# A spatially explicit fitness-based model of capelin migrations in the Barents Sea

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## ABSTRACT

The geographical distribution and production of the Barents Sea capelin (*Mallotus villosus*, Osmeridae) is modelled by the use of a state-variable optimization technique (dynamic programming), where the main objective of individuals always is to maximize fitness, or total expected reproduction ($R_0$), by selecting the most profitable habitats through time. Fitness is gained by successful reproduction (a function of size) during the spawning season on the breeding grounds off northern Norway. The environment (predators, temperature and zooplankton prey) is determined by a meteorologically forced circulation model for the year 1980, creating a spatial and seasonal fluctuation in the environment. Predation from cod is the main source of mortality, and the distribution of the cod (*Gadus morhua*) stock is assumed to vary with temperature. Growth is predicted from a bioenergetic model, incorporating the cost of swimming between feeding areas and spawning grounds. Field data of the capelin stock recorded during autumn cruises from 1979 is implemented at the start of the model, and then this stock is modelled through 1980 and the first months of 1981. Model predictions are compared with the observed distribution of capelin in autumn 1980. Habitat selection has consequences for the dynamics of the population and growth of individuals, demonstrating the importance of combining external (environmental) and internal (evolutionary) forcing to understand and predict the dynamics of fish populations. This study is the first application of dynamic programming to model the dynamics and ecology

of horizontal fish migration, and we suggest that the method may be developed into a useful tool for the management of short-lived species.

## INTRODUCTION

The horizontal distribution and individual growth of capelin, *Mallotus villosus*, in the Barents Sea varies seasonally and annually (Gjøsæter and Loeng, 1987; Loeng, 1989; Loeng et al., 1992; Skjodal et al., 1992). In "warm" years, when the north-eastern parts of the Barents Sea are influenced by Atlantic inflow leading to a rise in the sea temperature, capelin extend their range of habitats north- and eastwards, whereas they are constrained further to the south and west in "cold" years (Fig. 1; Ozhigin and Luka, 1985; Loeng, 1989). The variability of the environment in this area has a substantial impact on the life history of capelin, as maturation is size dependent (Forberg and Tjelmeland, 1985), the life span is short and capelin are semelparous. Managing stocks of short-lived fish species inhabiting variable environments has been a particularly difficult task. The common fisheries management tool, virtual population analysis (VPA), requires both a stable environment and that the fish live for several years after recruitment. To remedy such difficulties, Giske et al. (1992) suggested dynamic optimization models as a way of modelling capelin growth and distributions. These models can predict optimal distributions depending on the environment (including predators), the size (weight) of single individuals and the fitness-maximizing behaviour of the fish. Here, the model suggested by Giske et al. (1992) is realized and further developed. Such process- or theory-based models are still not likely to fit observations (with our current understanding of capelin bioenergetics and environmental variations of large marine ecosystems), but possess the novel ability of making predictions of how animals will respond to environmental change and the consequences on abundance of such perturbations (Giske et al., 1992, Mangel, 1994; Tyler and Rose, 1994).

**Figure 1.**    Generalized distribution patterns (hatched) and spawning areas (double hatched) of capelin during summer and autumn in (a) warm and (b) cold years. Feeding (white arrows) and spawning (black arrows) migrations are implemented. Redrawn from Ozhigin and Luka (1985), Loeng (1989) and Giske *et al.* (1992).
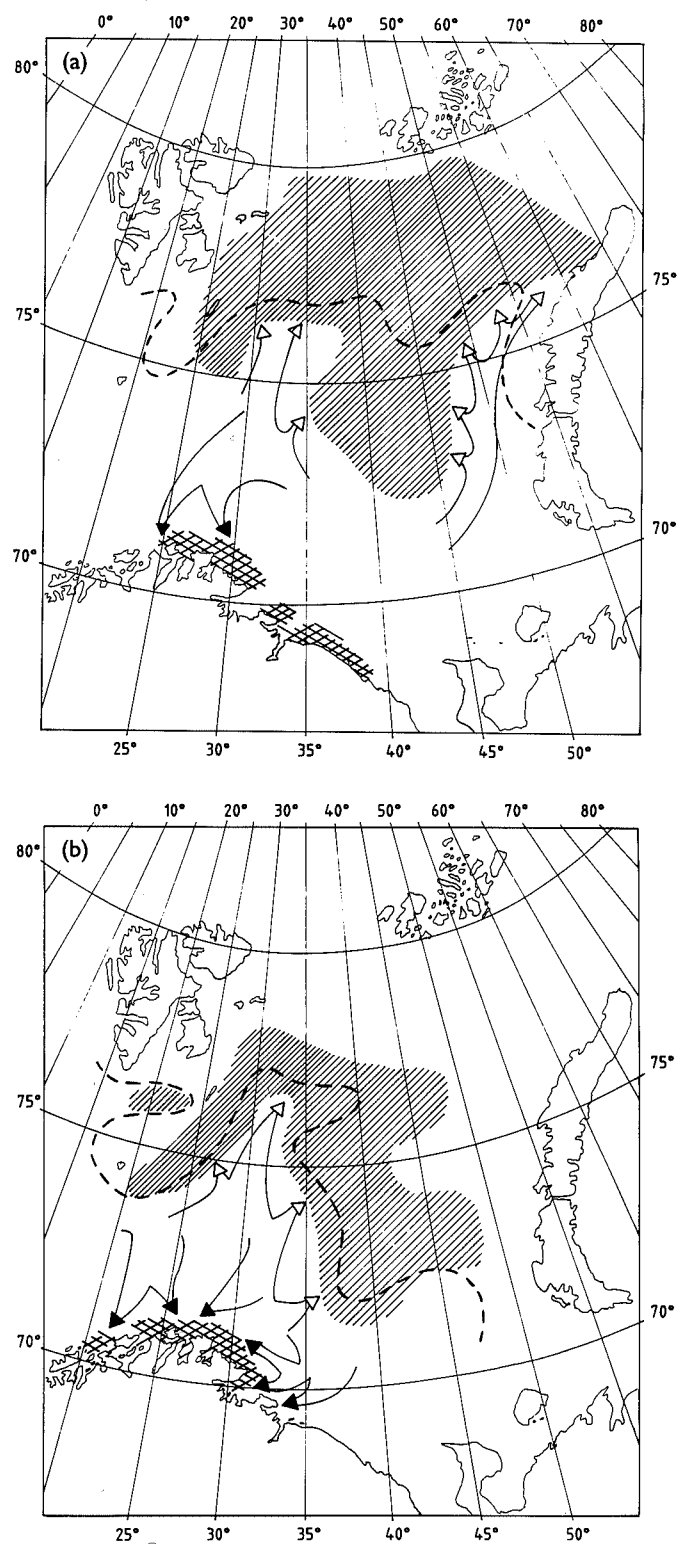
On small scales, fish are known to make decisions like whether to stay alone or to join groups, when to forage and when to hide from predators (Pitcher, 1993). Also at larger scales, the fish should, in order to maximize its contribution to future gene pools, enter new feeding areas as food becomes available, escape from areas with a high risk of mortality and visit the spawning grounds to spawn at times when eggs or larvae can drift into areas with favourable nursery conditions. Models describing the interaction between larval drift, survival and oceanographic conditions have become abundant lately (e.g. Bartsch *et al.*, 1989; Walters *et al.*, 1992; Bartsch and Kunst, 1994), but these models are not applicable when movement ability of fish can overrule the currents, or when fish actively utilize currents in their migration strategies. Also, several models of the vertical migrations of fish and planktonic organisms exist (Clark and Levy, 1988; Mason and Patrick, 1993; Rosland and Giske, 1994; Fiksen and Giske, in press) but fitness-based models of the active horizontal or geographical movements of marine animals are seldom encountered in the literature, and are absent at the scale of large marine ecosystems (Tyler and Rose, 1994). The difference between modelling the distribution of postlarval fish and particles is the ability of fish to swim and actively decide where to stay on a range of spatial and temporal scales. The migration habits of many fish will necessarily be important for their abundance and growth, as transitions between areas alter their overlap with predators, prey and other environmental factors (Clark and Levy, 1988; Mason and Patrick, 1993; Rosland and Giske, 1994). In addition, the shift from one area to another may be costly in terms of energy spent on the migration, at least for pelagic populations inhabiting large marine ecosystems (Jobling, 1994). To model fish populations in large ecosystems, we therefore need both physics and behaviour, with bioenergetics as the mechanism linking the two, and these very different branches of science must be unified in a cluster of models.

The model presented here is constructed by using results from a coupled physical–biological model as the environmental scenario for a capelin population. Data from the regular autumn cruise (September–October) in 1979 (Institute of Marine Research, Bergen) are used to initialize the spatial distribution and length frequencies of the stock. We have assumed that cod do not actively track aggregations of capelin, but simply correlate with the temperature field. Individual capelin move in this setting on a monthly scale and grow and die according to their spatial position. The fitness criterion in the dynamic optimization procedure is to maximize the number of eggs laid during the spawning season,

either in 1980 or 1981. Both options are given to individuals, and the year with the highest fitness value is chosen. Mature capelin migrate to their spawning area at the Finmark coast in February–June, while the immature fraction of the stock overwinter in deeper areas off the coast.

## THE MODEL

### Distribution of resources

Our conceptual understanding of how plankton is spread spatially and temporally in the Barents Sea has improved during the 1980s (e.g. Skjoldal and Rey, 1989; Skjoldal *et al.*, 1987, 1992), and a coupled physical–biological model including *Calanus finmarchicus* has been developed (Slagstad, 1981, 1987; Slagstad *et al.*, 1989; Støle-Hansen and Slagstad, 1991). We use results from this model to describe the thermal environment and food supply offered to capelin in the Barents Sea (Fig. 2). All copepodite stages (I–V) and adults are separated in the transport and growth processes, but summed up to biomass per volume in the capelin model. Only zooplankton in the upper 100 m are counted, while copepods located deeper are assumed safe from visual predation (Hassel *et al.*, 1991; Aksnes and Giske, 1993; Giske *et al.*, 1994; Rosland and Giske, 1994). The zooplankton model ignores alternative food like euphausids, amphipods and copepods other than C. *finmarchicus*, and thus underestimates prey abundance in the central and northern Barents Sea, where the stabilization of water masses following the melting of ice creates a phytoplankton bloom followed by the build-up of the zooplankton stocks. To compensate this, we assume spatially homogeneous, but seasonally fluctuating zooplankton (like *Calanus glacialis*) biomass in the temperature range 0.0–1.5°C. Also, we have used a minimum zooplankton abundance of about 10% of the global peak zooplankton abundance in all grid cells throughout the year. This is done to reduce the discrepancy between observed total zooplankton (Hassel, 1986; Skjoldal *et al.*, 1992) and modelled C. *finmarchicus* values.

### Capelin growth

Studies indicate that temperature and food abundance are the most important variables in determining capelin growth rates (Hassel *et al.*, 1991, Skjoldal *et al.*, 1992). Growth has been shown to follow a gradient from southwest to north-east (Gjøsæter and Loeng, 1987), maybe because of the supply of zooplankton and heat mediated by the Atlantic inflow from the south-west. We

**Figure 2.**   Maps of the Barents Sea (surrounded by northern Norway (lower left), Svalbard (upper left) and Novaja Zemlja (lower right) showing the horizontal distribution during four months of the year of temperature, zooplankton and predation risk. (a) Temperature °C of the Barents Sea during 1980 as predicted from the hydrodynamic model, averaged for the upper 100 m of the water column. (b) Densities of *Calanus finmarchicus* (biomass m$^{-2}$) from the zooplankton model, with an ice-edge bloom (conveyor belt) implemented. The simulation includes both the local production and the advected biomass, and the transport of individuals is regulated by their vertical migration. (c) Distribution of mortality risk (month$^{-1}$) resulting from eqns 6 and 7. Mammals are uniformly distributed, while cod distribution (ind. m$^{-2}$) is a function of temperature. Bottom depth influences the mortality risk by increasing predator density ($C_{i,j}$ + O) [ind. m$^{-3}$] in shallower areas. Low temperature in winter is coupled to high densities in nearshore areas of northern Norway.
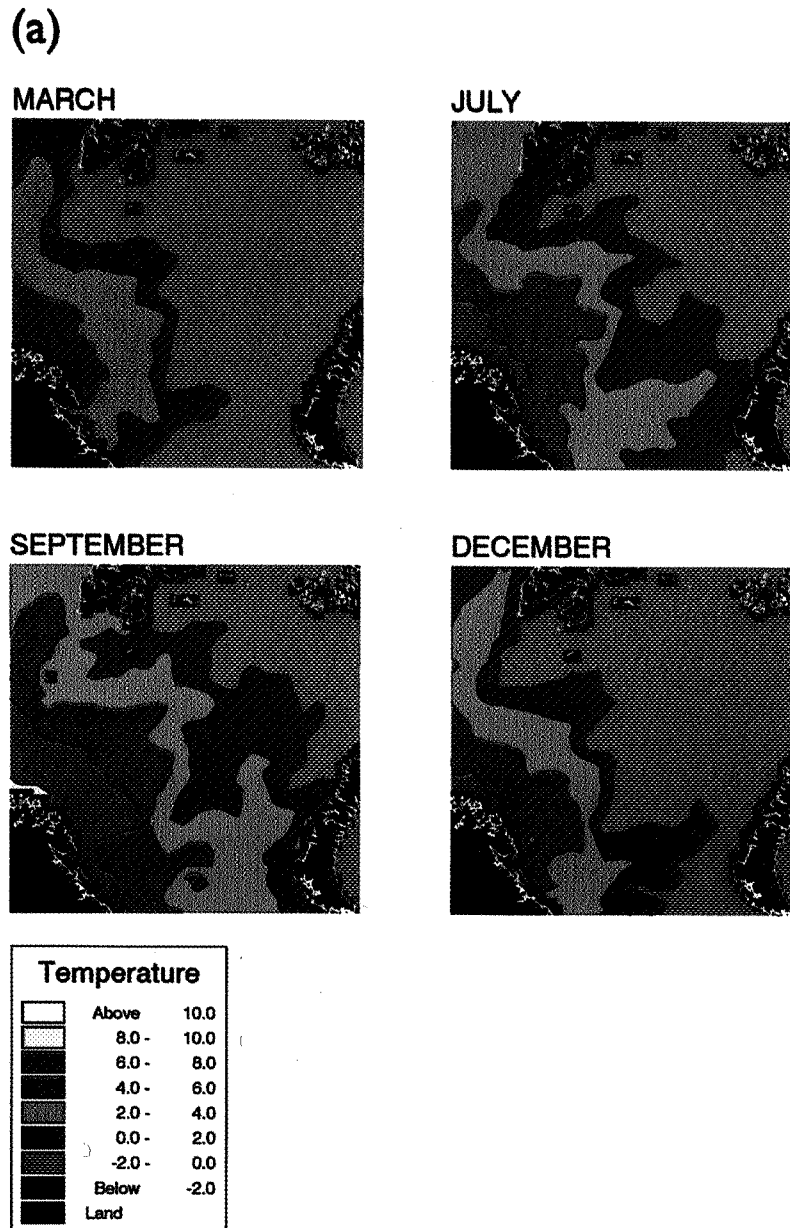
## (a)
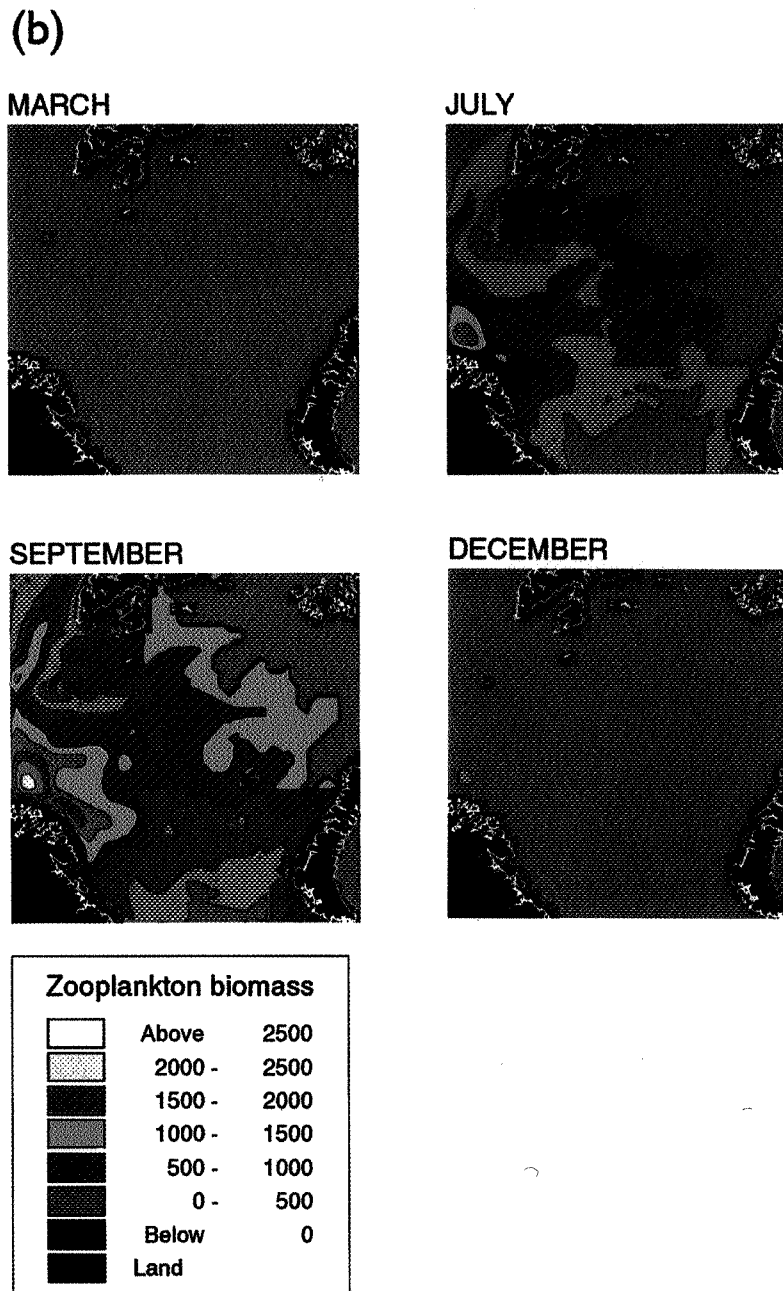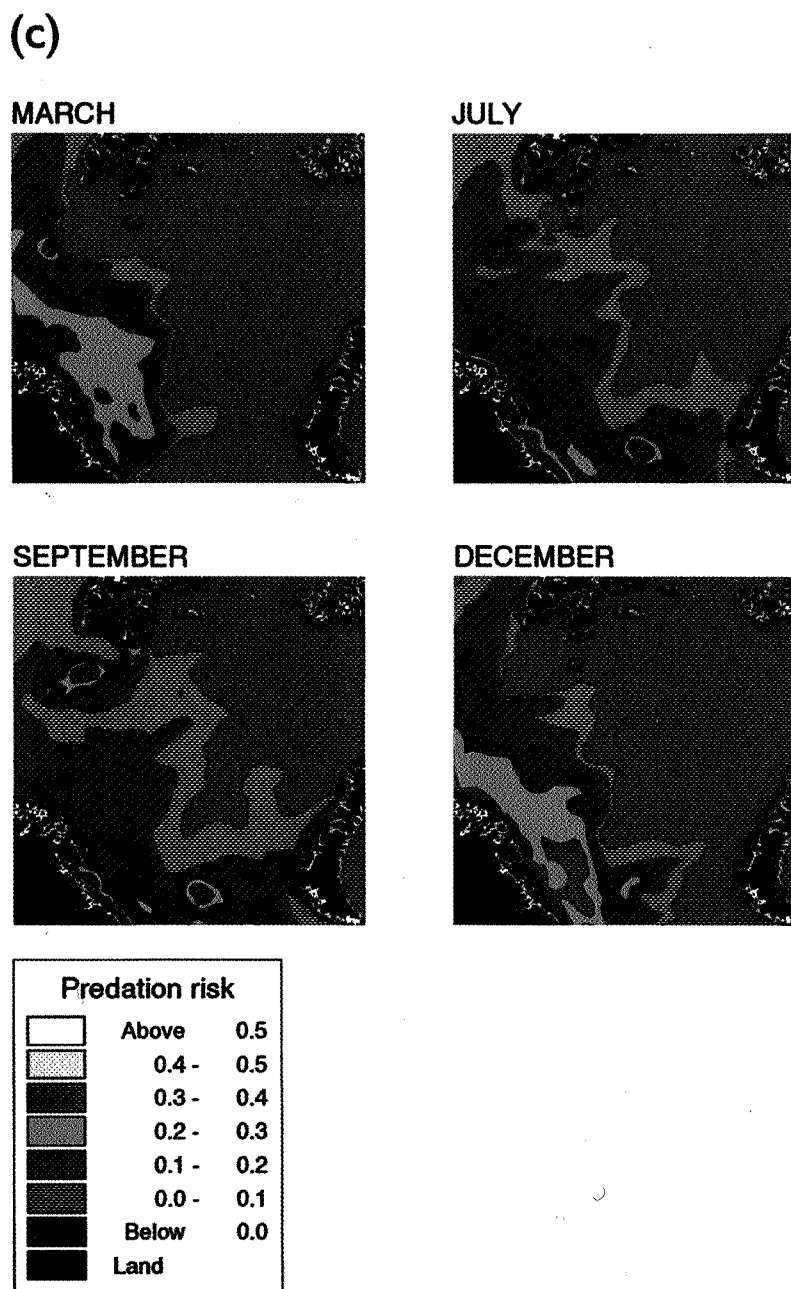
### MARCH

### JULY

### SEPTEMBER

### DECEMBER

| Temperature | | |
|---|---|---|
| Above | 10.0 | |
| 8.0 - | 10.0 | |
| 6.0 - | 8.0 | |
| 4.0 - | 6.0 | |
| 2.0 - | 4.0 | |
| 0.0 - | 2.0 | |
| -2.0 - | 0.0 | |
| Below | -2.0 | |
| Land | | |

Figure 2(b), see caption overleaf.

## (b)

**MARCH**

**JULY**

**SEPTEMBER**

**DECEMBER**

| Zooplankton biomass | | |
|---|---|---|
| | Above | 2500 |
| | 2000 - | 2500 |
| | 1500 - | 2000 |
| | 1000 - | 1500 |
| | 500 - | 1000 |
| | 0 - | 500 |
| | Below | 0 |
| | Land | |

approach the bioenergetics using the framework proposed by Kitchell *et al.* (1977) and Hewett and Johnson (1992) and assume a simple functional response as the 'P-value' in their model. No parameter values for the bioenergetic equations of capelin have been worked out, so we have used the parameters and equations

applying to herring, *Clupea harengus*, in Hewett and Johnson (1992), as this species also thrives in the cold, northerly waters and coexists with capelin in the Barents Sea (Table 1). The pros and cons of bioenergetic modelling are discussed by several authors, e.g. Ney (1993) and Hansen *et al.* (1993), and will not be

**Figure 2(c), see caption p. 196**

# (c)

**MARCH**

**JULY**

**SEPTEMBER**

**DECEMBER**

| Predation risk | |
|---|---|
| Above | 0.5 |
| 0.4 - | 0.5 |
| 0.3 - | 0.4 |
| 0.2 - | 0.3 |
| 0.1 - | 0.2 |
| 0.0 - | 0.1 |
| Below | 0.0 |
| Land | |

commented upon here. The basic equation for specific growth rate is defined by

$$\frac{\mathrm{d}W}{W\,\mathrm{d}t} = C - (R + S + F + U), \qquad (1)$$

where $W$ is fish weight (g wet weight), $t$ is time, $C$ is

consumption (feeding) rate, $R$ is respiration, $S$ is specific dynamic action, $F$ is egestion, and $U$ is excretion.

*Consumption* Consumption is calculated from fish weight, ambient temperature and food concentration:

**Table 1.** Description of parameter symbols and values used in the basic version of the model of the bioenergetics (all values are from herring, Hewett and Johnson, 1992). The temperature function $f_c$ (*T*) is not listed in text or tables, but is taken from Hewett and Johnson (1992).

| Symbol | Parameter description | Unit | Value |
|---|---|---|---|
| Consumption | | | |
| $\alpha$ | Intercept for maximum consumption | $g\,g^{-1}\,day^{-1}$ | 0.64 |
| $\beta$ | Body mass dependence of consumption | – | −0.26 |
| $k$ | Half saturation coefficient (prop. of $Z_{max}$) | – | 0.2 |
| Respiration | | | |
| $a$ | Standard respiration of 1 g individual at 0°C | $g\,O_2\,g^{-1}\,day^{-1}$ | 0.0033 |
| $b$ | Body mass dependence of metabolism | – | −0.23 |
| $\theta$ | Temperature dependence of metabolism | $°C^{-1}$ | 0.055 |
| $u$ | Swimming speed dependence of metabolism | $s\,cm^{-1}$ | 0.03 |
| $S$ | Specific dynamic action coefficient (SDA) | – | 0.175 |
| Excretion and egestion | | | |
| $m$ | Egestion coefficient | – | 0.16 |
| $n$ | Excretion coefficient | – | 0.1 |

$$C = \alpha W^{\beta} f_c(T)P, \qquad (2)$$

where $\alpha$ is the maximum feeding rate ($g\,g^{-1}\,day^{-1}$) of a 1 g capelin at the optimal temperature for feeding, $\beta$ is weight dependence of feeding, and $P$ and $f_c(T)$ are proportional adjustments due to food availability and temperature (range: 0–1). The function of $f_c(T)$ is rather complicated (Hewett and Johnson, 1992) and adapted to cold water species. From several parameters (listed in Hewett and Johnson, 1992), it calculates the temperature limitations on feeding. The functional response of capelin is incorporated in $P$ as a simple Michaelis–Menten-like function, scaling food limitation between 0 and 1:

$$P = Z/(kZ_m + Z), \qquad (3)$$

where $Z$ is the prey density and $kZ_m$ is the 'half-saturation constant' (the prey density where ingestion rate is half of its maximum), defined as a fraction $k$ (= 0.2) of the peak prey density $Z_m$.

*Respiration and SDA* Respiration is modelled as an allometric function of fish weight, temperature, specific dynamic action (SDA) and swimming speed (activity level):

$$R = aW^b \exp(\Theta T)A + S(C - F), \qquad (4)$$

where $a$ is minimum standard respiration rate ($g\,O_2\,g^{-1}\,day^{-1}$) of a 1 g capelin at 0°C with no swimming activity (converted to $g\,g^{-1}\,day^{-1}$ using oxycalorific coefficients from Stewart *et al.* (1983) and energy densities of capelin and copepods), $b$ sets the weight dependence of

respiration, $\Theta$ is the temperature (*T*) dependence of basic respiration, $A$ is the increment in respiration caused by activity, depending on how fast the animal is swimming, $S$ is the specific dynamic action coefficient, i.e. the metabolic cost of digestion and absorption of consumed material, $C$ is defined in eqn. 2 and $F$ is egestion. As we do not assume a constant optimal swimming speed, but rather let it be part of the optimality consideration, $A$ differs slightly from Hewett and Johnson (1992). Similarly to Hewett and Johnson (1992), we let $A = \exp(uv)$, where $u$ is a constant and $v$ is the swimming speed ($cm\,s^{-1}$). Swimming speed is the distance $d$ (in m) between current habitat ($i_t, j_t$) and the next ($i_{t+1}, j_{t+1}$) divided by time step length $\tau$ (in s) used on the distance:

$$d = D\sqrt{(i_t - i_{t+1})^2 + (j_t - j_{t+1})^2} \qquad (5)$$

which is a minimum estimate of the distance travelled. The variables *i* and *j* relate to grid cells in the north–south and east–west direction, respectively, and $D$ is the grid cell resolution (20 km). There is a minimum swimming velocity of 0.1 body length $s^{-1}$, applying to capelin not migrating but searching for food.

*Excretion and egestion* Egestion is assumed to be a constant proportion of consumption, $U = mC$; and excretion a constant proportion of consumption minus egestion, $F = n(C - F)$.

*Distribution of predators and mortality risk*

Cod is the principal predator of capelin, capable of consuming large proportions of the stock. Densities of

**Table 2.** Parameters of the predation process and the fitness premium used in the simulation.

|  | Description | Unit | Value |
|---|---|---|---|
| **Predation** | | | |
| $v_c$ | Swimming velocity of cod | m s$^{-1}$ | 0.2 |
| $v_m$ | Swimming velocity of mammals | m s$^{-1}$ | 0.5 |
| $v_l$ | Swimming velocity of capelin | m s$^{-1}$ | 0.1 |
| $R_c$ | Reactive distance of cod–capelin | m | 0.4 |
| $R_m$ | Reactive distance mammals–capelin | m | 0.5 |
| **Fitness** | | | |
| $x_c$ | Lower body mass | g | 5 |
| $x_m$ | Body mass at maturation | g | 14 |
| $\varepsilon$ | Scaling factor of fitness of immature survivors | – | 0.1 |
| $\omega$ | Number of eggs laid per gram body mass | eggs g$^{-1}$ | 500 |
| $\tau$ | Time step | days | 30 |
| $H$ | Final time (number of time steps) | months | 17 |

cod will generally be highest near the coastline, but young cod are known to migrate as far as to the Central Bank to feed (Nakken and Raknes, 1987). The overlap between cod and capelin is largest during the spawning period, when cod is feeding solely on capelin. Cod displays a major spawning migration to southern, warmer areas (Atlantic waters) and is likely to be less adapted to the cold Arctic water-masses than the endemic capelin. Mammals, however, are assumed equally likely to occur anywhere in the ocean. They will therefore not affect the distribution of capelin directly, but when the overall risk of mortality is altered, the optimal age and size at maturation may be changed, and so is the trade-off between growth and risk of mortality (mediated through habitat selection). We use the stock of cod in 1980 (about 1 million tonnes), and distribute it linearly increasing with temperature above −0.5°C. We have included a constant and uniformly distributed stock of other predators O (mammals) of half a million tonnes. Predation rates on capelin from cod and mammals are assumed to be proportional to their rate of encounter. Gerritsen and Strickler (1977) developed a model for the probability of intersection of randomly moving and distributed particles (predators and prey) in the pelagic. This model has recently been used to model ingestion rates of fish (Brandt and Kirsch, 1993; Mason and Patrick, 1993), and we assume the encounter rate for an individual capelin with its predators e is determined by predator reaction distance ($R_c$ and $R_m$), the swimming speed of both predators $v_c$, $v_m$ and capelin $v_l$, and, in this case, by local cod ($C_{i,j}$) and mammal (O) density (Table 2). The population biomasses (Table 1)

are converted to number of individuals by assuming individual body masses of 4 kg (cod) and 300 kg (mammals), so that capelin encounter rate with a uniform spatial distribution of predators is expressed by:

$$e_{i,j} = \pi R_c^2 \left(\frac{3v_c^2 + v_l^2}{3v_c}\right) C_{i,j} + \pi R_m^2 \left(\frac{3v_m^2 + v_l^2}{3v_m}\right) O;$$

$$v_m \geq v_l, \ v_c \geq v_l. \quad (6)$$

The mortality risk $\mu$ in each habitat during each time interval is

$$\mu = 1 - \exp(\tau e), \quad (7)$$

where $\tau$ is the duration of the time interval (one month) and e is the local encounter rate with predators, both cod and mammals (Fig. 2C). Equations 6 and 7 do not account for the time predators are concerned with activities other than searching (e.g. spawning or searching for other prey items), density-dependence, light- or stomach-limitations on ingestion or prey evasion, and will certainly overestimate predation risk. To compensate this, eqn 6 is scaled by a factor of 0.3, a parameter open to calibration.

We do not expect capelin to have adapted its migration pattern to the fisheries, and therefore we have simply omitted mortality from fisheries, though this has been a substantial mortality factor during recent decades.

### The dynamic optimization framework

The Barents Sea is divided into a horizontal grid of 60 intervals in the north–south direction and 60 discrete

intervals in the east–west direction, each covering a distance of 20 × 20 km. The time step used is 1 month. The state variables are specified by (1) capelin body mass, $x$, with intervals of 1 g (wet mass) and range 5–25 g, (2) the current position in the north–south direction, $i$, and (3) the current position in the east–west direction, $j$. For simplicity, at the maximum body mass, no increase in size or fitness will be allowed, and at body mass below 5 g the capelin is assumed to starve and die. Also, individuals starve if they lose more than 25% of their body mass during one month. In the model, maturation occurs at a body weight of 14 g (Forberg and Tjelmeland, 1985).

*Optimization criterion and the dynamic programming equation*

The capelin may be considered semelparous, and invests large proportions of its body mass into eggs. Egg production will therefore be a function of size, and we assume fecundity to increase linearly with body mass. But not only the number of eggs matter, eggs must be placed in gravels where the larvae will drift into viable nursery areas after hatching, that is at the coast of Finmark and Murman. The terminal fitness value $F(x, i, j, H, H)$ (notation as in Mangel and Clark, 1986, 1988; Houston et al., 1988) which specifies the premium of the behavioural track followed during the preceding year is then given by

$$F(x, i, j, H, H) = \begin{cases} \omega(x - x_m) & \text{for } x > x_m \quad (8a) \\ \varepsilon x & \text{for } x \leq x_m \quad (8b) \end{cases}$$

provided the individual capelin is situated within the specified spawning grounds during the breeding season (otherwise no terminal fitness is obtained). $H$ denotes the time of final spawning at the end of February 1981 (Table 2) and the parameter $\omega$ gives the number of eggs produced per body mass after the tissue-to-egg conversion is done. If the individual has not reached maturation $x_m$ at the end of the modelled period, then it is rewarded according to its achieved size, scaled down using the parameter $\varepsilon$ instead of $\omega$ (Table 2). If the state of the capelin at any time drops below the critical level $x_c$ or an individual loses more than 25% of its weight, the fitness value is set to zero (starvation). The model is deterministic: no stochastic variations in the environment or processes have been considered.

According to the principles of natural selection, capelin should seek to maximize fitness by maximizing lifetime fecundity, i.e. maximize growth and survival. Putting growth and risk of mortality together in a backward iteration equation, then for time $t = H - 1$, the beginning of the final time interval, the expression is

$$F(x, i, j, H - 1, H) = \max_{i,j} (1 - \mu_{i,j})$$

$$\times F(x + g_{i,j}, i_H, j_H, H, H), \quad (9)$$

where $F(x, i, j, H-1, H)$ is the fitness at the start of the time interval before the final time $t = H$ and $g_{i,j}$ the growth (change in body mass) in the grid cell $(i,j)$ during this time interval. For all habitats, the possible new habitats (within a range of 300 km, corresponding to swimming steadily at about one body length per second within one time step) are evaluated by eqn 9, and the habitat with the highest value is the optimal location $(i,j)$ in $t = H-1$ for capelin of size $x_{H-1} + g_{H-1}$ in grid cell $(i_H, j_H)$ at time $t = H$. By doing this backwards for all times $t$ until the first time step of the simulation, we obtain from the general dynamic programming equation a matrix of values tracking the optimal trajectory backwards in time for all combinations of the state variables $x$, $i$ and $j$:

$$F(x, i, j, t, H) = \max_{i,j} (1 - \mu_{i,j})$$

$$\times F(x + g_{i,j}, i_{t+1}, j_{t+1}, t + 1, H) \quad (10)$$

(see Mangel and Clark, 1988 for a detailed introduction to the use of dynamic models in behavioural ecology). By use of this matrix, only moving forward in time, we are now in a position to seed the model with an observed state $(x)$ and geographical $(i, j)$ distribution of capelin and simulate the stock development assuming optimal behaviour at all times. To modify the optimality criteria slightly, we have spread the individuals uniformly around the optimal habitat found from the backward iteration. This adjustment is made to increase model realism; all of the capelin will not end up at their very best location, but rather somewhere close by.

We simulate the period from September 1979 to February 1981, and therefore a fraction of the stock will mature, spawn and die during 1980. The main bulk of capelin spawning is generally accomplished in winter and early spring, but larval surveys suggest that spawning may occur as late as in June some years (H. Gjøsæter, pers. comm.). During 1980, we give our model capelin an option to spawn from February to June, by substitution of eqn 8 for eqn 10 at the spawning grounds in this period. Capelin always die after spawning in the model, and therefore no residual fitness is offered to spent individuals.

## SIMULATING THE PERIOD FROM LATE 1979 TO EARLY 1981

After the optimal trajectories through space and time are found for all possible combinations of positions and
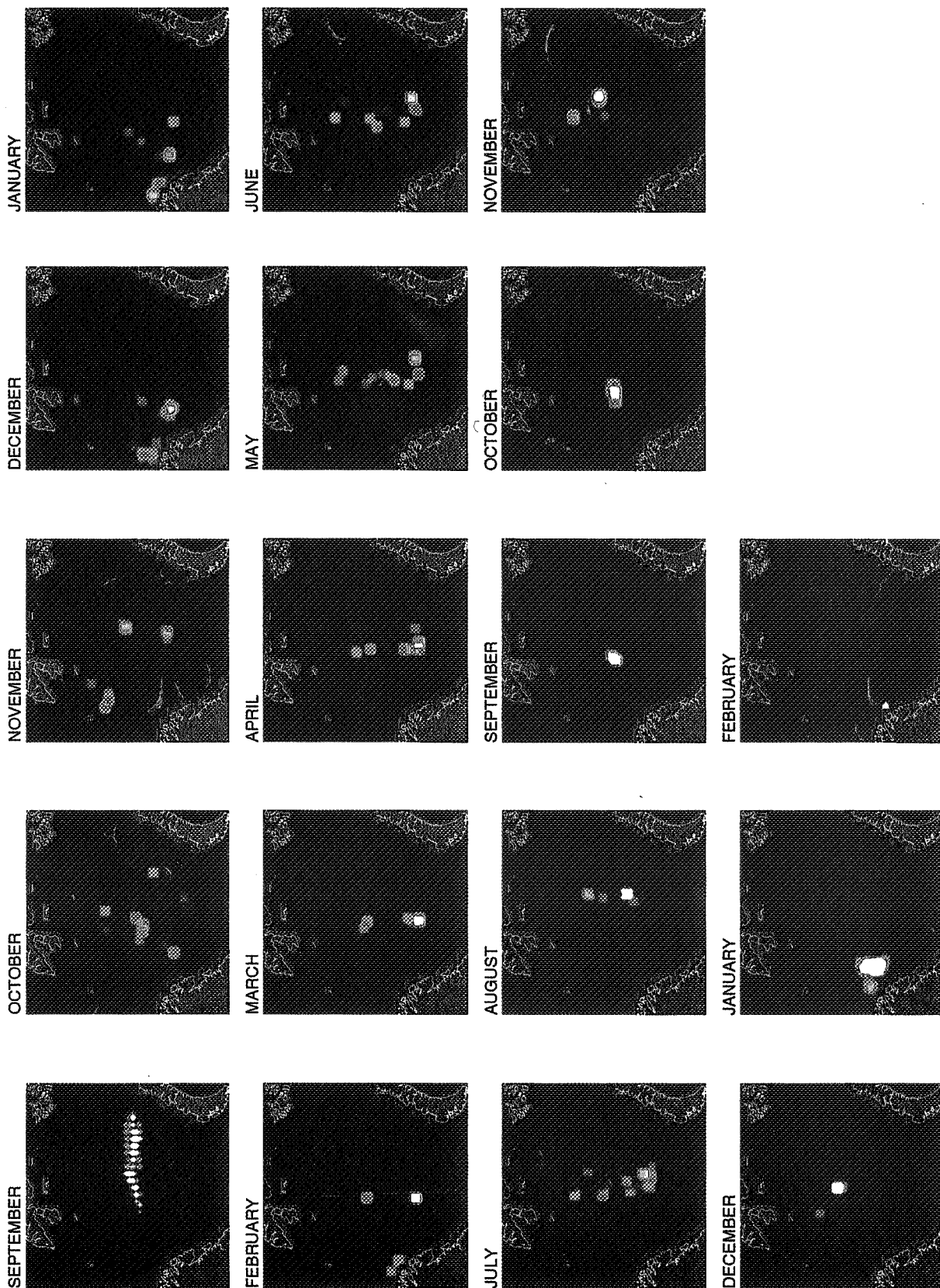
states, we can see how the population develops when all individuals follow their optimal paths. To do this, we have initialized the population with the distribution of individual body weight, numbers and geography recorded during the autumn cruise in 1979 (Fig. 3, first panel; fig 14 in Dommasnes and Røttingen, 1985). The fate of these capelin is modelled from September 1979 to February 1981 (Fig. 3). Initially, the capelin stock move south and west (Figs 3 and 4d), into warmer and more food-rich areas, and stay in these areas through the winter. Then they move north- and eastwards, to avoid cod as the water gets warmer and the cod stock spreads northwards. The spawning stock biomass is a key variable for management, and the model gives predictions about this. A large fraction of the stock spawn during February and March 1980 (Fig. 4a). Spawning biomass is very sensitive to the individual growth rate, due to the high number of individuals in the stock, so the shape of the average individual growth curve and the stock biomass will display similar trends (Fig. 4a, c). The predicted individual growth rate is very high during August and September 1980 (Fig. 4c) (probably too high), and this increases the spawning biomass in February 1981. It is likely that capelin and herring differ in their temperature-dependence of ingestion rate and metabolism, and that capelin will be less sensitive to higher temperatures than herring (which inhabit warmer Atlantic waters during large portions of their lives). The very high individual growth rate in late autumn is caused by the migration into warmer waters which also contain zooplankton, but is obtained at the cost of higher risk of predation (Fig. 4b). In autumn the modelled stock inhabits the warmest waters (Fig. 4c) and consumes the most zooplankton biomass (Fig. 4a), and during summer it stays in colder waters. Despite the uncertainties regarding growth and consumption, the model describes the general migration north- and eastwards in late summer, and the opposite direction as winter and spawning approaches.

Data from the capelin stock are collected from surveys during September–October, and the distribution pattern recorded from the cruise in 1980 (Dommasnes and Røttingen, 1985) can be schematically compared with results from the model (Fig. 5). The acoustic data are taken from Norwegian fisheries statistics, where the grid cells vary considerably in size and shape (fig. 6 in Dommasnes and Røttingen, 1985), while the model prediction is the joint distribution of capelin in September and October 1980. The model predicts distribution too far south and east at this time of year, although there is some overlap in the observed and predicted distributions.

## DISCUSSION

The model is only a first step towards a cluster of models that could become useful for management purposes. Yet, too many processes are poorly understood and not quantified. The bioenergetics of capelin has not been studied in the laboratory, and only tentative correlations of the environmental impact on growth exist (Gjøsæter and Loeng, 1987). The functional response is modelled as a simple decelerating function of prey density, but several other important factors like light, size distribution and depth distribution of prey and water clarity are ignored (Aksnes and Giske, 1993; Giske et al., 1994; Rosland and Giske, 1994). Currents will probably alter the metabolic costs of swimming, as their speed often will be in the same range as capelin swimming velocity. However, these currents have strong vertical gradients which could be utilized by flexible vertical migration, and in some areas dense shoals of migrating capelin have been observed to take advantage of tidal currents in this manner (E. Ona, pers. comm.). Further, schooling alters the risk of mortality and consumption rate, but is not included. Maybe most important, the depletion of prey (zooplankton) by predation is missed by the model, and other frameworks than dynamic programming must be used to accomplish this interaction. The zooplankton stock is very likely to be depleted if the calculations of ingestion by capelin are correct (Fig. 4a); a very high consumption is predicted from the bioenergetic equations. Obviously, the model presented here, like

**Figure 3.** The modelled two-dimensional distribution of capelin, initialized from the size and spatial distribution monitored during the 1979 autumn cruise in the central Barents Sea. The model grid is limited to two dimensions, with 20 km grid size and monthly time steps. Capelin density is drawn with increasing values from blue (no capelin) to red and yellow. The first panel shows the initial distribution of biomass, from cruises in 1979, while all the other panels show predictions from the model. First, mature and almost mature capelin swim south and west into the warm and food-rich areas to maximize body size before the first spawning season, but the smallest individuals keep out of areas of high risk and plan to spawn during the next season instead. After the spawning season the stock, divided into 2–3 main groups, stay in the central Barents Sea, and during winter (1981) they migrate south and west to spawn.
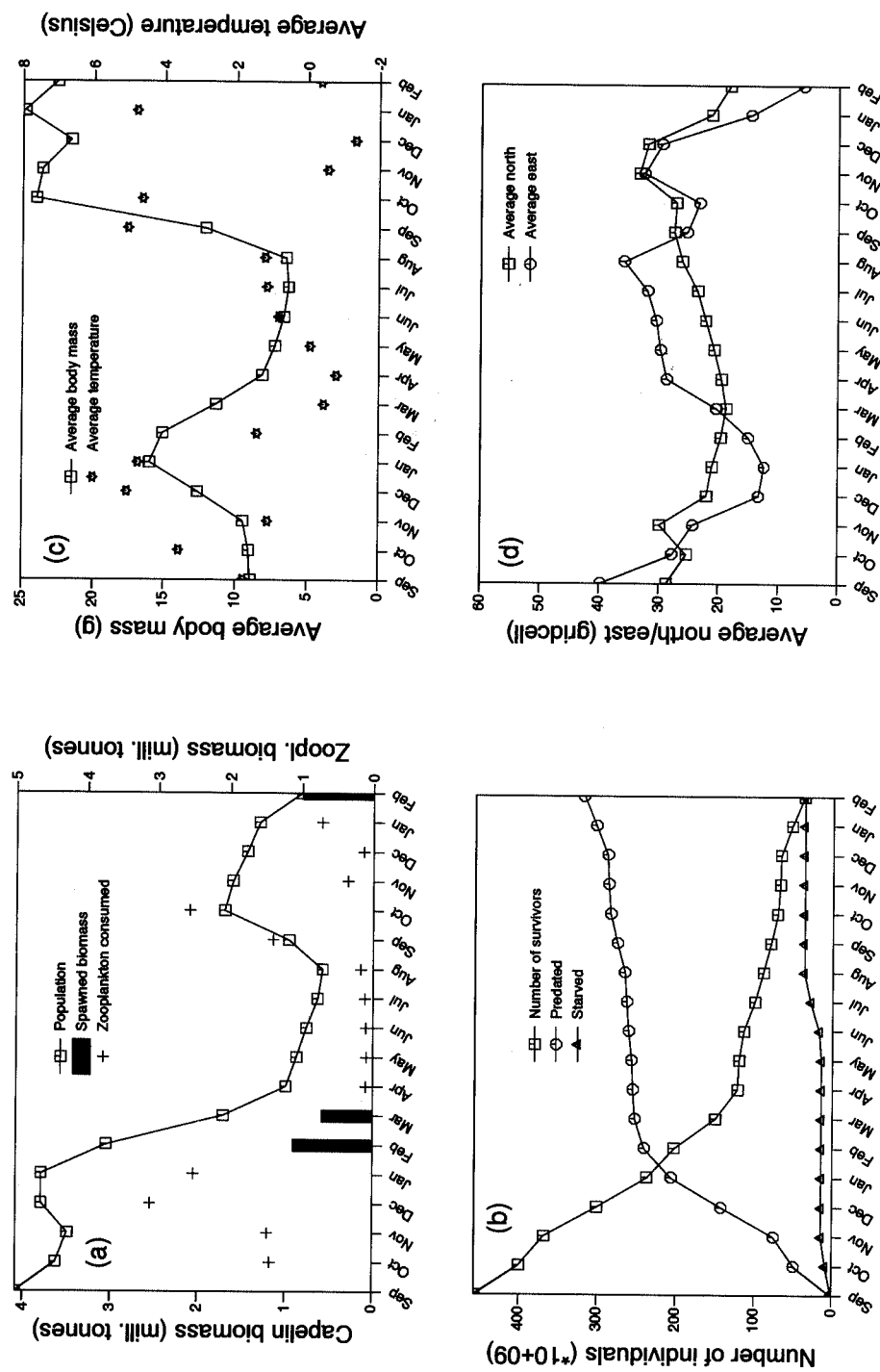
**Figure 4.** Dynamics of (a) total capelin, spawning and consumed zooplankton biomass; (b) numbers alive, starved and predated (cumulative values); (c) average individual biomass and temperature; and (d) average position in the north-east direction of the modelled population through the year (assuming no recruitment). Mortality increases as the spawning seasons approach, because the capelin distribution overlaps more with that of the cod stock. Growth takes place mainly during the periods November–December 1979 and October–December 1980, when the capelin inhabit warmer waters.

**Figure 5.**   (a) Predictions from the model of the distribution of capelin biomass during September and October 1980. Values in the panel are scaled against the maximum value of the data set (range 0–1), so that they can be compared directly. (b) Acoustic measurements of the spatial pattern of capelin biomass (relative values) from the autumn cruise in 1980. The original data are from Norwegian fisheries statistics, but have been transformed to the same grid as the model, to ease comparison.
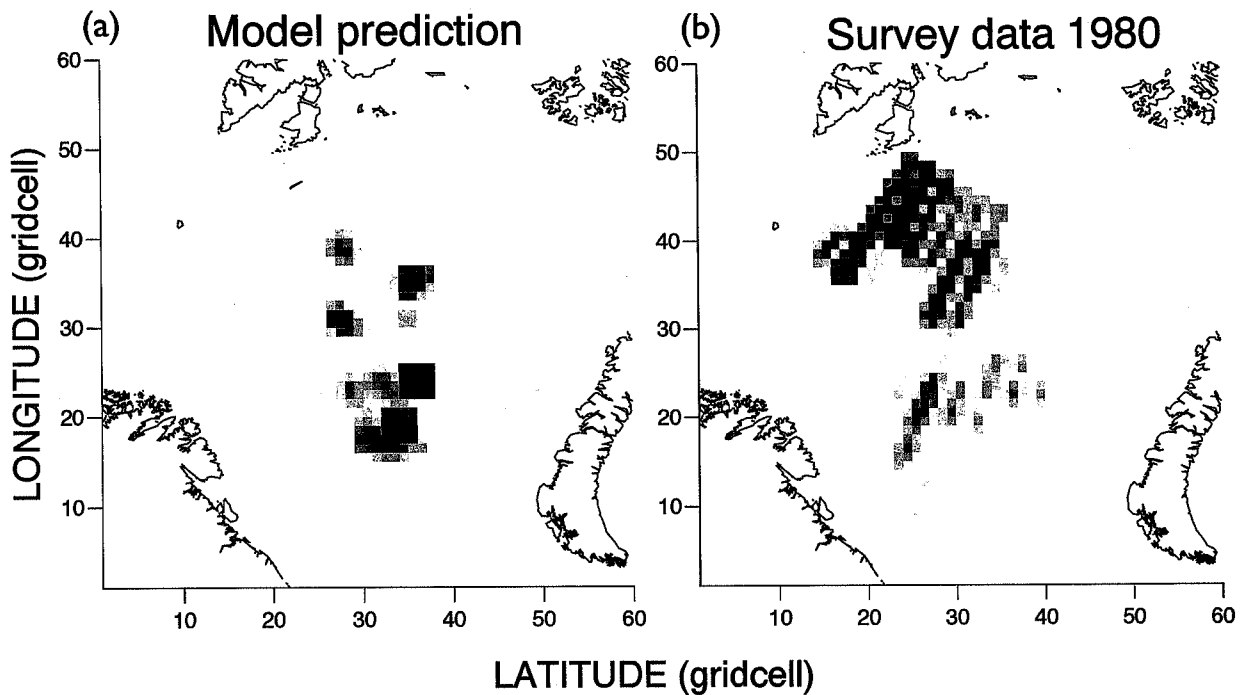


other models driven from below, is sensitive to the submodels or data supplying input of environmental forcing. Improving the effort in modelling or monitoring the zooplankton field will generally strengthen the reliability of models driven from below.

Fine temporal resolution is necessary to incorporate vertical processes. However, applying dynamic programming at temporal scales of years forces us to use long time steps, because it is impossible to use time steps at the scale of hours with current computer technology. This may be an important factor to include, as vertical gradients of growth and predation risk are orders of magnitude steeper than those in the horizontal direction (Aksnes and Giske, 1993; Rosland and Giske, 1994). However, virtually all modelling concepts will face computational difficulties if a large-scale population model of fitness-maximizing states or individuals interacting with their food source and predators is wanted. To accomplish the need for process-based models in aquatic ecology (Tyler and Rose, 1994), work like the early attempts by Balchen and colleagues (Balchen, 1976; Reed and Balchen, 1982) should be con-

tinued and improved by the use of recent developments in quantitative ecology, animal behaviour, oceanography and computer science.

*A spatially explicit individually based model of a fish population*

We have developed an approach or a tool to model the active migration pattern of fish in a large-scale marine ecosystem, with focus on the oceanographic environment and individual motivation and behaviour. We have tried to integrate emerging knowledge in hydrography and behavioural ecology to model the production of a commercial fish stock that is particularly difficult to manage due to a short life cycle, and have come close to the model class Tyler and Rose (1994) denoted 'spatially explicit IBMs': models with spatial heterogeneity, individual variability and individual movement. Much effort is put into a correct description of the fitness consequences of habitat selection and individual movement, and to simulate a fish population in a heterogeneous, seasonal environment. This is done at the expense of density dependence, depletion and

fine time resolution, which may be very important in the zooplankton–capelin interaction (Hassel *et al.*, 1991). Therefore, competing models and frameworks to the dynamic programming approach should be developed. The ideal free distribution (Sutherland and Parker, 1985; MacCall, 1990) or various departure rules (e.g. min $\mu$, max $g$, or min $\mu/g$) may be alternative ways to move individual fish in a heterogeneous environment, where depletion of food and density dependence may also be implemented. These rules were initially developed for juveniles (Werner and Gilliam, 1984), and a possibility is to model juveniles and adults separately, with different movement rules (e.g. Giske and Aksnes, 1992). On the other hand, the spawning strategy and patterns of a strategic nature (like seasonal variation in willingness to take risks and state-dependent motivation) will be difficult to model realistically in these settings.

The optimality criterion, or the assumption that capelin will respond in an optimal way to environmental conditions, is justified from the idea that individuals which come close to the optimal strategy are selected for, and multiply at a higher rate than individuals adopting suboptimal strategies. However, some obvious constraints on the perceptual abilities of fish (like being unable to foresee how the climatic situation will be later in the actual year, how food and predators will be distributed etc.) must limit the chance that they will hit the optimal trajectories every year. Probably, they will be adapted to some long-term environmental average, but with extensive abilities to respond to discrepancies from this average. The constraints capelin experience in anticipating their environment should be part of the dynamic programming equations, maybe as stochastic variations in the environmental variables. By finding long-time average situations of zooplankton, temperature and predator distributions from observations or from model simulations, the long-term pattern of capelin distributions could be found. Another way of handling uncertainty is to calculate the deterministic, optimal path of each year in the backward iteration, while letting the experienced habitat selection follow a probability distribution around the optimal track (as we did in our baseline simulation). In the simulations presented, swimming velocity is a major constraint on the options available to capelin.

*Future work*

The model goes some way in reproducing the general migratory pattern known from capelin in the Barents Sea, but the use of many uncertain parameters and processes makes an evaluation of the model difficult. Many alternative formulations of the mortality and foraging processes could be applied using the same framework. The model predictions should be confronted with the distributions, growth and abundance of capelin as measured during all the autumn cruises conducted in the Barents Sea. Then reasonable parameters may be fitted to the most sensitive variables in a hindcast analysis, and if the model passes this test, it may be used as a calculation tool for management purposes. We hope to develop a means to validate the model along these lines in the future.

However, we could anticipate many alternative models which should also participate in a competition for the most successful model (see above), arbitrated by data collected during a series of years. Future versions of the model may consider including vectors of currents in evaluating the costs of swimming from one point to the next, and to increase resolution in time and space. Vertical processes are important and fit within the scheme, but will require very efficient computers and algorithms.

Climatic forecasts for the next year can be statistically anticipated as warm, cold or intermediate (Loeng *et al.*, 1992). Knowledge about the present capelin stock, expected environment and size of the cod stock may be fed into the model to make tentative judgements about the near future. If the model represents processes satisfactorily, and the educated guess about the forthcoming oceanographic conditions is correct, the assessment of the capelin stock may be made more accurate.

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