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Effects of Biological and Physical Factors on Survival of Arcto-Norwegian Cod and 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 data on abundance indices of Arcto-Norwegian cod. The importance of environmental factors at the spawning grounds on the yearclass strength is discussed.

The results show that high temperature is a necessary but not sufficient condition for the production of strong yearclasses. Spawning of Calanus finmarchicus in Lofoten is very strongly influenced by the temperature in the upper layer. The time of peak spawning of Calanus differs by more than 1 1/2 month between the warmest year 1960 and the coldest year 1981. This cause large variations in the time of nauplii production.

The peak spawning of the Arcto-Norwegian cod is fixed within a period of one week from the end of March to the first days of 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 ^{0}C, causing a maximum difference in peak hatching of more than two weeks. This influence the transport time and distance from the spawning sites to the hatching and first feeding areas.

Both the newly hatched and the first feeding larvae are found to have the center of their distribution close to the spawning ground , where also the best feeding conditions for the larvae are found. This apparently indicates a "retention" area. However, the material on distribution of subsequent stages of eggs shows both spreading and transport. Feeding incidence and feeding ratio of larvae in different developmental stages from different areas , indicate that only the most advanced larvae are able to survive the drift through "poorer" feeding areas on their way from the "retention" area to the Barents Sea.

Results of gut analysis of first feeding larvae demonstrate the feeding response in cod larvae to different prey densities. These results indicate that the critical prey density for successful feeding must be in the order of 5-10 plankters per liter.

Length/ dry weight plot of cod larvae in the Lofoten area from the years 1982-1985 indicate the best growth conditions for the larvae in 1983 followed by 84, 82 and 85. In all the three years 1983-85 outstanding yearclasses of Arcto-Norwegian cod were produced, while the yearclass were of medium size in 1982. The yearclass in 1982 followed after 6 years of poor recruitment.

INTRODUCTION

The Arcto-Norwegian cod, (*Gadus morhua* L.) is a boreal species, migrating between the feeding area in the Barents Sea and the spawning areas 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). Low temperatures restrict the feeding area to the north and east. Annually temperature variations, as shown by SÆTERSDAL and LOENG (1984), will influence significantly upon the distribution area of cod. 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 area of egg incubation and larval stages, which is the coastal current in Lofoten and adjacent waters, also shows annual variation in temperature.The temperature conditions 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 yearclass 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 yearclass strength (BJØRKE and SUNDBY 1986). Thus it is reason to believe that the yearclass strength is established during the early stages. Many attempts have been made to demonstrate the factors responsible for the yearly variations in yearclass 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) , MELLE and ELLERTSEN (1984). Physical factors acting directly on the egg and larvae populations are shown to influence significantly on the mortality (GARROD and COLEBROOK 1978, KOSLOW 1984, SINCLAIR *et al.* 1985). The effect of the age distribution on yearclass strength is proposed by PONOMARENKO (1973).

In the present paper the yearclass variation will be discussed on the basis of 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 yearclass strength on three year old cod based on V.P.A. analysis.

The occurrence of *C. finmarchicus* from Skrova fixed station in Lofoten, were analysed for the period 1960-84. The data are based upon zooplankton material sampled weekly by a 36 cm Judaynet 180 µm mesh size from 300-0 meter depth. The frequencies of different developmental stages were found 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, by using small submersible electric pumps (200 l/min). Samples were usually taken from the following depths: 0, 2.5, 5, 7.5, 10, 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 % formaldehyde. The whole zooplankton sample was counted and identified under a binocular microscope. For a detailed study of the micro-zooplankton distribution a particle counter system was designed (TILSETH and ELLERTSEN 1984B).

The zooplankton data were compaired with sea temperature and time of appearance of the different developmental stages of *C. finmarchicus*. The temperatures used are the mean April temperature in the upper 30 meters at the fixed station in Lofoten.

Cod eggs were sampled from 3 localities 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, March- April 1983-85, (SUNDBY and SOLEMDAL 1984, SUNDBY and BRATLAND 1986). 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%. sea water.

One of the main objects of our investigations has been 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 the spawning product was calculated in 1983 and 1984. The number of 7-15 and 15-20 days old eggs and cod larvae in age groups 1-4, 4-8, 8-16 and 16-24 days post hatching were calculated from different surveys by the method described in SUNDBY and SOLEMDAL(1984). This number was compared with the estimated number of eggs spawned 1-5 weeks earlier calculated by the egg surveys described in SUNDBY and BRATLAND (1986). In this way different independant estimates of the survival can be calculated.

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 distributions 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 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 represents extreme cold and warm years. Hatching curves are calculated on the basis of the spawning curve and temperature. Adding 1 week to the hatching curve one get 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 1986). Fig. 6 shows 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 difference in distribution from the newly spawned eggs, but as the figure indicate there has been a considerable reduction in abundance.

Spawning in Calanus finmarchicus and naupliar distribution.

The time of spawning in *Calanus finmarchicus* is of importance for the food availability for cod larvae, as the larvae mainly feed upon *C. finmarchicus* nauplii (Ellertsen et al. 1977).

The content of *C. finmarchicus* samples are made up of 60-90 % in number of adult females in the end of March, only 4-5 % a month later when the copepodit stages I (CI) and II (CII) are dominating.

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

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

A more rapid development from eggs, nauplii to CI at higher temperatures could contribute to a curve shown in Fig. 9. However, a temperature difference of about 2.5 ^{0}C from a "cold" (1981, 1.9 ^{0}C) to a "warm" (1960, 4.4 ^{0}C) year would result in only a few days difference in developing time, not a month or more as shown in Fig. 9. The figure therefore expresses a temperature dependant spawning in *C. finmarchicus*.

The distribution of nauplii for the six successive years 1980-85 are 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.

The sheltered Austnesfjord usually have 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 colomn at each station. The actual density at a given depth might be considerably deviating from the intergrated value (TILSETH and ELLERTSEN 1984B).

The relation between yearclass strength and temperature.

Fig. 11 shows the relation between the yearclass strength represented by Virtual Population Analysis on 3 year old cod and the mean temperature in March and April for the upper 30 meters in Lofoten. All the data points are found below the hatched line. The figure shows that in cold years good yearclasses never occur, while in warm years good year classes may be produced.

Density dependant food uptake.

Table 2 shows the results of cod larval (stage 7) gut content analysis and the integrated density of nauplii in the water column 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.

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 successfull feeding must be in the order of 5 - 10 nauplii per liter.

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

"Good" and "bad" areas.

The distribution and abundance of larvae in the period 79-85 are shown in Fig 15. Large numbers of larvae were found in the period 1983-85, and the center of their distribution was found in the Vestfjord (for distribution of first feeding larvae see fig 8).

The feeding incidence and feeding ratio of the cod larvae from the different subareas are presented in Tables 3 and 4.

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 show larvae in an intermediate feeding condition.

Survival of the spawning products.

Fig. 16 shows the survival of the spawning products in 1983 and 84.

The figure shows that there is a heavy egg and larval mortality . This imply that only 10 % of the eggs will hatch and produce 2-3% first feeding larvae in these two years which both produced outstanding yearclasses.

Fig. 17 show larval length/ dry weight relationship in the years 82-85. The best growth was seen in 1983 followed by 84, 82 and 85.

DISCUSSION

SÆTERSDAL and LOENG (1984) found that rich yearclasses of cod occurred in the beginning of warm periods in the Barents sea, when the feeding areas are expanding. Their data show that the temperature starts to increase one year in advance of the occurrence of the rich yearclass. 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. However, looking into the data given by SÆTERSDAL & LOENG (1984) it seems that rich yearclasses occur the year after the temperature have started to increase. It is thereby possible that the improved feeding conditions for the mature population can contribute to a better survival through better egg quality. Both timing of spawning, fecundity and egg quality can be related to temperature/ feeding conditions (WOODHEAD & WOODHEAD 1965, HISLOP et al. 1978, DE VEEN 1976).

Investigations on the distribution and number of cod age groups I and II show that these age groups 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 yearclass 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 indexes from the postlarval surveys and the O-group surveys indicating that the major regulation of the yearclass strength takes place during the early developmental stages in Norwegian coastal waters.

The "triangle relation" between the temperature at the spawning field and the abundance of the produced yearclass 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 relation" as that for Vestfjorden is obtained when using the temperature in August and September, (it takes about 6 months for the watermasses of the Norwegian Coastal Current in the Vestfjord to reach the Kola section) which coincides with the time when the produced yearclass appear as O-group fish in that area.

Similar relation between temperature and yearclass strength is found for eggs and larvae from the West- Greenland cod population (HERMAN <u>et al.</u> 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 & COLEBROOK 1978).

The peak of spawning is found to be very stable from year to year as also found by CUSHING (1969). However, he used the mean date of catch in 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 fixity of the peak spawning "follows from the variability of the production cycle and dependence of the fish populations upon it during their larval lives".

We believe that the fixity 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 termocline, between the cold coastal water and the Atlantic water which have 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.

Analysis of the naupliar density and stomach content of cod larvae in Lofoten show that 5-10 nauplii per liter seem to represent a critical level for successful food uptake. This is in accordance with investigations in other areas (DEKHNIK <u>et al.</u> 1970, INCZE <u>et al.</u> 1984). This was also seen in the case studies reported in ELLERTSEN <u>et al.</u> 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 is usually corresponding to the area of high abundance of first feeding larvae (area 2-4).

Nauplii of other species (mostly <u>Oithona</u> spp.) are of minor importance since the nauplii in the cod larval guts almost exclusively belong to <u>C. finmarchicus</u>, although nauplii of <u>O. similis</u> occassionally are found in relatively high numbers in the area (ELLERTSEN, pers. comm.). A comparison between the gut content 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 <u>C. finmarchicus</u> 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 carapax 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 driftroute. 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 will take 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 will be about 14 days.High temperatures will therefore increase the chances 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 & SUNDBY 1981). This is a general phenomenon (HIEMSTRA 1962), and is the result of portion spawning, the first batches producing the largest eggs (HISLOP 1975, MAYENNE 1940). The positive correlation between egg size and size of larvae was demonstrated by KNUTSEN & 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 on pollock larvae by PAUL (1983).

Temperature also affects the timing of spawning in Calanus finmarchicus to a significant larger degree than the direct effect of temperature on the development of copepod eggs and nauplii. Developing time from spawning to copepodid I (CI) at 4.4 ^{0}C is about 30 days, and at 1.9 ^{0}C about 40 days (interpreted from TANDE 1981). In the warm year 1960 (mean April temp 4.4 ^{0}C, March 3.5^{0}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 temp 1.9 ^{0}C) suggest a peak spawning in the late April. An unusually early spawning of C. finmarchicus in Norwegian waters in 1960 has earlier been reported by BARANENKOVA (1965). This year the nauplii production was well over when the first feeding cod lavae occurred in the area, which may explain the resulting poor yearclass. The match/ mismatch in time between nauplii and cod larvae occurrence the other years is subject to a further investigation.

Good yearclasses produced in warm years might be attributed to a series of temperature- affected 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 chances 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 yearclass 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 (Fig. 17).

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 investigated 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 yearclass in the period 1979-85 as shown in Table 5. 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 rewieved by DAHLBERG (1979), makes it doubtful to draw any firm conclusions on yearclass strength from larval abundance estimates.

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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.

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 COP. NAUPLII,N/L	NUMBER OF COD LARVAE	FEEDING RATIO	FEEDING INCIDENCE
AUSTNESFJ.	(84)	31.5	26	3.5	96
AUSTNESFJ.	(77)	26.7	67	3.6	94
AUSTNESFJ.	(82)	21.0	8	1.9	88
AUSTNESFJ.	(82)	20.0	15	4.3	93
AUSTNESFJ.	(83)	16.0	26	2.3	81
VESTERÅLSFJ.	(82)	13.1	24	1.9	79
AUSTNESFJ.	(84)	10.3	20	2.8	90
HENNINGSVÆR	(82)	7.2	12	1.8	75
VESTERÅLSFJ.	(82)	6.7	91	1.0	55
VESTERÅLSFJ	(82)	6.0	8	2.7	88
BALLSTAD	(82)	4.8	5	1.2	80
AUSTNESFJ	(76)	4.7	88	1.8	86
SØRVÅGEN	(82)	4.1	11	1.0	45
HØLLA	(82)	3.6	12	1.0	58
LOFOTODDEN	(83)	1.5	9	0.6	44

Table 3. 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 4. 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	-

Table 5. Larval index, postlarval index and 0-group index (logaritmic) for the period 1979-85.

Year	Larval ind.	Postlarval ind.	0-group ind.
1979	30	7.2	0.4
1980	2	0.4	0.13
1981	15	15.4	0.1
1982	13	-	0.59
1983	89	74.7	1.69
1984	89	23.5	1.55
1985	125	56.5	2.46

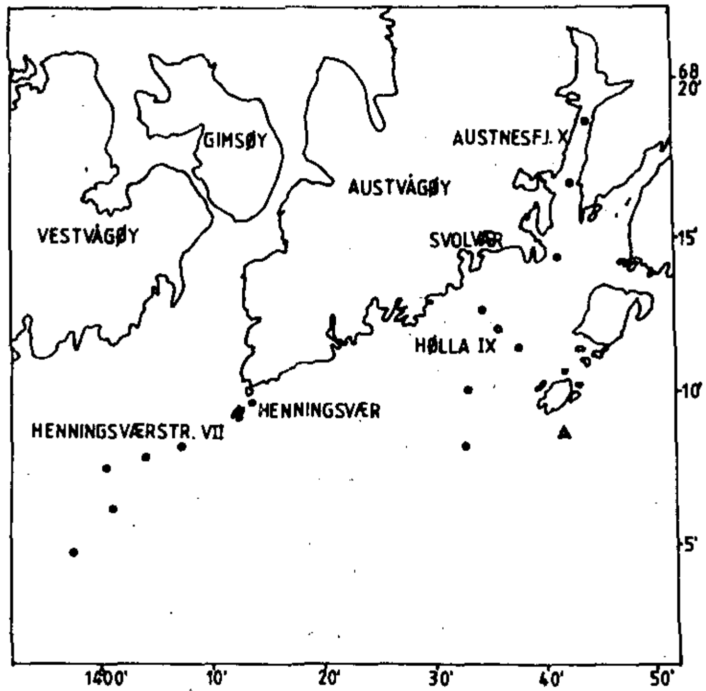

Fig.1. The main traditional spawning area of Arcto- Norwegian cod in Lofoten. Sampling stations for vertical net hauls are shown (●) and the fixed station Skrova (▲).

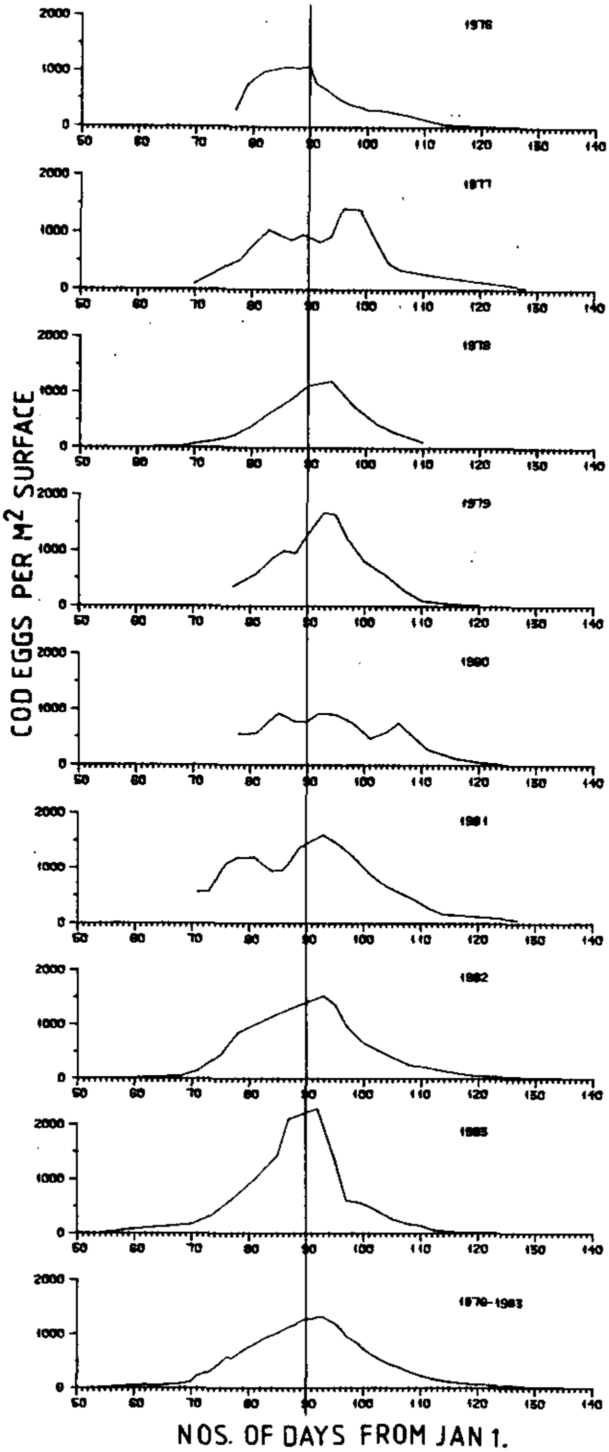

Fig. 2. Spawning intensity curves from *Lofoten* for the years 1976-83 and the mean spawning curve.

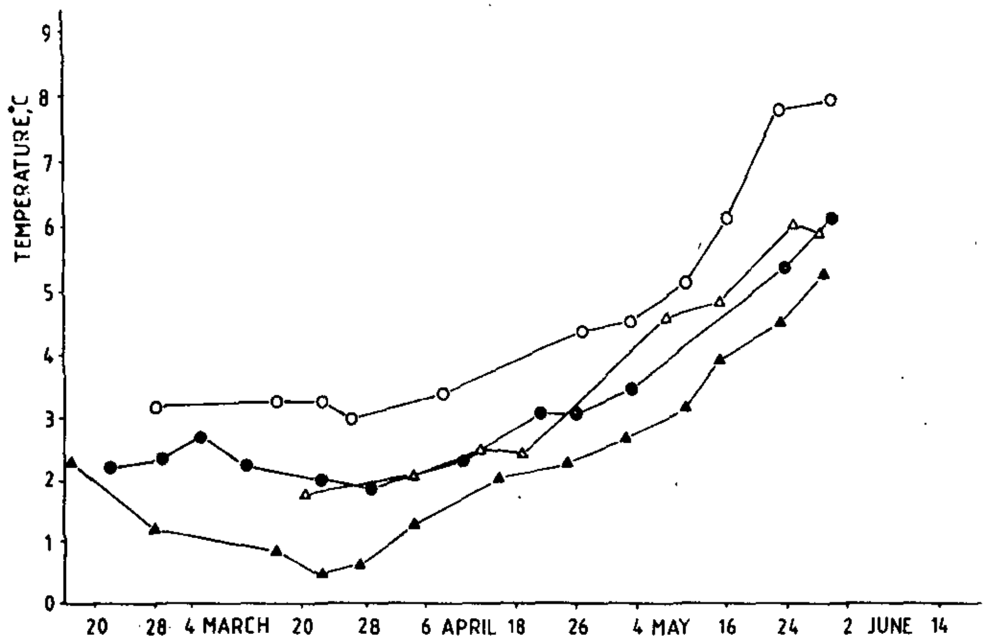

Fig. 3. Mean temperature in the upper 30 meters at the fixed station Skrova (see Fig. 1), (●) 1980, (▲) 1981, (△) 1982, (O) 1983.

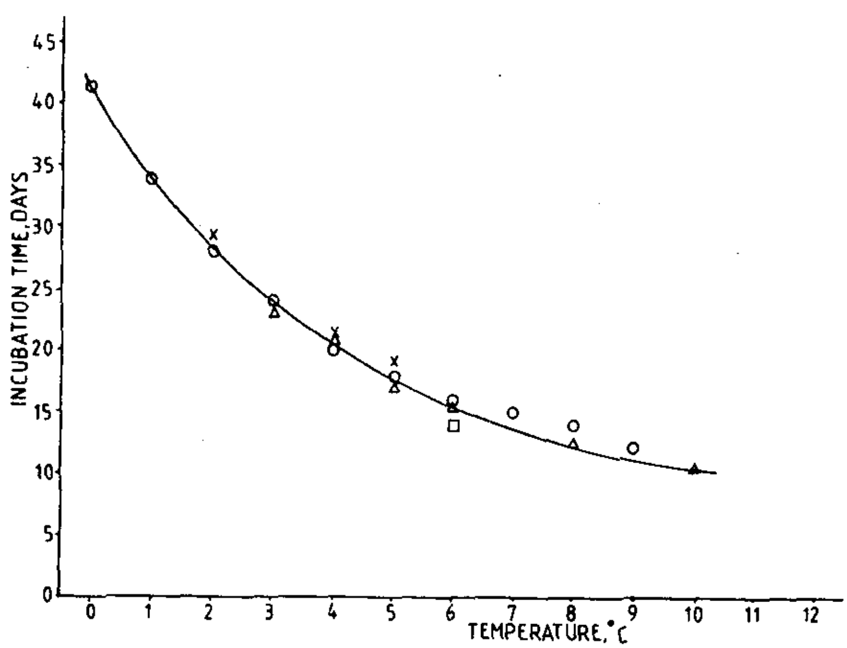

Fig. 4. Incubation period of cod eggs in different temperatures according to APSTEIN (1909) (O), DANIELSSEN and IVERSEN (1974) (□), DANNEVIG (1895) (△) and STRØMME (1977) (X).

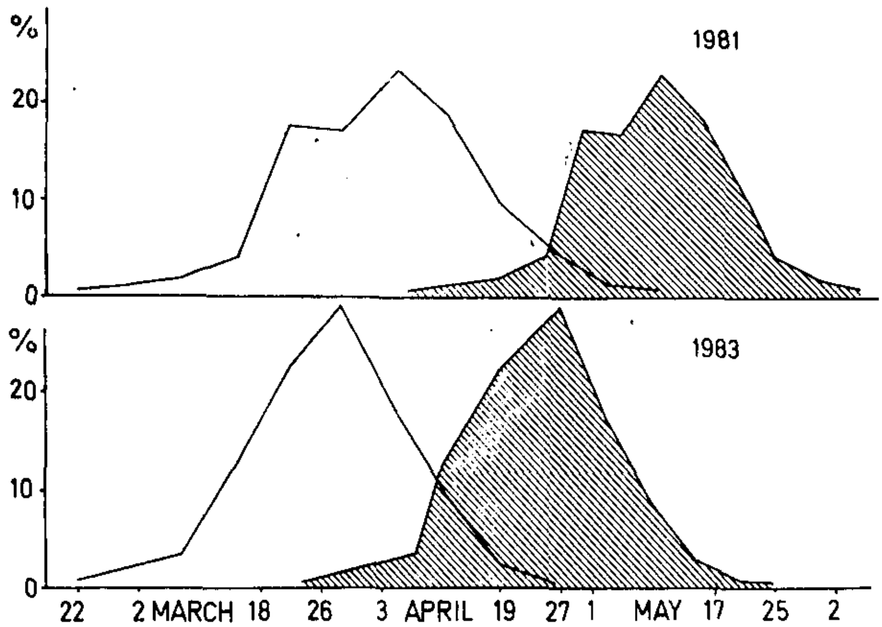

Fig. 5. Spawning curves (open) and first feeding curves (hatched) from the years 1981 and 1983.

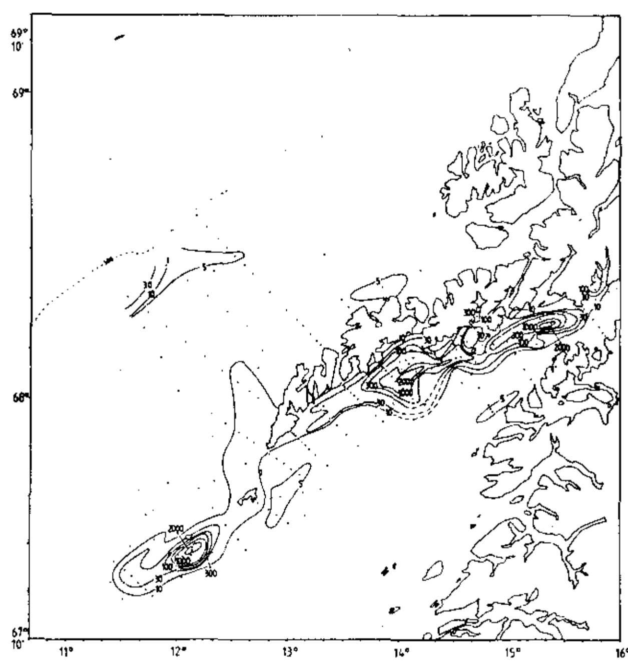

Fig. 6. Distribution and abundance of stage 1 eggs, 0-2 days old,nm^{-2}.

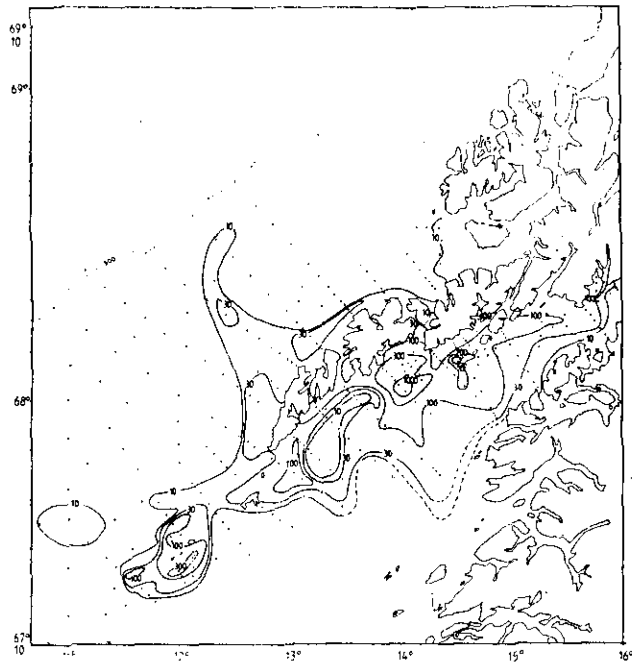

Fig. 7. Distribution and abundance of stage 3 eggs, 5-7 days old,nm^{-2}.

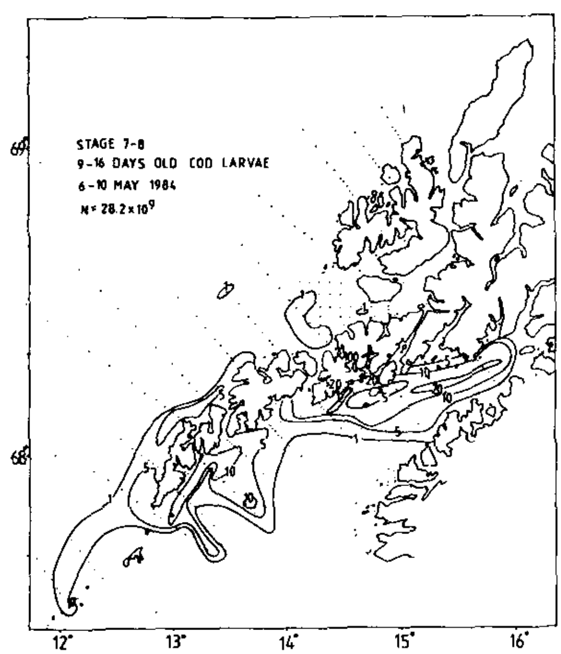

Fig. 8. Distribution and abundance of first feeding larvae, 9-16 days post hatching,nm^{-2}.

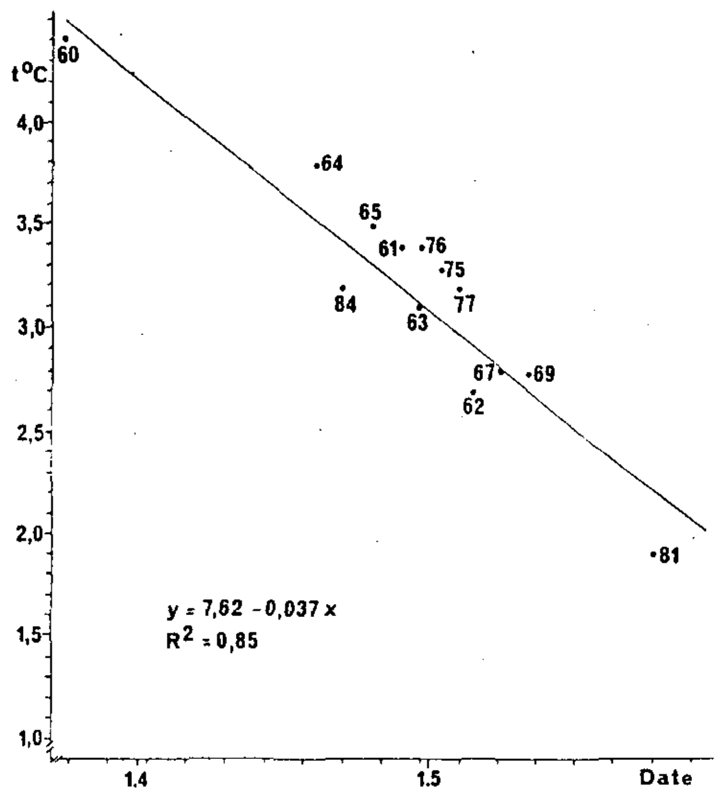

Fig. 9. Time of maximum occurrence of Calanus finmarchicus copepodite stage I versus temperature.

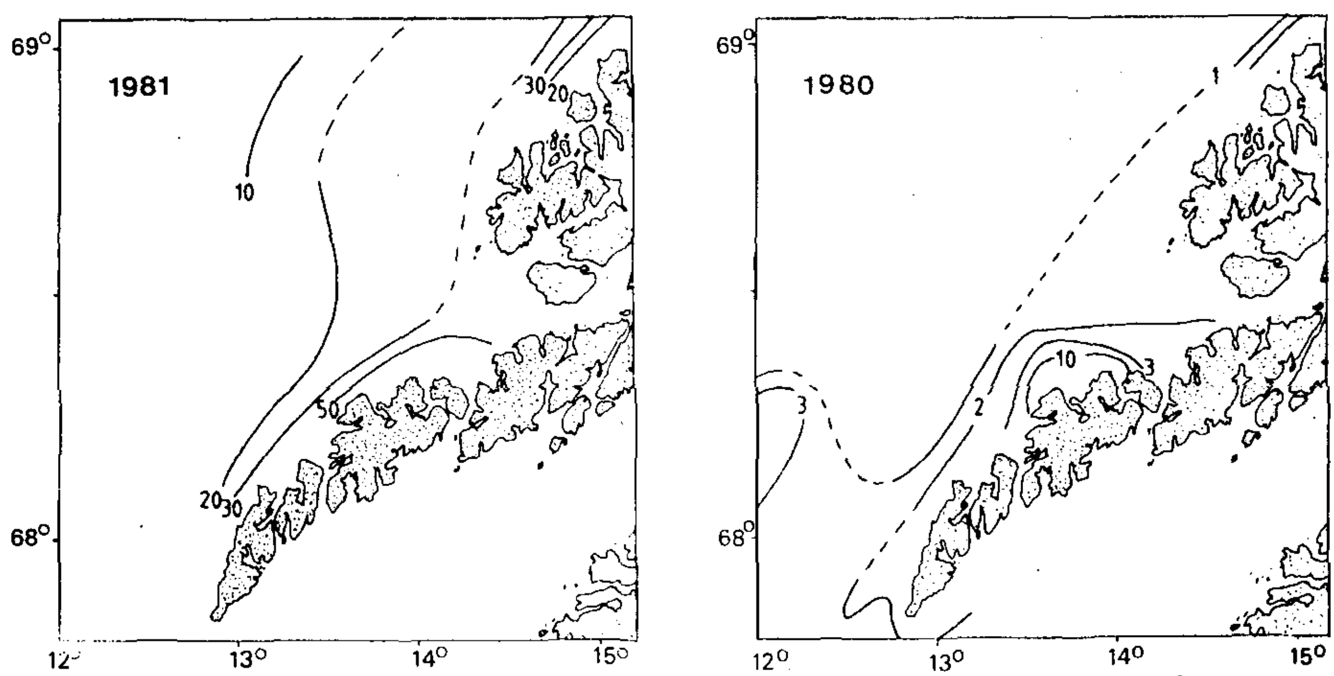

Fig. 10. Distribution and abundance of copepod nauplii 1980-85, nm^{-2}.

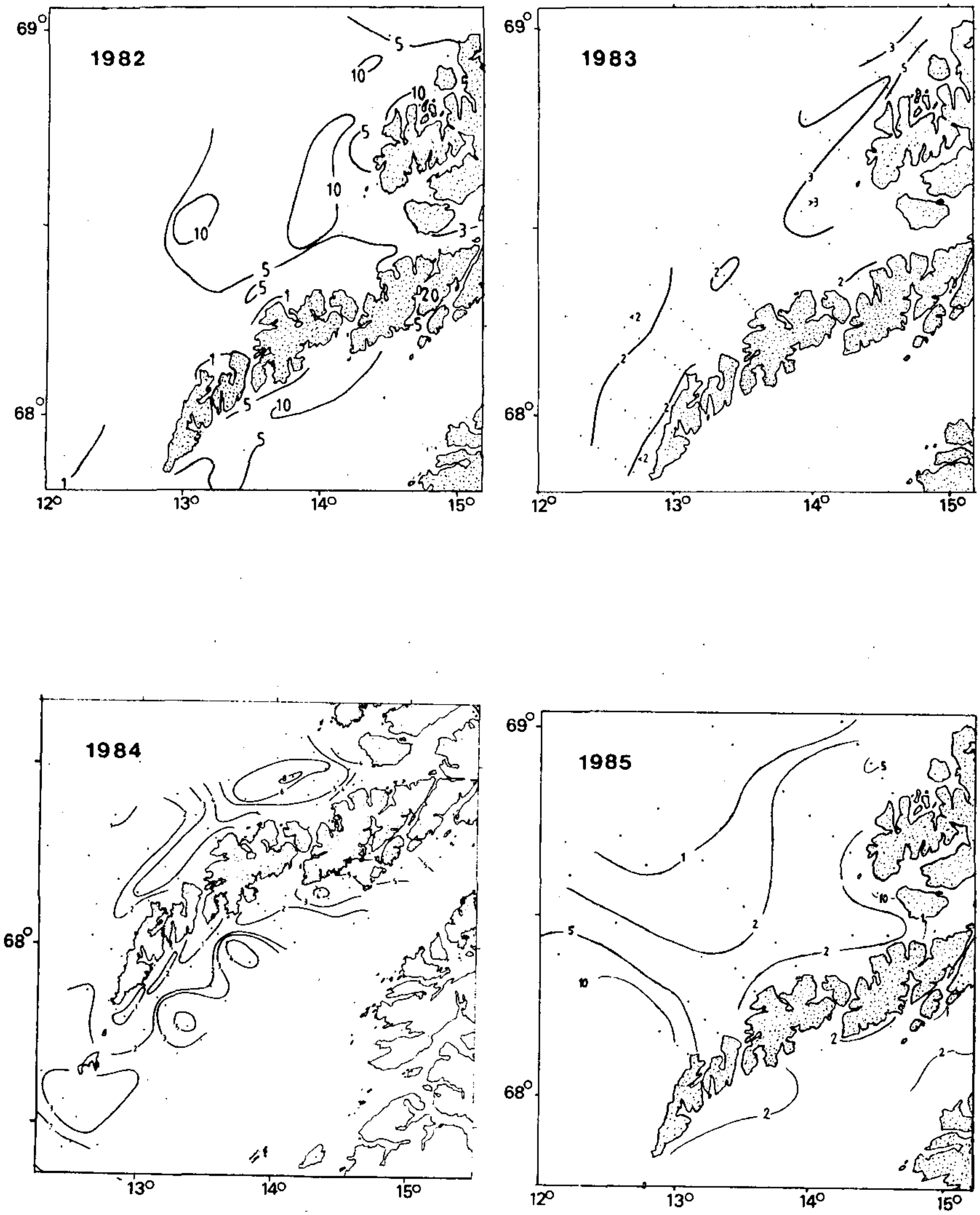

Fig. 10. Continued.

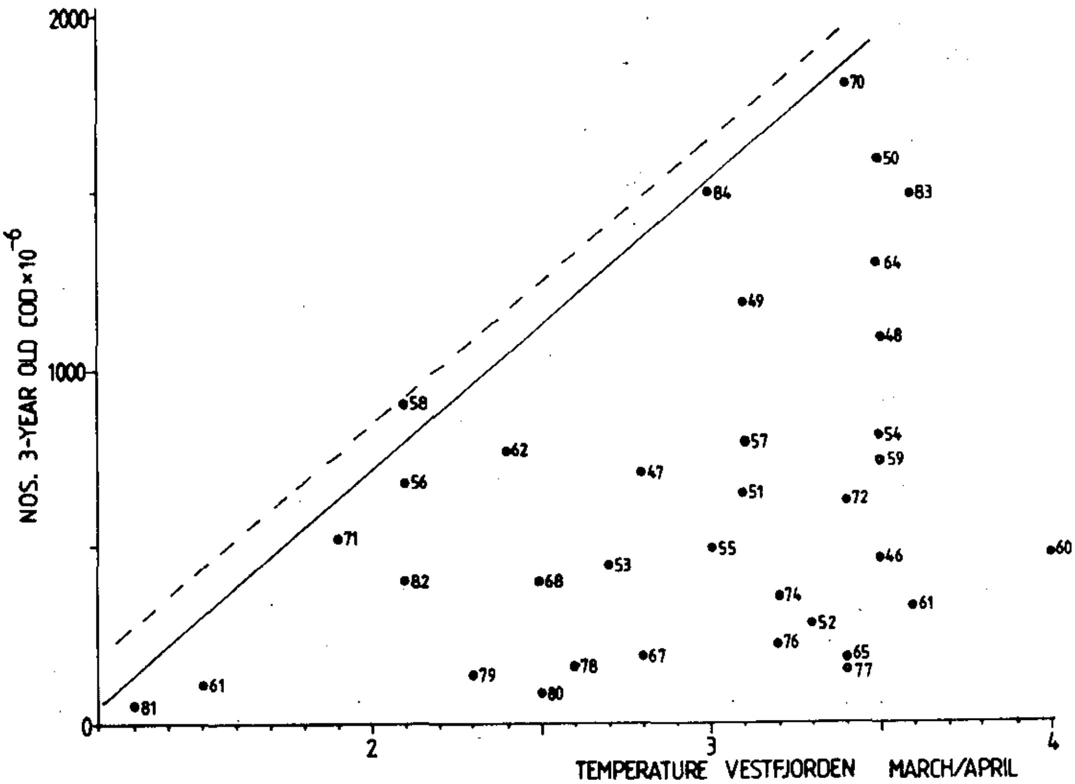

Fig. 11. The relation between the yearclass strength and the mean temperature in March-April in Lofoten.

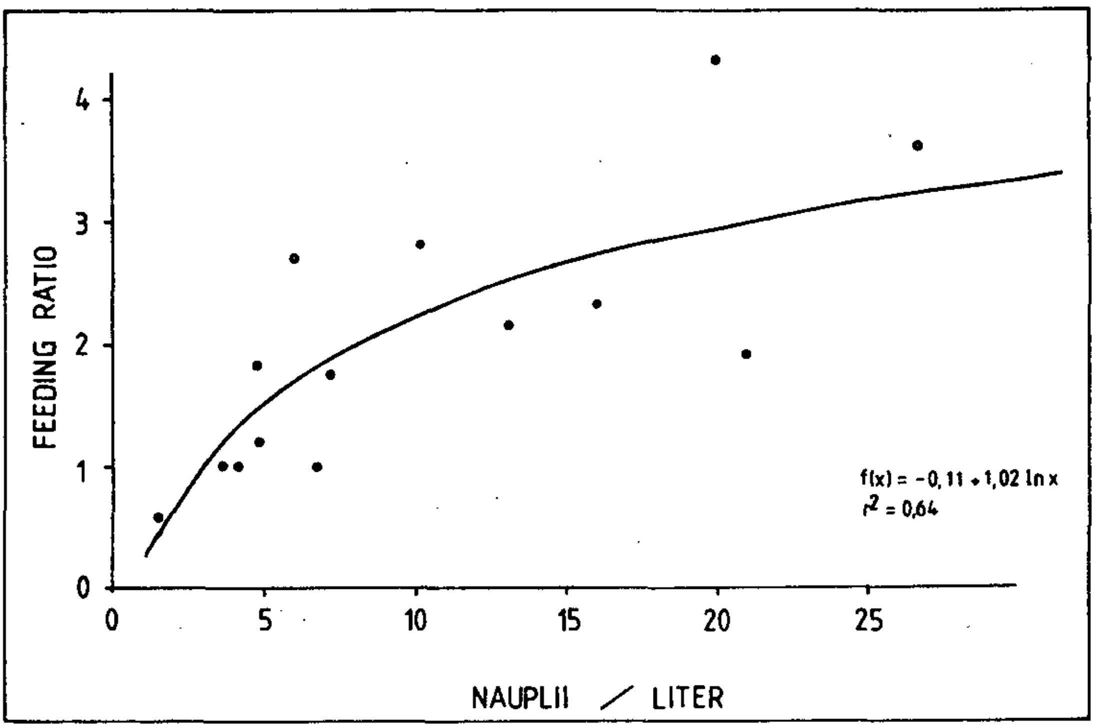

Fig. 12. Feeding ratio in cod larvae in relation to food density.

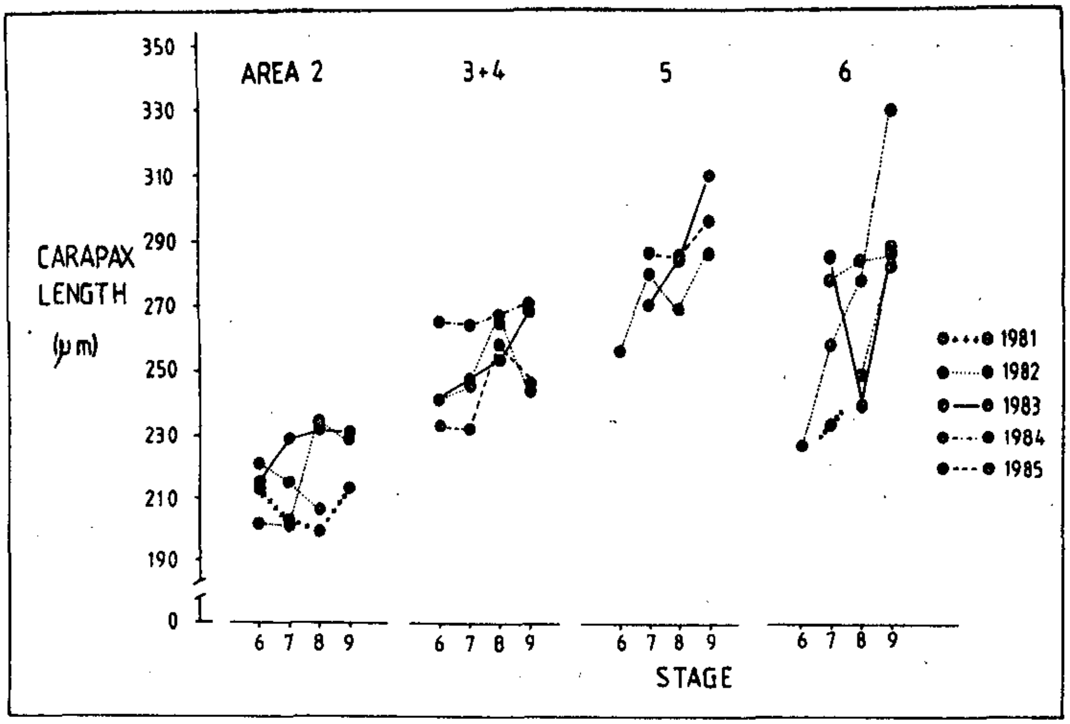

Fig. 13. Carapax length in stomach content of cod larvae in relation to area and cod larval stage.

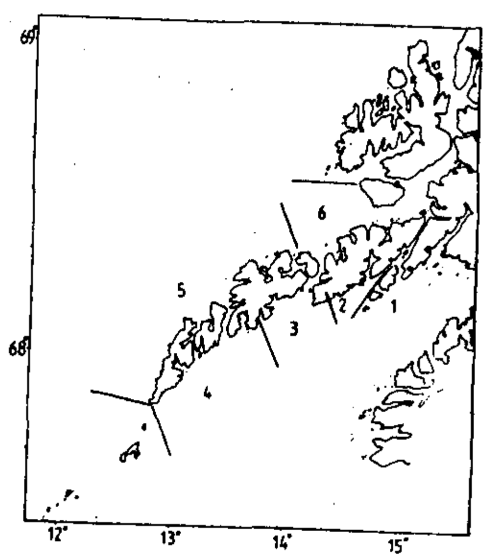

Fig. 14. Lofoten subareas 1-6.

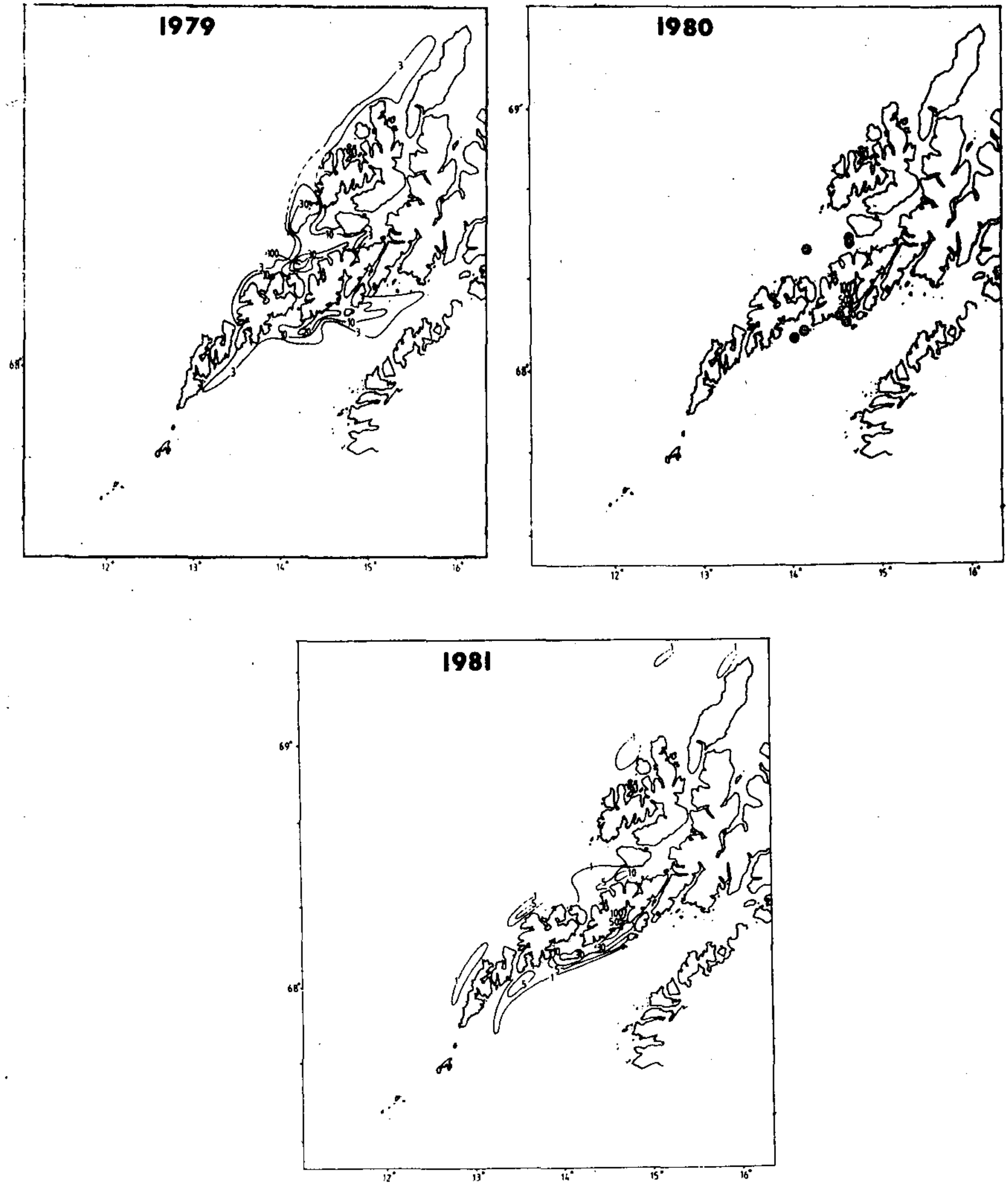

Fig. 15. Distribution and abundance of cod larvae 1979-85, nm^{-2}.

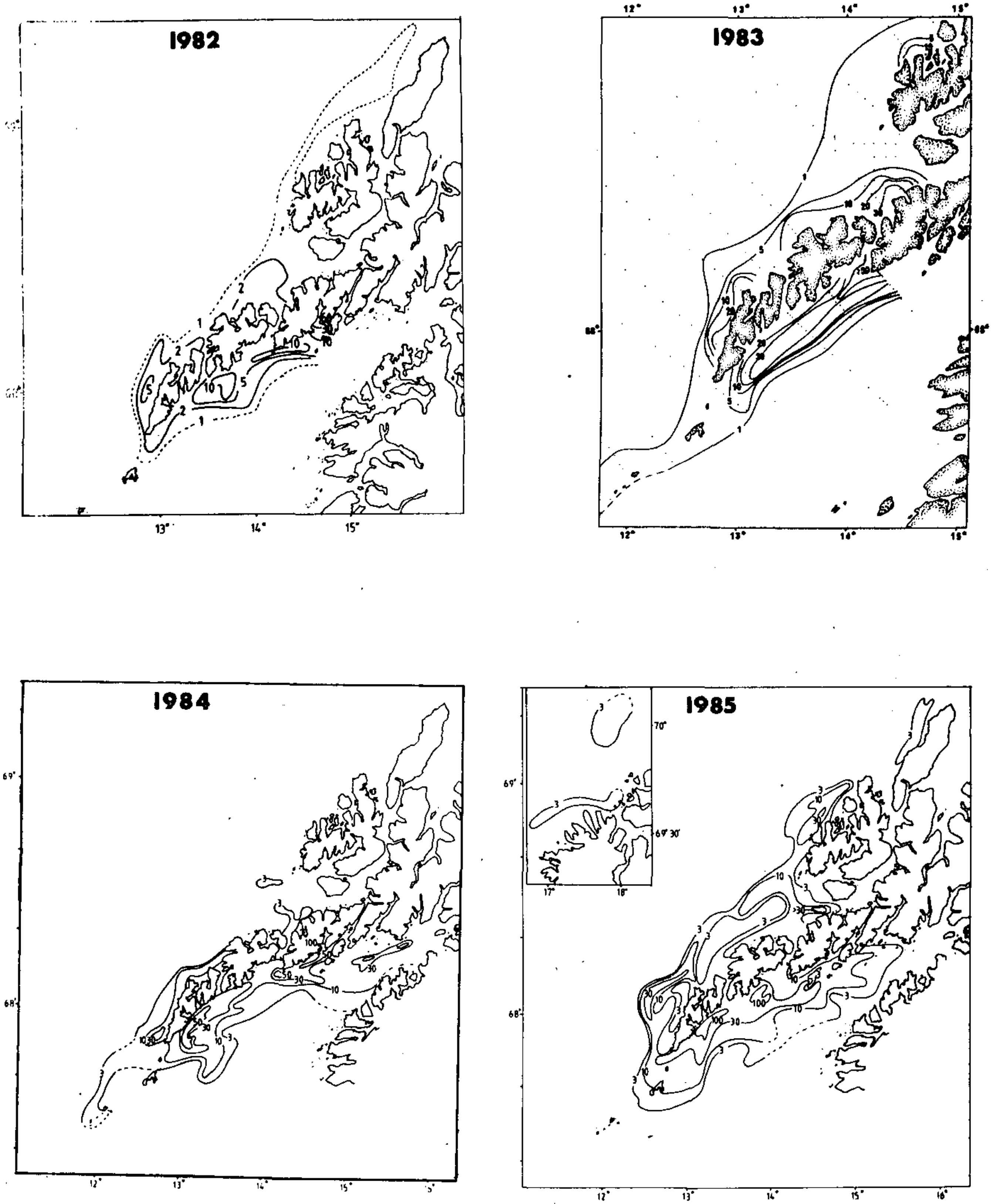

Fig. 15. Continued.

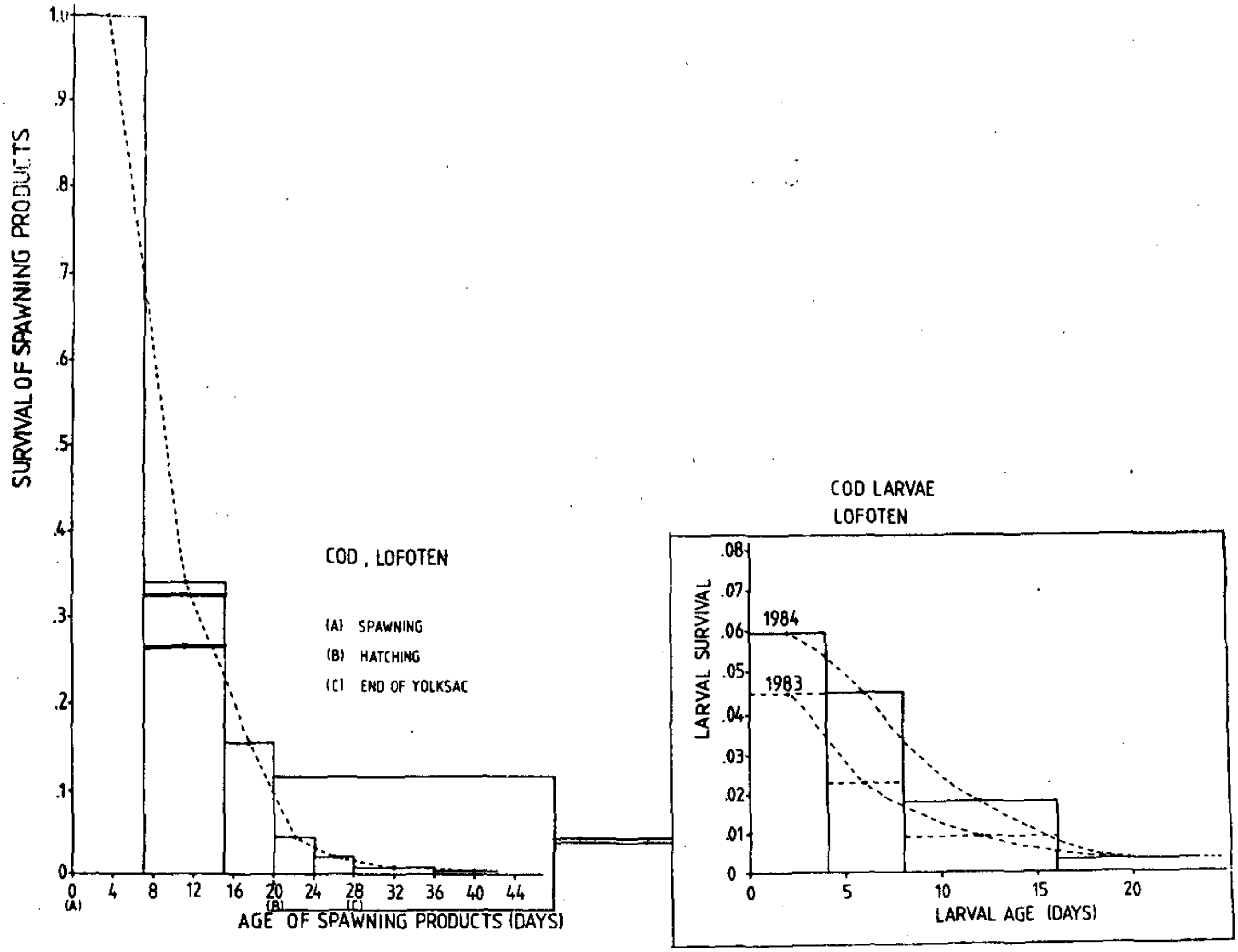

Fig. 16. Survival of cod eggs and larvae from spawning to larval age 20 days.

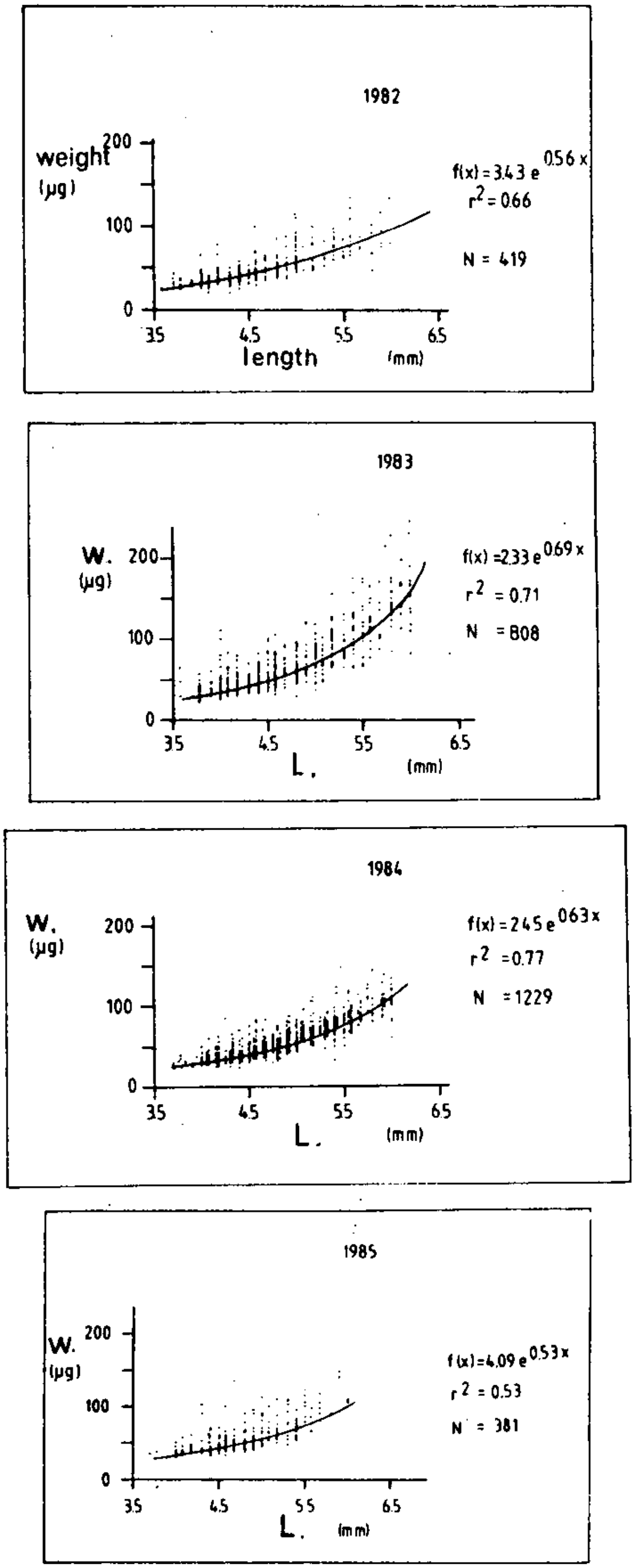

Fig. 17. Cod larval length/dry weight relationship in Lofoten area in 1982-85.