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SPAWNING STRATEGY AND A MECHANISM FOR ADAPTIVE LARVAL PRODUCTION IN ARCTO-NORWEGIAN COD.

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ABSTRACT
The Arcto-Norwegian cod is spawning in the temperature stable Atlantic water, and the eggs ascend into the more temperature variable coastal water. Changes in time of peak spawning, up to 10 days within the last 60 years, are caused by changes in the cod´s age composition, peak spawning of first-time spawners being somewhat delayed. In contrast, the peak spawning in the coastal water of Calanus finmarchicus, whose nauplii are the almost exclusively food organism for the first feeding cod larvae, vary with more than 40 days due to temperature variations. It is a clear tendency for the majority of nauplii abundance peaks to be situated ahead of the peak first feeding cod larvae, especially during warm years.

The temperature covariate in the spawning areas in the Norwegian coastal waters and the feeding areas of cod in the Barents Sea. High temperatures during the egg and larval stages favour the feeding condition of the larvae hatched first, since the concentration of nauplii is higher in the first part of the larval period. These larvae from the larger, high fecund cod females, are the largest and probably the most viable larvae produced during the season. During periods of decreasing temperatures in the feeding areas and the spawning sites, the production of viable larvae is more variable.

High temperatures also improve and extend the feeding areas in the Barents Sea, giving support for larger year-classes. In both temperature regimes the age compostition of the spawning population of Arcto-Norwegian cod will effect the degree of match between the production cycle of nauplii and first feeding cod larvae. The spawning strategy of Arcto-Norwegian cod in relation to Calanus finmarchicus can be named a modified match/mismatch hypothesis, ensuring a adaptive larval production to varying temperature regimes of the feeding areas of the cod.

INTRODUCTION

The spawning Arcto - Norwegian cod and Calanus finmarchicus, whose nauplii is the almost exclusive food for the first feeding cod larvae, are distributed in different parts of the water column. The mature cod migrates to the spawning areas in the deep temperature stable, warm Atlantic water and spawn in the transition layer between the upper coastal water and the Atlantic water below, in a temperature of 4 - 6 °C. In this way the cod spawn in the same temperature regime each year, while the Calanus is distributed and spawns in the temperature variable and colder coastal water.

The present ecological system is rather simple and have evolved during the 10000 years of postglacial period, when the Atlantic circulation reached the western and southeastern parts of the Barents Sea (Vorren et al. 1988). A very susceptible period in the life cycle of a fish species like the cod is supposed to be the timing of the spawning to the production cycle of the food organisms for the first-feeding larvae (Hjort 1914). Cushing (1972), introducing the term match-mismatch, used Sverdrup´s (1953) model to describe the variable onset of primary production in contrast to the fixed time of spawning.

In boreal and Arctic areas production cycle is short and varies in time primarily according to the temperature, and the variation in recruitment is much greater than in tropical and upwelling areas (Cushing 1982).

The present paper deals both with the general spawning strategy of the cod in relation to the production cycle of Calanus nauplii, and the effects of short - term changes in temperature and age of the spawning stock to the reproductive success.

Sætersdal & Loeng (1987) put forward the hypothesis that the reproduction of cod is adjusted to the variations in the size of and conditions in the feeding area, through evolutionary processes. A correlation between temperature and year class strength of cod in the Barents Sea was reported by Kislyakov (1959). The cooccurrence of large year classes of a series of species in some years on both sides of the Atlantic indicates a general key environmental factor (Templeman 1965). Hollowed et al. (1987) examining the recruitment of more than fifty fish stocks between California and Alaska, found a widespread synchrony of extreme year classes across the entire region studied and concluded that recruitment success is strongly influenced by environmental conditions.

A large scale covariation of the environmental parameters, mainly the temperature, as demonstrated by Blindheim et al. (1981) between the separated reproductive and feeding area of the migrating cod is a presupposition of an adaptive mechanism as called for by Sætersdal and Loeng (op. cit.).

Materials and methods.

Date of maximum concentration of Copepodite I of *Calanus finmarhicus* collected near Skrova in Lofoten (Inst. of Mar. Res., Bergen, unpublished data) was plotted against the mean temperature in the upper 30 meters in April, Fig.1, and is also taken to represent date of maximum abundance of *Calanus* nauplii. This figure has been improved by adding extra years to the figures given in Ellertsen et al. (1987, 1989). The linear relationship between temperature and maximum occurrence of *Calanus* Copepodite I is described by the equation

$$D(\text{date}) = 158.62 - 13.29\,t \qquad R=0.75 \qquad \text{(Equation 1).}$$

Fig. 2 shows the mean April temperatures at Skrova for the period 1936 - 88.

On the basis of Equation (1) and Fig. 2 the dates of maximum abundance of nauplii can be calculated for the period 1936 - 88.

The occurrence of copepod nauplii, cod eggs and first feeding cod larvae has been monitored in the Lofoten area in the spring since 1976. These investigations have provided information on duration of *Calanus* spawning in relation to cod larvae occurrence, horisontal and vertical distribution of nauplii and larvae, etc. (Ellertsen et al. 1988).

The date of 50 % spawning of cod in Lofoten in the period 1936 - 1988 is based upon the following information:

a, during the period 1936-1967 on data points based upon cod roe and fishery statistics given by Pedersen (1984)

b, peak spawning data from Smestad and Øiestad (1974) are used for the years 1968-1972, and

c, during the period 1976-1988 the date of 50 % spawning is based on abundance of egg stage I (0-2 days of development, (Solemdal 1989)), from frequent vertical net hauls from traditional spawning sites in Lofoten (Ellertsen et al. 1989).

Dates for maximum concentration of first feeding cod larvae are based on the above mentioned peak spawning data, adding both the incubation period found in Ellertsen et al. (1987) and 7 days from hatching to first feeding (Ellertsen et al. 1980).

Results.

Fig. 3 gives the spawning and first - feeding curves for Arcto - Norwegion cod and the production curves of nauplii for some years in the 1980íes. It was demonstrated that nauplii concentrations between 5 and 10 per liter is critical for succesfull feeding for first feeding larvae (Ellertsen et al. 1988). The different marking on the nauplii curves indicate periods with different nauplii concentrations.

Fig. 4a shows the date of peak spawning of the Arcto - Norwegian cod, described by the equation

$$D = -374.2998 + 0.2367\ x \qquad \text{(Equation 2)}$$

where D is Julian day of maximum abundance of stage I cod eggs, x is the year.

Fig. 4b shows the dates of first feeding cod larvae, described by the equation

$$D = -390.8872 + 0.2607\ x \qquad \text{(Equation 3)}$$

where D is Julian day of maximum abundance of first feeding cod larvae, x is the year.

Fig. 4c shows calculated dates of maximum abundance of Calanus nauplii during the period 1936-88, based upon April temperatures and Eq. 1, described by

$$D = -107.92 + 0.11489\ x \qquad \text{(Equation 4)}$$

Based upon the estimated dates of maximum concentration of first feeding cod larvae (Eq. 3), and the maximum abundance of copepod nauplii (Eq. 4), the differences in dates between these two maxima within a year is plotted against mean April temperature for the period 1936-88 (Fig. 5 a, b, c). Negative values mean that nauplii maximum is in front of first feeding larvae maximum.
Fig.5 a shows the period 1936 - 63 , 5 b the period 1964 - 88 and 5 c, the whole period.

More points are found on the left negative side of the figure, indicating that in most years the nauplii maximumis ahead of the

first feeding larvae maximum. With lower April temperatures there is a tendency to a larvae maximum simultaneous with or before the nauplii maximum.
During the period 1977 - 88 the spawning period was 60 days as an average, varying between 50 (1979) and 65 (1983, 1985). The period of spawning is here represented by a presence of stage I eggs exceeding 100 eggs per m^2. The period usually lasted from the ten first days of March to the two first weeks of May.

Discussion.

Temperature.
The temperature data from the fixed station at Skrova during the period 1936 - 88 reveals the following characteristics: the temperature oscillates with amplitudes of about 0.5 -1.0 centigrades and with intervals of 10 - 15 years. The periodicity is in good accordance with the temperature regime at the Kola section in the Barents Sea (Sætersdal & Loeng 1987). The mean temperatures in the upper 30 meters in April at Skrova during the period varied between 1.9 and 4.4 centigrades.There is a significant reduction in temperature from 1936 to present time, amounting to about 0.6 centigrades (Leinebø, pers. comm.). A long-term trend towards a decreasing temperature in southern (Ljøen and Sætre 1978) and northern (Blindheim et al. 1981) Norwegian coastal areas started in the 1940ies and this trend is still going on. Blindheim et al. (op. cit.) state that the temperature is a large-scale covariate, and that variations in temperatures along the coast are also reflected in the Barents Sea temperatures, as demonstrated in the Kola section. The temperature variations are the result of large - scale fluctuations in the Atlantic current into the Norwegian and the Barents Seas.

Peak spawning.
Three methods have been used to calculate peak spawning of the Arcto - Norwegian cod; frequent sampling of newly spawned eggs at the spawning sites (Ellertsen et al. 1981), cod roe and fishery statistics from Lofoten (Pedersen 1984) and the week of maximum catch from the Lofoten fishery statistics (Cushing 1969). The two first methods are in fairly good agreement during the overlapping period of 1976 - 82, while the week of maximum catch is systematically 14 days earlier. The cod roe method is biased by market conditions, since the criteria for accepting the roe at the fisheries stations are somewhat subjective. On this background a best fit relation was established for the years 1936 - 67 based upon Pedersen (1984), and data on sampling of newly spawned eggs used for the rest of the period (Smestad & Øiestad 1974, Ellertsen et al. 1989).

Comparing the period of almost 60 years a delay in spawning of about 10 days is found from the cod roe/egg sampling method, while the opposite trend was found by Cushing during the same period. During the last 40 years a more or less continous reduction of the spawning stock has taken place, followed by the reduction in the proportion of older spawners and an increased proportion of first time spawners (Jørgensen 1989). The minor, older part of the spawning population is more distributed in the western and warmer part of the Barents Sea (Nakken & Raknes 1987) and arrives first to the spawning grounds (Sund 1938), while the first time spawners, distributed in more easterly Barents Sea arrives later. The ratio between old and young fish and their different distribution patterns in the Barents Sea probably explain the varying peak spawning

Cushing and Dickson (1976) found a delay of about 10 days during the period 1894 - 1940, which is roughly a period of warming. The authors argues that this is an example which shows the ability of a fish species to alter its spawning strategy to short - term temperature changes. The question on the ability to alter peak spawning on a short time basis, as a response of a climatic change, is a very interesting one, but very little information exists in the literature. Cushing (1982) concludes; " Thus there is slight evidence that a fish stock can alter its peak of date of spawning , but the nature of the change remains obscure ".

During the present investigations in the period 1976-88, both an extremely cold year (1981) and a warm year (1983) have been experienced in the coastal waters of Lofoten. The peak cod spawnings these years were observed March 29 and April 1, respectively, indicating no short time effect of temperature on the peak spawning, as shown in Fig 4 a. On this background it is concluded that the variations in peak spawning of the Arcto - Norwegian cod is restricted to variations in the age composition of the spawning stock, and the variation in age composition observed within the last 50 years has affected the peak spawning in the order of about 10 days. Changes in peak spawning in general have no relation to changes in the temperature in the upper layer and hence no adjusting effect to the production cycle of nauplii. A spawning population with stable age composition will within a short time period have a fixed spawning peak.

During the period 1976 - 88 the spawning period has been about 60 days throughout the period, with a peak spawning about April 1. Wiborg (1957) states that the main spawning is from middle of March to the beginning of April during the 1950íes, while Rollefsen (1932) reports peak spawning in the last part of March. During the 1860íes Sars (1879) reports peak spawning in the end of March. The spawning period is constant during the period 1976 - 88 of about 60 days. No data from earlier periods on the total spawning period are reported from the Arcto - Norwegian cod.

Production of copepod nauplii.

Several investigations on the population dynamics in C. finmarchicus show that the date of peak abundance of nauplii is similar to date of peak abundance of copepodite stage I (Nicholls 1933, Kamshilov 1955, Fransz and Diel 1985). Other authors report a time lag of a few days between maxiumum concentrations of nauplii and CI (Wiborg 1954, Horwood 1973). Own investigations in the Lofoten area in 1987 reveal that maximum abundances of N and CI occurred at the same time (unpublished). We were therefore able to use a long-time series of data on occurrence of copepodite I when constructing a relationship between temperature and time of naupliar maximum. Investigations in the Lofoten area show that the C. finmarchicus nauplii are present over a period of about 12-16 weeks, with a pronounced maximum lasting 1-3 weeks, in locally defined areas the period of maximum abundance may be as short as a few days. Nicholls (1933) reports the nauplii to appear in the Clyde Sea area in March and to disappear in early July, indicating a naupliar period of about 16 weeks. According to Cushing and Tungate (1963) and Horwood (1973) C. finmarchicus nauplii in the North Sea are present for more than 60 days, all stages combined, while NI was observed for a period of about 40 days.

Baranenkova (1965) and Sysoeva and Degtyareva (1965) reported an unusual early spawning of C. finmarchicus in Norwegian waters in the warm year 1960. The maximum occurrence of CI in Lofoten was oserved about April 1, which is also taken to represent the date of maximum occurrence of nauplii, indicating the most intense spawning in early March. In the extremely cold year 1981, with temperatures in March and April 0.7 and 1.9 ^{o}C, respectively, maximum occurrence of CI was observed about May 20, which means that the spawning was at its maximum in late April. In 1929, with surface temperatures in the northern part of the Vestfjord about 2 ^{o}C, the most intense spawning in C. finmarchicus was also observed in the later half of April (Sømme 1934). This temperature dependent spawning in C. finmarchicus thereby causes a delay in spawning of about 1.5 months in the coldest year (1981) compared to the warmest (1960). Marshall and Orr (1972) report spawning in C.finmarchicus before the spring diatom increase, which may have been the case in 1960.

The abundance of nauplii in the first feeding larvae area varies between years. In most of the years investigated by the authors we observed a naupliar density of about 20 n/liter (average 0-40 m depth) at its maximum, and patches with densities above 50 n/liter (Tilseth and Ellertsen 1984). In 1987 the density of nauplii was rather low, with a density of 4 n/liter at its maximum. Disregarding the match or mismatch in time or space between larvae and their food organisms, some years must provide marginal food conditions for the larvae due to the low total production of nauplii. Wiborg (1978) investigating the annually varying zooplankton biomass along the coast of Norway, including Lofoten, in relation to temperature, failed to show a correlation between zooplankton abundance and temperature.

Spawning strategy of the Arcto - Norwegian cod.

The peak spawning of the Arcto - Norwegian cod produces a peak of the first feeding larvae lagging behind the peak of nauplii in most of the years during the period 1936 - 88. The same tendency is found using both direct sampling of nauplii, Fig. 3, or the relation between temperature and the spawning period of Calanus, Fig. 5. To characterize the general degree of match between the production of nauplii and first feeding cod larvae it is necessary to stress two independent phenomena influencing upon the match during the period 1936 - 88: the significant reduction in temperature (Leinebø, pers. comm.), amounting to a delay of about 10 days in peak abundance of nauplii, and a similar delay of peak cod spawning due to age reduction of the spawning population. In this period these two phenomena have neutralized each other to a large degree. It is reasonable to believe that the relation between peak nauplii and peak cod first - feeding larvae is an optimal reproductive situation for the cod, resulting from a long - term selection process during part of the 10 000 years of postglacial period. Since the cod and the Calanus inhabit different temperature regimes in the water column, and Calanus nauplii are, with few exceptions, the only prey organism for the first feeding cod larvae, the selection pressure must have been hard.

Since 1936, when the temperature measurements started in Lofoten, the temperature variations, and hence the variations in nauplii peak, are well within the match strategy of the cod, except in years with extreme temperatures. In this connection it should be stressed that the period of first feeding larvae is about 60 days at the present spawning stock level. The number of first feeding larvae in 1983 and 1984 are in the order of 1.4×10^{10} and

2.2×10^{10}, respectively (Fossum 1988), which means high numbers of larvae throughout the whole first - feeding period. With a 1 - 1 1/2 month period of sufficient nauplii concentrations, Fig. 3, there is usually a good match between first - feeding cod larvae and Calanus nauplii, except during warm and extreme cold years.
The spawning strategy seems to be different in other areas. Introducing the match/mismatch hypothesis Cushing (1972) presented a schematical figure with the nauplii curve lagging behind the first feeding larvae curve. The figure reflects the spawning strategy evolved by the North Sea cod (Cushing & Dickson 1976) and plaice from the Southern Bight (Cushing 1982). Thus the best feeding conditions are supposed to occur during the later part of the first feeding larvae period (Cushing 1982), contrary to the conditions for the Arcto - Norwegian cod. In the North Sea the period of nauplii production is longer than in Lofoten; Last (1978) report fish larvae feeding on copepod nauplii from February to June.

A modified match/mismatch hypothesis, adapting larval production to different temperature regimes in the Barents Sea.

Cod stocks reaching into subarctic regions, as the Arcto-Norwegian and the West Greenland cod stocks, show large fluctuations in stock size in relation to climatic changes (Rollefsen 1954, Ottestad 1969, Hansen and Buch 1986, Sætersdal and Loeng 1987). Analyzing data on stock size, temperature and ice condition throughout this century, Sætersdal and Loeng (op. cit.) conclude that large year-classes usually are associated with positive temperature anomalies. They put forward "the hypothesis of an adjustment of the recruitment to the fluctuating potential for stock biomass production". The connecting ecological factor to promote the adjustment must be temperature. A large scale current linkage between Norwegian coastal waters and the feeding areas of the cod in the Barents Sea has been demonstrated (Blindheim et al. 1981), the temperature relations lagging behind about half a year in the northernmost areas.
At higher temperatures at the spawning sites of the Arcto-Norwegian cod the nauplii peaks are situated more and more in front of the first feeding larvae peaks. This situation often lead to the formation of large year classes (Ellertsen et al. 1987). What is the positive effect on larval production in this situation? The egg population from a "normal" spawning stock is not homogenous according to size (Solemdal & Sundby 1981). There is a reduction in egg size during the spawning for two reasons: The older and larger high fecund fish producing larger eggs (Kjesbu 1988) arrive earlier in the Lofoten area (Sund 1938) to spawn. There is also a reduction

in egg size within a single female during the spawning season (Kjesbu, op. cit.). Knutsen & Tilseth (1985) demonstrated the positive correlation between egg size and larvae size at hatching. As a consequence, there is a reduction in larval size at hatching throughout the season. Similar intraspecific variations, based on varying feeding status, degree of spentness and age of female are demonstrated for several fish species (Nikolskii 1969, Solemdal 1970, Chambers & Leggett 1989). Chambers et al. (1989) also demonstrated a direct correlation between both condition and lipid indices of the female and initial yolk volume and viability of the capelin larvae, indicating reduced quality of the late spawned eggs. Combining the spawning strategy of the Arcto - Norwegian cod with the intraspecific variations of both spawning period and larval size relations, it becomes evident that the largest larvae, and probably the most viable, hatch early and will experience the best feeding conditions during the first - feeding period (Ellertsen et al. 1989). This is especially noticeably in the warm year 1983, showing both an early peak of Calanus nauplii and cod larvae of a significant better condition than in the years 1982, 1984 and 1985 (Ellertsen et al. 1989). The year class of 1983 turned out to be a large one. Supposing a peak spawning 10 days earlier than at present of the Arcto - Norwegian cod due to an increase of the age of the spawning population to the 1930 - level, and no change in the present temperature regime (see Fig. 5). This would result in a better match for the early hatched, larger larvae during mean and high temperature years, but worse during very cold years.

It must be stressed that he presented mechanism is based on the old idea of yearly variations in synchrony between the production cycles of fish larvae and their food organisms (Hjort 1914), named the match/mismatch hypothesis by Cushing (1972). The modifications are the following:
1. The inhomogeneous size distribution of eggs and newly hatched larvae during the production cycle, the larger being produced in the beginning of the cycle. 2. The production curve of nauplii being situated in front of the production curve of first feeding cod larvae during years with high temperatures.
In additon, the age composition of the spawning cod will influence upon the relation of the cycle of first feeding cod larvae to the production curve of C. finmarchicus, both in timing and larval size relations. It has also been demonstrated experimentally that both fecundity and the size of eggs are influenced by the nutritional status of the female to a high degree, which will also serve as a factor in the adaptive larval production to varying feeding conditions of the bottom stages of cod in the Barents Sea (Kjesbu et al,. in prep.). High temperatures are both increasing (Nakken and

Raknes 1987) and improving the feeding areas of the juvenile cod in the Barents sea, f.i. by the temperature controlled recruitment and distribution of euphausiids (Boytsov and Drobysheva 1987).
It must be borne in mind that the presented data and proposed mechanism will, of course, be only one of many factors determining the subsequent year class strength (predation, cannibalism, etc.). However, in contrast to these factors the modified match/mismatch hypothesis is explaining how population size can be adjusted to their later feeding conditions on a very early stage. Hence, the presented mechanism is regarded to be one of the results of evolutionary processes adapting reproduction to the optimum use of favourable periods and the survival in unfavourable periods, a mechanism asked for by Sætersdal & Loeng (1987).

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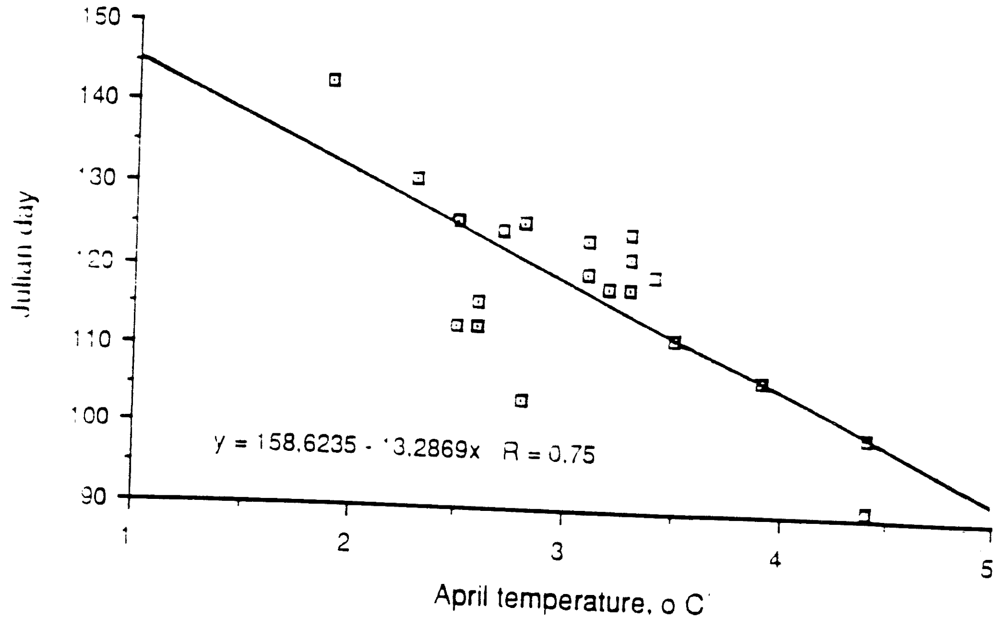

Fig. 1. Time of maximum occurrence of Calanus finmarchicus copepodite stage I versus the mean April temperatures in the upper 30 metres at the fixed hydrographical station at Skrova, Lofoten. Each dot represents one year in the period 1960-1984.

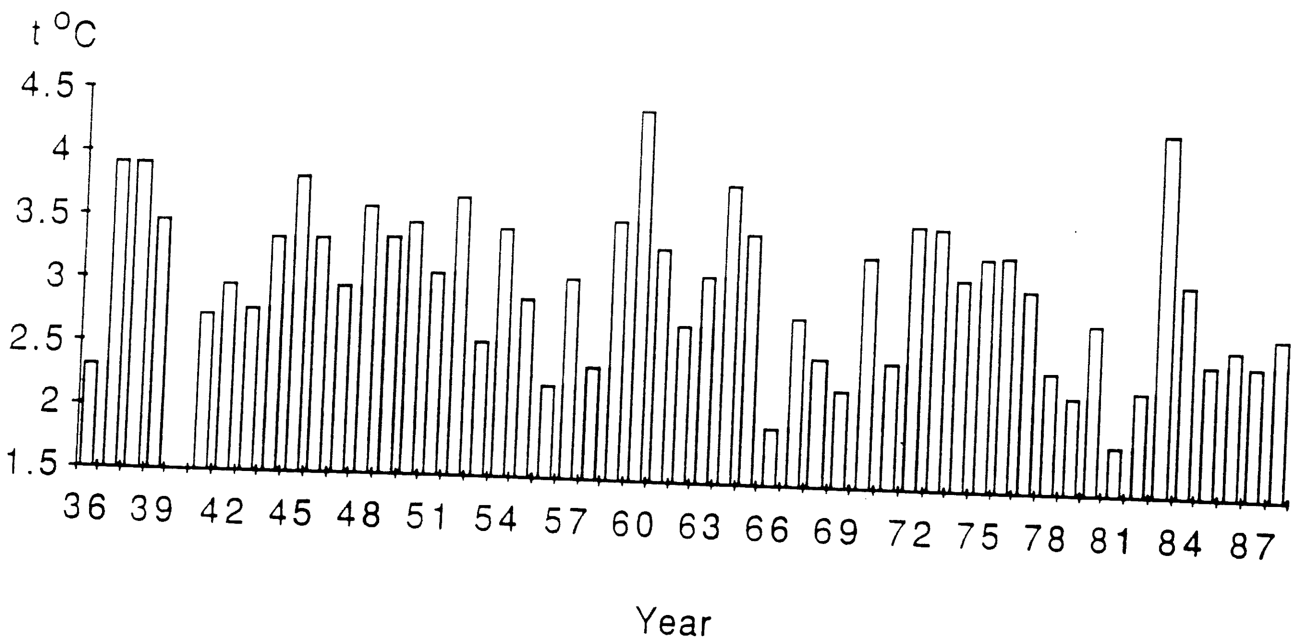

Fig. 2. Mean April temperatures in the upper 30 metres at the fixed hydrographical station at Skrova, Lofoten.

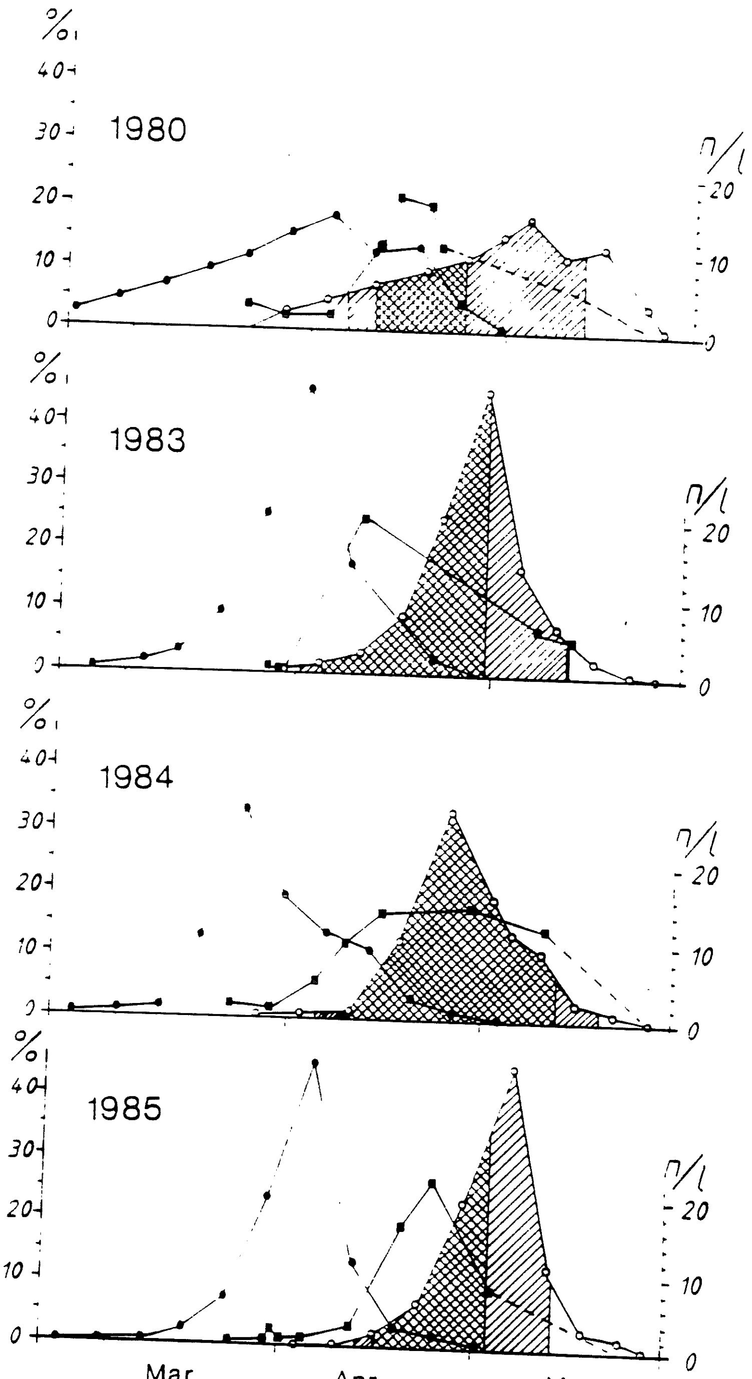

Fig. 3. The match and mismatch of larval production to that of their larval food. ●——● Percentage frequencies of newly spawned cod eggs, all data points sum to 100 %, ○——○ the subsequent distribution of first feeding cod larvae, and ■——■ the production of copepod nauplii.

////// the larval period when the naupliar concentration is between 5-10 n/l, XXXXX the larval period when naupliar concentration exceeds 10 n/l.

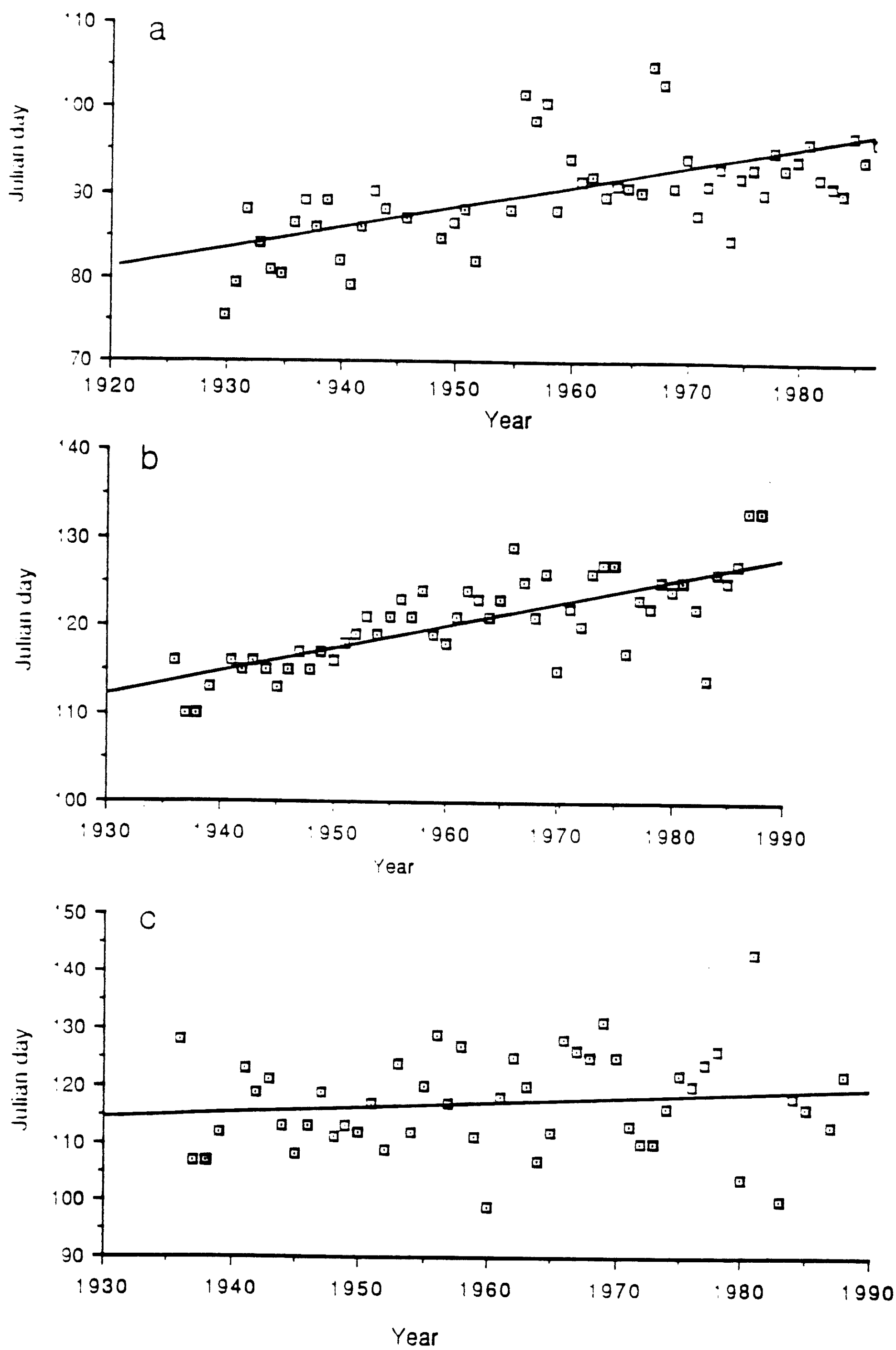

Fig. 4. A chronological sketch, through the period 1936-1988, of
a, dates of peak spawning of Arcto-Norwegian cod (1928-1988)
b, dates of peak abundance of first feeding cod larvae
c, dates of peak abundance of <u>Calanus finmarchicus</u> copepodite stage I.

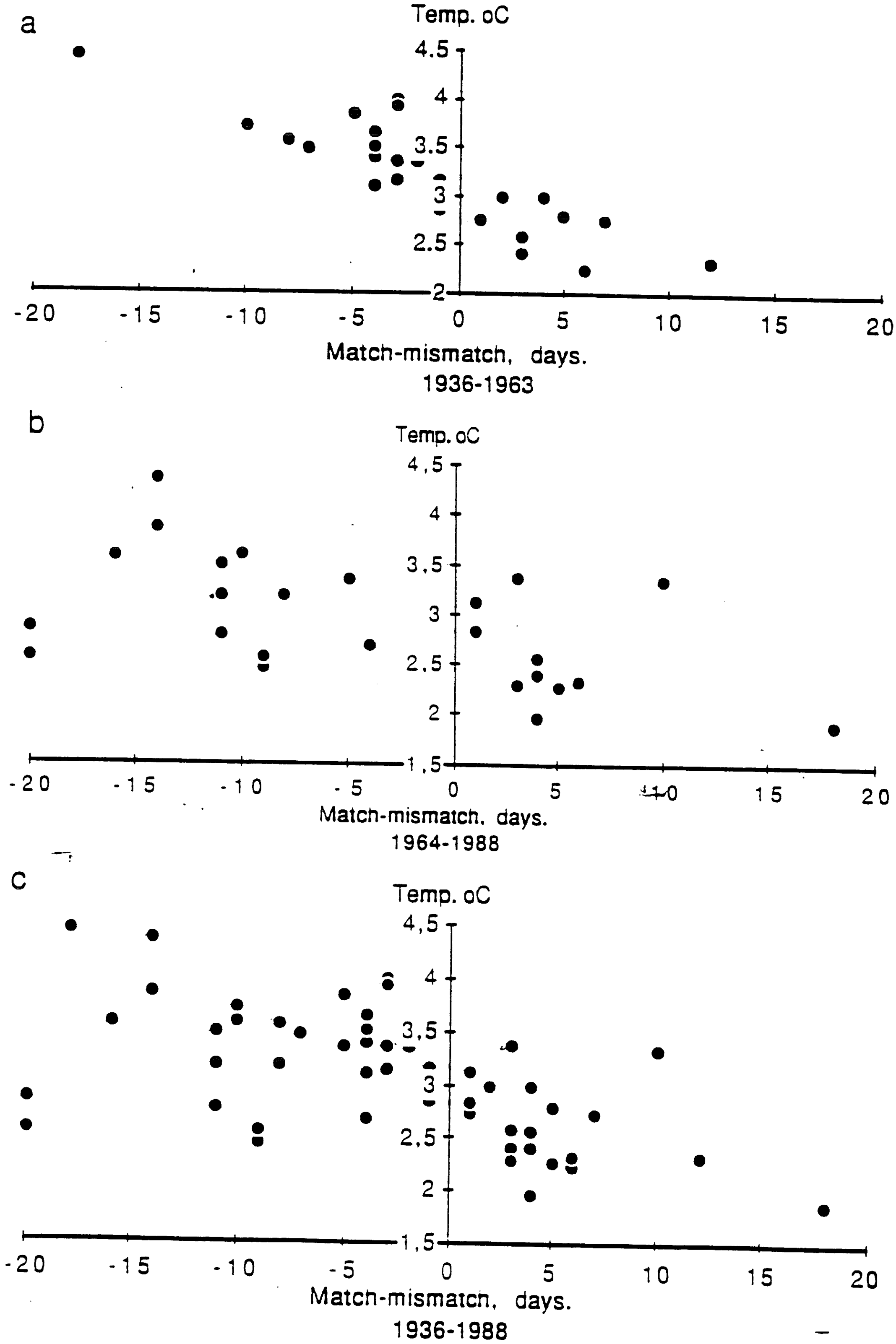

Fig. 5. Match/mismatch between dates of peak abundance of first feeding cod larvae and of copepod nauplii, in the periods
a, 1936-1963
b, 1964-1988
c, 1936-1988