

The Influence of Biological and Physical Processes on  
Early Juvenile Arcto-Norwegian Cod (*Gadus morhua* L.)  
with Special Emphasis on Zooplankton Abundance

by

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Dr. Scient. Thesis



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To my parents

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## Preface

It has been a long road to finish my doctor thesis, but to reach my goal I was very fortunate to receive help from a number of people whom I want to thank. First of all I want to thank my three advisors, Arne Johannessen, for being my official university advisor and providing me with comments and suggestions on the papers and the synthesis. Second, I want to express my sincere gratitude to Odd Nakken who became my advisor a little into my study and helped me get back on track when I needed it most. His comments and suggestions have always been of great help in addition to providing enormous encouragement and inspiration. Third, I want to thank Michael Pennington who has been my everyday support, mentor and my worst critic. He also helped me with the statistical problems and has been a very good co-author.

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*Kristin Helle*



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## List of papers

### Paper I:

Helle, K. 1994. Distribution of early juvenile Arcto-Norwegian cod (*Gadus morhua* L.) in relation to food abundance and watermass properties. ICES Marine Science Symposia, 198: 440-448.

### Paper II:

Helle, K., and Pennington, M. 1999. The relation of the spatial distribution of early juvenile cod (*Gadus morhua* L.) in the Barents Sea to zooplankton density and water flux during the period 1978 - 1984. ICES Journal of Marine Science, 56: 15-27.

### Paper III:

Helle, K. 2000. Distribution of the copepodite stages of *Calanus finmarchicus* from Lofoten to the Barents Sea in July 1989. ICES Journal of Marine Science (in press).

### Paper IV:

Helle, K. 2000. Does the midnight sun increase the feeding rate and hence the growth rate of early juvenile Arcto-Norwegian cod *Gadus morhua* in the Barents Sea? Marine Ecology Progress Series, 197: 293-297.

### Paper V:

Helle, K., Bogstad, B., Marshall, C. T., Michalsen, K., and Pennington, M. 2000. An evaluation of recruitment indices for Arcto-Norwegian cod (*Gadus morhua* L.). Fisheries Research, 48(1): 55-67.

## Background and objectives

Arcto-Norwegian cod (*Gadus morhua* L.) is one of the most important commercial gadoid species in the Northeast Atlantic (Garrod, 1988). The cod fishery has historically been and still is very important, and the large variations in cod abundance have been a matter of concern for centuries. Marine research on cod started in 1864 when G. O. Sars began his famous work on the biology of cod in Vestfjorden (Sars, 1879). Recruitment to the fishery varies greatly over time and thus it is crucial for management to have accurate and precise predictions of year class strength as early as possible. Hypotheses have been proposed that relate environmental quality with the feeding condition of larval fish and, ultimately, the year class success and strength (e.g. Hjort, 1914; Dragesund, 1970; Cushing, 1975; Lasker, 1975, 1978; Koslow *et al.*, 1985; Sinclair, 1988; Sundby and Fossum, 1990, Hansen *et al.*, 1994). A number of other hypotheses on when year class strength is established have been proposed, for example, during the egg and larval stages (Campana *et al.*, 1989; Sundby *et al.*, 1989; Astthórson *et al.*, 1994; Jákupsstovu and Reinert 1994; Anderson and Dalley, 1997), during the late larval and pelagic juvenile stages (Myers and Cadigan, 1993; Adams and Howard, 1996) or increased mortality during the early demersal stage (Beverton, 1984; Sissenwine, 1984).

Arcto-Norwegian cod spawn along a 1200 km coastline from mid-Norway to north Norway. The main spawning areas are in Vestfjorden and on the continental shelf outside Lofoten and Vesterålen between 67° 30' N and 69° N (Figure 1). Approximately 70 percent of the spawning takes place in this region (Sundby and Bratland, 1987). The time of spawning is remarkably consistent from year to year. Spawning starts in early March, reaches maximum intensity during the first weeks of April and terminates by the first half of May (Ellertsen *et al.*, 1987, 1989). The eggs and larvae drift north and north-eastward carried by the Norwegian Coastal Current and the Atlantic Current (Ellertsen *et al.*, 1981, Bergstad *et al.*, 1987). The advection of eggs, larvae and early juveniles is influenced by mesoscale circulation features created by the bottom topography of the shelf (Sundby, 1984). Because of a bottom topography induced gyre, early juvenile cod are especially abundant on Tromsøflaket Bank (Bjørke and Sundby, 1987; Sundby *et al.*, 1989). The

larvae and early juveniles caught in this clockwise circulation will be temporarily retained on the bank, while in other regions they will be subjected to rapid transport by coastal jets.

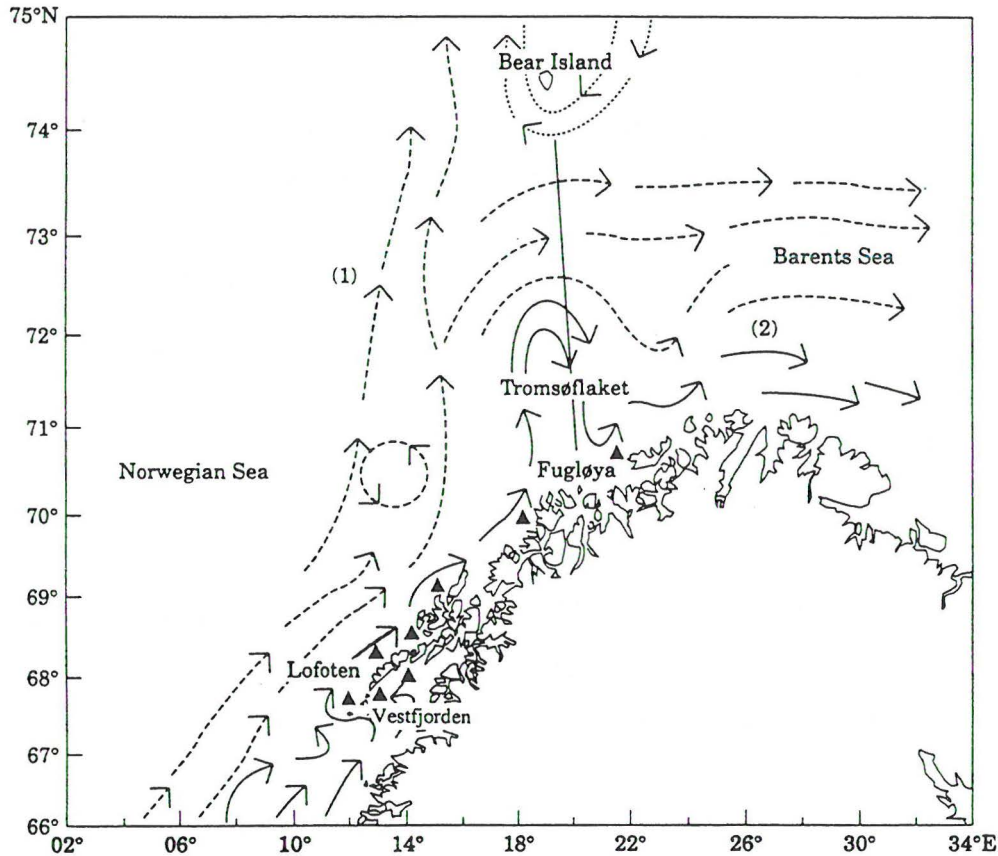


Figure 1. The main spawning areas for Arcto-Norwegian cod (denoted by ▲, adapted from Godø and Sunnanå, 1984; Sundby and Bratland, 1987) and the general system of water currents in the Norwegian Sea and the Barents Sea. Solid arrows denote the Norwegian Coastal Current, dashed arrows the Atlantic Current and dotted arrows, the Arctic Current. The West Spitsbergen Current branch is denoted by (1), and (2) is the North Cape Current branch (modified after Loeng, 1989a; Suthers and Sundby, 1993). The straight line denotes the section between Fugløya and Bear Island.

During the period 1977 through 1991, the Institute of Marine Research (Bergen, Norway) conducted an early juvenile fish survey along the coast of mid and northern Norway in June and July. The objectives of these surveys were to map the distribution of various fish species and to generate indices of abundance, with special emphasis on cod. Based on data from these surveys, Bjørke and Sundby (1987) examined the size distributions of



early juvenile cod from 1983 to 1985. Their analysis showed that early juvenile cod were on average 2-4 mm smaller in the northeastern part of the survey area compared with juveniles caught in the southwestern part. The early juveniles in the northeastern survey area should have been older and hence larger than in the southwestern area if they indeed drifted from the main spawning areas around Lofoten. To test this hypothesis, Suthers and Sundby (1993) used otolith microstructure techniques to examine the age and weekly growth of the early juvenile cod in 1988. They found that the juveniles in the north tended to be older and had a significantly lower growth rate compared with cod caught in the southwest. They concluded that temperature, either directly or indirectly, caused the difference in observed growth rates, which is confirmed by a number of other field studies (Sætersdal and Loeng, 1987; Ellertsen *et al.*, 1989; Houde, 1989; Pedersen and Jobling, 1989; Sundby *et al.*, 1989; Blaxter, 1992; Suthers and Sundby, 1993).

Laboratory experiments have been conducted to study the effect temperature has on growth. Fulton (1904) showed that juvenile cod kept in heated tanks (9.3°C) grew nearly twice as fast as those kept in colder water (4.5°C) and that fish in warm water had a far better appetite than those in cold water. Otterlei *et al.* (1999) found that an increase in temperature from 6 to 12°C generates a 17-fold higher dry weight after eight weeks.

Although the growth of larval and early juvenile cod seems to be influenced most by temperature, growth is also related to zooplankton abundance (Koslow *et al.*, 1985; Bailey, 1989; Suthers *et al.*, 1989; Karakiri *et al.*, 1989). Nesterova (1990) examined zooplankton biomass from 1959 to 1990 in the Barents Sea and found that it varied with water temperature. In warm years there is a large biomass, while in cold years biomass is low. The large inter-annual variation in biomass is due to variation in the stock of *C. finmarchicus* (Skjoldal *et al.*, 1987), which is the principal zooplankton species in the Barents Sea (Sysoeva and Degtereva, 1965; Skjoldal and Rey, 1989). The Norwegian Sea is a source of zooplankton for the Barents Sea and the amount of zooplankton transported from the Norwegian Sea into the Barents Sea depends on the rate of Atlantic inflow (Ozhigin and Ushakov, 1985). The abundance of zooplankton during summer is usually highest in the main current branches of the western entrance to the Barents Sea and

lowest in the central areas (Bliznichenko *et al.*, 1994; Degtereva *et al.*, 1985, 1986 a, b; Nesterova, 1990).

To examine the role that prey availability plays in determining the observed spatial size distribution of early juvenile cod, zooplankton was sampled at every station during the 1989 early juvenile survey. Instead of finding the smallest early juvenile cod in the east and the largest in the west as in Bjørke and Sundby (1987), the opposite was observed in 1989 (Helle, 1993). To examine if this was the beginning of a trend, the size distribution of early juvenile cod was determined for 1990 and 1991. Both these years showed that the size distribution was back to normal; the largest early juveniles were in the western part of the survey area (Helle, 1993).

Motivated by the Bjørke and Sundby (1987) study and results from my Cand. Scient. thesis (Helle, 1993), the main objectives of this thesis were:

1. Determine the effect of zooplankton abundance and spatial distribution on the size distribution and abundance of early juvenile cod.
2. Determine the relationship between the inflow of water to the Barents Sea and the abundance and distribution of zooplankton and early juvenile cod.
3. Determine other factors that may affect the growth of early juvenile cod.
4. Examine the relationship between a cohort's abundance as early juvenile cod and its abundance as recruits (i.e. three year olds).

## The Papers

### **Paper I: Size distribution of cod juveniles compared with food abundance**

In 1989, the spatial distribution of early juvenile Arcto-Norwegian cod (*Gadus morhua* L.) in the Barents Sea differed from the usual distribution. The juveniles were distributed much farther east than was observed in previous years, and the largest juveniles were also found farther east than usual. The highest abundance of early juvenile cod coincided with the areas of highest zooplankton biomass and a significant positive correlation was found between the abundance of early juvenile cod and the abundance of zooplankton. Although the largest juveniles (>40mm) were found in the areas with the highest zooplankton biomass, there was no significant correlation between the length of early juvenile cod and zooplankton biomass. No significant correlation was detected between length or abundance and temperature. However, there appeared to be a positive but not significant correlation between length and salinity.

### **Paper II: The relation between cod, zooplankton and wind driven flux in 1978-1984**

Arcto-Norwegian cod spawn along the coast off mid and northern Norway in March and April. The eggs and larvae are carried north by the currents and a large proportion of the early juveniles drift into the Barents Sea. Surveys of the early juvenile cod and zooplankton populations were conducted in late June and July from 1978 through 1984 off the coast of northern Norway and in the Barents Sea. Based on this survey series, the spatial distribution of the early juvenile cod was compared with the distribution and abundance of the zooplankton. In all years, there was more zooplankton, on average, in sub-areas in which early juvenile cod were observed than in those without early juveniles. The average water temperature was higher and salinity was lower in the sub-areas with cod than in the sub-areas without cod. The spatial distribution of the early juvenile cod and zooplankton appears to be influenced by the wind driven flux of water through the section between Fugløy and Bear Island and the correlation between the amount of zooplankton in the Barents Sea and the water flux was positive and significant.

### **Paper III: Advection of *Calanus finmarchicus***

The zooplankton biomass in the Barents Sea can vary by an order of magnitude from year to year. One reason for these large changes is the varying transport of *Calanus finmarchicus* from the Norwegian Sea into the Barents Sea. How much of the population is stationary in the Barents Sea

and how much is transported from the Norwegian Sea is unknown. Zooplankton samples were collected along the coast of North Norway from Lofoten into the Barents Sea during the early juvenile fish survey in July 1989. These samples were evaluated with special emphasis on *Calanus finmarchicus*, which were sorted to copepodite stages. By examining the distributional patterns of the different stages and the current pattern, the probable drift route of the zooplankton and its origin were determined. The different stages were distributed in very distinct bands, with the youngest stages in the south, while the older stages were found in bands stretching in an east-west direction with copepodite stage V farthest north and east. When these patterns are compared with current fields in 1989, the results support the theory that a large proportion of the *C. finmarchicus* stock is transported from the Norwegian Sea into the Barents Sea.

#### **Paper IV: The midnight sun and diurnal feeding**

The growth rate of Arcto-Norwegian cod juveniles in the Barents Sea during their first 4 months of life is about twice that of cod juveniles in areas farther south, such as Georges Bank and the Flemish cap. Cod larvae and juveniles in the Barents Sea experience 24 hours of daylight and thus the larvae and juveniles may continuously search for and capture prey. The stomach contents of cod juveniles caught in July 1989 were examined to determine if there were any diurnal patterns in stomach fullness or degree of digestion. No significant diurnal trends were detected. This suggests that feeding is continuous throughout the day, which enables the Barents Sea cod larvae and juveniles to grow more quickly than do cod juveniles farther south.

#### **Paper V: Evaluation of recruitment indices**

Abundance indices for Arcto-Norwegian cod (*Gadus morhua* L.) at various life stages were analysed to determine the index that provides the earliest reliable prediction of year class strength. The indices considered are: an egg abundance index; an early juvenile (approximately three-months old) abundance index; 0-group (age four to five months) abundance indices; bottom trawl and acoustic survey abundance indices for one-, two- and three-year-old cod, and VPA estimates of the abundance of three-year-old cod and of spawning stock biomass. Based on a regression analysis, a cohort's relative abundance as early juveniles is the best early indication of its abundance as two and three year olds.

## General introduction to factors affecting growth and survival of cod

The yearly abundance of Arcto Norwegian cod has for centuries been known to vary considerably. At the early juvenile stage the ratio between poor and good year classes is about 1:70 (Sundby *et al.*, 1989) while for 3 years old, the ratio is about 1:15 (ICES, 2000). In the past people thought that low abundance was a punishment for fishermen's indecent behavior. Today less godly hypotheses for the year-to-year variation have been proposed, although it has been very difficult to find "the" causal mechanisms for good or bad cod recruitment.

Hjort (1914) was one of the first to study the mechanisms behind cod recruitment and introduced the critical period hypotheses, i.e., that cod larvae would die from starvation if spawning did not coincide with annual primary production. As a refinement of Hjort's hypotheses, Cushing (1975) introduced the match-mismatch hypotheses. He observed that the time of cod spawning is almost constant while the time of maximum primary production is dependent on temperature and can therefore vary considerably from year to year. Hjort (1914) and Cushing (1975) focus on processes during the early larval stage, whereas Folkvord *et al.* (1994) suggest that there is also a "late critical period" in which early juvenile cod need an adequate amount of copepodites and the adult stage of *Calanus finmarchicus* to grow and survive.

Hjort's hypothesis is focused on starvation as the cause of larval mortality. The varying conditions described in his hypothesis are due to changes in climatic conditions (Koslow *et al.*, 1987; Cury and Roy, 1989; Ellertsen *et al.*, 1989; Loeng, 1989a, b; Dickson and Brander, 1993; Mann, 1993; Conover *et al.*, 1995; Ottersen and Sundby, 1995). Of the climatic factors, temperature is considered the most important factor affecting growth and survival. Ellertsen *et al.* (1987) and Ellertsen *et al.* (1989) come to the conclusion that good year classes never occur in cold years, they may be produced in warm years, and low temperatures during the egg stages always result in poor year classes. Even though temperature is assumed to be the most important factor influencing the growth of young cod (Sætersdal and Loeng, 1987; Campana and Hurley, 1989; Ellertsen *et al.*, 1989;

Pedersen and Jobling, 1989; Sundby *et al.*, 1989; Suthers and Sundby, 1993; Brander, 1994), temperature may only be a proxy for enhanced growth.

The amount of zooplankton in the Barents Sea varies considerably from year to year (Skjoldal *et al.*, 1987). It is not known if this is due to variation in the inflow of zooplankton from the Barents Sea or if it is due to variation in the endemic production. Zooplankton abundance is an important factor that determines the growth and survival of planktivorous fish stocks (Hjort, 1914; Skreslet, 1989; Cushing, 1995; Sundby, 1995; Nakken *et al.*, 1996) and low abundance leads to increased competition for food and cannibalism among the larval and pelagic juvenile cod (Folkvord, 1991). In addition other species, such as gelatinous planktivore predators, may be competitors for food (Fraser, 1970; van der Veer and Sadée, 1984; Frank, 1986). Competition for food and space between the settled 0-group and older fish may lead to increased mortality caused by increased cannibalism when the number of suitable habitats is reduced (Bailey and Houde, 1989; Hop *et al.*, 1992; Myers and Cadigan, 1993; Bogstad *et al.*, 1994; Nakken, 1994; Fromentin *et al.*, 1997; Bjørnstad *et al.*, 1999).

Hjort (1914) also hypothesized that larvae can drift out of favorable habitats and into less favorable ones. An example of this may occur in years when the currents drive the larvae and juveniles far to the west. If the juveniles are in deep water areas at the time of settling, high mortality is quite likely.

Not only currents but also the wind velocity may influence survival. The larvae and early juveniles are in the mixed layer, and therefore variable contact rates with prey induced by wind mixing may be an important regulatory mechanism for year class formation (Rothschild and Osborn, 1988; Sundby and Fossum, 1990).

Also processes before spawning may influence the success of a year class. Variation in year-class strength has been attributed to variation in the reproductive condition of the spawners, often called “the maternal effect”, which influences the amount and quality of egg production (Marshall *et al.*, 1998, 1999).

## Climatic changes in the Barents Sea

The connection between cod recruitment and climate changes has been studied extensively and Mann (1993) states: “*If it becomes possible to forecast fish stock changes from changes in atmospheric and ocean climate, this is likely to be of considerable assistance to management.*” To reach this goal, if it can be reached, one needs extensive knowledge about climate changes, the forces that drive the changes and how recruitment is influenced by these variations. In the search for correlations between environmental factors and recruitment care needs to be taken. Shepherd *et al.* (1994) state that:

*“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 invariability leads to a range of correlation coefficients which make it very difficult to decide whether or not a result might have occurred by chance.”*

The climatic conditions in the Barents Sea are closely related to the inflow of Atlantic water. Variation of the inflow is due to changes in the atmospheric conditions over the north Atlantic, with high and low pressure areas directing the wind and hence the water currents. Also local high and low pressure systems have an effect on the inflow of water into the Barents Sea (Loeng *et al.*, 1997). The climate in the Barents Sea alternates between warm and cold periods, and the length of each period is between 2.6 and 17.5 years (Loeng *et al.*, 1992). The warm periods are characterized by low air pressure, cyclonic circulation in the atmosphere, increased Atlantic inflow and little ice coverage. The cold periods are characterized by high air pressure, anti-cyclonic air circulation, decreased Atlantic inflow and more extensive ice coverage (Ådlandsvik, 1989; Ådlandsvik and Loeng, 1991). Salinity also varies and is synchronized with the variation in temperature (Loeng, 1989a).

Another process that influences the inflow of Atlantic water is the outflow of cold bottom water. Dense bottom water during winter is caused by cooling and ice formation (Midttun, 1985). It forms over the Central Bank and the shelf area of Novaya Zemlya and flows into the eastern basin, which occasionally is almost filled with this cold water. The

bottom water leaves the Barents Sea through the strait between Novaya Zemlya and Frans Josef Land and the outflow is replaced by inflowing water from the west (Loeng *et al.*, 1992). Thus outflow of water takes place for at least two reasons: first, the bottom water driven by its own density flows out of the Barents Sea, or second, an increased inflow of Atlantic water of higher density pushes the bottom water out. The latter explanation is, according to Ådlandsvik and Loeng (1991), the most likely. It is also the most probable explanation for the water transport patterns in 1989 and 1990. In early 1989, a large inflow of warm Atlantic water began. This inflow of water caused an outflow of dense bottom water between September 1989 and September 1990 (Loeng *et al.*, 1992). The inflow of Atlantic water continued in 1991.

### **Temperature**

Temperature is assumed to be the most important factor influencing the growth of young cod (Sætersdal and Loeng, 1987; Campana and Hurley, 1989; Ellertsen *et al.*, 1989; Pedersen and Jobling, 1989; Sundby *et al.*, 1989; Suthers and Sundby, 1993; Brander, 1994). Kislyakov (1959, 1961) came to the conclusion that there is a strong relation between the yield of a year class and the average water temperature during spawning. It has also been hypothesized that warmer temperatures stimulate gonad production so that a higher number of eggs are produced (Sætersdal and Loeng, 1987).

Sundby (2000) summarized the way temperature influences cod recruitment in different parts of the North Atlantic. He points out that in southern areas, such as in the North Sea, increased temperature leads to reduced cod survival (Dickson *et al.*, 1974) while in northern areas, such as in the Barents Sea and Greenland (de Young and Rose, 1993), increased temperature has a positive effect on survival. For the Faeroese and the Icelandic cod, no correlation between abundance at the 0-group stage and temperature was found (Astthorson *et al.*, 1994; Brander, 1995).



One of the most famous examples of how temperature influences cod's abundance and distribution is the cod stock off the west coast of Greenland. The stock appeared in the 1920s and disappeared in the 1970s with a peak biomass in 1950 of about 4 million tons (Buch *et al.*, 1994). The northern hemisphere underwent significant climatic changes around 1920 and water temperature increased off west Greenland. The warm period lasted until the end of the 1960s. It is not clear if it was the temperature that provided better conditions for survival and growth of cod or if it was due to increased inflow of cod larvae from southwestern Iceland along the Irminger current.

Although a number of possible explanations for the decline in the cod stock off Newfoundland have been given, such as over fishing and heavy predation by seals, it is also a fact that temperature has declined. A cooler ocean climate started in 1988 and in 1991 the Northern cod stock collapsed (Sundby, 2000). The cold conditions still prevail and the cod stock has not shown any sign of recovery (Haedrich and Hamilton, 2000).

### **Wind and currents**

The spatial distribution of early juvenile and 0-group cod varies from year to year. It has been suggested by Randa (1984) and Muchina *et al.* (1987) that the intensity of the inflow of Atlantic water into the Barents Sea influences the distribution of 0-group cod, and that the spatial distribution is determined by the strength of the current transport from the spawning ground. They also conclude that a high level of Atlantic inflow probably results in an easterly distribution of the 0- group in late August-September. At the early juvenile stage in June and July, the currents also play an important part in distributing the juveniles.

Based on the spreading pattern of the early juvenile cod in 1989, the strong inflow of Atlantic water appears to be the explanation for the easterly distribution of early juvenile cod and zooplankton (**Paper I, II and III**). In 1990, the distribution was more westerly and the main concentration of cod juveniles was found in the West Spitsbergen Current,

which indicates a large transport of water by this branch of the current system (Helle, 1993). In 1991, the concentration of juveniles had a more easterly distribution, and the flow into the Barents Sea was strong. These observations are confirmed by the current measurements modeled by Ådlandsvik *et al.* (1999). They estimated that there was a medium inflow of water into the Barents Sea in 1990 and a strong inflow of water in 1991.

The current patterns determine the nursery areas each year and the currents may also transport the larvae and juveniles out of these areas. Juveniles swept out of a nursery area were earlier considered lost to the system, but later investigations show that this may not be the case. Using a 3-D baroclinic hydrodynamic model, Ådlandsvik *et al.* (1999) examined different drift routes for Greenland halibut eggs and larvae under different current scenarios. The inspiration for this study was that they had observed that in spite of very few recruits found in the usual nursery areas, some year classes turned out to be much larger than predicted. Based on their model, they found that Greenland halibut could drift to areas farther north than expected and therefore were not in areas normally surveyed. The model also demonstrated that it is possible for particles with a westerly distribution to drift with the currents north and then west toward the coast of east Greenland. In years with a very westerly distribution of early juvenile cod, it is generally assumed that they are lost because they are carried to areas too deep for bottom settling. Alternatively the juveniles may drift to the coast of eastern Greenland, though this possibility has yet not been examined.

In other areas currents play an important role in the distribution, loss and import of larvae and juveniles. Bjørke and Sætre (1994) found that autumn spawned North Sea herring drift from the east coast of Scotland to the coast of southern, western and mid Norway. They also observed that juvenile seithe and haddock drift from the northern parts of the North Sea to the coast of mid-Norway, and finally that capelin spawned on the coast of Iceland are found in areas along the coast of mid-Norway. Iceland also loses eggs and larvae to Greenland. From the spawning grounds off the southwestern coast of Iceland, eggs and larvae usually are transported along the coast eastward and then north and east

to the northern coast of Iceland (Buch *et al.*, 1994). During some years the Irminger current transports eggs and larvae westward away from Iceland to the coast of east Greenland. It is not known how large this transport is and how much it influences the abundance of cod around Iceland or in east Greenland. However, tagging experiments show that it is rare that adult cod migrates from Iceland to Greenland, while a migration from Greenland to Iceland has been observed more frequently (Schopka, 1994).

On Georges Bank the yearly circulation pattern varies causing larvae in some years to be swept off the bank. The southeast flank of Georges Bank is particularly vulnerable to advective losses during periods of strong northerly wind stress (Walford, 1938; Cohen *et al.*, 1986). Larvae are also transported away from the bank by large storms, Gulf Stream rings or a combination of both (Serchuk *et al.*, 1994). Abnormal wind stress may also cause recruitment failure. For example, on the Faroe Plateau 0-group abundance was negatively correlated with wind stress towards the northeast during the period 1961 through 1991 (Hansen *et al.*, 1994).

These observations show that currents, wind, storms and other phenomena cause variations in the distribution and survival of fish eggs and larvae. Loeng *et al.* (1989) studied the general current pattern and the mesoscale current features in the Barents Sea important for the transport and dispersion of planktonic organisms and passively drifting pelagic fish larvae. They concluded that current tracks revealed a much more complex circulation pattern than indicated by earlier investigations (Ljøen, 1962; Sundby, 1976; Loeng and Sundby, 1986; Midttun and Loeng, 1987). **Paper II** shows that the wind driven current also influences the distribution of both early juvenile cod and zooplankton. A significant correlation was found between the wind driven flux through the section from Fugløy to Bear Island and zooplankton abundance in the Barents Sea. This result underlines the importance of including the wind driven flux as a factor influencing the abundance and distribution of both the early juvenile cod and the zooplankton.

## Zooplankton distribution and production

The advective transport of zooplankton by currents is known to vary with the rate of Atlantic inflow (Ozhigin and Ushakov, 1985). The main zooplankton species in the Barents Sea is *Calanus finmarchicus* (Sysoeva and Degtereva, 1965; Skjoldal and Rey, 1989). Zooplankton biomass in late spring and early summer in the north-south section of the central Barents Sea has had large inter-annual variations (Rey *et al.*, 1987), mainly due to variation in the stock of *C. finmarchicus* (Skjoldal *et al.*, 1987).

*C. finmarchicus* in the Norwegian Sea over winters in deep water. In spring, the mature females migrate upwards in the water column, where they spawn and die (Østvedt, 1955; Mauchline, 1998). Adults, eggs and nauplii are carried by the currents, and varying amounts are transported into the Barents Sea. The seasonal vertical migration interacts with fluctuations in the ocean currents. The inflow of water occurs in sporadic pulses and the timing and strength of the inflow will, therefore, determine the amount of zooplankton transported. If an inflow occurs during late autumn and winter, the transport of zooplankton will be low, and if an inflow takes place during spring and summer, the transport of zooplankton will be high (Skjoldal *et al.*, 1992). Consequently, changes in the current system will influence the growth of plankton feeders by varying the amount of prey (Loeng, 1989b). For a number of fish species, zooplankton is an important prey organism, e.g. capelin (Hassel *et al.*, 1991), cod (Lebour, 1918, 1919, 1920; Goodchild, 1925; Marak, 1960; Wiborg 1960; Sysoeva and Degtereva, 1965; Thorrisson, 1989; Helle 1993; **Paper I**), Greenland halibut (Michalsen and Nedreaas, 1998); herring (Dalpadado, 1993); haddock (Burgos and Mehl, 1987), polar cod (Ajiad and Gjørseter, 1990) and redfish (Dolgov and Drevetnyak, 1993, 1995). Thus knowledge of zooplankton abundance and distribution in the most important nursery areas for larval fish would provide a good indication of growth and survival conditions.

It is not known how much of the *C. finmarchicus* population is endemic and how much is transported into the Barents Sea. Pedersen (1995) constructed a model to determine the amount of zooplankton in the Barents Sea that is advected from the Norwegian Sea. His

results indicate that even with ideal conditions in the Barents Sea for endemic production, the advected biomass of *C. finmarchicus* is between six and ten times larger than the endemic production.

Nesterova (1990) examined zooplankton biomass in the Barents Sea from 1959 to 1990 and found that biomass is positively correlated with water temperature, that is in warm years there is a large biomass while in cold years biomass is low. **Paper II** demonstrates that there is even a stronger correlation between short-term wind driven flux and zooplankton abundance. In spite of high temperatures, Skjoldal and Rey (1989) and Skjoldal *et al.* (1992) found a record low zooplankton biomass during the summer of 1983. Neither Nesterova (1990) nor **Paper II** supports this observation, but these papers include data from areas farther south and west. The zooplankton biomass measurements used in Skjoldal and Rey (1989) and Skjoldal *et al.* (1992) were taken relatively far north (at 74, 75 and 76°N) and east in the Barents Sea and hence in areas probably not as strongly influenced by the inflow as are the more southwesterly areas. Internal processes, such as outflow of heavy bottom water, may influence the abundance of zooplankton in the central areas. During the winter of 1982 and 1983 a large outflow of bottom water and an inflow of Atlantic water took place. This outflow of heavy bottom water may have lead to a transport of over wintering *C. finmarchicus* out of the Barents Sea, which may be an additional cause for the very low zooplankton abundance in the areas examined by Skjoldal and Rey (1989) and Skjoldal *et al.* (1992). Sampling variability may also have caused the low biomass estimates.

The horizontal distribution of zooplankton during summer typically shows a pattern of high biomass in the main current branches in the western entrance of the Barents Sea and lower biomass in the central areas (Bliznichenko *et al.*, 1984; Degtereva *et al.*, 1985, 1986 a, b; Nesterova, 1990; **Paper II**). A discrepancy in the usual distribution of zooplankton biomass was found in 1989; the main concentration of zooplankton biomass was located much farther east than usual, with branches stretching eastwards out of the survey area (**Papers I and III**). Maps of the horizontal distribution of nauplii and the different copepodite stages of *C. finmarchicus* show that the main concentrations of all

stages extended from the south toward the northeast, with the smallest stages in the south and the largest in the north and east. The distribution of zooplankton in 1978 through 1984 and in 1989 (**Papers I and II**) and of the different copepodite stages in 1989 (**Papers I and III**) supports the theory that for the western Barents Sea the inflow of *C. finmarchicus* from the Norwegian Sea is a very important component of the total zooplankton biomass.

Temperature is a key factor for the development of *Calanus finmarchicus* that affects survival, egg production, spawning time and development of the nauplii and copepodite stages. Pedersen (1995) found that constantly high temperatures reduce the mortality rate of *C. finmarchicus*. He also observed that increases in temperature, even very slight ones, during spring tend to reduce mortality. Egg production is also related to temperature. Runge (1985) conducted laboratory experiments that showed that egg production by *C. finmarchicus* was strongly temperature dependent. At 5.3°C egg production was 26 eggs female<sup>-1</sup>d<sup>-1</sup> and when the temperature was increased to 13.5°C, egg production increased to 62 eggs female<sup>-1</sup>d<sup>-1</sup>. Egg production of *C. finmarchicus* also seems to be strongly dependent on the amount and quality of food available to the mature females before spawning (Melle and Skjoldal, 1989; Hirche, 1996). Runge (1985) concluded that egg production of *C. finmarchicus* on the Scotian shelf is food limited.

Temperature may influence the survival of cod larvae and early juveniles in a number of different ways. The timing of cod and Calanus spawning is an important factor for determining year class strength (Cushing, 1975). The spawning time of Arcto-Norwegian cod is remarkably consistent from year to year and is relatively insensitive to normal variations in temperature, with about 50 percent of the spawning occurring around 1 April (Ellertsen *et al.*, 1989; Jonsson, 1982). Calanus, on the other hand, is much more dependent on temperature. The spawning of Calanus is triggered by the spring bloom of phytoplankton (Marshall and Orr, 1955). The development time of copepod eggs and nauplii is directly related to temperature. However, temperature affects the timing of spawning for *C. finmarchicus* significantly more than it affects the development rate. Spawning is delayed by about 1.5 months in the coldest years as compared with the warmest years (Ellertsen *et al.*, 1989). In years with extreme temperatures, both high and

low, the mismatch between first feeding cod and nauplii production is large and may be the reason that weak year classes are produced. Figure 2 illustrates the scenarios in extremely warm and extremely cold years (Per Solemdal, personal communication). The largest cod females, who produce the largest eggs and larvae, arrive at the spawning grounds first (Solemdal, 1997) and thus the mismatch between the largest first feeding cod larvae and nauplii is greatest in extremely cold years (see Figure 2).

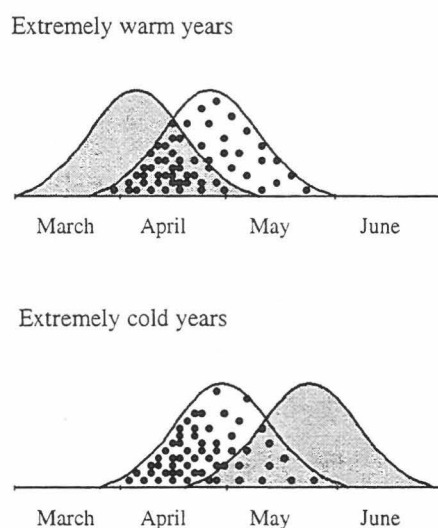


Figure 2. The nauplii production (marked with gray) and first feeding cod larvae in extremely warm and extremely cold years. The dots indicate the concentration of the largest first feeding cod larvae.

Although temperature is important for the production and abundance of zooplankton in the Barents Sea, in areas farther south, such as the Faroe Plateau, temperature does not seem to affect the production of zooplankton (Hansen *et al.*, 1994). It appears that wind stress on the shallow bank areas around the Faroe Islands is correlated with primary production, nauplii production and variations in the Faroe cod year-class strength. Hansen *et al.* (1994) hypothesized that increased wind stress delays the stabilization of water stratification, which negatively affects primary production. In spring zooplankton drift from over wintering grounds to the shallow bank area. A delayed or a low amount of primary production will, therefore, have a negative effect on the production of nauplii, the most important prey for larval cod in this area.

### **The distribution of cod in relation to zooplankton distribution**

Sysoeva and Degtereva (1965) state, regarding the distribution of zooplankton and cod juveniles in 1959-1961, that "In June a coincidence of quantitative distribution of cod larvae with that of *C. finmarchicus* was observed in separate branches of the currents in all 3 years investigated." A significant positive correlation was found between the abundance of zooplankton and the abundance of early juvenile cod at a station in 1989 (**Paper I**) and a significantly higher average zooplankton biomass was found in areas with cod than in areas without cod in the years 1978-1984 and 1989 (**Paper I and II**). The highest abundance of early juvenile cod was in areas with the highest abundance of the largest copepodite stages (CIV and CV) of *C. finmarchicus*, whereas the smallest copepodites, the nauplii and *Oithona similis*, were more abundant in areas without cod (Helle, 1993; **Paper I**). Comparisons of the distribution of early juvenile cod in the period 1978 to 1991 with the zooplankton distribution indicate a distinct overlap of the highest concentrations of cod and the highest concentrations of zooplankton (data from Bjørke and Sundby, 1987, Bjørke *et al.*, 1987, 1988, 1989; Helle, 1993; Nesterova, 1990; **Papers I, II and III**). Although the distribution of cod juveniles and zooplankton in 1989 was different from previous and successive years (**Paper I**), the distribution is consistent in that there was a large overlap of high concentrations of cod juveniles and zooplankton.

In a similar study, Morse and Meise (ms) related five variables to the density of fish larvae on Georges Bank during the period 1978-1985. The variables were temperature, depth, stratification, chlorophyll *a* and zooplankton density. Of the five variables, only zooplankton density was both significantly and positively associated with larval fish density in all months. In the southern Gulf of St. Lawrence Runge *et al.* (1999) examined the relation between mackerel recruitment and zooplankton biomass during the period 1981 to 1991 and found a positive and significant correlation. Blom *et al.* (1991) studied the association between feeding conditions and the production of cod fry in semi-enclosed marine ecosystems in western Norway, and Astthórsson *et al.* (1994) examined the distribution, abundance and length of early juvenile cod in relation to environmental conditions in Icelandic waters. In both studies there was a significant positive correlation between zooplankton abundance and the abundance of cod fry. The observations that



there are more cod juveniles, on average, in areas with a high abundance of zooplankton support the theory of Folkvord *et al.* (1994) that in addition to the critical period at the larval stage, there is also a late critical period for the juveniles in which they need an adequate amount of *C. finmarchicus* to grow and survive.

### **Growth and size distribution of juvenile cod**

A number of laboratory studies of the growth and survival of cod indicate that fast growth enhances the survival rate of larval and juvenile cod (Campana, 1996; Meekan and Fortier, 1996; Otterlei *et al.*, 1999). These results are supported by field data. For example, there is a positive correlation ( $r^2=61\%$ ,  $p < 0.001$ ) between the abundance index for early juvenile cod (**Paper V**) and average length for the same stage (data from Loeng *et al.*, 1995). Ottersen and Loeng (2000) found a positive correlation between the average length of pelagic 0-group cod and abundance at age 3, which was stronger than the correlation between estimated abundance at the 0-group stage and at 3-years old.

Among the factors influencing the growth rate of young fish in the field, temperature appears to be the most important (Houde, 1989; Blaxter, 1992). Increased growth rates at higher temperatures in the Barents Sea are also reported by Nakken and Raknes (1987), Loeng and Gjørseter (1990), Loeng *et al.* (1995) and Sundby (2000). All these authors agree that although a positive and significant correlation exists between the growth of larval and early juvenile cod and temperature, the mechanisms driving the correlations are complex.

Although temperature is considered one of the most important factors for cod growth, no correlation between temperature and average length of early juvenile cod at a station was detected during the period 1989-1991 (**Paper I**). A significant positive correlation between salinity and average length was found in 1990 and 1991 and a weak, but not significant correlation, was observed in 1989. The probable explanation for the weak correlation in 1989 is that temperature and salinity increased simultaneously in the southern Norwegian Sea, the West Spitsbergen Current and in the Barents Sea (Loeng *et*

*al.*, 1992; see Figure 5 in **Paper III**). Usually there is a temperature lag of about six months between the western and eastern Barents Sea (Loeng, 1989 a; Loeng *et al.*, 1992). The reason that length was correlated with salinity but not with temperature is, perhaps, that salinity changes to a lesser extent and more slowly than temperature after a water mass enters the Barents Sea. Therefore, salinity reflects more the history and origin of the water masses than does temperature (Loeng, 1989a). Gundersen (1993) found a correlation between length and salinity but not between length and temperature for larvae and 0-group capelin in the Barents Sea during the period 1981-1991.

The growth of larval and juvenile cod depends on the density of zooplankton (**Paper II**). Indeed, for the years 1983 to 1985 and 1989 the largest early juveniles were found in areas of the Barents Sea where zooplankton abundance was highest (Bjørke and Sundby, 1987; Nesterova, 1990; **Papers I, II and III**). For example, Figure 3 shows the size distribution of cod in 1984 (Bjørke and Sundby, 1987) and Figure 4, the zooplankton distribution for the same year (Nesterova, 1990). For comparison Figure 4 also shows the zooplankton distribution in 1989. Both the cod juveniles and the zooplankton had a very westerly distribution in 1984 with the largest sizes farther to the west. In 1989, the largest early juvenile cod and the highest abundance of zooplankton were in the east (**Papers I and III**).

However, larval survival is also a function of prey size (Jones and Hall, 1974). The right prey size range is not only important for growth at the larval stage, but also for the early juvenile stage (Volk *et al.*, 1984; Suthers *et al.*, 1989; Folkvord *et al.*, 1994). Based on these observations it is likely that the largest juvenile cod would be in areas with the highest abundance of zooplankton prey of appropriate size. Helle (1993) found that the proportion of *C. finmarchicus* copepodite, stages CIV and CV, in the stomachs of juvenile cod was higher than in the sea, which indicates that the early juvenile cod prefer larger stage copepodes. Size selection was apparent in all the sub-areas, but was strongest in the Lofoten area, which had the lowest proportion of CIV and especially CV in the sea compared with the areas farther north and east (see Table 1 in **Paper III**). In addition, the average length of the early juvenile cod in each area was positively correlated with the average density of stages CIV and CV (Figure 5).

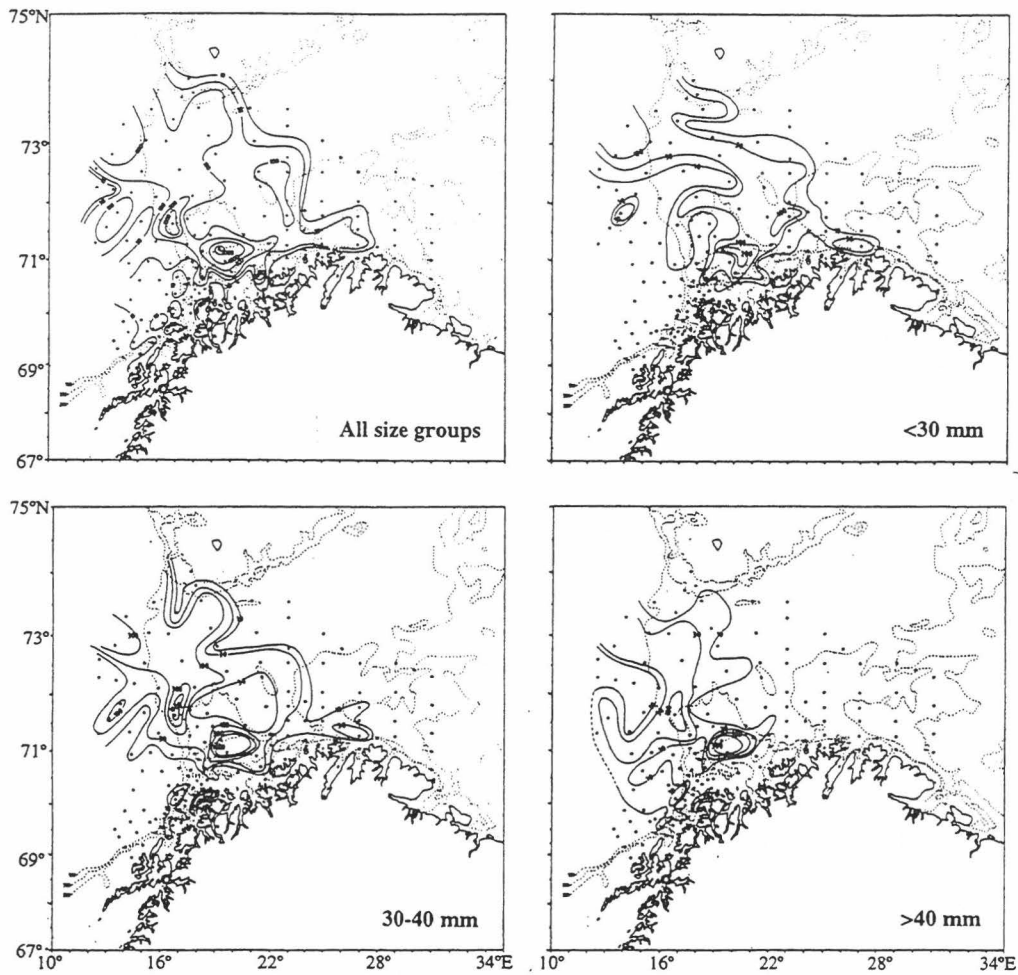


Figure 3. Distribution of early juvenile cod, 24 June-20 July 1984. Contours are the number per trawl hour, for all sizes, length: <30mm, 30-40 mm and >40 mm (modified after Bjørke and Sundby, 1987).

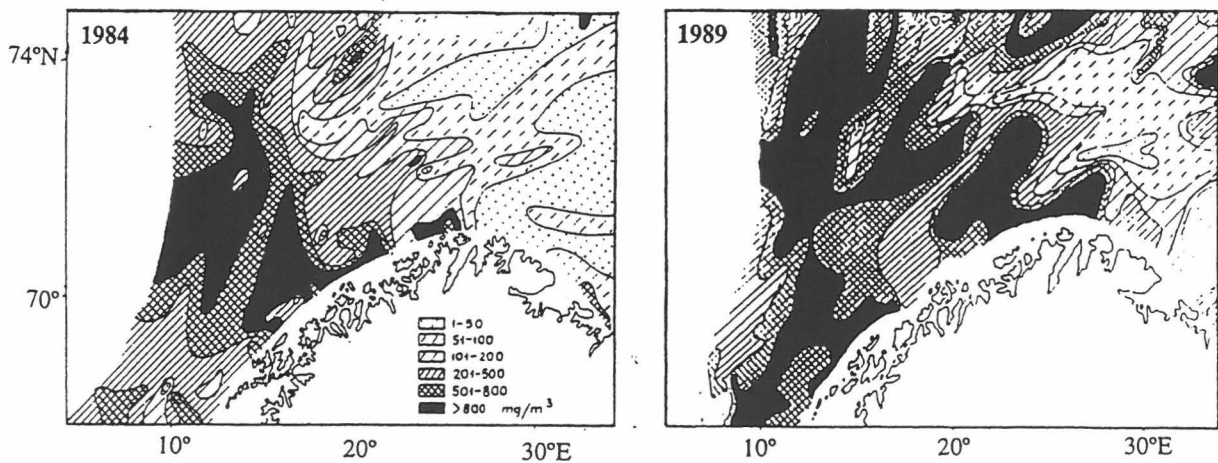


Figure 4. Biomass of zooplankton ( $\text{mg}/\text{m}^3$ ) in the 0-50 m layer in June/July 1984 and 1989 (modified after Nesterova, 1990).

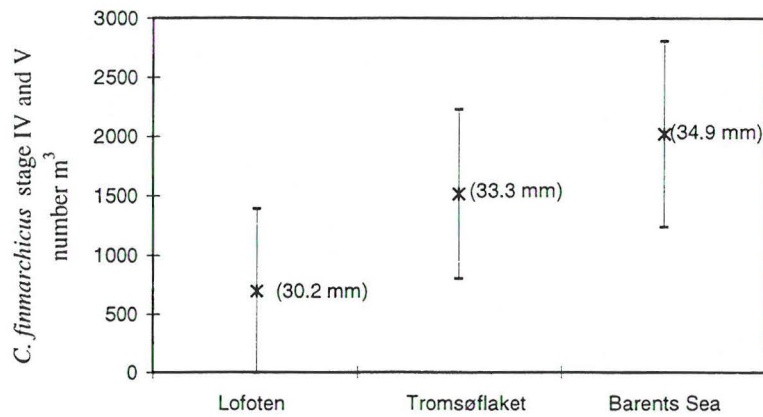


Figure 5. Average number  $m^{-3}$  of *Calanus finmarchicus* copepodite stages CIV and CV in three sub-areas. The lines denote 95% confidence intervals. In parentheses are the average lengths of the juvenile cod. (Data from Helle, 1993).

Blom *et al.*, (1991) and Astthorsson *et al.*, (1994) found a significant positive correlation between abundance of juvenile cod and abundance of zooplankton though no correlation was found between the average length of cod and zooplankton biomass. These results are consistent with the results for 1989; the largest juveniles were found in areas with the largest, on average, amounts of *Calanus finmarchicus*, especially stages CIV and CV, but no significant correlation was found between average size and zooplankton biomass at a station (**Paper I**). Thus it appears that zooplankton abundance may influence the survival of early juvenile cod. This observation also supports the claim by Koslow *et al.* (1985) that the condition of larval cod appears to be correlated with prey abundance and prey size, and that the relative prey availability per larvae may account for growth differences (van der Meeren *et al.*, 1994).

### **Growth rates in the Barents Sea compared with areas farther south**

The daily growth rate of larval and juvenile cod in the Barents Sea is higher than in areas farther south. Daily growth rates for juvenile cod off Nova Scotia are about half that of the juveniles in the Barents Sea (Suthers and Sundby, 1996). Other studies have also shown that larval and juvenile cod in areas farther south grow more slowly compared with the growth observed in the Barents Sea (Campana and Hurley, 1989; Suthers *et al.*, 1989; Thompson and Harrop, 1991; Anderson *et al.*, 1995; Anderson and Dalley, 2000).

To compare growth rates, coastal cod larvae and juveniles from the southwestern part of Norway at about 60°N were reared in the same enclosure as Arcto Norwegian cod (van der Meeren *et al.*, 1994; Otterlei *et al.*, 1999; Suthers *et al.*, 1999). The experiments indicated that Arcto Norwegian cod had either a lower growth rate (van der Meeren *et al.*, 1994; Otterlei *et al.*, 1999) or no significant difference in growth compared with coastal cod (Suthers *et al.*, 1999). Van der Meeren *et al.* (1994) concluded that the comparisons of the larvae from these two stocks were done under coastal cod conditions and that the superior growth of the coastal cod may represent a better adaptation by coastal cod larvae to the rearing conditions.

It is sometimes difficult to compare laboratory results with field observations since the conditions experienced by larval and juvenile cod in the laboratory or in enclosures may be quite different than in the field. For example, the maximum growth rate of cod larvae in relation to temperature on Georges Bank was observed at 7°C (Buckley and Lough, 1987), while for laboratory reared Norwegian coastal cod there was a continuously increasing growth rate with increasing temperature (Otterlei *et al.*, 1999). One reason for this divergence of laboratory and field results is that the food concentrations in the experiments and in the field may have been very different. The reared cod larvae and juveniles were raised in enclosures with a high density of prey organisms, while in the field food abundance is much more variable and more energy is needed to search and capture prey organisms. On Georges Bank 7°C is probably the equilibrium point for increased growth versus increased metabolism.

Growth differences among cod stocks may also be due to the environment in nursery areas. Juvenile cod experience 24 hours of daylight in the Barents Sea (Pedersen *et al.*, 1989) and in **Paper IV** an examination of stomach data shows that early juvenile cod feed around the clock. This may be the reason that the growth rate is higher in the Barents Sea than in more southern areas.

Another reason that larval and early juvenile cod may grow more quickly in the Barents Sea is the availability of high energy prey. *Calanus finmarchicus* is one of the most important and most numerous prey species for larval and juvenile cod in the north Atlantic and makes up a significant part of the zooplankton biomass (Sundby, 2000). In the Barents Sea there are many fewer species than farther south (Sømme, 1934) and *C. finmarchicus* makes up, on average, 90 percent of the total biomass (Nesterova, 1990), which is considerably more than in other areas (Gislason *et al.*, 1994; Runge *et al.*, 1999). Prus (1970) found that of all prey species available, *C. finmarchicus* has the highest calorific value (5.23- 7.67 kcal/g ash-free dry weight). Hence, the superior growth rate of cod juveniles observed in the Barents Sea may be due to the very calorie rich diet of the predominate *C. finmarchicus* (Helle, 1993), together with being in an environment in which they can forage 24 hours per day.

### **The early juvenile cod as a predictor of year class strength**

In **Paper V**, twelve different indices of abundance, ranging from spawning stock biomass to abundance as 3-years old, were used to determine the stage at which year class strength is established. Of all the indices considered, the early juvenile stage index was the best predictor of year class strength and a much better predictor of a cohort's abundance at 1, 2 and 3 years old than the 0-group index.

Although the index of abundance from the 0-group survey appears to be biased (**Paper V**), studies have shown that estimates of average length at the 0-group stage generated by the survey are correlated with abundance at later stages, and that the average length at the 0-group stage may be a better predictor of year class strength than the index of 0-group abundance (Ottersen and Loeng, 2000; Ottersen *et al.*, 2000). It has also been shown that

the average length at the 0-group stage is correlated with average length at later stages and that the length signal from the 0-group stage can be traced to when cod reach maturation (Helle *et al.*, 2000).

### **Concluding remarks**

For managing the cod fishery, it is important to have a prediction or indication of year class strength as early as possible. Since both the abundance of early juvenile cod and the average length reached at the 0-group stage are correlated with recruitment, it is important to know the factors controlling both survival and growth. For the various cod stocks in the North Atlantic, different factors appear to influence the year class strength of cod. High temperature in the Barents Sea may result in good recruitment, while on the Faroe Plateau temperature does not have any apparent effect, but wind stress on the nursery grounds seems to be related to recruitment success. For the northern cod stock on the Grand Banks, Anderson and Dalley (1997) suggest that there are three factors that influence recruitment: juvenile abundance, large size at settlement and geographic distribution prior to settlement.

When examining biological and physical factors, such as climatic conditions and variation in food availability, that may influence the distribution and abundance of early juvenile Arcto-Norwegian cod, four factors, which are interconnected, should be considered: water temperature, general current patterns, wind driven water flux into and out of the Barents Sea and zooplankton abundance and distribution.

At the time of first feeding it is important that the larvae have a sufficient amount of the right size prey. Given the large variation in zooplankton distribution and abundance both within and among years (Nesterova, 1990; **Paper II**), it is likely that larvae that are in a sufficient zooplankton patch at first feeding have a better chance of good growth and survival if they remain in the patch and the patch stays intact until the larvae reach the early juvenile stage. It may, therefore, be artificial to focus on an early “critical period” (Hjort, 1914) or a “late critical period” (Folkvord *et al.*, 1994). It is likely that the entire pelagic stage from hatching until the early juvenile stage is a “constant critical period”

with a continuous risk for the larvae and juveniles to get separated from the patch or for the patch to become depleted or dispersed. At what age the early juvenile cod are able to search for good patches of prey is uncertain. Sundby (1995) found that larvae and up to two months old early juvenile cod have little or no ability to swim across or against currents. As they grow older it is likely that the early juvenile cod's ability to stay within a patch increases, but given their small size at three months (2.5 to 4 cm long), it is not likely that they can actively swim over large distances to search for prey. **Paper V**, however, shows that the largest year-to-year variation in mortality occurs before the early juvenile stage, which may indicate that the larvae and juveniles are most vulnerable to variations in zooplankton abundance during the period from first feeding to 2-3 months old.

In my opinion much more field effort should be spent assessing zooplankton abundance on the nursery grounds during the larval and early juvenile stages, observing whether copepodite development is synchronized with the development of the larval and early juvenile cod and examining whether the larvae and juveniles are confined to one zooplankton patch. The five papers presented here show that expanding our understanding of the physical and biological factors influencing the abundance, distribution and growth at the early juvenile stage will provide new insights into the mechanisms underlying the recruitment processes.



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