Distribution of gadoids in the Barents Sea;
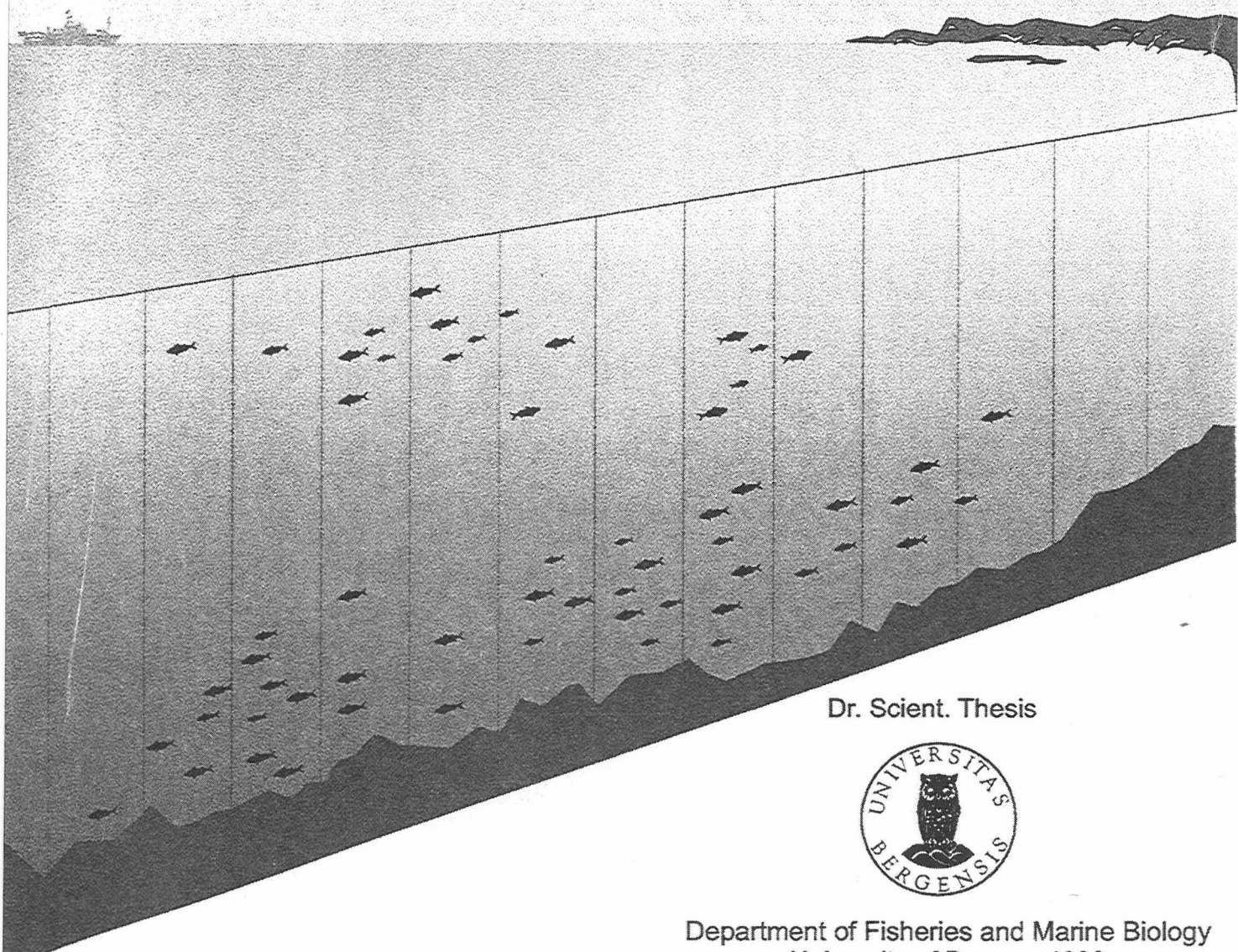# Impact on survey results

by

Kathrine Michalsen

Dr. Scient. Thesis

PREFACE

This thesis is a result of my participation in research activities which had the aim of improving the methodology for estimating fish abundance on the basis of survey-based data. The six papers included here, which are identified by the numerals 1-6, describe how the horizontal and vertical distribution of cod can affect survey results. All the papers except Paper 6 have been published or are in press. The project has received financial support from the Research Council of Norway and the Institute of Marine Research (IMR).

I wish to express my sincere gratitude to my supervisors; Anders Fernö, Olav Rune Godø and Odd Nakken for their guidance, encouragement and critical review throughout the study.

The results were obtained through extensive team-work, as signified by the many co-authors of the papers included here. In addition to my three supervisors, I would also like to thank Geir Ottersen, Asgeir Aglen, Ingvar Huse, Arill Engås, and Boonchai K. Stensholt for stimulating discussions and productive teamwork.

Thanks to the staff at the Institute of Marine Research, the crews of the research vessels and hired trawlers, and to the engineers and instrument operators for their skilful work and valuable co-operation. They have all contributed to an inspiring scientific environment and a pleasant social atmosphere. I also want to thank IMR for allowing me to participate on scientific surveys as well as supporting travel to symposia and meetings abroad.

Finally, I thank Lars Nese, my family and my friends for their support and encouragement throughout the study.

Bergen , December 1998
Kathrine Michalsen

CONTENTS

BACKGROUND

The assessment of north-east Arctic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) stocks is based on virtual population analysis (VPA). Landing statistics and relative abundance indices from scientific surveys are the basic data used. The indices of relative abundance have been derived from five different series of survey data, of which the most important is the Norwegian winter survey in the Barents Sea (ICES, 1998). Errors and biases in estimates of abundance from such surveys may thus have an important economic impact on the fisheries.

Warnings of a rapid decline in stock sizes of north-east Arctic cod in the Barents Sea (ICES, 1998) and of northern cod in Northeast Atlantic waters (Walters and Maguire, 1996) were observed earlier in the survey data than in the VPA. This has raised the question of whether more weight should be given to the survey indices in the assessment procedures. Whether future surveys are used to generate an assessment independent of catch statistics or are used to tune the VPA as is the case today, a better understanding of the survey errors is necessary in order to decrease uncertainty in abundance estimates and to improve the reliability of studies that aim to determine population-regulating mechanisms.

Combined bottom trawl and acoustic surveys have been carried out in the Barents Sea and Svalbard region since 1981 (Jakobsen *et al.* 1997). The length distributions and species compositions of trawl catches are used to calculate bottom-trawl indices and to convert echo abundance into estimates of fish density. In the tuning of the VPA both series of indices are assumed to reflect stock abundance, but neither of the two survey methods samples the complete vertical distribution of the stock. Fish close to the bottom are best assessed by the bottom trawl while acoustic measurements are more appropriate for pelagic concentrations (Figure 1). Variations in the availability of the fish to the two survey methods involve a complex set of factors, among which the behaviour of the fish is of major importance.
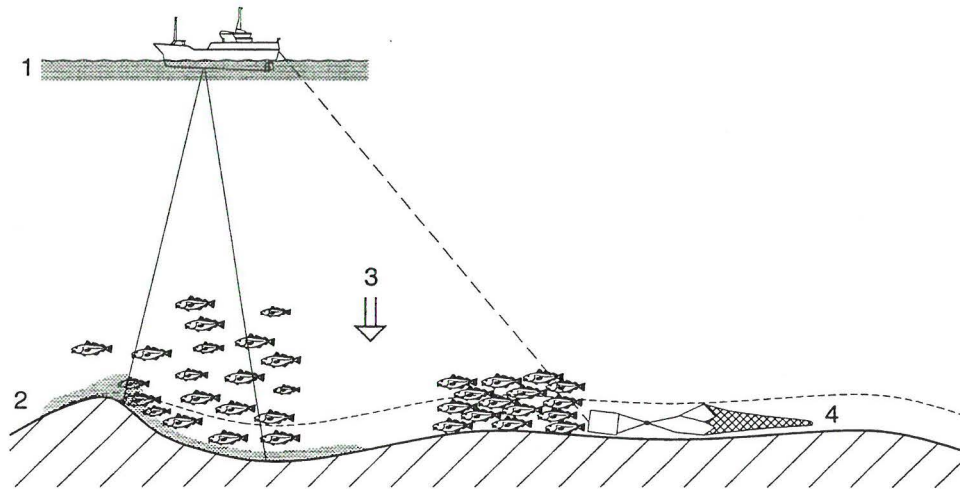
Figure 1. Examples of errors within the echo sounder beam and in the volume swept by the bottom trawl. 1) shows the upper acoustic deadzone, 2) the acoustic bottom deadzone, 3) vertical herding when fish are pelagically distributed above the bottom trawl and 4) the height of the trawl opening.

In periods of warm climate in the Barents Sea the area of cod distribution extends eastwards and northwards, unlike during cold periods when the fish tend to concentrate in the south-western parts of the Barents Sea (Figure 2). Young fish are distributed in colder waters farther east than older age groups (Nakken and Raknes, 1987). If the surveys covers only a fraction of the stock, or if the degree of coverage varies between years, this can cause an underestimate of the abundance and bias the size- and age-structure of the population.

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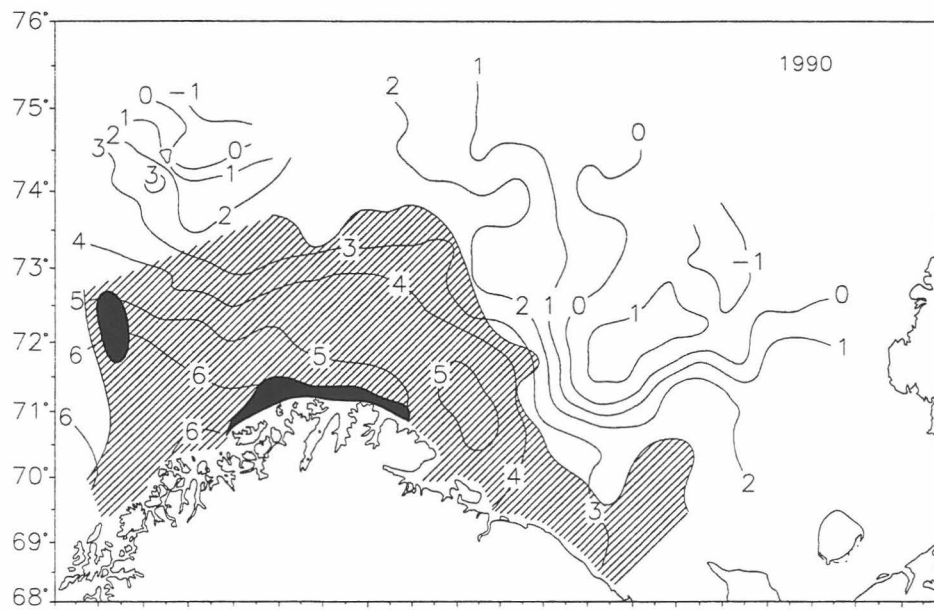
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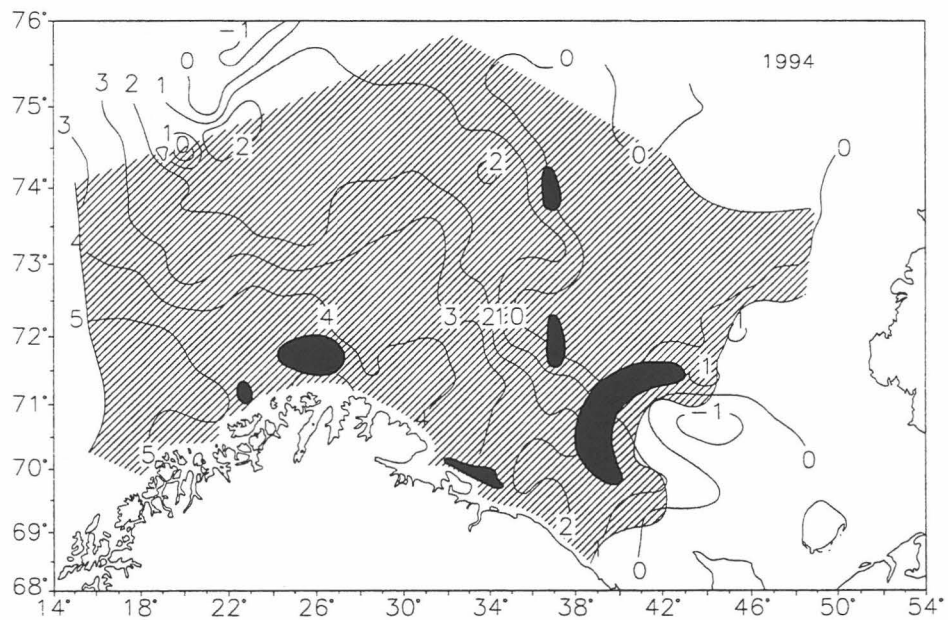
Figure 2. Distribution of cod density (hatched areas) and bottom temperature (isotherms, °C) in February 1990 and 1994. The graphs show echo densities (backscattering coefficient, s_A) of all age groups of cod. Dark shading for $s_A > 100$ m^2 (nautical mile)$^{-2}$, from Paper 1.

Because of the importance of the two survey methods for estimating the abundance of gadoid stocks in the Barents Sea, several studies of the assumptions underlying these methods have been performed. The reliability of abundance estimates based on acoustic surveys has been reviewed by Aglen (1989, 1994), survey design and efficiency have been evaluated by Vølstad (1990), trawl-sampling problems have been studied by Engås (1991, 1994), while the accuracy and precision of bottom-trawl and acoustic surveys have been discussed by Godø (1990, 1994). Knowledge of how environmental factors affect fish distribution, and thereby also abundance surveys, is essential for further improvements of the survey methodology. The principal objective of this study has been to identify environmental factors of explanatory importance for the vertical and horizontal distribution of gadoids in the Barents Sea and to improve the methodology for estimating fish abundance on the basis of survey data. The ultimate goal is to increase the reliability of survey estimates of abundance.

DISTRIBUTION OF GADOIDS

Throughout the centuries the gadoid fisheries have provided a substantial income to Norwegian fishermen. In order to maximise their catches, fishermen have always exploited their knowledge of the movements and likely distribution of the fish. Since the first recorded landing and until the present day, landings have fluctuated considerably, due to natural fluctuations in the environment and/or as a direct response to the exploitation rate (Nakken, 1994). Of all the gadoids, the stock of north-east Arctic cod is the largest and, in economic terms, the most important (Garrod, 1988). For this reason, the following discussion will concentrate on this species.

NORTH-EAST ARCTIC COD AND ITS ENVIRONMENT

The Barents Sea is a shelf sea with an average depth of 230m. It is characterised by an inflow of relatively warm and highly saline Atlantic waters in the southern area and

cold low-saline Arctic water in the north (Midttun, 1989; 1990). In years with high inflow the mean temperature rises, as is reflected in the long time-series of hydrographic observations from the Kola section (Loeng *et al.*, 1992). There is a horizontal variation in sea temperature across the Barents Sea, with higher temperatures in the western areas than in the east and north (Midttun, 1989). Within the area of distribution of north-east Arctic cod, annual mean temperatures range from 6-8°C at the spawning grounds along the west coast of Norway (Aure and Østensen, 1993) down to 0°C or even -1°C along the Polar front in the northern and north-eastern areas where the fish feed during summer and autumn (Woodhead and Woodhead, 1965; Mehl *et al.*, 1985; Jørgensen, 1992). At any given location seasonal variations in hydrographic conditions are quite large in the upper 50 m, while in depths below 100 m seasonal variations are relatively small, varying by no more than 1-3 °C (Ottersen and Ådlandsvik, 1993). The longest temperature time series available is from the Kola region, where observations have been made by Russian scientists at monthly or quarterly intervals ever since 1900 (Tereshchenko, 1996).

A detailed description of the production and distribution of the pelagic ecosystem in the Barents Sea is given by Sakshaug *et al.*, (1991, 1994). Some of the main features are summarised below. Zooplankton organisms reproduce during the spring phytoplankton bloom. During that period most of the zooplankton biomass is found in the surface layer. In summer, the bulk of the biomass is concentrated at depths similar to the phytoplankton maximum, mainly in the upper water masses. During the autumn, the zooplankton begin to descend to greater depths, while during the winter they are more or less evenly distributed throughout the water column. In warm years the biomass of phytoplankton and zooplankton have a high degree of temporal overlap, with peaks in June and July respectively. In cold years phytoplankton production starts earlier than usual while the zooplankton production starts later, resulting in very low degree of overlap and thus reduced biomass production of zooplankton.

During the summer months 90% of the total biomass of zooplankton may consist of the copepod *Calanus finmarchicus* (Sakshaug *et al.*, 1994). This species is mainly

distributed in Atlantic water in the polar front region (Skjoldal *et al.*, 1987; Melle, 1998). Two species of amphipods dominate in the western and central parts of the Barents Sea; *Themisto abyssorum* and *T. libellula*, where the former is common in sub-arctic water masses, while the latter is found in Arctic water masses (Dalpadado *et al.*, 1994). The two main krill species, *Thysanoessa inermis* and *T. longicaudata* are mainly found in Atlantic water in the area to the south and southwest of the Svalbard bank (Dalpadado and Skjoldal, 1991). In contrast to the copepods and amphipods, the highest concentrations of krill were found during the winter (Dalpadado and Skjoldal, 1996). Zooplankton is an important component of the diet of the main fish stocks in the Barents Sea, e.g. capelin (Hassel *et al.*, 1991; Dalpadado and Skjoldal, 1996), polar cod (Ajiad and Gjøsæter, 1990), herring (Dalpadado, 1993), cod (Mehl, 1989; Helle, 1994), haddock (Burgos and Mehl, 1987), redfish (Dolgov and Drevetnyak, 1993; Dolgov and Drevetnyak, 1995) and Greenland halibut (Michalsen and Nedreaas, 1998).

The habitat of north-east Arctic cod extends from the spawning grounds along the Norwegian coast south to about 62°N, up along the continental slope to west of Spitsbergen and through the whole of the southern and central Barents Sea east to Novaya Zemlya (Figure 3). The mature part of the stock migrates from its wintering grounds in the northern and eastern parts of the Barents Sea to the spawning areas along the coast of Norway. Spawning takes place at several locations, including the banks off Møre and the coastal areas between Lofoten and Sørøya. However, the most important spawning area is outside Lofoten and Vesterålen (Bergstad *et al.*, 1987). Spawning occurs from February to June, with a peak between about 20 March and 10 April each year (Ellertsen *et al.*, 1981). After hatching the fry remain in the upper 50 m of the water column, feeding on zooplankton, particularly eggs and nauplii of *Calanus finmarchicus* (Ellertsen *et al.*, 1984). In contrast to cod, copepod spawning is closely related to temperature conditions rather than to a specific time of year. Consequently, in extremely cold years the cod will hatch before the copepods have spawned and the cod larvae will be totally dependent on their yolk sack to survive (Skreslet, 1989). Since the locomotive abilities of the larvae are limited, they drift more or less passively with the warm Atlantic surface current from the spawning areas to the nursery areas (Ellertsen *et al.*, 1981). A year with a greater inflow of Atlantic

water will be warmer than average and will advect the pelagic 0-group cod further eastwards into the Barents Sea (Loeng *et al.*, 1995). Cod of age 1 appear to remain in the areas where they settled during autumn as 0-group, at the end of their pelagic drift phase (Maslov, 1944, 1960; Baranenkova, 1957). As the fish grow bigger the range of their seasonal migrations increases (Figure 3). Immature fish (ages 3-6 years) prey on capelin migrating towards the coast of Russia and northern Norway in winter-spring. The mature part of the stock (>7 years), migrates from the feeding areas in the northern and eastern parts of the Barents Sea to the southern and western part of their distribution area to spawn (Bergstad *et al.*, 1987).
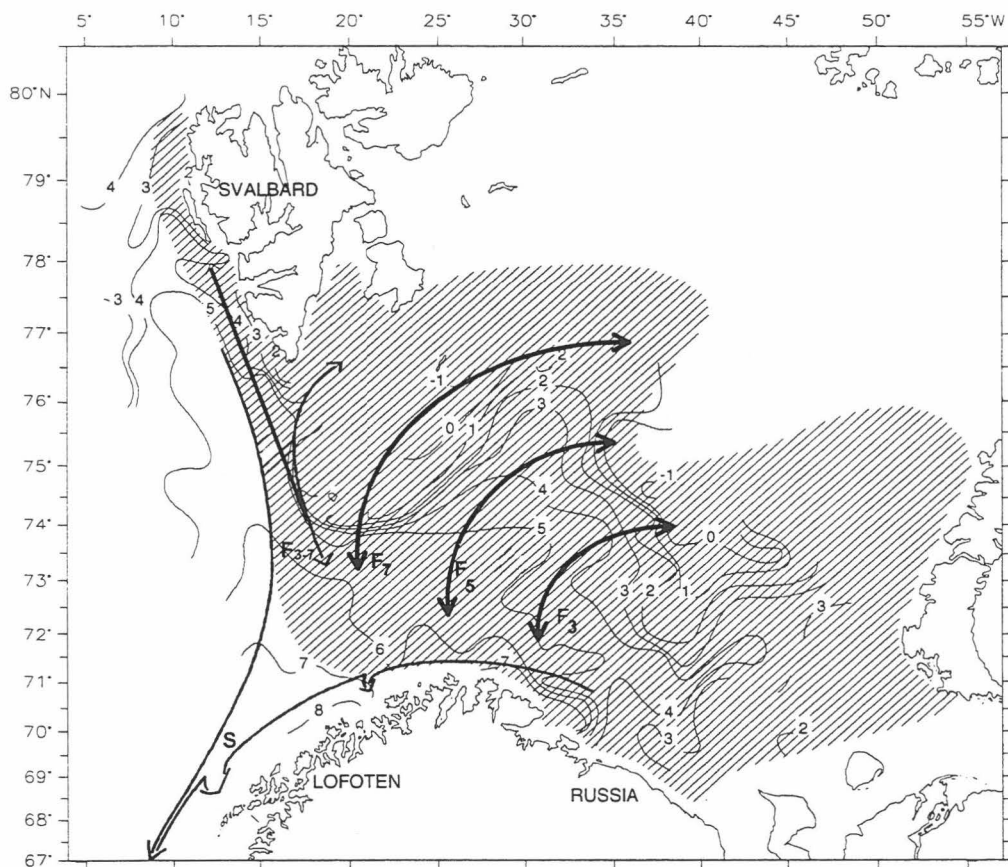

Figure 3. The area of distribution of north-east Arctic cod, and isotherms (^{0}C) at 100 m depth. Feeding area (hatched), seasonal feeding migrations (F) for age groups 3, 5 and 7, and spawning migrations (S) are indicated (redrawn from Mehl, 1991 and Mehl, et al., 1985). Temperature distribution is for August 1995 (ICES, 1996).

HORIZONTAL AND VERTICAL DISTRIBUTION

The connection between temperature and the distribution of north-east Arctic cod, as shown in Figure 2, has been described in several studies (Eggvin, 1938; Konstantinov, 1967, 1969; Nakken and Raknes, 1984). Temperature-related displacements have also been reported for some of the most important prey species for cod; krill (Dalpadado and Skjoldal, 1996), shrimp (Nilssen and Hopkins, 1992) and capelin (Gjøsæter, 1997). Because north-east Arctic cod inhabit a area with large horizontal temperature gradients, the temperature actually experienced by the fish, the ambient temperature, may be quite different from those in any geographically fixed point.

In Paper 1, the mean ambient winter temperatures for each age group were calculated from the spatial distribution of fish density and temperature, for the period 1988-1995. The estimates of ambient temperature were compared with temperature series in specific fixed areas and with the standard section along the Kola meridian. Inter-annual variability in ambient winter temperature was found to be greater than in the fixed areas and in the Kola-section series. In accordance with the increased migration with age, the older age groups which were distributed further west and in warmer waters experienced higher winter ambient temperatures than the younger groups. An eastward displacement during a relatively warm period in the Barents Sea coincided with an increase in abundance of young cod which caused a reduction in the ambient temperature. The inter-annual variability in ambient temperature was highest for the younger age groups, ranging from 3-4 ^{0}C in 1990 to 0.5-1.5 ^{0}C in 1994.

Myers and Stokes (1989) have identified three ways in which the geographical distribution of a fish population might change as its abundance increases. The patterns identified were; 1. A proportional increase throughout its range; 2. A range extension in which the population increases relatively more in marginal habitats; and 3. A relatively greater increase in the prime habitat, i.e. increased population density leads to higher concentration. The results of Paper 1 indicate that young cod respond according to the second manner with an extension of their range towards the east, with the result that they experience low ambient temperatures during periods with a general increase in population size. In an evolutionary perspective, the optimal response of the

young fish, in years with extensive overlap with older cod, would be to move eastwards into colder waters, which are less favourable to growth but which have a lower cumulative predation risk. However, the possible effect of cannibalism on our data should not be ignored. A geographical variation in predation on young fish from large cod could have counteracted a more westerly distribution with age of ages 1 to 3 from 1990 onwards. According to ICES (1998) cannibalism on fish aged 0-3 increased considerably from 1991 to 1993/1994. It is likely that this increase in predation was more pronounced in areas of extensive overlap between prey and predator, i. e. in the more western parts of the distribution area of the small fish. Thus the densities in these areas would be reduced at a higher rate than further east. In order to quantify changes in distribution of cod due to changes in prey availability, there is a need for more detailed and systematic information about the horizontal distribution for the main prey items.

Vertical migrations are often a result of a trade-off between the gain of feeding and the risk of predation (Clark and Levy, 1988). These movements are often affected by changes in light (Neilson and Perry, 1990). Differences in activity have been observed, alternating between an active day period and a more passive phase at night (Clark and Green, 1990; Løkkeborg and Fernö, *in press*). Reduced activity at night could be related to a poorer ability to detect visual stimuli. In general, the visual reaction distance in fish decreases with decreasing light level (Confer *et al.*, 1978; Utne, 1997) and in proportion to fish size (Mangel and Clark, 1988). Thus, at a certain light level small fish can utilise the pelagic water masses without the increased danger of being preyed upon by larger individuals (Clark and Levy, 1988). Since small fish have to balance the feeding opportunities found in the upper water column against the risk of predation, while large fish can concentrate on maximising food consumption, a diel size difference in patterns of vertical migration, such as was found in Paper 5, is likely to take place. In this study, juvenile haddock and redfish were pelagically distributed at night whereas a pelagic distribution of large haddock was observed during the day.

Water currents are also known to influence the vertical distribution of fish, with some species avoiding increased current speed, others utilising them for transport, either by

passive or by modulated drift (Harden Jones *et al.*, 1979; Arnold , 1981; Arnold *et al.*, 1994; Arnold and Metcalfe, 1995). In some cases selective tidal transport can offer a gain in speed of more than 50% (Weihs, 1978). Since current speed and direction may vary with depth, it may be energetically advantageous to move between different depths in a tidal cycle. In Paper 4, the results showed that tidal currents seemed to affect the vertical distribution of cod and haddock. It was argued that the observed ascent from the bottom at the time of strong eastward currents could be a behavioural adaptation to modulated drift, maximising the overlap with capelin in distribution areas at the same time as saving energy.

Maintaining neutral buoyancy at all depths involves continuous secretion of gas to, and resorption of gas from, the swimbladder (Harden Jones and Scholes, 1985). Alexander (1971, 1972) calculated that fish making diel migrations between surface and 250 m need more energy to maintain neutral buoyancy than they need to control their depth by swimming alone. Large cod can probably compensate for reduced swimbladder lift by using their pectoral fins (Alexander, 1971) and altering the angle of attack of the body (Harden Jones and Scholes, 1985). In both of these studies it is argued that fish which maintain neutral buoyancy at the top of their vertical range and rest on the bottom for part or all of the remainder of the time would save energy. This assumption has since been supported by Arnold and Greer Walker (1992). In Paper 6 it was observed that cod make large vertical movements within a shorter time period than is required to equalise pressure changes and to maintain constant buoyancy. As well as supporting the above assumptions, these observations also suggest that current knowledge about the ability of fish to control their buoyancy is limited. Diel vertical movements were only observed during limited periods of time, at different times of the year and only for some of the fish. This suggests that the factors that affect vertical movements may vary according to the season, the availability of prey, the physiological state of the fish, the geographical area or even between individual fish.

DISTRIBUTION AND CONSEQUENCES FOR GROWTH

Fish growth depends on the availability of prey, but is also an integration of a series of processes (feeding, assimilation, metabolism, transformation and excretion) all of which are controlled by temperature (Brett, 1979; Wootton, 1990; Jobling, 1994). Since temperature affects all species to a greater or lesser extent, it is an important indicator of changes in the ecosystem (Daan, 1994). The importance of temperature is further emphasised by Brander (1995), who argues that studies of differences in growth can only move on to consider other factors, such as food availability, if and when the effects of temperature have been taken into account.

In Paper 2 it was found that mean lengths at age increased as ambient temperature rose for cod aged 2-6. Mean individual growth was highest for year classes that had experienced high temperatures during the two first years of their life. From Paper 6, in which individually tagged cod experienced temperatures of 3-4 °C during the winter and 0-2 °C in the autumn, it can be concluded that the ambient winter temperatures used in Paper 2 were close to the maximum annual values. Thus, the effect of temperature on growth was probably underestimated. Since the range of the seasonal migrations increases with age (see Figure 3) it is expected that the amplitude of the annual temperature cycles experienced by the fish will also increase as they grow older (Figure 4). Considering that the age groups of cod maintained their relative distribution more or less independently of the absolute ambient temperature values (Paper 1), it may be expected that the relation between the curves in Figure 4 will be almost fixed from year to year. The absolute value of ambient temperatures for all age groups will shift up and down the y-axis according to the current temperature regime and stock abundance (for the youngest cod).

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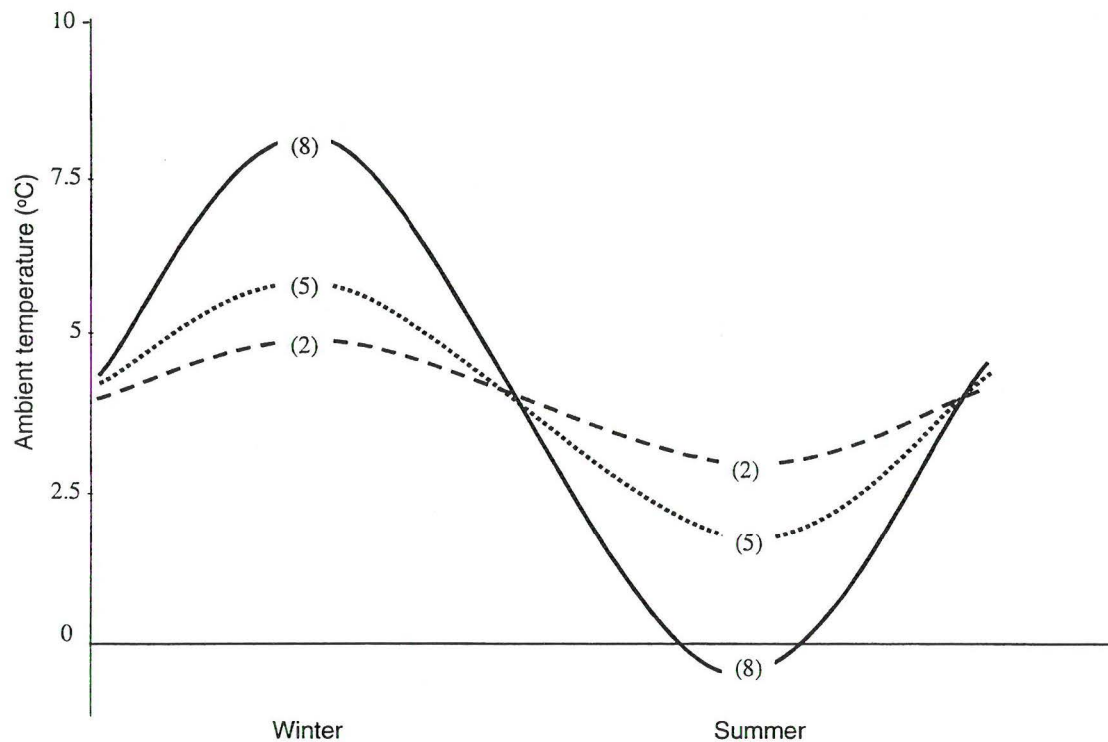
Figure 4. Annual temperature cycles experienced by the fish at different ages. Numbers in brackets indicate age group. The cycles are drawn based on the findings of Papers 1 and 6.

The energy source for growth and migration comes from ingested food. Young cod prey mainly on crustaceans (krill, deep sea shrimp and amphipods), while older cod incorporate larger proportions of fish in their diet (Mehl, 1991). Figure 5 shows the annual consumption, as a percentage of the weight of different prey species, in two years. In 1993, the main prey item for 2-year-old and older cod was capelin, while younger fish mainly preyed upon krill (Figure 5a). In 1996, which was a year with low availability of capelin, the proportion of krill, shrimp and cod in the diet of cod more than one year old increased (Figure 5b). The average consumption of fish prey in the diet of medium and large cod varies from about 65% in the winter to 35% in the fall (Burgos and Mehl, 1987; Mehl, 1989). Lipids and proteins are more effectively digested than carbohydrates (Brett and Groves, 1979). In addition to the composition of various organic compounds, the diet will exhibit differing energy contents depending on the prey species, prey size and meal size (dos Santos, 1990).

The easterly extension of the distribution area, the high population size and the low ambient temperatures observed in Paper 1 were also accompanied by slower growth (Paper 2). In a theory which assumes density-dependent growth, individual predators will obtain reduced food rations at high abundance, leading to a reduction in the growth rate (Nilssen *et al.*, 1994). Stomach analysis shows that the individual consumption of capelin by cod was relatively high at the beginning of the 1990s (Figure 5; Bogstad and Mehl, 1997). The observed reduction in growth rate in 1993 can therefore not be regarded as a direct consequence of reduced prey availability. Our interpretation was that the high abundance of cod influenced the horizontal distribution in a manner that affected the ambient temperature, and thus also their growth rates, negatively. Hence a growth-temperature relationship may wrongly be interpreted as a growth-density (abundance) relationship if only biological data are considered. A even more detailed description of the factors affecting growth could probably have been achieved if the annual liver index had been included in the analysis. Since excess energy is stored in the liver of the fish, such an index will be an integrator of combined food/temperature effects (Lambert and Dutil, 1997). As an example, it has been shown that for mature fish the annual liver index provide a more sensitive measure of the reproductive potential for the stock than estimates of spawning biomass do (Marshall *et al.*, 1998).
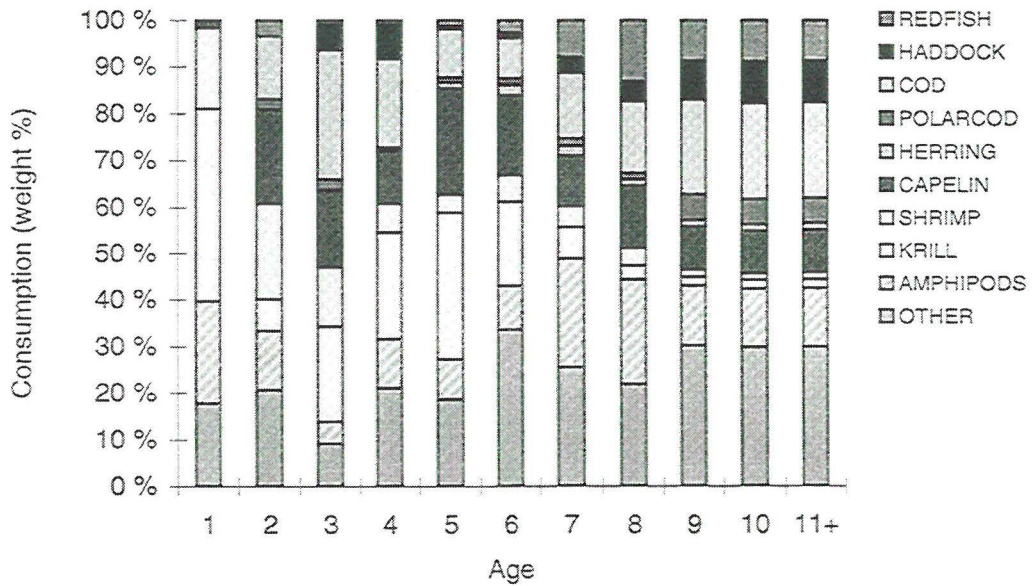
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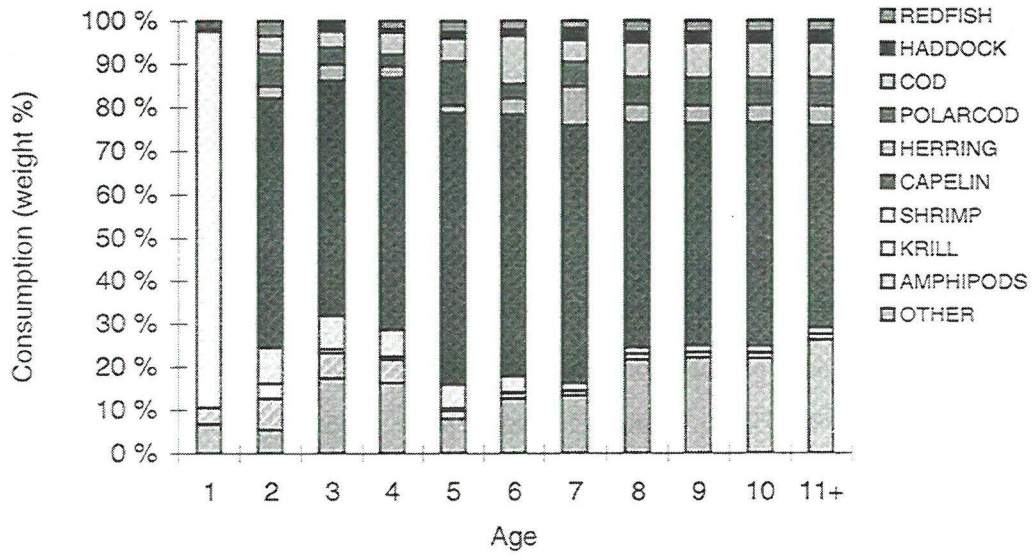
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Figure 5. The annual consumption of cod by age (based on data from the joint IMR-PINRO stomach content data base, and Bogstad and Mehl, 1997). Percentage weight of the different prey species in a) 1993, b) 1996.

Even though temperature has been identified as an important factor influencing growth, the mechanisms involved are several. Within a certain range of temperatures the metabolic rate rises exponentially with increasing temperature, while the rate of ingestion peaks at an intermediate temperature and then declines as the temperature continues to rise (Jobling, 1994). The optimum temperature for growth rate, however, is slightly lower than that at which the ingestion rate reaches its maximum (Jobling, 1994). The efficiency of the ingested food, the conversion efficiency, used for growth, is highest at a slightly lower temperature than the optimum temperature for growth (Jobling, 1994). In situations where the temperature falls, the metabolic processes slow down and the maximum food intake will also fall, reducing the growth rates regardless of the availability of prey (Jobling, 1994). On the other hand, if the food supply is limited, growth rates may be higher at lower temperatures than in warmer areas because metabolic costs fall with decreasing temperatures. In addition, there might be a energetic gain from thermocycling. It has been observed that growth may be increased by exposing fish to fluctuating temperature regimes, e.g. the Kaufman effect (Cossins and Bowler, 1987). An experimental study in which juvenile sockeye salmon were exposed either to a temperature cycling or to a constant temperature showed that when fed moderate rations sufficient to sustain growth, the fish on the cyclical regime had growth rates equal to or greater than fish on constant regimes (Biette and Geen, 1980). In this sense vertical movements can also be considered as a behavioural mechanism conducted in order to maximise fish growth. This can be achieved either by feeding in warm water layers and otherwise remaining in cold water when prey availability is low, or by remaining in warm water layers and feeding in colder layers when food concentration is high.

IMPACTS ON SURVEY RESULTS AND STOCK ASSESSMENT

The horizontal and vertical distribution as well as the migration patterns of target species are critical factors in planning scientific surveys. Surveys are supposed to cover the total volume utilised by the fish, but occasionally parts of the geographical area and vertical layer are left out. If the degree of coverage varies from one year to another this can bias abundance indices. Lack of area coverage can be adjusted for by establishing relations with environmental factors of explanatory importance for the vertical and horizontal distribution of the fish.

HORIZONTAL DISTRIBUTION AND LACK OF AREA COVERAGE

Migration of fish stocks during the survey can result in either overestimation or underestimation of distribution area and stock size, depending on whether the survey track is in the same, or in the opposite direction to that of the migrating fish. Migration is thus regarded as a major source of error for acoustic abundance estimates of pelagic species (MacLennan and Simmonds, 1992; Hafsteinsson and Misund, 1995). At the time of year when the combined bottom trawl and acoustic survey for demersal fish in the Barents Sea is conducted, it is expected that mature cod will be outside the survey area, while immature cod are assumed to be relatively stationary during the survey (Jakobsen *et al*, 1997). However, this need not always be the case. In a study conducted immediately after the annual abundance survey, vertical movements connected with strong eastwards currents could have resulted in substantial horizontal displacements of immature cod (Paper 4).

The presence of other species can also affect the horizontal distribution and thus the catchability coefficient. In Paper 3, a hierarchy among fish species was revealed, where a large wolffish (*Anarhichas sp.*) was observed to be dominant over smaller cod and haddock. When wolffish are present, their aggressive bait-defence behaviour may scare away other fish species. If long-line catch data are used for stock assessment

purposes, the presence of wolffish might reduce the hooking rate for cod and haddock, and should therefor be considered as a potential source of error.

At the beginning of the 1990s the geographical distribution of the younger age groups of north-east Arctic cod extended far beyond the standard survey area in east and north and the survey area was therefore extended in 1993 (Jakobsen *et al.*, 1997). As shown in Paper 1 the increase in the distribution area occurred during a relatively warm period in the Barents Sea when there was high abundance of the youngest age groups of cod. Because the youngest age groups and the smallest fish within each age group are distributed farther to the east (Papers 1 and 2), insufficient coverage of the distribution area prior to 1993 has caused an underestimate of the abundance and biased the size- and age-structure of the population as well as the growth rates of the youngest age groups. Inspection of fish distribution maps (Ottersen *et al.* 1996) indicated that in 1988, 1989 and 1990, the eastern (and northern) boundaries of cod were well within the area sampled. However, in 1991 and 1992 fish aged 1-3 years were present at several of the easternmost (and northernmost) stations. Catches of older fish (age ≥ 4 years) were lacking or very low at the boundaries of the surveyed area in all years. To improve the comparability of the abundance indices from the surveys within the whole time series 1981-1998, variation in the area covered ought to be corrected for. This could be done by using indices based on data from the old standard survey area only or by adjusting the survey indices for those years with insufficient area coverage. Figure 8 in Paper 2 indicates that the amount of fish to the east and north of the old standard area is positively correlated to abundance as well as to temperature. This apparent dependency might be used to adjust the indices of abundance for the years with insufficient area coverage. However more years with complete coverage are needed before such a relationship can be quantified satisfactorily.

VERTICAL DISTRIBUTION AND SAMPLING ERRORS

Since the two methods used for abundance estimation, the bottom trawl and acoustics, covers different fractions of the true stock it has been argued that a combination of the two density estimates would improve the reliability of the survey results (Godø and Wespestad, 1993; Godø *et al.*, 1998). For bottom trawl surveys the volume swept by the trawl is considered to be the most important source of error, while for acoustic measurements the quantities of unrecorded fish in the bottom zone and the target strength are regarded as being most important (Paper 5). Since the length and species compositions from trawl catches are used to convert echo abundance into estimates of fish density, the quality of both estimates is greatly affected by the ability of the bottom trawl to obtain representative samples of the fish in the area. In addition, comparisons of the acoustic recordings and bottom trawl catches in Papers 4 and 5 revealed diel changes in the relationship between the two measurements of relative abundance.

Fish close to or on the bottom can not be distinguished from bottom echoes, in an area defined as the acoustic bottom dead zone (Ona and Mitson, 1996). The extent of the bottom dead zone is a function of pulse length, transducer beam width, depth and bottom configuration (MacLennan and Simmonds, 1992). For the Barents Sea surveys, the height of the dead zone is approximately 1m above the seabed (Aglen, 1994). Since the hull-mounted transducer is usually located at a depth of about 5 m and since echo integration starts some metres below, the volume of water above this depth (about 10 m) produces another acoustic dead zone (see Figure 1). When the bottom is sloping or rough, or when the vessel is pitching and/or rolling, the dead zone area will increase and fish densities will be even more underestimated.

The use of a constant backscattering cross-section is based upon the assumption that swimbladder volume and shape are independent of depth. This assumption has been the basis for applying a mean target strength function for several fish species, including the north-east Arctic cod and haddock, in abundance estimation (Foote, 1987). The greatest potential source of variation in target strength is the orientation of

the fish relative to the horizontal plane (the tilt angle, Aglen 1994). Since a change in aspect angle of only a few degrees has a marked effect on target strength (Nakken and Olsen, 1977; Rose and Porter, 1996), a combination of negative buoyancy and a head up position could cause a dramatic reduction in target strength measurements, leading to a masking of the proportion of fish and thus reducing the efficiency of the echo sounder. Noise from gear and vessel also result in a change in tilt angle when the fish dive (Olsen *et al.*, 1983a, 1983b; Ona and Godø, 1990). Systematic tilt angle differences between day and night have been observed in herring (Beltestad, 1974; Huse and Ona, 1996). The observed variation in vertical distribution recorded in Papers 4 and 5 indicates that a diel change in tilt angle probably also exists for cod and haddock. However, the individual tagged cod described in Paper 6 only occasionally conducted vertical migrations within a clear diel rhythm. This might imply that the collective pattern in vertical distribution, apparent from bottom trawl and acoustic measurements, is not necessarily caused by an identical diel pattern in movement of the individual fish. Since cod generally require five to six days to digest a meal of capelin (dos Santos, 1990), and the process used to level out pressure changes is slow, is not likely that individual fish will have a diel rhythm in their vertical migration pattern. Other cycles in the vertical migration pattern may occur during horizontal migration, especially where tidal currents are being avoided/utilised. Further tagging studies of fish of different length and age groups, within different areas, and during different times of the year might provide information about individual fish behaviour that would be useful for interpretations of the survey data.

The effective fishing height of the trawl is taken to be constant between hauls, but as shown in Paper 5, this is not always the case. In response to vessel noise, fish in the pelagic zone may swim towards the bottom (Ona and Godø, 1990; Nunnallee, 1990). The bottom trawl will thus catch fish that had been swimming higher in the water column than the height of the trawl opening (Paper 5). Vertical herding is highly dependent on the size of the fish and their vertical distribution pattern (Aglen, 1996). Effective fishing heights of 30 m for large fish and 4 m for small fish were used for estimating the amount of fish (mainly haddock) unavailable to the bottom trawl in Paper 5. These values are in general agreement with those reported by Aglen (1996).

Correction factors adjusting for species and length-dependent vertical herding ought to be calculated in the same way as for horizontal herding (Dickson, 1993a, 1993b). In addition, diel variations in herding efficiency should be accounted for. To quantify the effect of vertical herding several approaches can be adopted. One is to compare acoustic and bottom trawl estimates of density directly, as was done by Aglen (1996) and in Paper 5, but to extend the study by also covering other times of the year as well as several geographical areas. Another approach could be to assess the diving reaction of fish acoustically by monitoring fish reactions as the survey vessel passes an acoustic buoy (Godø and Totland, 1996).

Aglen *et al.* (1997) described day-time video observations of fish in front of the ground gear. When only one or two fish were observed, they searched actively along the gear, and a high proportion escaped below the gear. When more than four fish were present, they adopted a schooling behaviour, swimming polarised along the direction of towing , and only a few escaped. This indicates that the number of fish entering the trawl mouth will affect its catching efficiency. If schooling is more common during the day than at night, the above mechanism will result in higher catch efficiency during the day. In addition, if the degree of schooling also increases with stock size, it could contribute to a stock size-dependent day/night ratio, as observed by Godø and Wespestad (1993), and Korsbrekke and Nakken (1997). However, if the fish densities continue to increase, the efficiency of the trawl might be reduced because accumulation of fish in front of the trawl could force those arriving later to overflow and escape (Godø *et al.*, 1990).

The vertical distribution of fish may be size-dependent or it may depend on the interactive behaviour between different sizes of the same species or between different species (Papers 4 and 5). Little is known about how behaviour alters as size and species compositions change. If fish populations distribute themselves by depth according to size, the availability of a given size to the two sampling methods will be a function of the length distribution of the populations.

The bottom trawl catches not only depend on how the fish react to the trawl, but also on the shape and movements of the trawl during a tow. Instruments that can make detailed in situ measurements of the performance of the trawl (changes in the vertical opening of the trawl, distance between the doors, bottom contact of the ground gear, distance towed, towing speed, angle between trawl and vessel etc.), are essential to confirm that the trawl is operating properly and to ensure reliable measurements of the volume being swept by the trawl. A detailed description of the effects of trawl performance and fish behaviour on the catching efficiency of bottom trawls has been given by Engås (1994). From his description it seems impossible to construct trawls which sample all species and length groups with the same efficiency.

In Papers 4 and 5 it is shown that changes in the availability of the fish can generate a large variable bias for both acoustic recordings and bottom trawl catches. A promising step in the direction of reducing the bias generated by vertical movements of the fish seem to be the combination of acoustic and swept area estimates; using acoustics to estimate the density of fish unavailable to the bottom trawl (Paper 5). Such a combination will require more studies on the effective fishing height of the bottom trawl. An alternative observation method proposed is to have an upward-looking transducer at the trawl headline to measure the density of fish above the trawl. The main uncertainty would be the species and size composition of the unavailable fish, which would still have to be sampled by other gears. There is also a need for more knowledge of horizontal avoidance of fish as response to trawl gears and vessels. When correction factors for vertical and horizontal herding are established, the density of fish unavailable to the bottom trawl has been measured and the coefficient for converting acoustic measurements to fish density (TS) adjusted, then acoustic density can be added directly to the swept area densities, giving an absolute estimate of fish density at each station. These can further be summed to provide an absolute estimate of fish abundance for each survey.

FOOD CONSUMPTION OF THE COD STOCK AND ITS AMBIENT TEMPERATURE

In the cod stock assessment process, natural mortality rates are based on consumption models and adjusted for temperature-dependent predator-prey considerations, including cannibalism (Bogstad and Gjøsæter, 1994; Bogstad and Mehl, 1997). The temperatures used in these calculations are monthly climatological temperatures (Ottersen and Ådlandsvik, 1993) at three fixed locations which are regarded as representative of the western, eastern and northern parts of the distribution area for cod. The comparison of these temperatures and the mean ambient temperature at age in Paper 1, showed that the variability between years for all ages and the variation between age groups were largest for the ambient temperatures. For the period 1992-1995 the mean ambient winter temperature of age 1-3 years were 1-3 °C lower than those used in the evacuation models, a difference that would generate an overestimate of 10-30 % in the consumption estimates (Bogstad and Gjøsæter, 1994).

Since capelin is the main prey item for cod, a prediction of how much capelin will be eaten by cod is crucial for the capelin quotas. An overestimate of the ambient temperature of 1°C would lead to a 10 % overestimate of the consumption of capelin (equivalent to about 25% of the fishing mortality of capelin). In addition, the consumption of cod and haddock by cod would influence the recruitment estimates of these two species. If the consumption is overestimated then the numbers of recruits are overestimated in the VPA. Hence, both mortality rate and recruitment as estimated by the surveys might be influenced by temperature.

There are several methods to calculate ambient temperatures that all give different results. As an example 4 different estimates of ambient temperature were calculated in Paper 1. These were based on observations from acoustic and swept area densities, and for temperature recordings at the bottom as well as averaged from 100m depth to the bottom. Although the estimates differed from each other, they were more similar than the temperature series in any fixed geographical location. In this study no conclusion regarding which temperature to use was drawn. Since it is known that the vertical distribution of fish varies between years (Paper 1), the choice of sampling method and vertical temperature representation should be defined by the availability

of the fish for the two sampling methods each year. One way of evaluating this could be to construct a vertical profile showing mean echo density at increasing height above bottom. During 1993-1995 a change in distribution took place; with cod being closer to the bottom in 1995 than in 1993 (Paper 1). Hence, it is expected that the availability to the bottom trawl increased over the period and that the availability to the acoustics decreased due to more fish in the acoustic dead zone in 1995 than in 1993. Therefore, it is recommended that in years when fish stays close to the bottom, swept area and bottom temperature should be used, while in years where a higher proportion of the fish are distributed high up in the water column, swept area or acoustics together with mean temperature from 100m to the bottom should be used.

Due to their seasonal migration pattern, cod are in the warmest part of their distribution area during the winter and in the colder parts of this area in the summer (Paper 6). To adjust for these seasonal variations in temperature the mean ambient autumn temperature should also be calculated. Cod can experience just as large a difference in temperature within a single day as they experience between seasons (unpublished data). In order to arrive at a reliable estimates of annual cod consumption, the extent of this diel temperature variation has to be studied more thoroughly and the magnitude quantified. Through extending the use of data storage tags, more detailed information about the effect of temperature on the growth of cod can be provided. Hopefully, by combining ambient winter temperature, ambient autumn temperature and data from tagging experiments it will be possible to create a annual ambient temperature curve at age, as described earlier, with the resolution in time needed to improve the consumption estimates. To incorporate the functional relationship between temperature and growth, predictions of temperature are needed. Reliable models for forecasting ocean climate one year ahead are currently only at a preliminary stage (Ådlandsvik, 1998).

CONCLUDING REMARKS

The reviewed papers describe how horizontal and vertical distribution of gadoids can affect survey results.

By using ambient temperature instead of geographically fixed temperatures, estimates of the quantity of food consumed by cod will be made more reliable. Hence, estimates of mortality rate and recruitment for cod and haddock would also be improved. It has been shown that temperature affects the growth of north-east Arctic cod. Estimates of annual temperature cycles would improve further studies on the effects of temperature on fish distribution and growth.

Demersal fishes such as cod and haddock migrate vertically, causing diel and semi-diel variation in the availability of the fish to the two tools used in abundance surveys (bottom trawl and echo sounder). Obtaining reliable correction factors that take into account biological as well as environmental factors is currently an unrealisable goal. A promising first step, however, would be to combine acoustic and swept-area estimates, using acoustics to estimate the density of fish that are unavailable to the bottom trawl. To do this further studies on vertical herding and horizontal avoidance will have to be carried out.

The understanding of fish migrations demands studies which cover a range of scales in time and space from hours and metres, through days and tens of kilometres, to years and hundreds or thousands of kilometres. A more fundamental understanding of the relationship between the environment and observed behaviour is therefore needed. This can only be achieved if observations of both the physical and biological environment are made on scales of time and space that are relevant to the processes under investigation. By studying individual fish rather than parts of the population, the factors that actually affect fish movements and the mechanisms behind them may be revealed, quantified and integrated in a form that will be representative of the whole population and applicable for assessment purposes.

The modifications in the methodology used for estimation of fish abundance from survey-based data, that have been proposed here, would reduce sources of error and increase the reliability of estimates of abundance.

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