

Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations

Svein Sundby

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The recruitment of Atlantic cod stocks shows different responses to temperature changes. Cod stocks inhabiting the lower temperature range show generally an increase in recruitment with increasing temperature, while cod stocks inhabiting the uppermost part of the temperature range show a decrease in recruitment with increasing temperature. In the present paper possible functional relationships between temperature and cod recruitment mechanisms are analysed. Temperature influences the recruitment processes in a large number of ways; partly directly on vital rates in cod, and partly indirectly through trophic transfer. The copepod *Calanus finmarchicus* is the dominant prey species for the early stages of cod. It proposed that the recruitment-temperature relation of Atlantic cod is a proxy for the food abundance during the early stages, and that advection of *C. finmarchicus* from the core production regions in the central parts of the North Atlantic Subpolar Gyre to the fringes where the cod stocks have their habitats explains the particular recruitment response to temperature.

Svein Sundby, Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway.
E-mail: svein.sundby@imr.no

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INTRODUCTION

Fish recruitment studies often emphasise the importance of small spatial and temporal scales to be essential for understanding the basic mechanisms linked to individual growth of fish larvae. Particularly, such recruitment studies in cod have substantially contributed to increased understanding of the effects of basic biological processes (e.g. Fiksen & al. 1998) which are important elements in more complex models on individual transport, growth and survival of the early stages within a certain stock or subpopulation (e.g. Werner & al. 1996). However, there are limitations to our ability to understand the dynamics of marine ecosystems from basic processes alone, but combined with holistic approaches (e.g. Wiegert 1988) we might gain synergistic effects in analysing ecosystem functioning. In the present context this means that large-scale processes, particularly linked to climatic events, need to be considered (Mann 1993).

Ishevskii (1961, 1964) found positive correlations between temperature and recruitment of cod stocks in the Barents Sea and in the Northwest Atlantic region, and he noticed that temperature and recruitment seemed to vary inversely in the two regions. Subsequently, Rodionov (1995) analysed the recruitment in ten different North Atlantic cod stocks by factor analysis, and confirmed Ishevskii's conclusion that there was a trend of east-west opposition in year-class strength across the

Atlantic. Rodionov further associated the temporal pattern of variation with similar patterns in the North Atlantic Oscillation index (NAO). In the northwest Atlantic region Koslow (1984) found consistent positive correlations in recruitment among stocks within such species as cod, haddock, and herring. He suggested that the spatial extent of these patterns which span the region from West Greenland to Georges Bank, indicated that large-scale physical forcing rather than local biological interactions, regulated fish recruitment.

Despite the early concern of the influence of temperature on Atlantic cod, it is only over the last 15 years that the issue has been heavily focused with respect to mechanisms and functional relationships between environmental parameters and recruitment. An extensive collection of papers on Atlantic cod stocks were presented at the ICES Symposium on Cod and Climate Change in Reykjavik in 1993 (Jacobsson & al. 1994), but we still lack basic understanding of how large-scale climate variations are functionally linked to basic biological processes of importance to fish recruitment.

Temperature has a direct effect on growth (e.g. Jobling 1988; Brander 1995) and distribution (e.g. Nakken & Raknes 1987; Rose 1993) of adult cod. However, growth of early life stages and recruitment processes are linked to temperature in more complex ways. This is because vital rates in early life stages are also strongly dependent on other climate parameters as turbulence and light

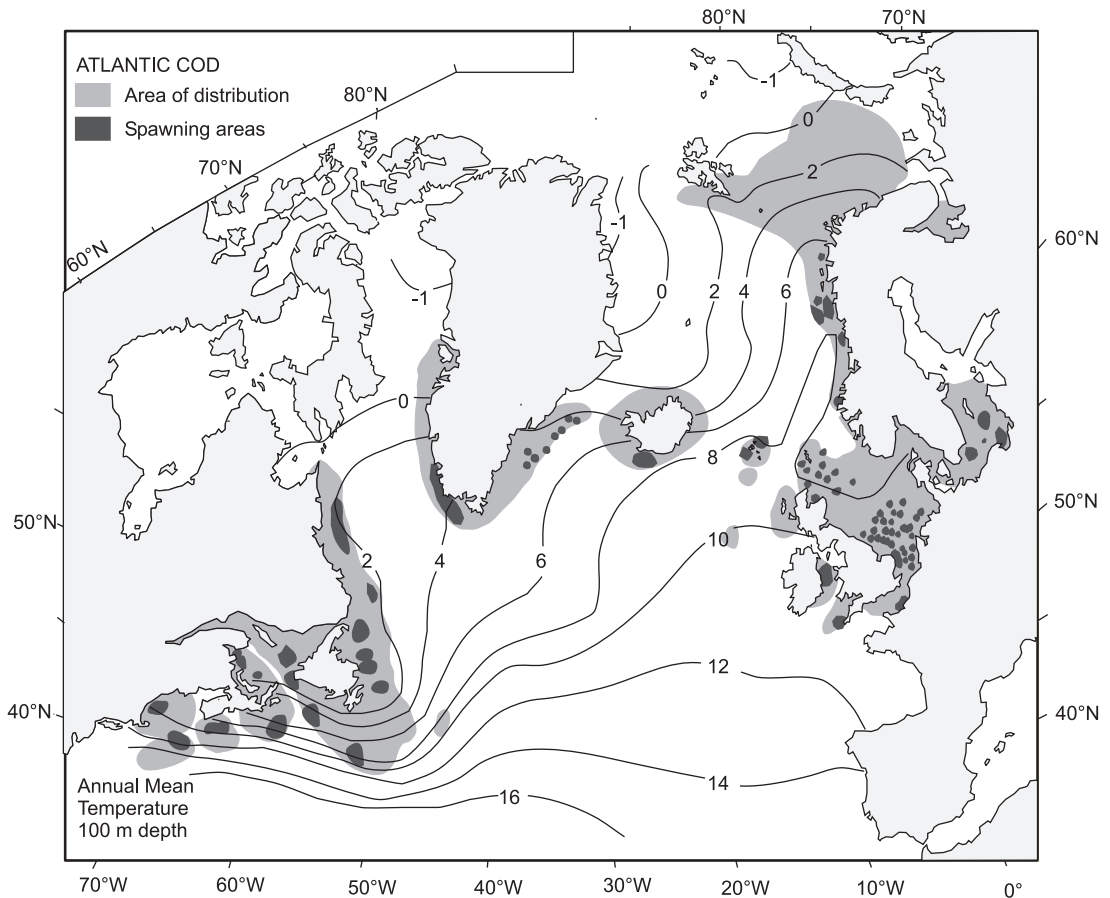


Fig. 1. Spatial distribution of Atlantic cod stocks (*Gadus morhua*) (shaded), their spawning areas (darkly shaded) and the annual mean temperature at 100 m depth in the North Atlantic. (Cod distributions are modified from FAO (1972) and Garrod (1977). Temperatures are based on Antonov & al. (1998)).

conditions which in some regions are correlated with temperature, and because temperature influences larval processes indirectly through lower trophic levels. The parameters of importance to basic biological processes influencing fish growth are food concentration, temperature, motion (e.g. turbulence) and light (Rothschild 1988). In some sectors of the North Atlantic these parameters partly covary, and in other sectors they do not. Consequently, a correlation between growth or recruitment and an environmental parameter in one stock should not necessarily be present in another stock.

By going from individual growth to population growth and ecosystem responses the complexity increases. There are many ways in which marine ecosystems respond to ocean climate variability (Cushing & Dickson 1976). Most of the responses are complicated and far from fully understood because of interactions between trophic levels, but still the basic components of the ocean climate

influencing the ecosystem are limited to the basic physical parameters mentioned above.

As pointed out by Shepherd & al. (1984) the problem with correlations of recruitment with climatic variables is that “there is no limit to the number of comparisons a curious investigator will want to make. Succumbing to this curiosity, however, inevitably leads to a range of correlation coefficients which make it very difficult to decide whether or not the best result might have occurred by chance”. They concluded that it is very desirable that the selection of environmental variables is based on clearly stated prior hypotheses concerning the mechanisms involved, and not on posterior selection simply on the basis of high correlations.

The aim of the present paper is to analyse possible causal relationships between physical and biological environmental factors and recruitment of Atlantic cod. The direct and indirect effects of temperature are em-

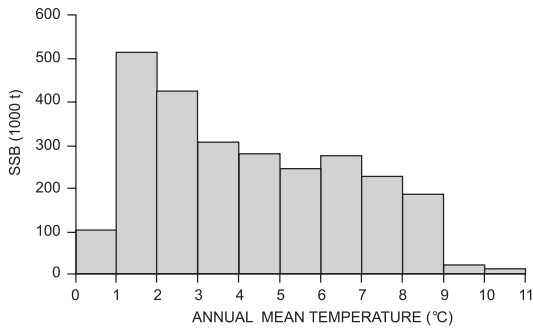


Fig. 2. Ambient temperatures of the spawning stock biomasses of Atlantic cod stocks. (Cod stocks in strongly stratified waters are excluded, i.e. the cod stocks in the Baltic Sea and the Gulf of St. Lawrence).

phased, and particularly the role of temperature as a proxy for other environmental factors and how it influences fish recruitment indirectly through lower trophic levels. A basin-scale generic mechanism for Atlantic cod recruitment is proposed where temperature change is linked to advection of *Calanus finmarchicus* from core production regions. This provides favourable feeding conditions for young stages and strong recruitment of the cod stocks which are distributed around the fringes of the core regions of *C. finmarchicus*.

DISTRIBUTION OF ATLANTIC COD STOCKS IN RELATION TO TEMPERATURE

Atlantic cod populations are distributed at the shelves on both sides of the North Atlantic from about 40°N (south of Georges Bank) to 80°N (to the north of West Spitsbergen). The ambient temperature, expressed as the yearly mean over the area of distribution, ranges from about 1°C for the West Greenland and northern Labrador stocks to about 11 °C for cod in the southern part of the North Sea, the Irish and the Celtic Seas. Fig. 1 shows the geographical distribution of Atlantic cod with their spawning areas. The distributions are based on FAO (1972) and Garrod (1977) and is updated and modified based on information from members of the ICES Working Group on Cod and Climate Change. The overlaying temperature distribution, annual mean at 100 m depth, is drawn based on the global hydrographic data base (Antonov & al. 1998) where the temperature values are resolved in an array of 1 × 1 degrees longitude and latitude. Fig. 2 shows the spawning stock biomass of Atlantic cod distributed in its annual mean ambient temperatures. The figure is constructed by taking the tabulated values on spawning stock biomass of each stock in Brander (1994) and locating them geographically according the distributions in Fig. 1. The ambient temperatures

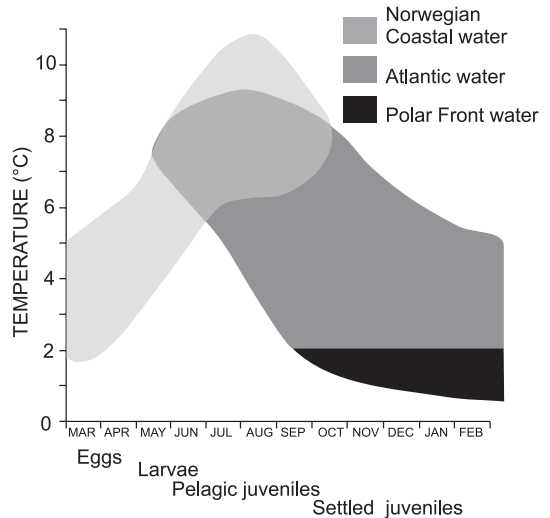


Fig. 3. Ambient temperatures of Arcto-Norwegian cod during the first year of life. (After Loeng & Sundby 1986).

of each stock is then obtained by integrating the areas between each 1 °C. The overall pattern shows a general decline with increasing ambient temperature. The cod stocks in the arctic and arcto-boreal regimes which cover the lower temperature range, consist of some of the historically known largest stocks, mainly of the Greenland cod, the cod stocks off Labrador and Newfoundland and the Arcto-Norwegian cod. The middle range consists mainly of the Icelandic cod which occupies waters more influenced by Atlantic water. The upper temperature range consists mainly of the North Sea cod and with the small Irish Sea cod and the Celtic Sea cod stocks at the upper extreme.

When including the seasonal amplitudes of the temperatures for each stock, the actual ambient temperature range is somewhat wider than the yearly mean temperature shown in Fig. 2. Particularly, during the period from the egg stage to pelagic juvenile stage the fish undergo the largest temperature changes through lifetime. Spawning occurs for most stocks between February and May (Brander 1994) when the temperature in the upper layer is at its seasonal minimum. Russian scientists reported developmental time for cod eggs from the northern Labrador stock to be about 3 months as they develop under the ice at temperatures of -1 °C. At the other end of the temperature range cod eggs hatch within about one week. As most of the Atlantic cod stocks spawn during spring, the temperature increases as the eggs and larvae develop throughout late spring and summer and reaches the seasonal maximum in late summer before juveniles settle to the bottom. Fig. 3 shows an example of how the ambient temperature develops for Arcto-Norwegian cod over the

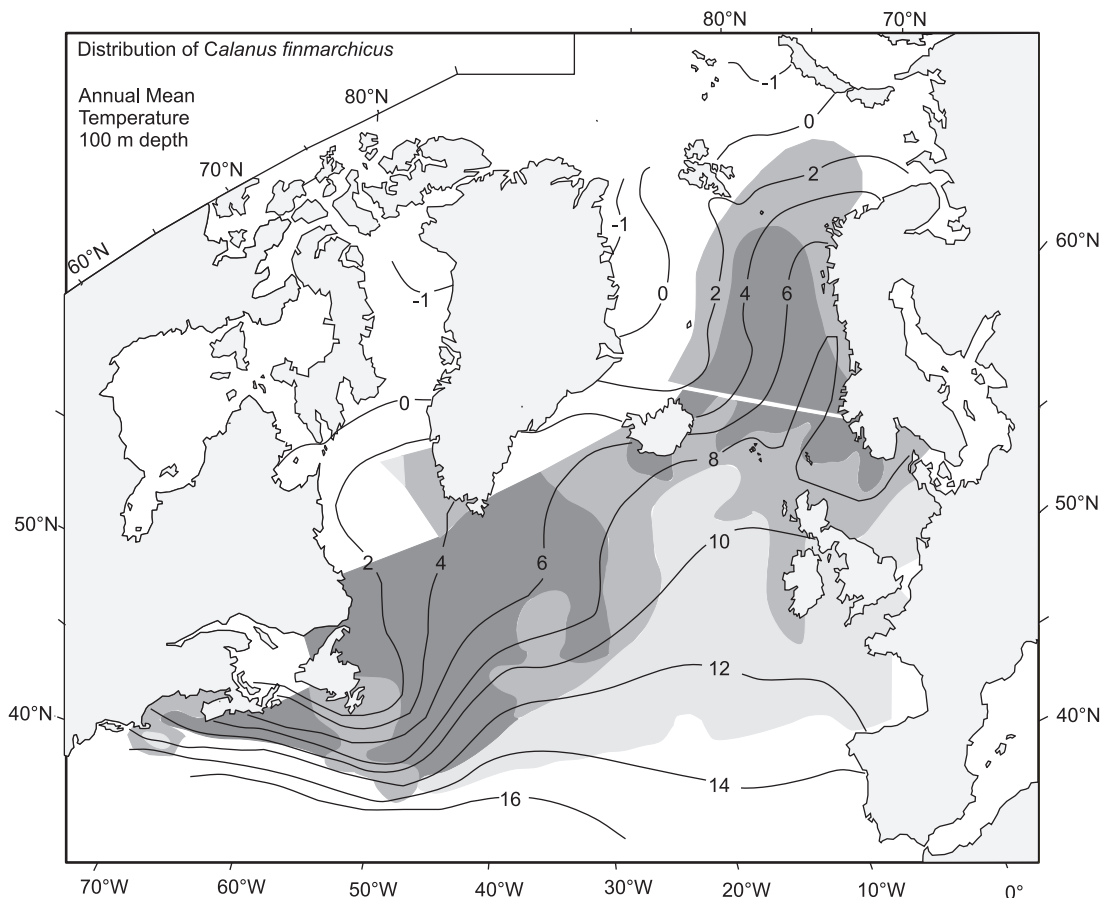


Fig. 4. Spatial distribution of the *Calanus finmarchicus* and the annual mean temperature at 100 m depth in the North Atlantic. (The data on *C. finmarchicus* is from the Continuous Plankton Recorder Program of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). The cut-off line indicates northern boundary for the SAHFOS data. Distributions in the Norwegian Sea to the north of this line are based on data from Conover (1988), Nesterova (1990), and Holst & al. (1998)).

first year of life with rapidly increasing temperature until the juveniles settle to the bottom in the Barents Sea in September-October (Loeng & Sundby 1985). Even though the absolute temperature varies between cod stocks, it is a general feature of all those Atlantic cod stocks spawning during spring that temperature increases from the egg stage to the pelagic juvenile stage. For the demersal juveniles and adult stages of the Arcto-Norwegian cod Godø & Michalsen (2000) found that the annual temperature cycle varied inversely compared to that of the early stages with the highest ambient temperature in spring/winter and lowest in late summer/autumn. This is due to the seasonal migration pattern with feeding in the warm southwestern parts of the Barents Sea and/or spawning at the coast off mid- and North Norway during winter/spring (4-7 °C), and with feeding during summer at the polar front in the north (< 0 °C).

Larvae from the Northern cod stock off Labrador/Newfoundland has been found at temperatures well below 0 °C (Serebryakov 1967), and it is expected that eggs and larvae from this stock are distributed down to the level of larval freezing of -1.35 °C (Valerio & al. 1992). Also adults of the Northern cod may be found living down towards the limit of mortality by freezing (Templeman 1965). Arcto-Norwegian adult cod may enter waters of -0.5 °C during summer in the northern Barents Sea (Woodhead & Woodhead 1965). At the upper temperature limit, the summer habitat of cod in the southern part of the North Sea and in the Celtic Sea may reach temperatures of about 16 °C.

The cod have been shown to have certain temperature preferences within the habitat of a specific stock unit. Sars (1879) became aware of that the spawning cod in Lofoten were found in certain depth layers which he

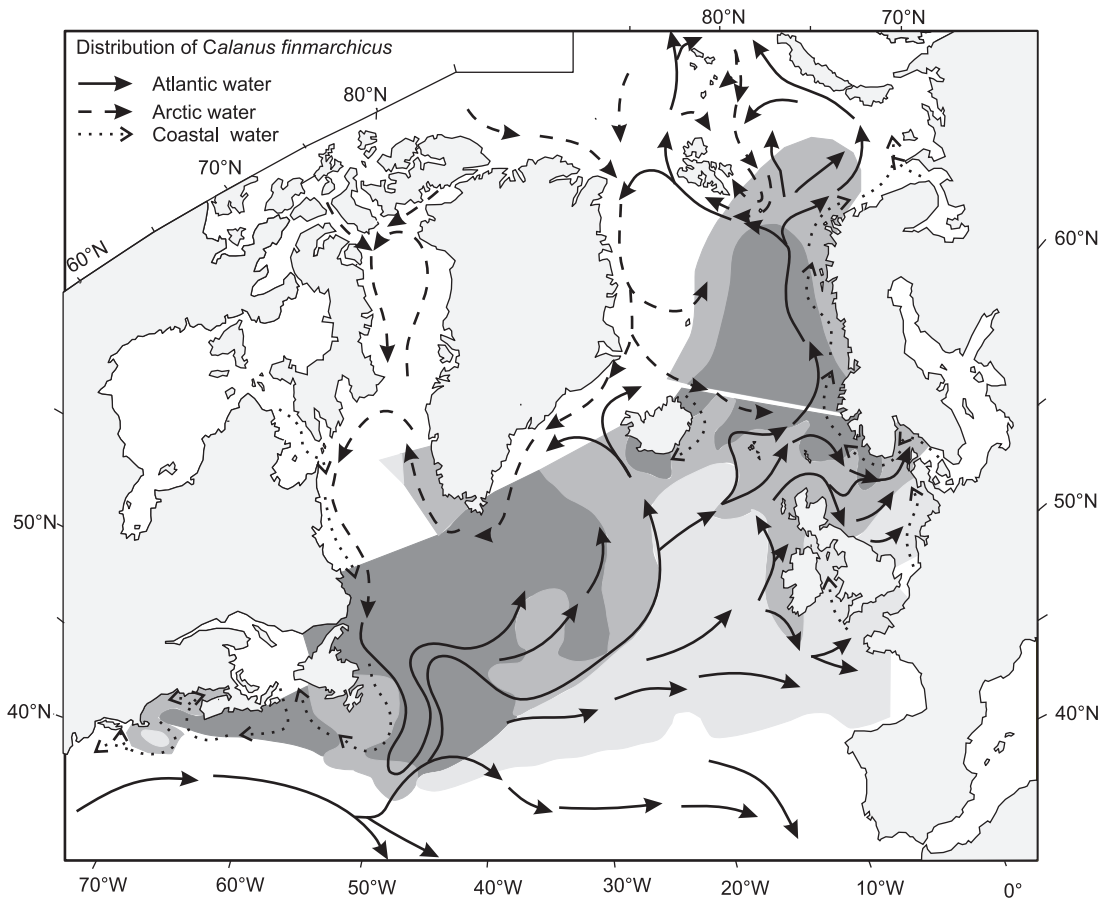


Fig. 5. Spatial distribution of the *Calanus finmarchicus* (as in Fig. 4) and circulation patterns in the North Atlantic. (Circulation pattern is based on Dietrich & al. (1980)).

believed coincided with a specific temperature range. Already in the late 1880s some Lofoten fishermen used deep-sea thermometers to find the depth layer where the spawning cod were most abundant (Nordgaard 1899). Gade (1894) investigated the issue in more details and concluded that the spawning cod was most abundant in the depth layers of temperatures from 4 to 6 °C. After more than one hundred years this statement still holds for the spawning cod in Lofoten. Similarly, Rose (1993) found that the Northern cod off Labrador and Newfoundland on its way from the offshore feeding areas to the onshore spawning habitats followed the temperature layer from 2.0 to 2.7 °C. In the Barents Sea, the juvenile and adult cod are distributed over a temperature range from less than 0 °C in the northern and eastern parts (mainly during summer) to more than 6 °C in the western part. Nakken & Raknes (1987) found that older fish were distributed more westerly in the warmer water than younger

fish. The interannual variability in ambient temperature was considerable higher than the interannual variability of mean temperature of the Barents Sea (Ottersen & al. 1998), indicating that the cod was not stationary distributed during a temporal change in temperature, but also changed their distribution in relation to the spatial temperature field.

DISTRIBUTION OF THE KEY PREY SPECIES *CALANUS FINMARCHICUS* IN RELATION TO TEMPERATURE, CIRCULATION AND TO ATLANTIC COD STOCKS

The copepod *C. finmarchicus* is a key prey species for many fishes in the North Atlantic, and it constitutes the major biomass component of the mesozooplankton within the North Atlantic Subpolar Gyre (Figs 4 & 5). (The North Atlantic Subpolar Gyre is here defined as the region limited by the cool East Greenland Current,

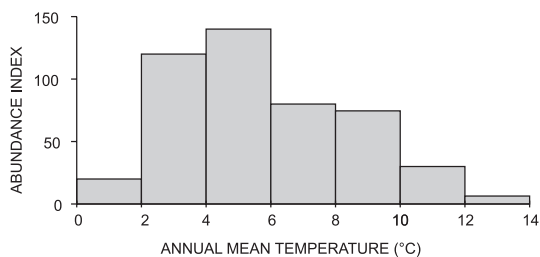


Fig. 6. Ambient temperature of biomass of *Calanus finmarchicus* in the North Atlantic.

West Greenland Current and Labrador Current in north and west and the warm North Atlantic Current and Norwegian Atlantic Current in south and east. This definition is slightly different from the subpolar gyre mentioned in figure 2 by Dickson & al. (1988), who define the subpolar gyre as limited by the Arctic Front in north and west and limited by the Subarctic Front in south and east. The difference between these two definitions is that the latter excludes the eastern part of the Norwegian Sea from the gyre).

For the major part of the cod stocks *C. finmarchicus* is the main prey species for the larval and pelagic juvenile stages (Sysoeva & Degtereva 1965; Ellertsen & al. 1984; Thorisson 1989; Brander 1994, Helle 1994). Through trophic transfer *C. finmarchicus* may also be an important species for the older stages of the cod. In contrast to the distribution of the cod stocks, which are found at the continental shelves around the fringes of the North Atlantic Subpolar Gyre, *C. finmarchicus* is most abundant in the deep sea within the Gyre. Helland-Hansen & Nansen (1909) who first described the cyclonic gyre in the Norwegian Sea noticed that the position of the gyre coincided with the area where Damas (1905) found the highest concentrations of *C. finmarchicus*. They concluded that the gyre was found in the mixed water masses of the warm Atlantic water and the cold, fresher Arctic water. Also, they noticed that high concentrations of *C. finmarchicus* were found in the area over the Feroes-Iceland Ridge. Kanaeva (1963) who studied the entire subarctic region of the North Atlantic found that in addition to high zooplankton concentration in the Norwegian Sea, there was also another large region of high concentrations located to the south and southeast of Greenland and east of Newfoundland. Later these qualitative features have been confirmed quantitatively by the long time series on zooplankton collected in the Continuous Plankton Sampler Programme by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) (e.g. Planque & al. 1997). The data from SAHFOS are not covering the entire Nordic Seas but the boundary data between Norway and Iceland do indicate higher concen-

trations of *C. finmarchicus* into the Nordic Seas. Timokhina (1964) estimated the annual production of *C. finmarchicus* in the Nordic Seas of about 74 mill. tons while Ellertsen (1996) estimated the abundance in the same area of about 200 mill. tons. In Figs 4 and 5 the SAHFOS data are combined with other zooplankton data from the Nordic Seas and the Barents Sea (Conover 1988; Nesterova 1990; Holst & al. 1998). It is evident that the central part of the Nordic Seas is the other core region of mesozooplankton biomass, and the major part of that is *C. finmarchicus* (Østvedt 1955; Pavstikts & Timokhina 1972; Blindheim 1989). In Fig. 4 the *C. finmarchicus* distribution is combined with the annual mean temperature distribution at 100 m depth (as in Fig. 1). In Fig. 5 the *C. finmarchicus* distribution is combined with the general circulation projected from current map of the North Atlantic by Dietrich & al. (1980). From the figure it appears that its habitat extent is bounded by the circulation features of the North Atlantic Subpolar Gyre which is also pointed out by Aksnes & Blindheim (1996). The basin scale distribution of the *C. finmarchicus* might therefore be an evolutionary life cycle adaptation to the circulation features of the northern North Atlantic, and particularly in the two smaller gyres within the large North Atlantic Subpolar Gyre, i.e. the gyre to the south of the Greenland and the Nordic Seas Gyre (Bryant & al. 1998). The temperature regime (Fig. 4) within these two gyres might also be a key factor in the life cycle adaptation as in both of these two core regions where *C. finmarchicus* concentrations peak, the temperatures of the upper 100 m layer ranges from about 4 to 7 °C. At higher and lower temperatures the abundance of *C. finmarchicus* declines. The shape of the southern boundary seems to be formed by the Gulf Stream, the Irminger Current and the North Atlantic Current. The southernmost oceanic extent of the *C. finmarchicus* coincide with the 13 °C yearly mean isotherm, although locally in certain coastal areas (Celtic Sea, North Sea, and the eastern seaboard of North America) *C. finmarchicus* is found at higher temperatures (Williams 1985). Along the northern boundary the *C. finmarchicus* seems to be limited approximately by the 1 °C isotherm. Fig. 6 shows the abundance of *C. finmarchicus* as a function of the ambient temperature. The figure is constructed similarly to that of the cod spawning stock biomass in Fig. 2. The abundance data amalgamated in Fig. 4 are spatially integrated over the temperature range to display the biomass of *C. finmarchicus* as a function of temperature. The temperature ranges for the two species, *C. finmarchicus* and Atlantic cod (Figs 2 and 6) appear to be approximately the same, but the *C. finmarchicus* is most abundant nearer the mid part of the temperature range, while the Atlantic cod is most abundant nearer the lower range of the temperature distribution.



RECRUITMENT OF ATLANTIC COD STOCKS IN RELATION TO TEMPERATURE

Most of the Atlantic cod stocks living at the lower end of the temperature range have a tendency to respond positively with respect to recruitment on an increase in temperature, although strong positive correlations between temperature and recruitment does not exist for each individual stock. Hermann (1953) found a positive correlation between the year class strength of the West Greenland cod and the temperature at the Fylla Bank during summer. Hansen & Buch (1986) reanalysed the data using a longer time series and showed that the recruitment generally was higher in years with high temperatures, although the correlation was not as high as for the former time series. Particularly, there was a period of high abundance of cod at West Greenland in the 1950s and 1960s, and they suggested that the causal relationship was linked to increased influx of the warm Irminger Current which carried eggs and larvae from the Icelandic cod stock that recruited to the Greenland cod stock.

The recruitment of the Arcto-Norwegian cod stock has been shown to respond positively to high temperatures in various ways. Sætersdal & Loeng (1987) analysed recruitment of the Arcto-Norwegian cod through the 20th century and showed that strong year classes tended to occur in periods of warm years and particularly at the beginning of the warm periods. They proposed that in warm periods the gonad production increased resulting in better recruitment. Ellertsen & al. (1989) analysed the time series 1946-1985 of year class strengths of Arcto-Norwegian cod based on virtual population analysis of 3-year-old fish. They found that year class strength was always low in cold years, but in warm years both good and bad year classes occurred. They concluded from this that a high temperature is a necessary but not sufficient condition for the formation of strong year classes. Ellertsen & al. (1989) proposed that the causal mechanism might be linked to the production of the main prey item for cod larvae, the *Calanus nauplii*, since the onset of the *Calanus* production was found to be strongly temperature dependent. In warm years the peak abundance of *Calanus nauplii* at the first-feeding areas of cod larvae occurred up to six weeks earlier than in cold years. The time of cod spawning and larval hatching, however, was remarkably constant between years and showed no variation with temperature. Hence the interannual temperature variations might produce more or less synchrony in the production of cod larvae and its prey in correspondence to the hypothesis by Cushing (1969). Sundby & Fossum (1990) indicated that the temperature might be a proxy for the wind-induced turbulence which might increase the recruitment. Campana (1996) found that individual growth of juvenile Georges Bank cod was

positively correlated with year-class strength. Ottersen & Loeng (2000) showed that there was also a strong relationship between individual length of Arcto-Norwegian 0-group cod and year-class strength. These investigations indicate that the causal mechanism might be that increased growth increases survival as outlined by Shepherd & Cushing (1981) and this supports the “bigger is better” hypothesis (e.g. Leggett & DeBlois 1994). Ponomarenko (1984) showed that extreme low winter temperatures in the northeastern part of the Barents Sea may cause increased mortality of 1- and 2-group cod, and thus the causal relationship between temperature and recruitment might as well be linked to increased temperature-dependent mortality.

The Northern cod stock off Labrador and Newfoundland is also one of the Atlantic cod stocks living at the lower temperature range. Elizarov (1963) found a positive correlation between temperature and catches of cod in the region. deYoung & Rose (1993) demonstrated a similar response of cod recruitment to low temperature as for the Greenland cod and the Arcto-Norwegian cod. They related the temperature effect to changing spawning locations of the fish in warm and cold years, and suggested that a southward shift in the distribution of spawning cod in cold years led to a reduced recruitment because of lower retention of the eggs and larvae in the southern region. The cool ocean climate that developed at the Labrador Shelf after 1988 was followed by a collapse in the Northern cod. Although it has been claimed that overfishing alone was the cause of the collapse (Myers & al. 1996), it cannot be rejected that the cool climate was an important additional factor. Taggart & al. (1994) found that the recruitment variability in the 1980s was in part determined by environmental conditions, but pointed out that the causal relationship is unclear since the thermal environmental conditions are correlated with most of the other climate parameters. Planque & Frédou (1999) reanalysed the Northern cod recruitment data based on Myers & al. (1995), and they did not find a similar positive correlation between temperature and recruitment.

The Icelandic cod stock inhabits warmer water masses than the Greenland cod, the Arcto-Norwegian cod and the Northern cod. The positive response of recruitment to increased temperature is here less than for the previously mentioned stocks (Planque & Frédou 1999). Malmberg (1988) and Malmberg & Blindheim (1994) described the relation between recruitment to the Icelandic cod stock and the physical conditions in more detail. They showed that strong year classes are more frequent in years of strong influence by Atlantic water masses and absence of severe ice conditions to the north of Iceland, i.e. influence of Arctic water masses. Malmberg (1988) emphasised that favourable hydro-

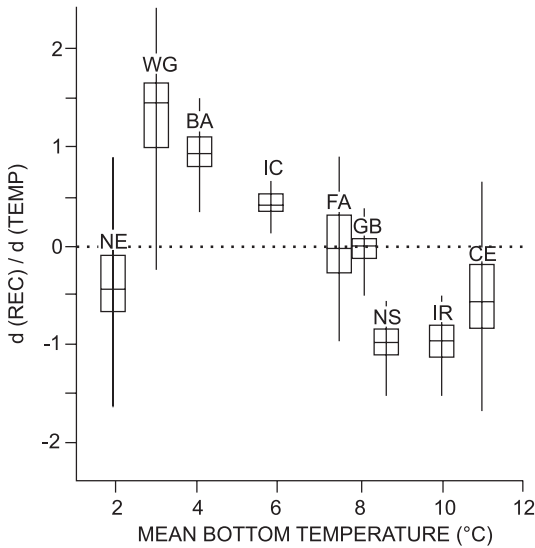


Fig. 7. After Planque & Frédo (1999): Change in recruitment with change of temperature for nine Atlantic cod stocks in relation to mean ambient bottom temperature. Boxes and lines indicate the 50 % and 95 % limits of the empirical distribution of the slopes determined by bootstrapping procedure. NE: Northern cod, WG: West Greenland cod, BA: Arcto-Norwegian cod, IC: Icelandic cod, FA: Faroese cod, GB: Georges Bank cod, NS: North Sea cod, IR: Irish Sea cod, and CE: Celtic Sea cod.

graphic conditions for recruitment are linked to other factors than temperature only, and that the food availability might be important. Astthorsson & al. (1994) who analysed the time series from 1971 to 1992 concluded that neither the abundance indices nor the mean lengths of 0-group cod were correlated with temperature. On the other hand, they showed that there was a significant correlation between the zooplankton biomass in southwestern Icelandic waters and the 0-group index of cod indicating a direct link between cod recruitment and zooplankton abundance.

The Faroese cod stocks, where the weight of adult fish has been shown to be strongly dependent on temperature (Brander 1995) show no response of temperature on recruitment. Instead, Hansen & al. (1994) indicated that the most important limiting factor for recruitment might be strong winds which have a tendency to sweep off both cod eggs, larvae and their prey from their natural nursery grounds.

North Sea cod occupies an environment near the upper limit of the temperature range for North Atlantic cod stocks. Dickson & al. (1974) showed that cod recruitment in the period 1954-1968 was inversely related to the sea surface temperature along the Hull-Hanstholm section in the middle part of the North Sea. Svendsen &

al. (1995) developed a multi-regression model to predict cod recruitment in the North Sea and found that a low heat content represented as the area of water masses of less than 7.5 °C, was favourable for good recruitment. The two other components of the model favouring good recruitment were reduced spread of the Norwegian coastal water and a strong wind mixing. O'Brien & al. (2000) showed that recruitment of North Sea cod was low in years when temperature during the first half of the year was high, while in cold years both high and low recruitment occurred. The weak year classes in cold years were associated with a low spawning stock biomass while the strong year classes were associated with high spawning stock biomass.

The Irish Sea and the Celtic Sea cod stocks are found at the uppermost limit of the temperature range. These stocks clearly show a negative correlation between temperature and recruitment (Planque & Fox 1998). The authors state that there might be a number of possibilities with respect to causal mechanisms. They indicate that the causal effects might be the influence on the reproductive biology of the adult fish, physiological effects on the eggs and larvae, temperature effects on the food production, or a combination of these factors.

Ottersen (1996) analysed the temperature-recruitment relationship for eight Atlantic cod stocks. He concluded that the response of recruitment to an increase in temperature was positive among the low-temperature stocks, negative for the stock with the highest temperature (North Sea stock) and indeterminate for the cod stock with a temperature habitat in between. Planque & Frédo (1999) re-examined in a comparable and unified way the temperature-recruitment relations for nine of the Atlantic cod stocks across the temperature range, including the results from the Irish Sea stock (Planque & Fox 1998). Even though the linear temperature-recruitment correlations for single stocks were generally low, they found a significant linear correlation between environmental temperature and change in recruitment as a function of temperature change when all nine stocks across the temperature range were included in the analysis. Consequently, their results statistically strengthened the general analysis and conclusion of Ottersen (1996) that cod stocks at the lower temperature range show a positive change in recruitment with increasing temperature, that the cod stocks at temperate waters show no clear response in recruitment to changing temperature, and that a negative relationship between recruitment and temperature is present at the upper range of temperature habitats. Fig. 7 is taken from Planque & Frédo (1999) and shows the change in recruitment with change in temperature for nine Atlantic cod stocks in relation to mean ambient bottom temperature. The Northern cod stock data (having the lowest ambient temperature but a slightly negative



recruitment response to increasing temperature) were considered as uncertain and when the Northern cod was removed from the analysis the correlation coefficient increased to $r = 0.83$ ($p = 0.0016$). Planque & Frédo (1999) pointed out that there are several problems with the temperature data of the Northern cod stock: both the temporal homogeneity through the recruitment stage and the spatial homogeneity are very low, and the large fall of the spawning stock biomass in the late 1980s before the stock collapse might have over-ruled the temperature effect on recruitment. As pointed out above, deYoung & Rose (1993) found a positive relationship between recruitment and temperature as shown for Arcto-Norwegian cod by Ellertsen & al. (1989). However, they used the vertically averaged annual mean temperature at hydrographic station 27 off St. John's, Newfoundland, and it might be possible that these data do not represent the actual ambient temperature for neither the pelagic eggs, larvae and juveniles nor the demersal spawning stock.

It can be questioned whether the effect of temperature on recruitment acts functionally through the conditions for the spawning stock rather than the conditions for the early larval and juvenile stages. Ottersen & Sundby (1995) reanalysed the recruitment time series for Arcto-Norwegian cod including the effects of spawning stock biomass and wind conditions. They found that the variation in spawning stock biomass was equally important for the recruitment variability as the variation in temperature. Kjesbu & al. (1998) found a doubling in the individual potential fecundity of Arcto-Norwegian cod from a cold to a warm year in the Barents Sea. Hence, it can be concluded that the temperature also influence recruitment through the egg production, but it does not account for all of the variation in recruitment.

In spite of uncertainties about the temperature-response of specific stocks, it can be concluded that the dome-shaped pattern of recruitment response to temperature presented by Planque & Frédo (1999) seems to be a generic feature for the Atlantic cod. Whether there exists a generic causal process which can explain this temperature response is presently less clear. As shown for the above mentioned stocks a multitude of causal relationships between temperature and recruitment have been proposed, partly explained by the direct influence of temperature on recruitment, partly explained by temperature as a proxy for other processes. The temperature-induced match-mismatch between larval production and their food items (Ellertsen & al. 1989), the increased gonad production due to increased temperature (Sætersdal & Loeng 1987), and increased larval growth during the most vulnerable stages (Ottersen & Loeng 2000) all belong to the category of more direct influence of temperature. The advection of larvae and juveniles by

warm water masses from neighbouring stocks (Hansen & Buch 1986), temperature as a proxy for wind-induced turbulence (Sundby 1995), temperature as a proxy for food abundance (Malmberg 1988), and displacement of spawning areas to more unsuitable regions (deYoung & Rose 1993) belong to the category of more indirect effects of temperature. At the upper limit of the temperature range where the cod stocks show a negative correlation between temperature and recruitment, the investigators seem to be less certain about the causal mechanisms.

RECRUITMENT OF ATLANTIC COD STOCKS IN RELATION TO COPEPODS ABUNDANCE

Field documentation on recruitment responses to the variations in food abundance during the early larval stages, as hypothesised by Hjort (1914), are more scarce than documentation on the influence of temperature, even though some of the authors above indicate that temperature might be a proxy for the food abundance (Malmberg 1988; Ellertsen & al. 1989). Most thoroughly treated is the zooplankton situation in the North Sea. In a series of works Cushing (1962, 1967, 1969) pointed to the importance of plankton production on the recruitment of fish stocks. Particularly, he showed that herring stocks in the northeast Atlantic spawn at the same time as plankton production peaks and introduced the match-mismatch hypothesis (Cushing 1974) that variations in recruitment are linked to the variations in the onset and peak plankton production. Cushing (1984) pointed out that in certain periods there have been a weak positive correlations between North Sea haddock recruitment and abundance of *C. finmarchicus* ($r^2 = 0.25$, $p < 0.02$) and between North Sea cod recruitment and abundance of *C. finmarchicus*. In these cases he related the increase in *Calanus* abundance to increased inflow of water from the Norwegian Sea and the East Icelandic Current which is the region where *Calanus* is most abundant in the Northeast Atlantic. He also pointed out that during influges of *Calanus*-rich water from the Norwegian Sea the temperatures decreased as shown by Dickson & al. (1974). However, Cushing (1984) tended to focus on the effect of delayed *Calanus* production by the cooler water and hence a better temporal match in abundance between the early larval cod and zooplankton rather than the effect of increase in total zooplankton abundance as a result of increased advection. Rothschild (1998) analysed the relationships between abundance of zooplankton and year-class strengths of North Sea cod and herring, including also the variations in fishing mortality. He found that large year classes of cod co-occurred with either high abundances of *Calanus* or *Paracalanus/Pseudocalanus*. He also found that high abundance of



both *Calanus* and *Paracalanus/Pseudocalanus* rarely occurred. In years with low abundance of *Calanus* or *Paracalanus/Pseudocalanus* good recruitment of cod occurred only once while in all the other ten years with low zooplankton abundance bad cod recruitment occurred.

Astthorsson & al. (1994) showed that there was a positive correlation ($r^2 = 0.37$, $p < 0.05$) between zooplankton biomass in southwestern Icelandic waters (the region where the larval stages of cod are found) and the abundance of 0-group cod during 1971-1992. They did not find a significant correlation between mean length of 0-group cod and zooplankton abundance, but concluded that it is less likely that food conditions in the very early stages should be correlated with length at the 0-group stage.

Helle & Pennington (1999) analysed a limited Norwegian time series of surveys on zooplankton in the western Barents Sea and Arcto-Norwegian early juvenile cod during the period 1978-1984. Using a model on volume flux of water into the Barents Sea developed by Ådlandsvik (1989) (see also Ådlandsvik & Loeng (1991) and Loeng & al. (1997)), they found a significant positive correlation ($r^2 = 0.65$, $p < 0.04$) between zooplankton abundance and the influx of Atlantic water from the Norwegian Sea. They also found a positive correlation, although weaker, between the abundance of early juvenile cod and zooplankton abundance. Nesterova (1990) reporting on an extensive time series on Russian zooplankton surveys during the early stages of cod larvae (April/May) for the period 1959-1990, found that the zooplankton abundance was higher in warm years than in cold years. Closer inspection of the data showed a similar feature between temperature and zooplankton abundance as shown between temperature and cod year-class strengths by Ellertsen & al. (1989): i.e. always low abundance in cold years, while in warm years both high and low abundances occurred leading to the conclusion that a high temperature is a necessary but not sufficient condition for high zooplankton abundance. Hence, a similar relation between cod recruitment and zooplankton abundance, as shown by Rothschild (1998) for the North Sea cod, might also be present for the Arcto-Norwegian cod.

GENERAL FEATURES OF COD GROWTH AND MORTALITY IN RELATION TO TEMPERATURE

Recruitment and growth are processes that are expected to be strongly linked. Therefore, it is of interest to examine how temperature in general influences growth rates across the temperature range of Atlantic cod and to explore whether similar responses to changes in temperature occur for growth and for recruitment. Theilacker &

Dorsey (1980) listed temperature-dependent processes related to survival in early life stages: Hatching time, development in the yolk-sac stage, efficiency of yolk absorption, time to exogenous feeding, time to point of no return (which is the stage when the larva is in a condition too poor to recover from starvation), feeding rates, growth, activity, respiration rates and gross growth efficiency. It is not evident how these processes interact on influencing growth and survival in a larval fish population. For cod living near the lower limit of temperature tolerance metabolism will speed up as the temperature increases, but in larvae and early juveniles, survival does not necessarily increase with increasing temperature. The energy turnover in larvae is large compared to the total energy content of the individuals, and the effect of temperature becomes less simple than for larger juvenile and adult fish. Yolk-sac larvae will burn their energy reserves faster at higher temperatures and reach starvation (Houde 1974) and point of no return earlier (McGurk 1984).

Houde (1989) investigated growth, mortality and energetics of marine fish larvae world-wide at temperatures from 5 to 30 °C, and found that both growth and mortality increased with increasing temperature. He concluded that the increase in growth rate at high temperatures must be supported by an increased food consumption. The maintenance ration for larval cod will increase with increasing temperature. It implies that larval cod can benefit from increasing ambient temperature only if they encounter food at rates above the maintenance level. The mortality rate is highest during the egg and early larval stages and decreases exponentially towards the 0-group stage (Sundby & al. 1989). As the larvae are growing larger they will be more capable to survive periods with poor food conditions and be more capable to escape predators. Hence, it has been argued that an increased larval growth rate will decrease total larval mortality because the accumulated time spent in the early and most vulnerable stages will be reduced. Support for this hypothesis is given by Mekan & Fortier (1996) on larval and juvenile cod on the Scotian Shelf and by Hare & Cowen (1997) on bluefish. When considering the importance of rapid growth for survival of larvae, the full advantage of an increasing temperature can only be obtained when they are given enough food, since the energy demand to grow at mean rates increases with increasing temperature (Houde & Zastrow 1993). Ellertsen & al. (1989), Sundby & Fossum (1990), and Sundby & al. (1994) all showed that satiated larvae are occurring only occasionally in the field.

From the above-mentioned temperature-dependent vital processes, it is not obvious how temperature influences survival of the early life stages of cod in the field. In addition, there are many interacting physical and trophodynamic processes accompanied by a temperature

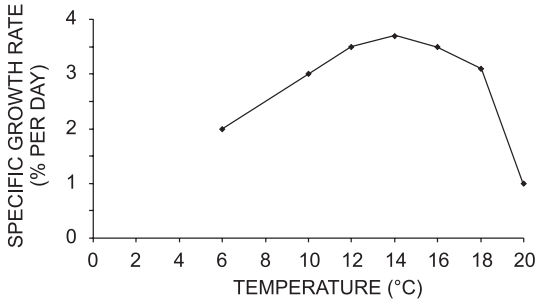


Fig. 8. After Otterlei & al. (1996): Specific growth rates of early juvenile cod (weight 2 - 20 g, reared in the laboratory) as a function of temperature.

change which makes it a very difficult task to single out mechanistic relationships to temperature. In the laboratory, however, where the various environmental factors can be kept constant or controlled, functional effects of temperature are easier to record. Such experiments have been conducted by Otterlei & al. (1996) and Otterlei & al. (1999) on larval and juvenile cod and by Jobling (1981) and Jobling (1988) on adult cod. Both the experiments for juveniles and adults show increasing growth rates up to a temperature of about 14 °C, then decreasing rapidly above 18 °C. Pedersen & Jobling (1989), however, found that sexually mature cod probably have the optimum growth temperature 2-3 °C lower than for the juveniles and younger adults. Fig. 8 shows the results of Otterlei & al. (1996) who measured the growth of larval and juvenile cod under various temperatures. It should be emphasised that the above-cited experiments were made for fish fed at satiation. The optimum growth temperature might be lower under food limitation as shown for sockeye salmon by Brett & al. (1969). In lack of similar experiments on Atlantic cod it is not possible to indicate how much the optimum growth temperature might be reduced under natural food concentrations. Brander (1995), however, who investigated weight at age (2-4 year-old-fish) of 17 Atlantic cod stocks in the temperature range from 1 to 11 °C showed that the weight of the cod increased through this temperature range, indicating that the optimum growth temperature is at least as high as 11 °C (Fig. 9).

While growth rates of satiated cod peaks at about 14 °C it starts to decrease dramatically first when the temperature exceeds 18 °C (Otterlei & al. 1996). Yin & Blaxter (1987) found a 50 % mortality of yolk-sac larvae at 15.5-18 °C, but Otterlei & al. (1996) still had more than 80 % survival from larval to juvenile stage at 20 °C. It is evident that the survival rate drops dramatically for both juveniles and adults above 20 °C just as the growth rate drops above 18 °C. McKenzie (1934) found that the up-

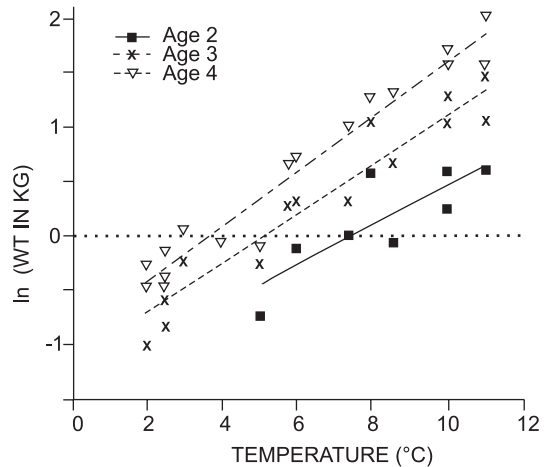


Fig. 9. After Brander (1995): Weight of 2-4 year-old cod for 17 Atlantic cod stocks as a function of ambient temperature.

per level of temperature tolerance in adult cod is 23-24 °C in laboratory experiments. Jobling (1988) reviewed the physiological and nutritional energetics of juvenile and adult cod and estimated the final temperature preferendum of cod at 13.5 °C. This is also close to where (15 °C) physiological processes such as the gastric evacuation rate, appetite, feeding and metabolic rate peak (Jobling 1988).

Are extreme low temperatures directly lethal for cod? One should expect that adults would have the ability to migrate out of the lethal areas. As mentioned above Ponomarenko (1984) recorded that extreme low winter temperatures in the Barents Sea may cause increased mortality of the north-eastern distribution of 1- and 2-group cod. On the other hand, Goddard & al. (1992) found that the juveniles of Northern cod continuously produce antifreeze proteins to avoid freezing. The adults would produce such proteins only after a certain period of time from the time of exposure to extreme cold water. This is probably due to the high energy requirements for producing the antifreeze proteins, and because they have the alternative to migrate out of the cold region. However, larvae and early juveniles have no other alternative than producing antifreeze proteins because of their limited ability to migrate. Whether these mechanisms also are found in other Atlantic cod stocks are left to show. Blood samples from Arcto-Norwegian cod during the winter 1993 showed absence of antifreeze proteins (Goddard pers. comm), but unfortunately all of the samples were from adult cod caught at temperatures above 0 °C. However, Leivestad (1965) kept Barents Sea cod permanently supercooled in laboratory for 2 months. At that time they were not able to identify antifreeze pro-



teins, but he observed that the potassium/sodium ratio of the tissue fluid decreased as the temperature decreased. Whether this result might be a proxy for possible production of antifreeze proteins or it is an indication of the opposite, i.e. development of a poor condition, is not known.

In conclusion, only the Atlantic cod stocks distributed at the uppermost range of ambient temperatures (i.e. in the southern North Sea, in the Irish Sea and in the Celtic Sea) may experience super-optimal temperature at certain times of the year (summer season) with respect to growth rates when fed to satiation. But in most years cod live at sub-optimal temperatures with respect to growth rates even in these rather warm regions. At the lower temperature range cod is found down to $-1\text{ }^{\circ}\text{C}$ and even lower. The major Atlantic cod stocks are all distributed at lower temperatures compared to those giving optimal growth at excess rations. More than 80 % of the Atlantic cod biomass is distributed at annual mean temperatures below $7\text{ }^{\circ}\text{C}$ (Fig. 2). It implies that most cod stocks, at least the adult part of the stocks, increase their growth rates over their entire natural range of temperatures ($1\text{--}11\text{ }^{\circ}\text{C}$) found in the North Atlantic.

THE INFLUENCE OF TEMPERATURE AND ADVECTION ON ZOOPLANKTON ABUNDANCE AND PRODUCTION

The importance of variable advection causing variability in zooplankton biomass has been a focused issue in many investigations in the Nordic Seas and adjacent continental shelves. Ishevskii (1961) claimed that fluctuations in the oceanographic conditions in the Barents, Greenland, and Norwegian Seas were mainly linked to variations in the intensity of influx of warm Atlantic water to the region. Degtereva (1979) demonstrated a positive correlation between the abundance of zooplankton biomass and the temperature in the Barents Sea. Later Russian zooplankton surveys conducted in the northeastern Norwegian Sea and in the western Barents Sea in spring (April/May) during the period 1959-1990 showed higher abundance in warm years than in cold years (Nesterova 1990), and the temperature effect was stronger for the Barents Sea than for the Norwegian Sea part. A similar Russian time series of summer cruises (in June/July) (Nesterova 1990) do not indicate such a relationship. The Russian time series also show that the zooplankton concentrations are generally higher in the Norwegian Sea than along the Norwegian coast and in the Barents Sea. This implies that variable volume transports onto the northern Norwegian shelf and into the Barents Sea, as demonstrated by Ådlandsvik (1989), may cause variations in the zooplankton biomass in these regions. This may also explain the stronger positive rela-

tionship between zooplankton biomass and temperature in the Barents Sea than in the Norwegian Sea because there is a negative gradient both in the zooplankton concentrations and in temperature downstream along the inflowing Atlantic water from the Norwegian Sea into the Barents Sea. The functional relationship to zooplankton abundance in the Barents Sea might therefore be caused by the advection of warm and zooplankton-rich Atlantic water from the Norwegian Sea rather than by temperature itself. Skjoldal & al. (1987) linked the variations in the zooplankton abundance in the western Barents Sea to the variations in the inflow of zooplankton-rich Atlantic water from the Norwegian Sea. Skjoldal & Rey (1989) showed that the large fluctuations in the zooplankton biomass in the Barents Sea in late spring during the period 1978-1985 were due to variations in the influx of Atlantic water from the Norwegian Sea. Helle & Pennington (1999) found a high positive correlation between the average zooplankton abundance in the western Barents Sea in June-July and the influx of Atlantic water in June from the Norwegian Sea to the Barents Sea.

To what extent copepod production in the Norwegian Sea is food limited or limited by temperature is not known, but interannual variations in zooplankton biomass in the region may vary by a factor of six (Nesterova 1990). Considering the interannual variation of the temperature, it is to be expected that temperature variations must be an important factor for regulating growth of copepods in the Norwegian Sea.

As pointed out in a former section, Cushing (1984) showed that there was a correlation between cod recruitment and the abundance of *Calanus* in the northern North Sea and pointed out that advection of copepods from the Norwegian Sea influenced the *Calanus* abundance in the North Sea. Heath & al. (1997) tested the hypothesis that concentrations of overwintering *C. finmarchicus* in the North Sea are not sufficiently apparent to support the abundances observed in the spring, and that the population is sustained by invasion from an overwintering stock located beyond the shelf edge. Their results showed that the main source of overwintering animals entering the North Sea in spring occurs at depths greater than 600 m in the Faeroe-Shetland Channel where concentrations greater than $100\text{ animals}\cdot\text{m}^{-3}$ are found in association with the overflow of Norwegian Sea Deep Water across the Iceland-Scotland Ridge. Further, Heath & al. (1999) compared model results and observations in the field of the abundance and distribution of *C. finmarchicus* in the North Sea and concluded that advection of spawning individuals from the Norwegian Sea Deep Water, mainly via the Norwegian Trench, is an important source for replenishing the stock of *C. finmarchicus* and long-term changes in this current might be one of the important



causes of the similar long-term changes observed in the abundance of *C. finmarchicus* in the North Sea (Colebrook & al. 1984). Stephens & al. (1998) correlated time series of annual mean zooplankton abundance from the Continuous Plankton Recorder Surveys in the North Sea during the last three decades with transports from a circulation model and found that in the northern parts more than half the variance of *C. finmarchicus* can be accounted for by inflow during winter. They concluded that the *C. finmarchicus* population enters the North Sea in early spring from the Atlantic water masses, and that the variability in *C. finmarchicus* abundance also was positively correlated with the NAO index.

In the Faroese region the importance of advection of *C. finmarchicus* from deeper water masses of Norwegian Sea origin have been studied by Gaard (1996) and Hansen & al. (1994). Gaard (1996) found that *C. finmarchicus* was transported from the deep Norwegian Sea Basin via Faroese-Shetland Channel and the Faeroe Bank Channel deep overflow. He indicated that the northern part of the Faeroe Plateau is receiving overwintering *C. finmarchicus* from the Faeroe Bank Channel. Hansen & al. (1994) found that one of the important conditions for having a strong recruitment of cod is that *C. finmarchicus* is advected from the Faeroe Bank Channel onto the Faroese shelf regions. They found evidence that during the period of recruitment collapse, spring winds were abnormally strong from the southwest, increasing the probability that cod eggs, cod larvae and copepods were transported off the shelf and possibly also affecting the primary production and hence the production of copepod nauplii.

The stage composition of *C. finmarchicus* in Icelandic waters indicates that the nearshore shelf populations in southern Iceland are replenished from the adjacent deep oceanic waters. Gislason & Astthorsson (1998) found that younger stages dominated the nearshore regions in May-June, while the adult stages were more abundant in the offshore regions. Astthorsson and Gislason (1998) found that the mean zooplankton biomass in Icelandic waters was higher in warm years than in cold years, particularly in the cool water masses off northern Iceland. They suggested this could be caused by three factors: Higher food availability for zooplankton in warm years, faster zooplankton growth in warm years and larger influx of zooplankton-rich Atlantic water in warm years.

It has been discussed whether the Irish Sea may harbour endemic populations of *C. finmarchicus* and *C. helgolandicus* or their occurrence are based on advection from north (Malin Shelf) and south (Celtic Sea) respectively. Gowen & al. (1997) did not find a significant horizontal gradient in the abundance of the two species based on two zooplankton stations in the Irish Sea, one in the

North Channel in the northern Irish Sea adjacent to the Malin Shelf and one in the stratified region in the more central parts of the Irish Sea, and concluded that the two species are breeding within the Irish Sea. On the other hand, Planque & Fromentin (1996) clearly concluded that the Irish Sea lies between the population centres of the two species with increasing concentrations of *C. finmarchicus* in the region to the north of the Irish Sea and increasing concentrations of *C. helgolandicus* in the Celtic Sea to the south. It should therefore be expected that a change in volume fluxes of water masses into the Irish Sea also would result in a corresponding change in advection of *Calanus* which would add to the locally produced biomass. Also it should be expected that a lower temperature would favour local production of *C. finmarchicus* since the temperature of the regions are at the higher range within the species distribution. This is supported by Williams (1985) who found that *C. finmarchicus* dominated the colder and deeper part of the water column below the thermocline in the Celtic Sea while *C. helgolandicus* dominated the upper warmer water.

In the northwest Atlantic the documentation on advection of copepods from oceanic regions to the shelf is more limited. Koslow & al. (1989), however, reported that the highest concentrations of the most abundant zooplankton species, *C. finmarchicus*, were found over deeper waters on the edge of the Scotian Shelf. Numerical modelling studies by Hannah & al. (1997) showed that *C. finmarchicus* on the Georges Bank was supplied from the deeper basin of the Gulf of Maine. Hence, these studies from the northwest Atlantic give support to the general mechanism shown from the northeast Atlantic that *C. finmarchicus* populations on the shelves might be replenished from adjacent deeper regions.

Is it possible that increased growth of copepods, induced by high temperatures, results in more food for larval and juvenile fish? Higher temperatures will influence generation time of copepods (Huntley & Boyd 1984). On the other hand, Carlotti & al. (1993) found in addition that the size of the stages of *C. finmarchicus* decreased with increasing temperature, and this effect was more pronounced for the copepodite stage V and for the adults where storage weight in the form of lipids is a larger fraction of the total weight than for the younger stages. Egg production of *C. finmarchicus* is dependent on the availability of food resources (Hirche 1989; Skjoldal & Melle 1989). Runge (1985) also found in the laboratory that the egg production of *C. finmarchicus* fed to satiation was temperature dependent, increasing from 26 eggs female⁻¹ d⁻¹ at 5.3 °C to 62 eggs female⁻¹ day⁻¹ at 13.5 °C. Temperature will therefore influence the initial number of copepod eggs spawned as a direct effect and indirectly if the phytoplankton production is en-

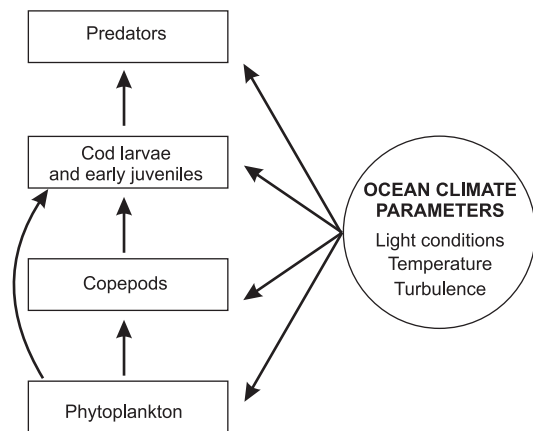


Fig. 10. Direct effects and indirect effects through lower trophic levels of climate parameters on fish growth.

hanced of higher temperatures. It has been reported that *C. finmarchicus* may produce two or even three generations per year (Conover 1988) even though the spring generation is the dominant one throughout its habitat. Increased temperatures may cause parts of the *C. finmarchicus* population to produce more than one generation per year, and in this way considerably increase the food availability for juvenile fish.

A SYNTHESIS ON EXPLANATORY MECHANISMS OF THE RELATIONSHIP BETWEEN TEMPERATURE AND RECRUITMENT OF ATLANTIC COD

The causal effects of temperature on cod populations growth and recruitment in the North Atlantic can partly be a direct effect by changes in physiological processes of cod and partly indirect effects through trophic transfer. I will here evaluate several of these possible pathways from temperature to cod recruitment:

1. The large temperature effects on adult growth measured in laboratory (Jobling 1981; 1988; Pedersen & Jobling 1989) compared with field observations of various cod stocks (Brander 1995) and within a stock (Michalsen & al. 1998) indicate that the direct influence of temperature on adult growth is a major factor. These authors all show that growth rate continues to increase all through the ambient temperature range, and consequently the optimum cod recruitment temperature at about 8 °C found by Planque & Frédou (1999) can not be explained by temperature-induced growth of spawning stocks.
2. Another possible pathway is that the optimum growth temperature is lower at sub optimal feeding con-

ditions that are normally found in nature. The laboratory experiments by Jobling (1981, 1988) and Pedersen & Jobling (1989) on juvenile and adults and by Otterlei & al. (1996, 1999) on larvae and early juveniles were conducted at excess food conditions. There are strong indications that optimum growth temperature of juvenile and adult cod of 13.5 °C cannot be considerable lower in the field since Brander's (1995) field data indicate no decline in growth rates up to the highest ambient temperature of 11 °C. The early stages, however, might show a lower optimum growth temperature as suggested by Blom (1999) since they are more exposed to lethally low food concentrations. Consequently, this effect cannot be neglected even though there are presently no data to confirm it. Campana & Hurley (1989) used field data from the region of Georges Bank-Gulf of Maine-Browns Bank to calculate the larval growth of cod under various environmental conditions. They used the ambient temperature as the environmental variable in their growth model and found that the optimum growth temperature was 5.9 °C. However, they did not measure the ambient food concentration (or other parameters of the water masses), and consequently this temperature value can not be interpreted as the functional optimum growth temperature, but should rather be interpreted as a proxy for the water masses giving optimum growth.

3. Growth and survival of larvae and early juveniles are probably more influenced by temperature through indirect effects. The simplest indirect effect of temperature on the growth is through the influence of the availability of the main prey species, *C. finmarchicus* (Fig. 10). *C. finmarchicus* feeds the entire ecosystem in the subarctic region of the North Atlantic as it is an important food item for pelagic fishes and thereby influence food conditions for adult cod, and it has a major direct influence on growth of larvae and early juvenile cod as they mainly prey on the nauplii and smaller copepodite stages of *C. finmarchicus* (Brander 1994). If *C. finmarchicus* has a lower optimal growth rate than 11 °C this might be an explanation why recruitment is inversely related to temperature at the upper range of ambient temperature. There are few studies on temperature-dependent egg production of *C. finmarchicus*. From Hirche (1990) and Hirche & al. (1997) it can be concluded that egg production increases continuously throughout the temperature range from -1.5 °C to 8 °C. Runge (1985) found higher egg production at 13.5 °C than at 5 °C, but overall the egg production was lower than in the experiments by Hirche & al. (1997), and thus they cannot be directly compared. It is therefore uncertain whether egg production maximises in the temperature range from 8 to 13.5 °C, but these experiments indicate at least that there is not a great decrease in egg production in the



upper temperature range from 8 to 13.5 °C. From this I find it unlikely that the decline in cod recruitment above about 8 °C as demonstrated by Planque & Frédou (1999) is linked to a temperature-induced decline in the egg production of *C. finmarchicus*.

4. It is also to be expected that the indirect effect of temperature acts through the phytoplankton production, i.e. the main food production for the copepods. The experiments above were made on female *C. finmarchicus* fed super-abundant food, and egg production is strongly dependent on food concentration (Hirche & al. 1997). Optimum egg production might be found at a lower temperature when food abundance is less than excessive. Trophodynamic modelling applied on the Northeast Pacific (Robinson & Ware 1994, Robinson 1994) demonstrate that a high temperature is beneficial for a high phytoplankton production and a high rate of trophic transfer from phytoplankton (diatoms) through zooplankton (copepods and euphasiids) to fish (Pacific hake and Pacific herring). This system of trophic transfer is quite similar to that of Atlantic cod. Hence it is quite probable that temperature might also act on Atlantic cod recruitment through trophic level one. However, there are no data for the Northeast Atlantic to conclude that the phytoplankton production is optimal at 8 °C and declines above that temperature.

5. This pathway is also linked through trophic transfer under the influence of advective transport of *C. finmarchicus* from its core regions to the fringes of distribution where the recruiting cod are feeding. As presented earlier in this paper the Atlantic cod stocks (Fig. 1) are distributed around the rim of the two major habitats of *C. finmarchicus* (Figs 4 and 5) within the North Atlantic Subpolar Gyre, that is the deeper parts of the Nordic Seas and the deep-sea region to the south of Greenland and to the west of Newfoundland. The copepod concentrations are on average more than 10 times larger in these regions than along the surrounding continental shelves where the cod stocks are found. The ambient temperatures of these two core regions for *C. finmarchicus* are 4–7 °C (Fig. 4) which are equal to the mid-range of cod stocks temperature habitats, e.g. the Icelandic and Faroese cod stocks. The Arcto-Norwegian cod is found at ambient temperatures lower than that of the core region of *C. finmarchicus*, while the North Sea cod and, particularly, the Irish Sea cod and Celtic Sea cod stocks are found at higher temperatures than that of the core region temperature of *C. finmarchicus*. These distributions can be pictured in a conceptual way as in Fig. 11. The Atlantic cod stocks are distributed around the fringes of the region of *C. finmarchicus* core abundance. The cod stocks located at the upper fringe of *C.*

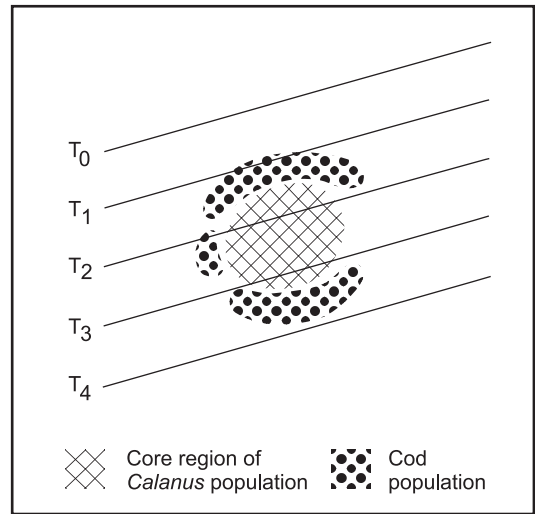


Fig. 11. Conceptual figure of spatial distributions of Atlantic cod stocks around the core regions of *C. finmarchicus* in the North Atlantic Subpolar Gyre. The temperature distribution is indicated by isotherms of increasing temperature from T_0 to T_4 .

finmarchicus distribution have a lower ambient temperature than in the core region. The cod stocks located at the lower fringe have higher ambient temperature, while the cod stocks on the left side fringe have an ambient temperature equal to that of the core region. An increased advection of water from the copepod rich core region to the fringes will result in improved food abundance for larval and juvenile cod resulting in better recruitment. If the increased advection is directed along a negative temperature gradient, i.e. towards the habitats of cod stocks at lower ambient temperature, the import of *C. finmarchicus* from the core region will be accompanied by an increased temperature (Fig. 12A). This is the situation for the Arcto-Norwegian cod documented by several authors with various data (Ishevskaia 1961; Degtereva 1979; Skjoldal & al. 1987; Helle & Pennington 1999). If the increased advection is directed along isotherms from the region of *C. finmarchicus* core abundance, the increased import of copepods will not be accompanied by a significant change of temperature (Fig. 12B). This is the situation for the Icelandic cod and in accordance to what was reported by Astthorsson & al. (1994) who found a positive correlation between cod recruitment and zooplankton abundance at the first feeding region, but no correlation with temperature. Also for the Faroese cod a similar situation has been described. Gaard (1996) and Hansen & al. (1994) explicitly focused on the importance of advection of copepods from the Norwegian Sea into the feeding areas of larval and juvenile Faroese cod. If the increased advection is directed along a positive

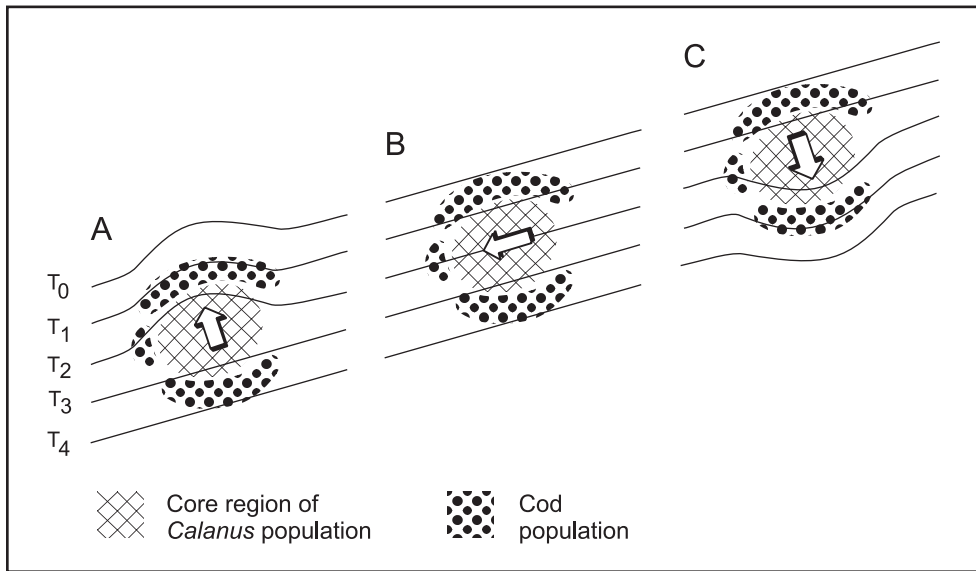


Fig. 12A. Conceptual figure of spatial distributions as in Fig. 11 under increased volume flux along a negative temperature gradient from the core region of *C. finmarchicus* to cod stocks at lower ambient temperature.

Fig. 12B. Conceptual figure of spatial distributions as in Fig. 11 under increased volume flux from the core region of *C. finmarchicus* to cod stocks at approximately equal ambient temperature.

Fig. 12C. Conceptual figure of spatial distributions as in Fig. 11 under increased volume flux along a positive temperature gradient from the core region of *C. finmarchicus* to cod stocks at higher ambient temperature.

temperature gradient i.e. towards the habitats of cod stocks at higher ambient temperature, the import of *C. finmarchicus* from the core region will be accompanied by a decrease in temperature (Fig. 12C). This is potentially the situation for the cod in the North Sea and particularly for the Irish Sea and Celtic Sea cod. As pointed out earlier the idea of the role of advection of *Calanus* from the Norwegian Sea to the northern North Sea as a factor in fish recruitment was already emphasised by Cushing (1984), and Dickson & Cushing (1974) showed that the advection of water masses from this region was accompanied by a lower temperature. Svendsen & al. (1995) found a positive correlation between strong cod recruitment and the low temperature in the subsurface water. Heath & al. (1999) who investigated the transport of copepod-rich water into the North Sea from the adjacent off-shelf regions to the north, confirmed by observations and modelling that advection is an important factor for the abundance of *C. finmarchicus* in the North Sea. For the Irish Sea it has been documented a highly significant negative correlation between temperature and cod recruitment (Planque & Fox 1998). It should be expected that higher recruitment is associated with an increase of water masses from north. However, there is no documentation that such a change also is accompanied by higher concentrations of *C. finmarchicus*. On the other

hand, there is clear documentation that there are higher concentrations of *C. finmarchicus* on the Malin Shelf to the north of the Irish Sea (Planque & Fromentin 1996), and therefore it should be expected that a higher influx of water from the north also should be accompanied by higher *Calanus* concentrations. The results of Campana & Hurley (1989) showed that optimum growth of larval cod was found in the water masses of 5.9 °C. They did not present the salinity of these water masses, but one interpretation of their result could be that the temperature was a proxy for copepod-rich Atlantic water masses of offshore origin.

Long-term changes in the abundance of *C. finmarchicus* in the North Atlantic have been linked to similar changes in the North Atlantic Oscillation (NAO). Fromentin & Planque (1996) and Planque & Taylor (1998) found that there had been a long-term decrease in the *C. finmarchicus* abundance in the region around the British Isles and an increase in the abundance of *C. helgolandicus* during the period when the NAO increased. Piontkovski & al. (in press) found an opposite response of the *C. finmarchicus* abundance in the Gulf of Maine to the NAO. In the northeastern Norwegian Sea and in the western Barents Sea, the Russian zooplankton time series by Nesterova (1990) also show an increase in the zooplank-



ton abundance. Zooplankton abundance based on time series from southwestern Icelandic waters (Astthorsson & al. 1994) show their own characteristic pattern of variability with large interannual variation but no clear long-term trend. These adverse patterns of variability in the zooplankton abundance around the North Atlantic Subpolar Gyre are not inconsistent with a change caused by variable advection of *C. finmarchicus* from the two core regions of the Gyre (Figs 4 and 5). An increase in the inflow of Atlantic water to the Nordic Seas could result in lower concentrations of *C. finmarchicus* in the Atlantic region around the British Isles which would be upstream of the core region in the Norwegian Sea (although also more complex responses with an increase in the return flux of overwintering *Calanus* in the deep water also might be expected (Backhaus & al. 1994)). Similarly, it is not inconsistent with an increase in the abundance of *C. helgolandicus*, because the waters around the British Isles are downstream of the core regions of *C. helgolandicus*. The increase of *C. finmarchicus* downstream to the core region in the Norwegian Sea (which would be the Barents Sea (e.g. Helle and Pennington 1999)) coincides with increased influx of the warm Atlantic water.

The question of the effect of local production versus advection on the abundance of zooplankton and its availability as food for fish is an important issue. As the individual life cycle of the plankton increases the importance

of the advection term increases. With a life cycle of several months, as is the situation for *C. finmarchicus*, the advection term may become very important. Aksnes & al. (1989) investigated the carrying capacity for fish in Masfjorden in western Norway and found that 90 % of the zooplankton production was advected from the outside of the fjord. The present paper does not address a similar quantification of the copepod advection on a basin scale. But this literature study shows that the advection of copepods from the North Atlantic Subpolar Gyre onto the adjacent continental shelves is similarly important for the carrying capacity on the shelves. Further the inverse response of Atlantic cod recruitment to temperature change in the upper and lower range of ambient temperatures is likely to be the result of advection of zooplankton from the core regions. Monitoring of the long-term changes in the oceans water mass fluxes would be an important issue in the task of assessing the ocean productivity, since the subsequent change in zooplankton abundance is expected to be lagged compared with the change in flux of water masses, and thus might have a predictive value.

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