9			
Year	82	83	84	85	82	83	84	85	82	83	84	85	82	83	84	85
A.1	-	-	0.2	-	-	-	1.2	-	-	-	2.4	-	-	-	3.3	-
A.2	0.6	1.7	1.2	0.3	1.4	3.4	2.4	1.8	2.5	5.1	3.0	-	4.5	7.7	4.4	-
A.3	0.2	0.5	-	1.2	1.6	1.5	-	3.3	2.1	2.5	-	-	2.0	4.5	-	-
A.4	0.2	0.5	0.5	0.5	1.2	2.1	2.3	2.0	-	1.7	3.3	2.4	-	-	5.4	5.8
A.5	0.7	0.1	0.6	0.5	0.9	0.8	1.4	1.3	2.3	1.8	-	2.6	2.2	1.8	-	-
A.6	0.7	0.4	-	-	2.4	1.7	-	-	2.2	3.8	-	-	4.3	6.0	7.4	-

The dry weight is a more conservative factor and dependant on the conditions some time in advance of the catch of the larvae. The dry weight of the larvae after fixation and removal of the gut and liver is given in Table 6.

There is larger differences in dry weight between years than areas. 1983 was an outstanding year, and the stage 9 larvae from 1983 were heaviest compared to the other stage 9 larvae in all areas. The results with larvae in stage 7 and 8 are more variable and there are little consistency in these data. Small variations in dry weight may be camouflaged by variable loss of dry weight during fixation as indicated by the results on larvae in stage 5-7 in Table 7.

Survival of the spawning products

Fig. 16 shows the survival of the spawning products in 1983 and 1984. The

Table 6. The dry weight of the different larval stages in the different areas, during the years 1982-85. Mean=weighted mean of all larvae in a certain stage. Mean/area=weighted mean of all larvae (stage 5-9) in a certain area.

Stage	7				8				9				Mean/area			
Year	82	83	84	85	82	83	84	85	82	83	84	85	82	83	84	85
A.1	-	-	54	-	-	-	76	-	-	-	124	-	-	-	66	-
A.2	41	53	51	56	65	78	66	-	115	139	101	-	45	60	52	59
A.3	51	51	54	62	68	66	68	77	91	119	97	-	44	54	56	57
A.4	44	52	50	51	65	71	70	71	102	143	138	113	42	70	58	49
A.5	53	53	48	54	58	71	70	79	133	156	114	-	66	91	53	57
A.6	40	75	40	58	83	94	72	84	196	201	161	147	129	155	195	76
Mean	50	53	52	56	68	75	69	79	146	170	117	131	60	84	59	58

Table 7. Shrinkage due to fixation.

Larval stage	Before fixation	After fixation	Shrinkage,%
5	4.7±0.06mm (N=10)	4.4±0.3 mm (N=35)	6
	60 ± 7 γg "	46 ± 6 γg "	23
6	4.7±0.3 mm (N=24)	4.4±0.3 mm (N=12)	5
	53 ± 10 γg (N=11)	45 ± 11 γg "	15
6	4.7±0.2 mm (N=15)	4.4±0.2 mm (N=53	6
	65 ± 11 γg "	46 ± 6 γg "	29
7	4.9±0.4 mm (N=24)	4.6±0.4 mm (N=9)	6
	69 ± 13 γg "	57 ± 10 γg "	17
7	5.2±0.3 mm (N=12)	4.7±0.3 mm (N=35)	10
	83 ± 14 γg "	59 ± 10 γg "	23

figure shows that there is a heavy egg and larval mortality. Only 10% of the eggs were hatched and produced 2-3% first feeding larvae in these two years which both produced outstanding year classes. Fig. 17 shows larval length/dry weight relationship in the years 1982-85. The best growth was seen in 1983 followed by 1984, 1982 and 1985.

DISCUSSION

SÆTERSDAL and LOENG (1984) found that rich year classes of cod occurred at the beginning of warm periods in the Barents Sea, when the feeding areas were expanding. Their data show that the temperature starts to increase one year ahead of the occurrence of a rich year class. Similar yearly variations in temperature are found in the coastal waters of northern Norway (BLINDHEIM, LOENG and SÆTRE, 1981), indicating that most of these variations are large scaled. It is possible that the improved feeding conditions for the mature population contribute to a better survival through better egg quality. Both timing of spawning, fecundity and egg quality can be related to temperature

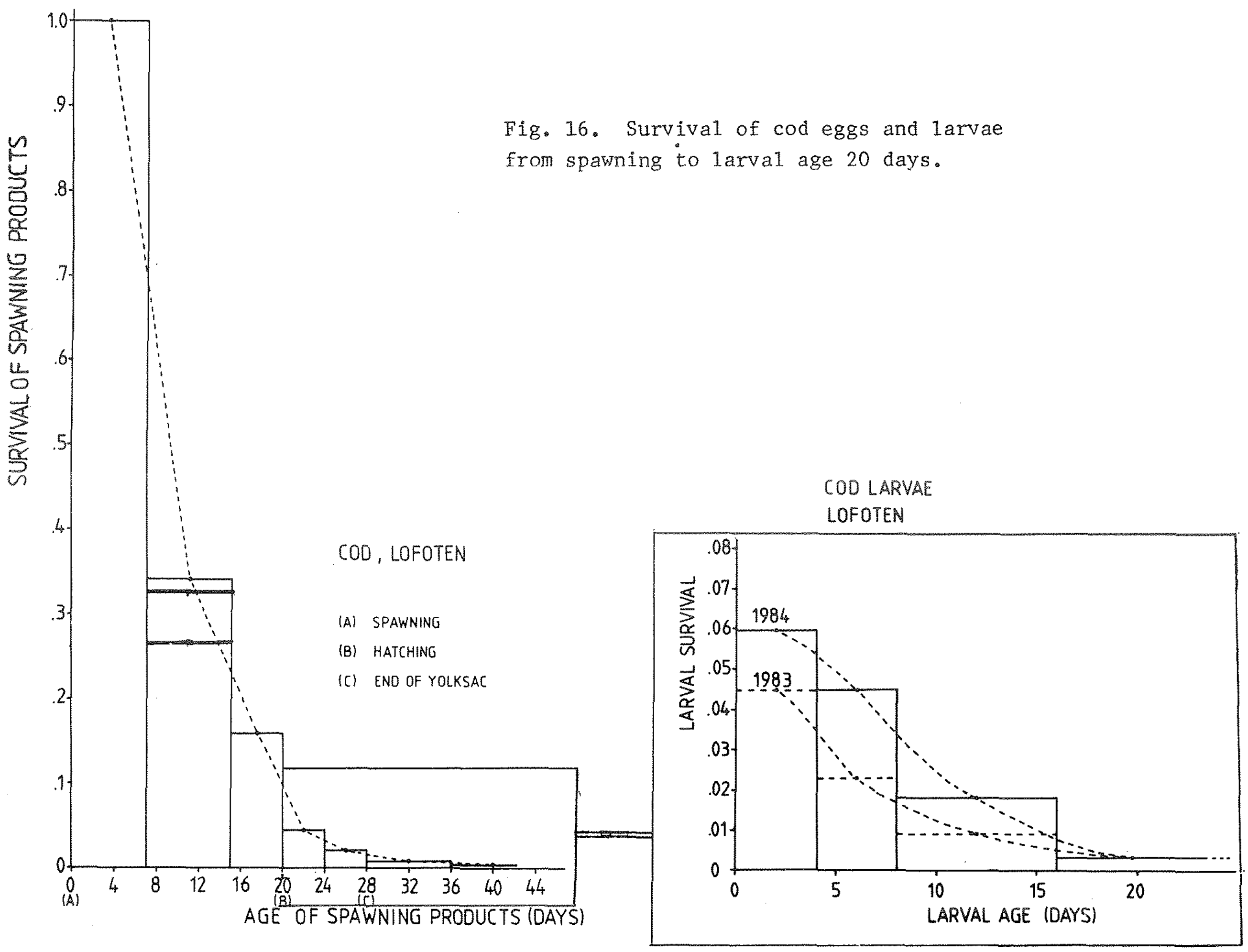


Fig. 16. Survival of cod eggs and larvae from spawning to larval age 20 days.

and feeding conditions (WOODHEAD and WOODHEAD 1965, HISLOP, ROBB and GAULD 1978, DE VEEN 1976). However, these factors have not been proved to influence the year class strength in Arcto-Norwegian cod.

Investigations on the distribution and number of cod age groups I and II show that they are found in the easternmost parts of the distribution areas in the Barents Sea with lowest temperatures (PONOMARENKO 1973). It has been postulated that the adaption force of the year class to the ambient feeding area is mortality on these stages due to temperature/feeding conditions acting at these stages. However, it has recently been shown by BJØRKE and SUNDBY (1986) that there is a good correlation between the indices from the postlarval surveys and the 0-group surveys indicating that the major regulation of the year class strength takes place during the early developmental stages in Norwegian coastal waters.

The "triangle plot" between the temperature at the spawning field and the abundance of the produced year class only appears when using the temperature during the spawning period in March/April. As earlier mentioned the temperature in the Barents Sea is to some extent correlated with the temperature in the coastal waters of Northern Norway. The correlation coefficient between the annual mean temperature of the Kola section in the Barents Sea and the mean temperature at the spawning field is 0.6 (r^2=0.6) (SUNDBY, pers. comm.). Using the Kola section temperature a similar "triangle plot" as that for Vestfjorden is obtained when using the temperature in August and September, (it takes about 6 months for the watermasses of

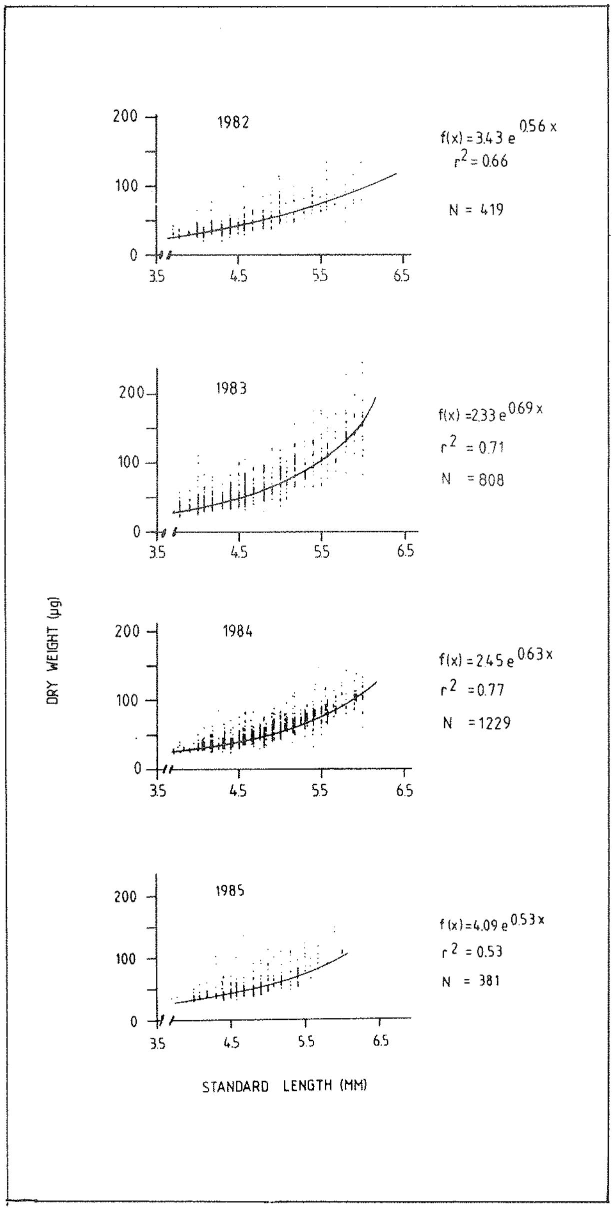


Fig. 17. Cod larval length/dry weight relationship in Lofoten area in 1982-85.

the Norwegian Coastal Current in the Vestfjord to reach the Kola section) which coincides with the time when the produced year class appear as 0-group fish in that area.

A similar relation between temperature and year class strength is found for eggs and larvae from the West-Greenland cod population (HERMAN, HANSEN and HORSTED 1964), but not on the older stages. The same phenomenon is also found in other cod populations living close to the limits of their distribution range (GARROD and COLEBROOK 1978).

The peak of spawning is very stable from year to year as also found by CUSHING (1969). However, he used the mean data of catch in the Lofoten area as an index of peak spawning and arrived at a date 14 days earlier than was found in the present paper. CUSHING (1969) argues that the stability of the peak spawning in fish has indirect adaptation to "the variability of the production cycle and dependence of the fish populations upon it during their larval lives".

We believe that the stability of the peak spawning is the result of the constant temperatures during spawning migration and spawning, since the cod migrates and spawns in the subsurface thermocline between the cold coastal water and the Atlantic water which has a constant temperature that do not vary between years.

PEDERSEN (1984) showed a delay in peak spawning of about 1 week since 1929 which correlates well with the increasing proportion of first-time spawners during the same period. It is well known that larger fish spawn earlier than the first-time spawners (SOROKIN 1957). Contrary to PEDERSEN (1984), CUSHING (1969) found an opposite trend in the peak spawning during the same period, probably as a result of a change in fishing pattern in Lofoten.

SINCLAIR et al. (1985) focus on Hjort's second hypothesis which stress "the differential loss of larvae from their appropriate larval distribution area due to interannual differences in advection".

Such an area is described in the present paper, corresponding to the main spawning area of the Arcto-Norwegian cod. According to the current system in the Vestfjord (FURNES and SUNDBY 1981) the first feeding larvae should be transported 240 kilometers away from the spawning area. The fact that most eggs and larvae are still found over the spawning grounds in April-May implies that the Vestfjord is a "retention area". Similar retention areas, where eggs and larvae are kept within a certain area caused by different physical forces (gyres, transition zones etc.), are described by ILES and SINCLAIR (1982).

The release of larvae from the "good area" is a continuous but highly variabel process. The larvae which happen to stay within the area for the longest time period, will have the best conditions for growth and survival.

Analyses of the naupliar density and stomach contents of cod larvae in Lofoten show that 5-10 nauplii per liter seem to represent a critical level for successful food uptake. This agrees with investigations in other areas (DEKHNIK, DUKA and SINYUKOVA 1970, INCZE et al. 1984). This was also seen in the case studies reported in ELLERTSEN et al. 1984, where the larvae, stage 6-9, exposed to plankton densities in the Austnesfjord, above 20 nauplii per liter, were in a good state of feeding. The larvae caught in the Vesterålsfjord diurnal station, however, exposed to a mean naupliar density of 6.7 per liter, had a much lower feeding ratio.

In the beginning of May the naupliar density is often less than 10 nauplii per liter in most of the investigated area. However, the area of high naupliar densities usually correspond with the area of high abundance of first feeding larvae (area 2-4).

Nauplii of other species (mostly Oithona spp.) are of minor importance since cod larvae feed almost exclusively on C. finmarchicus. Nauplii of O. similis are occassionally found in relatively high numbers in the area (ELLERTSEN, pers. comm.). A comparison between the gut contents of equal staged cod larvae, showed that the size of the copepod nauplii in their guts increased along their drift route. The reason for this may be that the time of spawning of C. finmarchicus is somewhat delayed in the inner part of the Vestfjord compared to the mouth of the fjord and outer side of Lofoten (ELLERTSEN unpublished data, SØMME 1934, WIBORG 1954). Then the mean age of the nauplii, the carapace length and the calory content, will increase along the drift route of the cod larvae as the watermasses containing the cod larvae mixes with watermasses containing some retained nauplii in older stages along the drift route. This will give some compensation for the decreasing prey densities found on the outer side of the Lofoten archipelago (area 5).

The incubation of cod eggs takes place in the upper 50 meters of the water column in the Coastal Current, which shows a relatively large variation in temperature between years. The difference in incubation time between a warm and a cold year is about 14 days. High temperatures therefore increase the changes for a first feeding larvae to stay within the good area.

Another important point is that the size of the cod eggs is reduced significantly during spawning (SIVERTSEN 1935, SOLEMDAL 1970, SOLEMDAL and SUNDBY 1981). This is a general phenomenon (HIEMSTRA 1962), and is the result of portion spawning. The first batches contain the largest eggs (HISLOP 1975, MAYENNE 1940). The positive correlation between egg size and size of larvae was demonstrated by KNUTSEN and TILSETH (1985). This means that if the feeding conditions are favourable early in the season, this will coincide with the occurrence of large larvae better suited for feeding. It is also possible that high temperature will have a positive effect on feeding as demonstrated by PAUL (1983) on pollock larvae.

The development time of copepod eggs and nauplii is directly affected by the temperature. However, the temperature affects the timing of spawning in Calanus finmarchicus to a significant larger degree than the effect upon development rate. Developing time from spawning to copepodid I (CI) at 4.4°C is about 30 days, and at 1.9°C about 40 days (interpreted from TANDE 1981). In the warm year 1960 (mean April temperature 4.4°C, March 3.5°C) the time of maximum occurrence of CI was about April 1. This implies that the spawning was most intense in early March, while a maximum occurrence of CI in 1981 about May 24 (mean April temperature 1.9°C) suggest a peak spawning in the late April. An unusually early spawning of C. finmarchicus in Norwegian waters in 1960 was reported by BARANENKOVA (1965). That year the nauplii production was well over when the first feeding cod larvae occurred in the area, which may explain the resulting poor year class. The match/mismatch in time between nauplii and cod larvae occurrence the other years needs further investigation.

Good year classes produced in warm years might be attributed to a series of temperature related biological phenomena:

1. Good feeding conditions early in the season, favouring the large larvae that are produced in the beginning of the spawning season (KNUTSEN and TILSETH 1985).

2. Short incubation period increasing the changes to stay in the "good area" during first feeding.

3. Facilitated feeding. PAUL (1983) found a better feeding success at higher temperature in Pollock (Theragra chalcogramma).

The year class produced in 1983 was especially strong at the postlarval stage. This may be due to the above mentioned phenomena: Short incubation period of the eggs as seen from Fig. 5, and good feeding conditions as indicated by the fast growth at all larval stages.

The reasons for the relatively high mortality, also found in other species (see DAHLBERG (1979) for a review on the subject), are not fully known. Dispersal of spawning products out of the investigation area may account for a minor part of what is estimated as mortality, since the whole distribution area of eggs and larvae is supposed to be covered by the investigation. Part of the mortality may be due to predation, as herring (Clupea harengus), ctenophors (Bolinopsis infundibulum) and medusae (mainly Aurelia aurita ephyrae) are found to feed on cod eggs and larvae in the area (MELLE and ELLERTSEN 1984, MELLE 1985). An additional effect can be that low success at the onset of feeding of larvae exposed to low prey densities can make them more vulnerable to predation.

There is good agreement between the abundance of larvae in early May and the size of the resulting year class in the period 1979-85. No such agreement was found by WIBORG (1957) on the same stock for the period 1948-56.

The large variability in larval survival reported in the literature reviewed by DAHLBERG (1979), makes it difficult to draw any firm conclusions on yearclass strength from larval abundance estimates.

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