

# Optimal selection of temperature areas by juvenile cod (*Gadus morhua* L.) in the Barents Sea modelled by dynamic optimisation

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The trade-off between growth rate in areas with different temperatures and predation rates was modelled for juvenile cod living in the Barents Sea by a dynamic optimisation model. The choice of optimal temperature area of a juvenile (1-group) cod growing from a start weight (50 g, 15 cm) to a size refuge (640 g, 40 cm) was modelled for two scenarios with distributions of predators (4+ groups cod) similar to those observed in the Barents Sea in February 1990 and 1994, respectively, and without food limitations. The model predicted that when there was an overlap in distribution between large cod and younger cod (0–3 group), the younger year classes would move to areas with lower temperature and less predators, offering higher survival rates. Fish predators forced the prey to inhabit less optimal areas, and both growth and survival rates fell in comparison with a scenario with fewer fish predators (cannibals) and less overlap. Increased fish predator density increased these effects, and the juveniles would stay in colder water for a longer period and their growth rate would be further reduced. Higher mortality, independent of area and size, made it more profitable to stay in warmer water, leading to higher growth but increased mortality rates.

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## Introduction

This study addresses the problem of small juvenile cod living in the Barents Sea and their choice of habitat with respect to the temperature and predation risks that will optimise the probability of survival, until they reach a size where they will not be eaten by most fish predators. The problem is solved by a state-variable model using stochastic dynamic programming (SDP; Mangel and Clark, 1988). In the model, the growth rate of the cod is only related to ambient temperature and fish size, and predation risk is related to prey size and densities of large cod in areas with different temperatures. The goal is to achieve better understanding of the processes behind observed variations in the growth and distribution of juvenile cod in the Barents Sea.

During the last few decades, dynamic modelling has been widely used in behavioural ecology (e.g. Sibly and McFarland, 1976; Mangel and Clark, 1988; McNamara and Houston, 1992). This method has also been useful for explaining vertical and horizontal migrations of fish and plankton (Mangel and Clark, 1988; Rosland and Giske, 1994; Tyler and Rose, 1994; Fiksen and Giske, 1995; Fiksen *et al.*, 1995; Giske *et al.*, 1998). This approach makes it possible to predict optimal habitats over various time scales for animals that are trading off predation risk and growth, to include important life history characteristics, and to account for, both short- and long-term behaviour patterns. One of the most obvious advantages of this model is the possibility it offers of quantifying changes in behavioural patterns due to changes in environmental factors and internal state (Krebs and Davies, 1984).

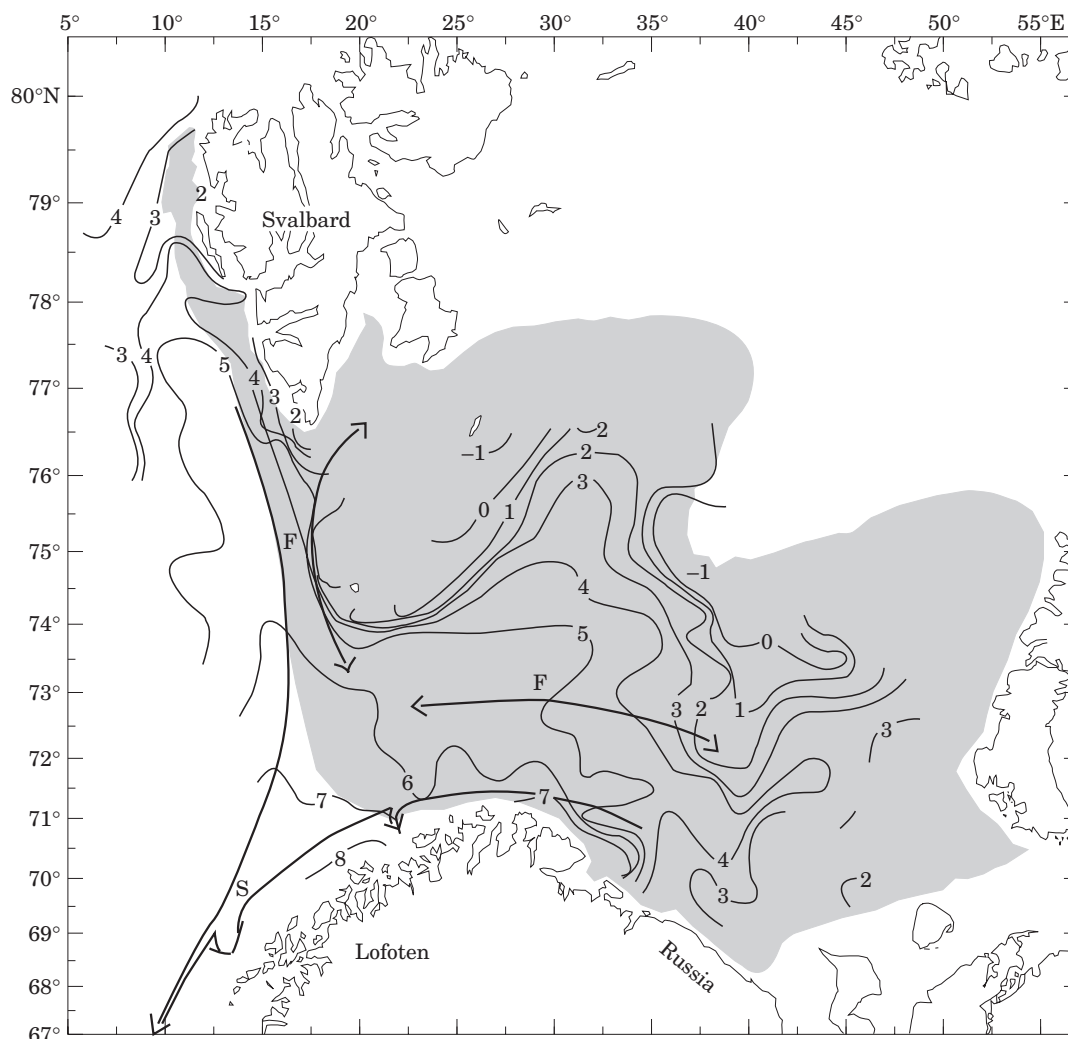


Figure 1. The area of distribution of northeast Arctic cod and isotherms ( $^{\circ}\text{C}$ ) at 100 m depth. Feeding areas (hatched), seasonal feeding migrations (F) and spawning migration (S) are indicated. Temperature distribution is for August 1995. (Reprint of Figure 1 in Ottersen *et al.*, 1998).

Dynamic modelling is based on the idea that organisms respond to changes in their environment, given their current physiological state, in order to maximise their fitness. This theory is based on the assumption that individuals that come close to the optimal strategy are selected for, and reproduce at a higher rate than individuals adopting suboptimal strategies. One might be tempted to ask whether cod rationalize about predation risk or how cod measure cumulative mortality rate or reproductive potential. These questions are outside the scope of this paper. However, we accept that the behaviour of a cod in response to various environmental, biological and internal physiological cues operates in such a way as to maximise its future survival probability on a given time horizon.

### The cod in the Barents Sea

Within the area of distribution of Northeast Arctic cod (Figure 1), annual mean temperatures experienced by the fish range from 6–8 $^{\circ}\text{C}$  at the spawning grounds along the west coast of Norway (Aure and Østensen, 1993) down to 0 $^{\circ}\text{C}$  or even –1 $^{\circ}\text{C}$  along the Polar Front in the north and northeast where the fish feed during summer and autumn (Woodhead and Woodhead, 1965; Mehl *et al.*, 1985). The Barents Sea is characterised by an inflow of relatively warm Atlantic water (Midttun, 1990). In years with high inflow, the mean temperature and areas without ice cover both increase. In these warm periods cod distribution extends towards the east and north as compared to periods with low inflow, when the

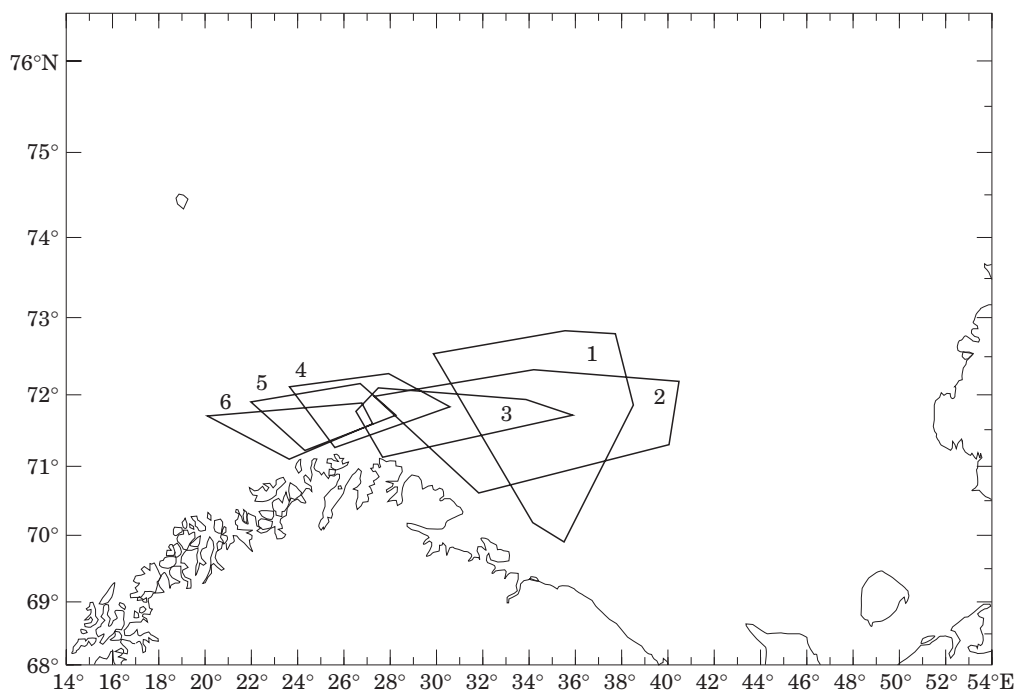


Figure 2. Areas within which the centre of mass distribution of each age group (1–6 years) were located in February 1988–1995. (Reprint of Figure 5 in [Ottersen et al., 1998](#).)

fish tend to concentrate in the southwestern part of the Barents Sea.

Cod are mainly found at depths below 100 metres ([Korsbrekke et al., 1995](#)), where seasonal variations in temperature at given locations are rather small, 1–3°C ([Ottersen and Ådlandsvik, 1993](#)). As a result, cod experience the greatest temperature differences during their seasonal horizontal migration. Generally speaking, the smaller cod are found in colder water than larger cod and have shorter seasonal migrations. The 1–2 year-old cod seem to remain mainly in the areas where they settled during the autumn as 0-group at the end of their pelagic drift phase ([Maslov, 1960](#)). When they are large enough (age three or more) to prey on capelin (*Mallotus villosus*), they start to follow the capelin migrations towards the coasts of Russia and northern Norway in winter, and north and eastwards in the summer. The majority of mature specimens, from about seven years of age, migrate to the spawning grounds in the Lofoten area, or further south, in November–February. They migrate back to the feeding areas in the western and northwestern part of the Barents Sea in April–May, and further north and east during the summer and early autumn to feed on capelin ([Mehl et al., 1985](#)).

In accordance with these seasonal movements through areas with different temperatures, the mean ambient temperatures of the fish will increase with age, as

demonstrated by the horizontal distribution of the centre of mass of each age group ([Figure 2](#)), where older age groups are found further west and in warmer waters than the younger ones ([Ottersen et al., 1998](#)). A clear tendency of reduced inter-annual variability with age in the location of the centre of mass for each age group can also be observed. Individual age groups also maintain their relative distribution to each other, more or less independently of absolute temperature ([Ottersen et al., 1998](#)).

It is likely that there are geographical variations in predation pressure on small cod by large cod, and that the risk of predation is more pronounced in areas of extensive overlap between prey and predator, i.e. the western parts of the distribution area of the small fish. The number of fish species is low in the Barents Sea. In terms of number and biomass, cod is the dominant predator on other fish, especially on fish larger than about 15 cm, and cannibalism is probably the main cause of mortality of 1–3 group cod ([Bogstad et al., 1994](#)). Because of the seasonal and annual variations in geographical overlap between large and small cod, the predation risk for a small cod will vary, both during the year and from year-to-year, dependent on the biomass of large cod and the availability of the preferred prey of large cod, e.g. capelin and deepwater shrimp (*Pandalus borealis*) ([Mehl, 1989](#); [Bogstad et al., 1994](#); [Nilsen et al., 1994](#)).

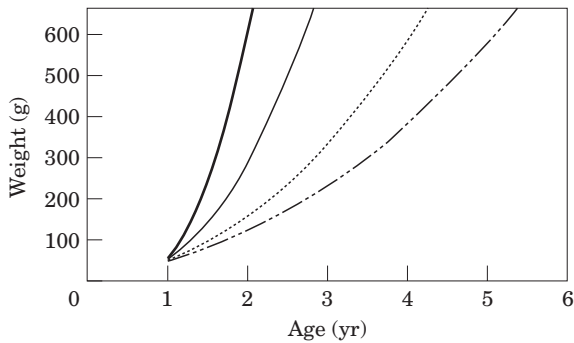


Figure 3. Growth of a 50 g cod (age 1) at 1 (— · — · —), 2 (·····), 4 (— — —), and 6°C (—) when fed to satiation according to the growth model (Jobling, 1988).

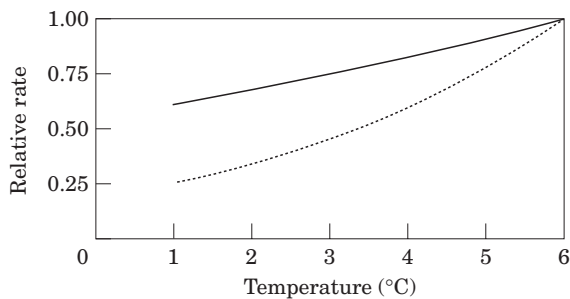


Figure 4. Relative decrease in consumption (—) and growth (·····) rate compared to consumption and growth rate at 6°C for a cod fed to satiation (Jobling, 1988).

### The model

For most fish there is a trade-off between maximising food intake and avoiding predation (Sogard, 1994). For cod living in areas with geographical variations in temperature, such as the Barents Sea, the ambient temperature is also a part of this trade-off. The maximum growth rate of cod is very temperature-dependent, as shown in Figure 3, where growth of cod fed to satiation at temperatures from 1–6°C is calculated according to a model developed by Jobling (1988). Given that there is sufficient food and no predation, the cod should stay in the warmest water in the southwestern part of the Barents Sea to optimise growth. We assume that cod are able to modify their directional movements on the basis of differences between ambient and preferred temperatures (Neill, 1979).

Both low prey density and high predation risk in warmer areas can make it more profitable to remain in colder water. If we look at these factors separately, the trade-offs are somewhat different. As the temperature falls, the metabolic processes slow down and maximum food intake and growth rate both decrease (Figure 4). However, the relative decrease in growth rate is greater than the decrease in consumption (Jobling, 1988).

The risk of being eaten by larger fish usually decreases with increasing size. This relationship is dependent on the size and number of predators, the density of alternative prey, and the food intake of the predators (which is temperature dependent). Cod make up only a small part of the diet of large cod (Bogstad *et al.*, 1994), so the distribution of the predators ought to be little influenced by the distribution of small cod. However, the opposite situation is not true, and small cod ought to avoid areas with many predators (large cod). With the same predator density, the daily predation risk will be lower in colder water due to the lower food intake of the predators. However, these relationships are complex, because the growth rate of the small fish also decreases. Since consumption decreases relatively less than growth, cumulative mortality per growth step will actually increase. The optimal strategy for the small cod will therefore depend on factors such as temperature, available prey, growth rate, relative distribution of the predators, total biomass of predators, and other mortality risks.

This complex trade-off can be optimised by a dynamic model. We developed a simplified model, in which we looked at optimal habitat choice of a juvenile (1-group) cod growing from a start weight (50 g, ca. 15 cm) to a size refuge, i.e. a terminal weight where there is assumed to be no risk of being eaten by other fish (640 g, ca. 40 cm). Optimal fitness is defined as the maximum probability of survival until the cod reaches terminal weight. The cod can choose between areas with different temperature and predation risks. The optimal choice is found by a backward iteration process, where the optimal choice for each growth increment (10 g) is found, starting at the terminal weight  $W_N$  and going backwards to the start weight  $W_0$ . The basic methods and terminology are taken from Chapter 8 in Mangel and Clark (1988), but the model deviates from the original patch choice models by optimising survival in fixed growth steps (weight intervals) instead of fixed time steps.

### Dynamic modelling equations

The model has the following essential components:

State phase:  $W(k)$  = Weight of cod at the start of step  $k$ .

Constraints: Growth rate,  $G$ , as a deterministic function of temperature and weight,  $G_1(T, W(k))$ , is explained in Equation (3) below. The probability of growing (finding food) in each temperature area is set at 1 in all patches. The metabolic cost of moving between different temperature areas is not taken into account.

Strategy set: Choice of temperature area (patch). Temperature  $T = 1$ –6°C.

Optimisation criterion: Probability of survival over  $N$  periods;  $N = \text{integer}((W_N - W_0)/\Delta w)$ .

State dynamics:  $W(k+1)=(W(k)+\Delta w)$  with probability  $S(W(k),T)$ , where  $S(W(k),T)$  is size- and temperature-dependent probability of survival through a weight step at weight  $W(k)$  and temperature,  $T$ .

The stochastic dynamic programming equation then becomes:

$$F(W(k),W_N)=\max[S(W(k),T)]*F(W(k+1),W_N) \quad (1)$$

with terminal fitness function:

$$F(W(N),W_N)=1 \quad (2)$$

The optimal fitness  $F(W(k),W_N)$ , is the maximum probability of survival from weight  $W(k)$  to terminal weight  $W_N$ .

The size and temperature-dependent growth rate

The probability of being preyed on during the time the fish grows one growth increment,  $\Delta w$ , depends on how fast it grows through the increment and the daily mortality risk in the area. The growth rate is dependent on available food, temperature ( $T$ ), and the weight of the fish  $W(k)$ . If we assume that the growth rate is constant within each step and that the fish feed to satiation (no food limitations), the specific growth rate can be expressed by the following formula (Jobling, 1988):

$$G_1(T,W(k))=e^{f(T)+h(W(k))} \quad (3)$$

where  $f(T)=(0.216+0.297T-0.000538T^3)$  and  $h(W(k))=-0.441\ln W(k)$ .

To calculate the time needed by the fish to grow through growth step  $k$  at temperature  $T$   $\Delta t(k,T)$ , we use the common formula for specific growth rate:

$$G_2=100[(\ln W(k+1)-\ln W(k))/\Delta t(k,T)] \quad (4)$$

If we multiply by  $\Delta t(k,T)$  and divide by  $G_2$  on both sides of Equation (4) and then substitute  $G_2$  with  $G_1(T,W(k))$  we get the following equation for  $\Delta t(k,T)$ :

$$\Delta t(k,T)=100(\ln W(k+1)-\ln W(k))/G_1(T,W(k)) \quad (5)$$

The cumulative mortality rate

If we assume that the biomass of predators per area is the same in all temperature areas, the daily predation mortality decreases with increasing size, and decreasing temperature. This is due to the growing ability of the prey to escape with increasing size and decreased metabolism and consumption by the predators at lower temperatures. Maximum instantaneous mortality per day for the smallest fish in the warmest area, due to predation by fish, is given as  $M_d$ =constant. Minimum probability of survival per day is  $s_{\min}=e^{-M_d}$ , given no

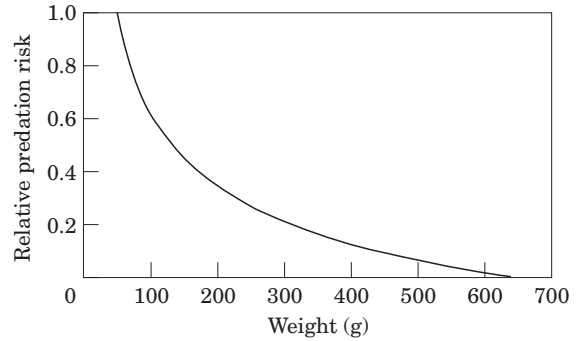


Figure 5. Weight-dependent predation risk relative to the predation risk of a 50 g cod.

other causes of mortality. In addition, we assume there is mortality independent of fish predation, which is set to a constant,  $M_0$ , at all temperatures.

The relative decrease in mortality rate,  $c(T,W(k))$ , compared to  $M_d$ , caused by decreased temperature, increased prey size and decreased predator density is calculated as follows: The relative reduction,  $r_1(T)$ , of the consumption by predators relative to the consumption at the highest temperature, was calculated using the formula for consumption (6) from Jobling (1988).

$$C(T,W_p)=e^{f_2(T)+h_2(W_p)}, \quad (6)$$

where  $f_2(T)=(0.104T-0.000112T^3-1.50)$  and  $h_2(W_p)=0.802\ln W_p$ .

The relative decrease in consumption,  $r_1$ , by predators at decreased temperature, is independent of predator size,  $W_p$ , since the weight disappears in the division:

$$r_1(T)=C(T,W_p)/C(T_{\max},W_p)=e^{f_2(T)+h_2(W)-f_2(T_{\max})-h_2(W)}=e^{f_2(T)-f_2(T_{\max})} \quad (7)$$

The relative fall in predation mortality as prey size increases,  $r_2(W(k))$ , from  $W_0$  to  $W_N$  is expressed by this assumed relationship:

$$r_2(W(k))=(\ln(W_0)/\ln W(k)-0.605)/(1-0.605); \quad W_0=50 \text{ g}; W(N)=W_N=640 \text{ g} \quad (8)$$

The value of  $r_2(W(k))$  decreases from 1 at  $W_0$  to 0 at  $W_N$  (Figure 5). The weight at zero predation risk (size refuge) was set at  $W_N=640$  g ( $L=40$  cm), on the basis of analyses of cod stomachs sampled in the Barents Sea (Bogstad et al., 1994). This relationship between relative predation risk and weight is a reasonable assumption, where the predation risk falls most steeply at the beginning and slowly approaches zero towards the end (Figure 5).

The relative distribution of predators in the different temperature areas is regulated by  $r_3(T)$ , which gives the

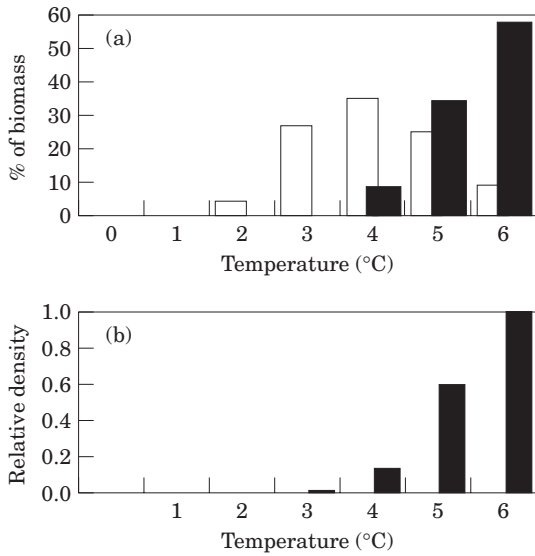


Figure 6. (a) Observed distribution of cod at age 1–3 (open) and 4–7 (filled) years in 1990 in different temperatures (°C). (b) Relative distribution of predators (age 4–7 years) calculated from Figure 6(a) and used as input values for the 1990 scenario.

scenario we wish to study. The area with the highest predator density has factor 1, whilst the factors in the other areas are calculated as:

$$r_3(T) = (\text{predator density area } T) / (\text{predator density in temperature area with highest predator density})^{-1} \quad (9)$$

Two scenarios were chosen: the year 1990, when most large cod (the predators) were found in the warmer 4–6°C water; and the year 1994, when the predators were distributed throughout the whole temperature range (1–6°C) of the Barents Sea. The relative biomass distributions of 1–3 and 4–7 year-old cod within each 1°C temperature interval (Figures 6 and 7) were calculated from survey data recorded in February (Table 2 in Ottersen *et al.*, 1998). See Ottersen *et al.* (1998) for details on the distribution of cod and temperature in the Barents Sea in these two years.

In the model it is possible to pass through several temperature areas in one growth step. There are no costs of moving through temperature areas with high predation risk, and there is no cost of migration. Due to the relatively low predator biomass at 6°C in 1994 [Figure 8(a)], the model will always choose the highest temperature as the optimal one with the parameters used in the basic run. To avoid the fish moving through temperature areas with higher mortality, the relative predator distribution was set at maximum at all temperatures above the temperature with the highest predator biomass [Figure 7(b)].

The correction factor,  $c$ , is the product of the equations describing the effects of increased prey size,

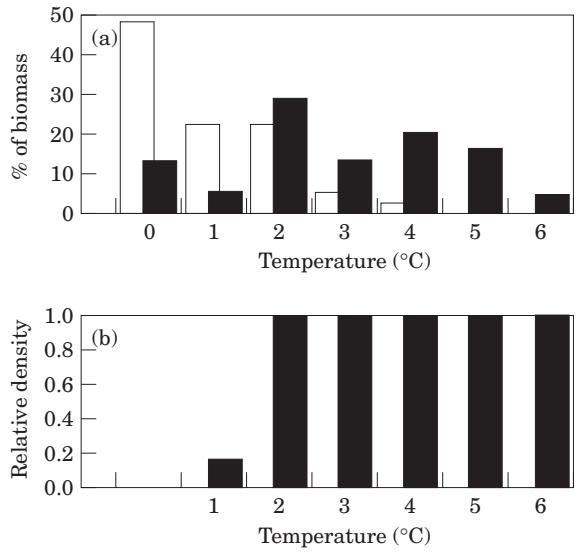


Figure 7. (a) Observed distribution of cod at age 1–3 (open) and 4–7 (filled) years in 1994 in different temperatures (°C). (b) Relative distribution of predators (age 4–7 years) calculated from Figure 7(a) and used as input values for the 1994 scenario. To avoid the fish moving through temperature areas with higher mortality, the relative predator distribution was set at maximum at all temperatures above the temperature with the highest predator biomass.

decreased temperature, and relative predator distribution:

$$c(W(k), T) = r_1(T) r_2(W(k)) r_3(T) \quad (10)$$

whilst survival per day in area  $T$  of a cod of size  $W(k)$  is:

$$s(W(k), T) = [1 - (c(T, W(k))(1 - s_{\min}))] s_{M0}; \quad s_{M0} = e^{-M_0} \quad (11)$$

The probability of survival through weight step,  $k$ , in temperature area,  $T$ , is then:

$$S(k, T) = s(W(k), T)^{\Delta t(k, T)} \quad (12)$$

which is the value we wish to maximise in each growth step, such that the product of the survival in all time steps  $[\Pi S(k, T); k = N \text{ to } 1]$  is maximised.

### The basic run

The model was run with relative distribution of predators according to the 1990 and 1994 scenarios [Figure 6(b) and Figure 7(b)], with maximum predation mortality  $M_y = 3 \text{ yr}^{-1}$  ( $M_d = M_y/365$ ) and other natural mortality  $M_0 = 0.1 \text{ yr}^{-1}$ . The  $M_y$  and  $M_0$  values were chosen as reasonable values based on a sensitivity analysis and general knowledge of the mortality of Barents

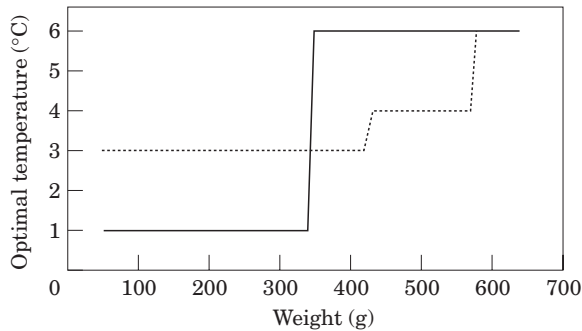


Figure 8. Predicted optimal choice of temperature areas relative to weight, under the 1990 (.....) and 1994 (—) scenarios.

Sea cod. This method of choosing parameters has also been used by Bull *et al.* (1996).

In the basic run we assume that there is surplus food in all patches and we thus restrict the analyses to the trade-off between predation risk and temperature.

The model was written in SAS<sup>®</sup> Language (SAS Institute Inc.).

### Sensitivity analysis

To test the effects of increased total predation mortality,  $M_y$ , the model was run with  $M_y=0, 1, 2$  and  $3$ , predator distribution as in 1994, whilst the other parameters were kept as in the basic run. To test the effects of natural mortality  $M_0$  due to other causes, the model was run with  $M_0=0, 0.1, 0.2$ , and  $0.3$ , predator distribution as in the 1994 scenario, whilst the other parameters were kept as in the basic run.

## Results

### Optimal temperature preferences (habitat choices)

Given the conditions set in the basic run, the optimal strategy for a small cod living in the 1990 scenario (Figure 6) would be to stay in a temperature regime of around 3°C up to a weight of about 400 g (Figure 8), representing a growth period of more than 1.8 years (Figure 9). At this weight the size-dependent mortality risk becomes lower in the 4°C temperature regime due to the increased growth rate and reduced predation risk with increased size. When the fish has reached a weight of about 550 g it is large enough to migrate further west into the 6°C temperature regime, where it stays until the terminal weight is reached (Figure 8).

In the 1994 scenario (Figure 7), the optimal strategy is to stay in the 1°C temperature regime up to 350 g (Figure 8), representing a growth period of 2.8 years (Figure 9). After reaching this size, it migrates to the highest temperature regime of 6°C, as predation in the

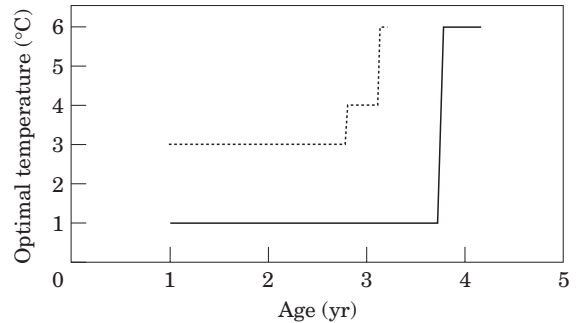


Figure 9. Predicted optimal choice of temperature areas relative to age, given the 1990 (.....) and 1994 (—) scenarios, assuming weight=50 g at age 1.

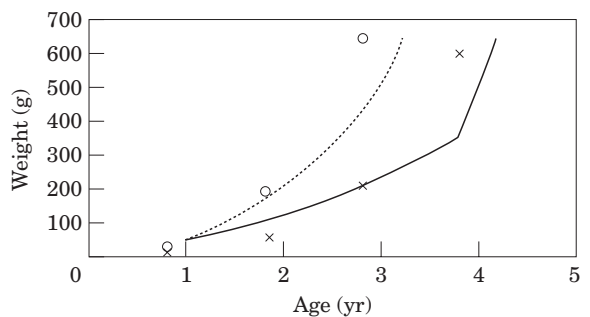


Figure 10. Predicted growth for a 50 g cod in the optimal areas given the 1990 (.....) and 1994 (—) scenarios, and observed mean weights at age of the 1989 year-class (○) and 1993 year-class (×) in the Barents Sea.

model is set to be equal in the temperature regimes above 1°C for this scenario [Figure 7(b)].

### Optimum growth rate

In the 1990 scenario, the small cod should remain in warmer water, resulting in higher growth rates compared to the 1994 scenario (Figure 9). According to the growth model the terminal weight was reached one year later in the 1994 scenario than in the 1990 scenario (Figure 10). The mean weights of the real 1990 and 1994 year classes in the Barents Sea (1–3 group) are also shown in Figure 10. Even if the model is based on constant scenarios (winter 1990 and 1994) the model weights showed quite a good approximation to the real weights.

### Maximum probability of survival

In the 1990 scenario the probability of survival to the terminal weight was higher than in the 1994 scenario (Figure 11). This was a combined effect of the higher temperature in the optimal area for fish smaller than

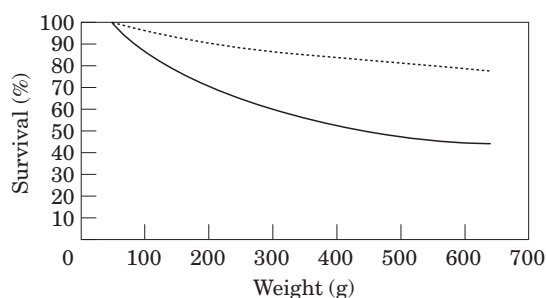


Figure 11. Probability of surviving to different weights of a 50 g cod to weight in the optimal areas given the 1990 (.....) and 1994 (—) scenarios.

350 g in the 1990 scenario and the distribution of most of the predators in the warmest water (Figures 6 and 7).

## Discussion

The model is constructed as a “dynamic state variable” model in order to study the optimal behaviour of juvenile cod attempting to grow through the predation field with as high probability of survival as possible. The present model is a modification of a “traditional patch type” model (e.g. Mangel and Clark, 1988) and can be compared to a one-dimensional version of the two-dimensional fitness-based model of capelin migrations in the Barents Sea (Fiksen *et al.*, 1995), where spatial or horizontal movements in our model are linked through the temperature conditions in the Barents Sea.

One of the conclusions from our model is that in the 1990 scenario (Figure 6), translated to the Barents Sea temperature distributions, young cod tend to have a more westerly distribution than in the 1994 scenario (Figure 7). This is mainly because the older fish are found further towards the warmer waters to the west, thus allowing the younger ones to shift westwards. In the years when the older age groups are more evenly distributed and the overlap between the age groups increases, the potential for cannibalism is also greater. The response of the young fish is to move eastwards into colder waters. These areas are less favourable to growth but have a lower cumulative predation risk. This observed change in distribution is partly in agreement with the results from Ottersen *et al.* (1998), who illustrated the horizontal distribution of cod by presenting the centres of mass for each age group from 1988–1995 (Figure 2) by taking the co-ordinates for the longitude displacement and comparing them with the calculations of mean ambient temperature (Figure 10 in Ottersen *et al.*, 1998). At rising sea temperature levels from 1989–1990, fish distributions tended to shift eastwards. During the warm period from 1990–1993, all age groups were moving further eastwards, leading to continuously decreasing ambient temperatures as predicted from the

model. From 1993–1994 the temperature in the Barents Sea fell, and one should expect that the fish would have a more westerly distribution in 1994 than in previous years. Instead, the mass centre of fish aged three and older shifted even further to the east. In this period the biomass of young fish increased considerably (ICES, 1996). Although temperature seems to be an important factor influencing the horizontal distribution of cod, at high abundance the fish are distributed over a wider area, extended towards the east and thus shifting the centre of mass of distribution eastwards, apparently independent of temperature conditions. Although the effect of increased abundance seems to be of considerable importance, this is not taken into account in our model.

To enable the model to represent a more realistic picture of the ecosystem, we might have included some information about the availability of food in the different temperature areas, but no such quantitative documentation was found, and we recommend making investigations of ambient temperature and prey distribution in the future. In the colder, eastern areas, the young cod might benefit from a higher abundance of prey suitable for small fish (Burgos and Mehl, 1987), as krill and amphipods are generally abundant in the areas close to the Polar Front (Loeng *et al.*, 1995). In addition the amount of alternative prey for the predators can influence the predation pressure. However, Bogstad *et al.* (1994) found little support for the hypothesis that the frequency of cannibalism increased when the abundance of capelin, the major prey of cod, was low.

Another limitation of our model is the fact that we have ignored seasonal variations in temperature, geographical distribution (centre of mass), food availability (quality and quantity), and assumed that the February situation is representative for the whole growth period up to the terminal weight. The model could have been improved by implementing the change in distribution of predators with season and time. Some of these data are available, but they remain to be analysed.

We have not taken into account the mechanisms of aquatic feeding, nor of the visual attack/detection range of a predator in relation to fish size. The feeding of most fish stops at the “visual feeding threshold” below 0.1 lux (Blaxter, 1974). In the Barents Sea during the winter months, the daylight period is short, restricting the feeding rate and predation risk on young cod. The visual reaction distance decreases proportionally more for a large fish than for small fish with decreasing light (Mangel and Clark, 1988, using data from Hall *et al.*, 1979; Aksnes and Giske, 1993), and thus the predation pressure on young cod is considered to drop faster compared to the limitation for the small cod to find food.

We also know that fish make vertical migrations in order to reduce the predation risk (Clark and Levy,



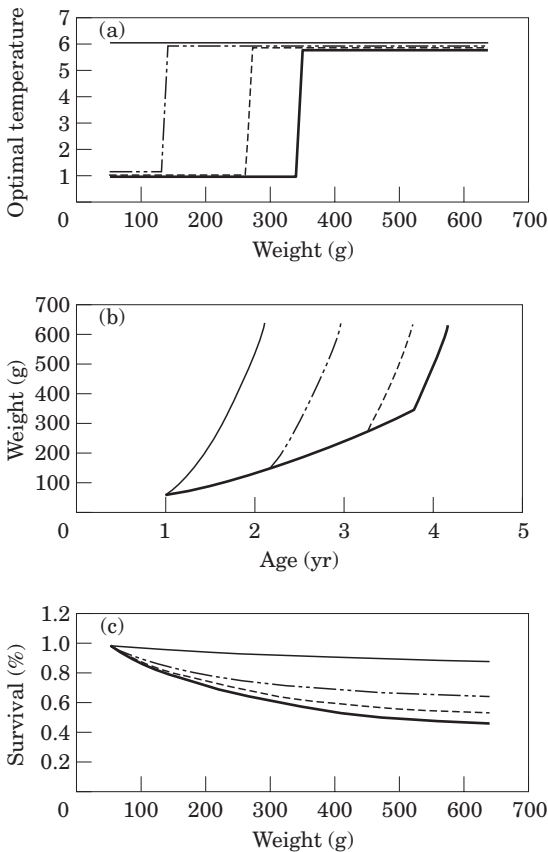


Figure 12. Effects of increasing total predation mortality,  $M_y$ . (a) Optimal temperature area at weight; (b) weight at age; (c) survival probability at weight. —,  $M=0$ ; - · - ·,  $M=1$ ; - - - -,  $M=2$ ; ———,  $M=3$ .

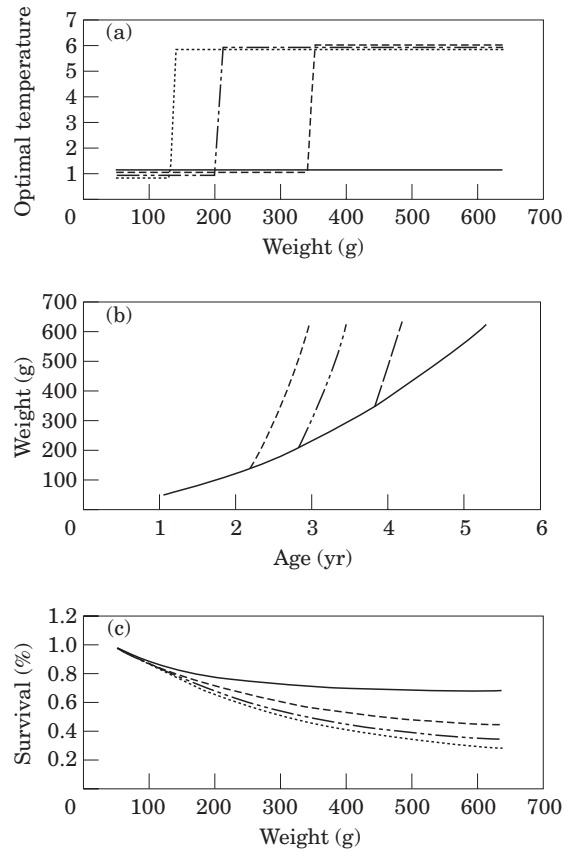


Figure 13. Effects of increasing other natural mortality,  $M_0$ . (a) Optimal temperature area at weight; (b) weight at age; (c) survival probability at weight. —,  $M_0=0.0$ ; --,  $M_0=0.01$ ; - · - ·,  $M_0=0.2$ ; · · · ·,  $M_0=0.3$ .

1988; Michalsen *et al.*, 1996); however, vertical movement is ignored in our model.

**Sensitivity analysis**

The biological significance of increasing total fish predation mortality  $M_y$ , is that the total biomass of fish predators increases, without changing the relative distribution in the different temperature areas. Increasing  $M_0$  means adding a constant mortality to all areas. The different values of both parameters are analysed for their effects on optimal habitat, growth and total probability of survival to  $W_N$ .

Using the predator distribution of the 1994 scenario, the effect of increasing the maximum predation rate  $M_y$  from 0–3 is shown in Figure 12. With no predation mortality ( $M_y=0$ ) it is optimal to stay in the warmest water. Increasing mortality due to predation ( $M_y$ ) makes it profitable to stay longer in the coldest water, because of the low ratio of predators to prey in this area in the

1994 scenario. This leads to a slower rate of growth and decreased survival with increasing  $M_y$ .

Increasing the predation-independent mortality  $M_0$  from 0.0 to 0.3 has the opposite effect on habitat choice and growth (Figure 13). Because of the increased time taken to grow one growth step in cold water the cumulative mortality risk will increase more in cold water when  $M_0$  increases. A low  $M_0$  enables the fish to select areas with a low risk of mortality, making it profitable to stay in this area even if it is at the lowest temperature.

How large must differences in mortality probability be, to make a “significant” differences for the cod? If the difference is very small or not detectable, we assume that the cod will choose the area with the highest growth rate. To test the effects of a minimum detectable difference in cumulative mortality between two temperatures in a growth step, the model was run with minimum detectable differences of 0–0.025, in steps of 0.005, predator distribution as in the 1994 scenario and other parameters as in the basic run. The results show that with an

increasing threshold factor the fish tended to choose warmer and more risky habitats than with no threshold. In the basic run we did not use any minimum detectable difference.

In the model there was a need for uncertainty ( $M_0$ ) in areas with low temperatures and no predation risk. The modelled cod always preferred the “safe” area when no natural mortality was included in the model. Bull *et al.* (1996) also found that non-zero mortality had to be included in their model so that there was a trade-off between starvation and predation risk, otherwise the model failed to reflect foraging effort. In the real world there is probably no safe haven, and in a changing world the animal must also take into consideration the probability of increased abundance of predators in the future. We assume that, through evolution, the fear of an unknown future is inherited in most animals and is expressed through their behaviour. There is, therefore, probably a minimum growth rate (or food intake) that the animal can accept, even when there is no risk of mortality.

The function used to describe the relation between weight and relative predation risk is not based on data, except the general impression obtained from stomach-contents data (Daan, 1983; Bogstad *et al.*, 1994). This relationship is difficult to estimate and depends on the size distributions of predators and amount of alternative prey. The effect of making the relationship less size-dependent (flattening the curve in Figure 5), will diminish the benefit of fast growth and make predation mortality more important. In the 1994 scenario the cod should thus remain longer in cold waters with fewer predators. This would have led to slower growth and lower probability of survival. If this relationship was more size-dependent (steeper curve), it would lead to an opposite effect. Experimental data on this relationship are required.

The availability of prey is one of the most important factors governing the distribution of fish populations. In the model we have assumed that there is a surplus of food at all temperatures. In addition to avoiding predation, the other reason for moving into cold waters is lack of food in the warmer areas. This will diminish the benefit of higher temperatures. Using the 1994 scenario, the relative decrease in growth rate of 5% per degree will make the 1°C area the optimal choice for a longer period of time, leading to decreased growth and survival. The fish is then predicted to stay in the cold water until it has grown 100 g more.

In a world with limited resources, the availability of prey is also dependent on what the other individuals of the same and other species do. In our model we only consider the optimal strategy of one fish in a static environment, but, in a fish community, density-dependent effects may occur when many fish make the same choice. This problem is considered in ideal free

distribution models (see references in Tyler and Rose, 1994; Giske *et al.*, 1998). One possible way to include the actions of conspecifics and competitors may be to combine dynamic programming and individually based simulation models (see suggestions in Giske *et al.*, 1998).

### The predictive value of the model

In summary, the model predicts that when there is overlap in distribution between large (4+ groups) cod and younger cod, the younger year-classes should move north and eastward to areas with lower temperature and less predators, offering higher survival rates. The fish predators force the prey to inhabit sub-optimal areas, and both growth and survival rates will fall compared to a scenario with less fish predators (cannibals) and overlap. Increased predator density will enhance this effect, and the juveniles will stay in cold water for a longer period and their growth rate will be further reduced. An increase in other natural mortality, if evenly distributed in all areas, will have an opposite effect on migration, and increase the total mortality and growth rate. Density-dependent effects of younger year-classes (small cod) are not considered in the model, but if these decrease the growth rate in a temperature area, the stage-dependent probability of survival will decrease, which may change the optimal choices. The predictions agree fairly well with observed historical data (Nilsen *et al.*, 1994; Michalsen *et al.*, 1998), but the data should be reanalysed to take a closer look at the mechanisms considered in the model.

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