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Capelin migrations and climate change – a modelling analysis

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Abstract The capelin is a small pelagic fish that performs long distance migrations. It is a key species in the Barents Sea ecosystem and its distribution is highly climate dependent. Here we use an individual based model to investigate consequences of global warming on capelin distribution and population dynamics. The model relies on input on physics and plankton from a biophysical ocean model, and the entire life cycle of capelin including spawning of eggs, larval drift and adult movement is simulated. Spawning day and adult movement strategies are adapted by a genetic algorithm. Spawning has to take place in designated near-shore spawning areas. The output generated by the model is capelin migration/distribution and population dynamics. We present simulations with present day climate and a future climate scenario. For the present climate the model evolves a spatial distribution resembling typical spatial dynamics of capelin with the coasts of Northern Norway and Murman as the main spawning areas. For the climate change simulation, the capelin is predicted to shift spawning eastwards and also utilize new spawning areas along Novaya Zemlya. There is also a shift in the adult distribution towards the north eastern part of the Barents Sea and earlier spawning associated with the warming.

1 Introduction

Migrations and phenology of organisms can often be altered without any genetic modifications and will therefore be among the first biological parameters that are affected by changes in currents, temperature and ecosystem productivity (Murawski 1993). Our ability to make sensible forecasts about the impact of global change on the higher trophic levels partly rests on skills in predicting changes in behavioural and life history traits. Modelling movement behaviour of organisms and life stages with large movement ranges remains challenging, but is nevertheless a key issue for understanding the responses of higher trophic levels to global warming. Since marine environments are heterogeneous,

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growth and survival potential differ greatly among habitats, and habitat choices are therefore important to individual fitness. The migrations of fish need to be understood in terms of food, predation and reproduction (Leggett 1977; Krebs and Davies 1997). This entails that individuals optimise the trade off between growth and survival throughout their lives and eventually choose a spawning ground that optimise both the conditions for the parents prior to and during spawning and not least those of the emerging offspring. Consequently, the spatial distribution of migratory fish may be understood better if the entire life cycle is considered in an integrated manner, rather than looking at each ontogenetic stage in isolation (Harden Jones 1968; Fernö et al. 1998).

Capelin (*Mallotus villosus*) is a small pelagic fish, and due to its climate sensitivity it has been referred to as a sea “canary” for marine ecosystem change (Rose 2005). The capelin performs long distance migrations between feeding, overwintering and spawning locations in the Barents Sea (Fig. 1, Gjøsæter 1998). There is considerable variability on several time scales in the physical and biological characteristics of the Barents Sea, and the migration pattern of capelin is adapted to this variability. The spawning location of capelin depends on the climate, and there tends to be easterly spawning in warm years and westerly spawning in cold years (Ozhigin and Luka 1985). Similarly the capelin distribution extends much further to the north and east in the Barents Sea during warm years than in cold years (Dommasnes and Røttingen 1985; Gjøsæter 1998; Gjøsæter et al. 1998). Adult capelin is subjected to high predation rates from cod (*Gadus morhua*) and marine mammals (Mehl 1989; Mehl and Sunnanå 1991; Bogstad et al. 2000), and the larvae is exposed to predation from juvenile herring (*Clupea harengus*) (Hamre 1994; Gjøsæter and Bogstad 1998; Huse and Toresen 2000; Godiksen et al. 2006). The capelin abundance has varied substantially during the last decades due to its key role as a major predator on zooplankton and as a prey fish in the ecosystem (Skjoldal et al. 1992). The Barents Sea has been warming in recent years, which has been associated with changes in the fish community. Most notably there has been increased abundance of blue whiting (*Micromesistius poutassou*) and juvenile herring in the Barents Sea. Furthermore the warming has reduced the ice coverage and increased the area of plankton production. The warming is expected to continue and it is likely to affect a number of features of the Barents Sea including the population and spatial dynamics of capelin. Even though the capelin is rather small, maturing at about 14 cm (Forberg and Tjelmeland 1985), it undertakes long distance migrations between feeding and spawning areas. Extensive migrations are energetically costly for such a small fish, and swimming capacity is likely to constrain the range of spawning migrations (Huse 1998b). In order to study capelin responses to climate change it is therefore important to view the entire life cycle in an integrated manner, considering both the distribution of eggs, larvae, juveniles and adults.

Individual based modelling (IBM, Huston et al. 1988; Grimm and Railsback 2005) is a versatile modelling approach that follow the fates of discrete individuals. This approach is therefore ideal for studying the entire life span of individuals and consequences of environmental variability on different life stages. Furthermore individuals in IBMs can easily be fitted with behavioural and life history traits. This is important when modelling adult fish which have a comprehensive behavioural repertoire (Huse 1998a; Strand et al. 2002). IBMs have previously proven successful in describing both vertical and horizontal migration in fish (Huse and Giske 1998; Huse et al. 1999; Strand et al. 2002). Due to the close link between ocean climate and capelin distribution (Ozhigin and Luka 1985), it is necessary to forecast ocean dynamics before considering capelin responses to climate change. A biophysical ocean model run for the Barents Sea (Fig. 1) for the period 1996–2059 provides plausible scenarios for developments in physics and plankton (Ellingsen et al. 2008). Here we present an IBM of

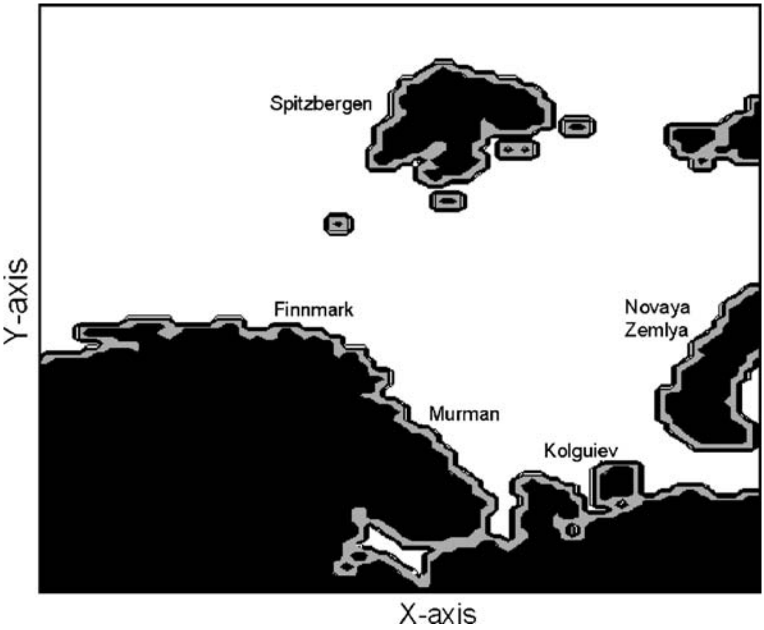


Fig. 1 The model area with potential spawning areas (*grey areas*) drawn in. The names in the map are referred to below

capelin life history to investigate how global warming may affect population and spatial dynamics of capelin based on predicted developments of climate and plankton dynamics in the Barents Sea.

2 The model

The model description is written in accordance with the PSPC+3 protocol for presenting IBMs proposed by Grimm et al. (2006), with an initial overview of the model components followed by a detailed description of process implementation and model functioning under Submodels.

2.1 Purpose

The model was designed to investigate the impact of climate change on capelin distribution and population dynamics. The model predicts spatial dynamics over the entire life span of capelin from eggs to adults given a description of the environment. Output from a 54 year (1996–2049) simulation of a biophysical model for the Barents Sea was used as input in the capelin model. Three different simulations were performed, utilising different time slices of the output from the biophysical model. In the capelin simulations, the time slices were run in sequence, and repeated when the end of the time slice was reached. In simulations 1 and 2 environmental forcing for a 10 year slice of the biophysical model were repeated 30 times throughout the 300 year simulation. The period 1996–2005 (simulation 1) was contrasted with the warmer period 2040–2049 (simulation 2, Fig. 2). In simulation 3 the period from

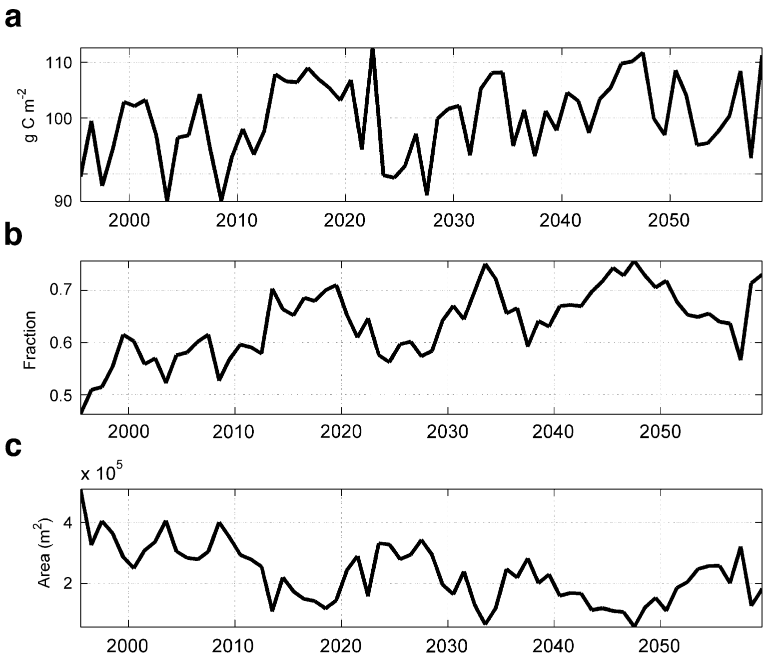


Fig. 2 Aggregated results from the biophysical model. Barents Sea: Simulated mean annual primary production (**a**), fraction of water with $T > 1°C$ (**b**) and ice covered area (**c**)

1996–2049 was used and repeated throughout the 300 year simulation. Four replicate model runs were performed for each simulation.

2.2 State variables and scales

The model domain is a lattice of 90 by 100 squares of 20 km side lengths. The biophysical model (Slagstad and McClimans 2005; Ellingsen et al. 2008) was used to generate fields for temperature, currents and plankton biomass. To simplify the model and reduce the considerable computation time associated with 3D simulations, we disregard the vertical dimension and rather used physical and plankton fields for the surface layer.

Super-individuals (Scheffer et al. 1995) were used to allow the IBM to represent the capelin population in the Barents Sea. Thus millions of identical individuals were pooled together in super-individuals. The number of siblings in a super-individual (internal number) is reduced due to mortality, and new super-individuals are born through reproduction. Super-individuals are specified by using attribute and strategy vectors (Fig. 3) where the former stores the states of the individuals (Chambers 1993) and the latter the behavioural and life history strategies (Huse 2001; Huse et al. 2002). The attribute vector of the capelin contained weight, age, energy density, internal number and position (Fig. 3). The strategy vector contained date for spawning and weights of the artificial neural network (ANN) used for calculating movement (see below). Length was related to weight by a regression based on capelin data. The model was structured so that the number of super-individuals actually simulated was kept at maximally 1,000 per age group. The abundance of the population is varied by the internal number. The individuals are moved up one age class on 1 January. At age 6 individuals are terminated. This assumption is

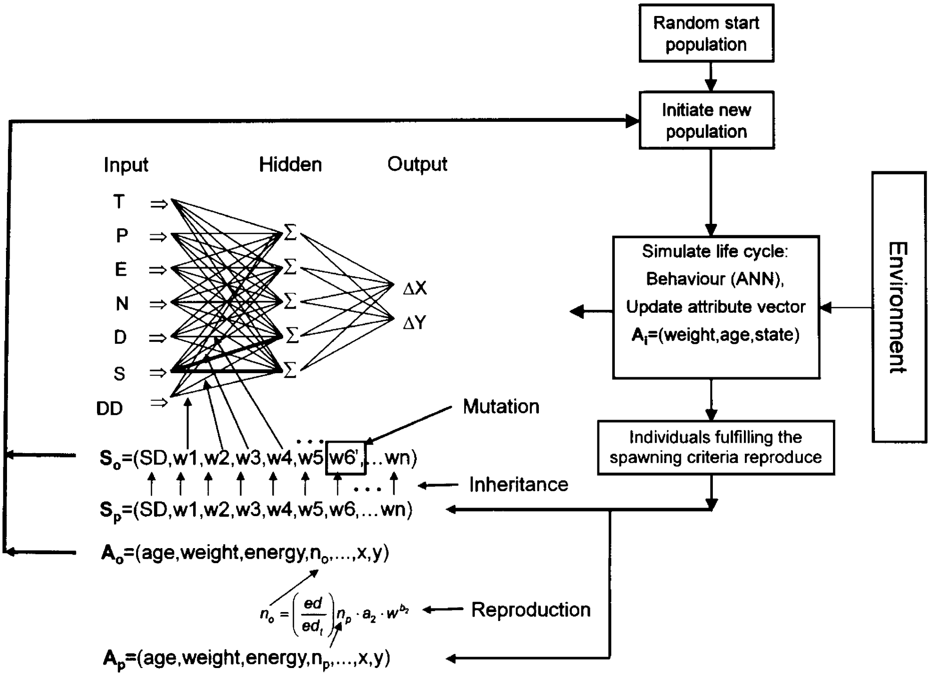


Fig. 3 The ING modelling concept with ANN based behaviour and GA based evolution in an individual-based setting. Individuals with randomly set "genetic" S_i that code for the weighting of the ANN, are initiated in the first time step. Individual states are kept track of by the attribute vector A_i. Individuals who fulfil the criteria set for reproduction produce a number of offspring (*o*) which is a function of the internal number of parent individuals (*p*). Offspring inherit the strategy vector of the parent. The strategy vector of offspring changes if mutations occur. Differences between the strategy vectors are expressed through differences in weights of the ANN, which can lead to behavioural differences

reasonable since very few capelin in the Barents Sea live beyond age 5 (Gjøsæter 1998) and also a fixed maximum age reduces computational demand.

2.3 Process overview and scheduling

The capelin model involved growth, mortality, movement and reproduction. For the larval fish, growth was calculated using temperature, plankton and fish size dependent equations for herring (*Clupea harengus*) larvae (Fiksen and Folkvord 1999), which is similar to capelin larvae. For the 1 year and older capelin, growth was calculated using a bioenergetics model (Hewett and Johnson 1992) dependent on temperature, prey biomass, fish size and activity level.

Egg mortality was set at a constant level. Larval mortality was calculated as a function of body size (Fiksen et al. 2002). For 1 year and older capelin, mortality was inflicted through predation from cod and marine mammals, and starvation. Capelin in the Barents Sea experience a high mortality associated with spawning (Gjøsæter 1998), and here we assumed a 100% mortality following reproduction.

The capelin eggs are demersal and adhere to the bottom substrate. The currents from the biophysical ocean model represent the sole horizontal movement of the larvae (age 0 years). Active movements of the adults (1 year and older) are decided by using the ANN (Fig. 3), and in addition the currents transport them passively.

Reproduction is conditional on the super-individual being at least 3 years old and at a spawning location (see Fig. 1) within ±20 days of the inherited spawning date. If so, a batch of eggs proportional to body weight and energy density is laid. The potential spawning locations (Fig. 1) were chosen as all areas within the model domain that are next to a shoreline. This includes the known spawning areas of capelin along the Finnmark and Murman shores (Sætre and Gjøsæter 1975; Ozhigin and Luka 1985; Gjøsæter 1998), and other areas that may be potentially utilised in case of a climatic change. The capelin prefers to spawn on gravel (Sætre and Gjøsæter 1975), but we were not able to access substrate maps for the Barents Sea, which could have restricted the area of possible spawning locations in a more realistic way. After a given time span that depend on ambient temperature, the eggs hatch and drift as larvae for the rest of the year. On 1 January, the larvae produced in the previous year are sorted by the product of their internal number and weight, which is a proxy for their Darwinian fitness, and the 1,000 best are transferred to the 1 year old group. The internal numbers of the rest of the larva are distributed equally among the 1,000 new 1 year olds. In this manner the total recruitment each year is passed on to the population, but only the best super-individuals (or strategies) are reproduced. If less than 1,000 larval super-individuals are alive at the end of the year, the population of alive larvae is resampled until a complete cohort of 1,000 larval super-individuals is achieved and passed on to the 1 year olds. Reproduction thus adds up to the recruitment of the population, but in addition the relative number of offspring passed on to the next generation is a measure of the Darwinian fitness of individual spawners. The model was run with daily time steps over 300 years. Some test runs showed that this time span was sufficient to stabilise the fitness and evolve good strategy vectors through selective mortality, growth and reproduction. This procedure is conceptually similar to the genetic algorithm (GA, Holland 1975) although the present model differs technically from the original implementation.

2.4 Design concepts

Some key conceptual features of the capelin IBM are listed below.

Emergence Movement trajectories, spawning time, and population dynamics are emergent properties of the interactions between the individuals and their environment.

Adaptation Movement behaviour and spawning time are the adaptive traits that the individuals can utilise to improve their fitness.

Fitness Fitness is emergent (Strand et al. 2002) and depends on the ability of the spawners to survive until reproduction and lay a batch of eggs in a valid spawning area (Fig. 1), and finally on the product of the number and size of larvae surviving to the end of the year.

Prediction Prediction is implicit through the adaptation to the environment.

Sensing Individuals are assumed to sense spatial position, day length, time remaining to spawning, density of food and conspecifics, and ambient temperature.

Interaction There are density dependent feeding interactions between individuals so that the food intake in each square depends on the biomass of food as well as the biomass of competitors.

Stochasticity Initiation of strategy vectors and spatial position of individuals is random, and there is a random walk component in the horizontal transport. Mutations of strategy vectors occur stochastically.

Collectives Individuals are grouped into super-individuals.

Observation The results on population- and spatial dynamics and strategy vectors are taken out on a yearly basis throughout the simulations.

2.5 Input

The capelin model relies on the biophysical ocean model for input on temperature, currents, and phytoplankton biomass. Light at latitude and day was calculated from a model based on sun height (Skartveit and Olseth 1988) in the same manner as in Rosland and Giske (1994).

2.6 Initialisation

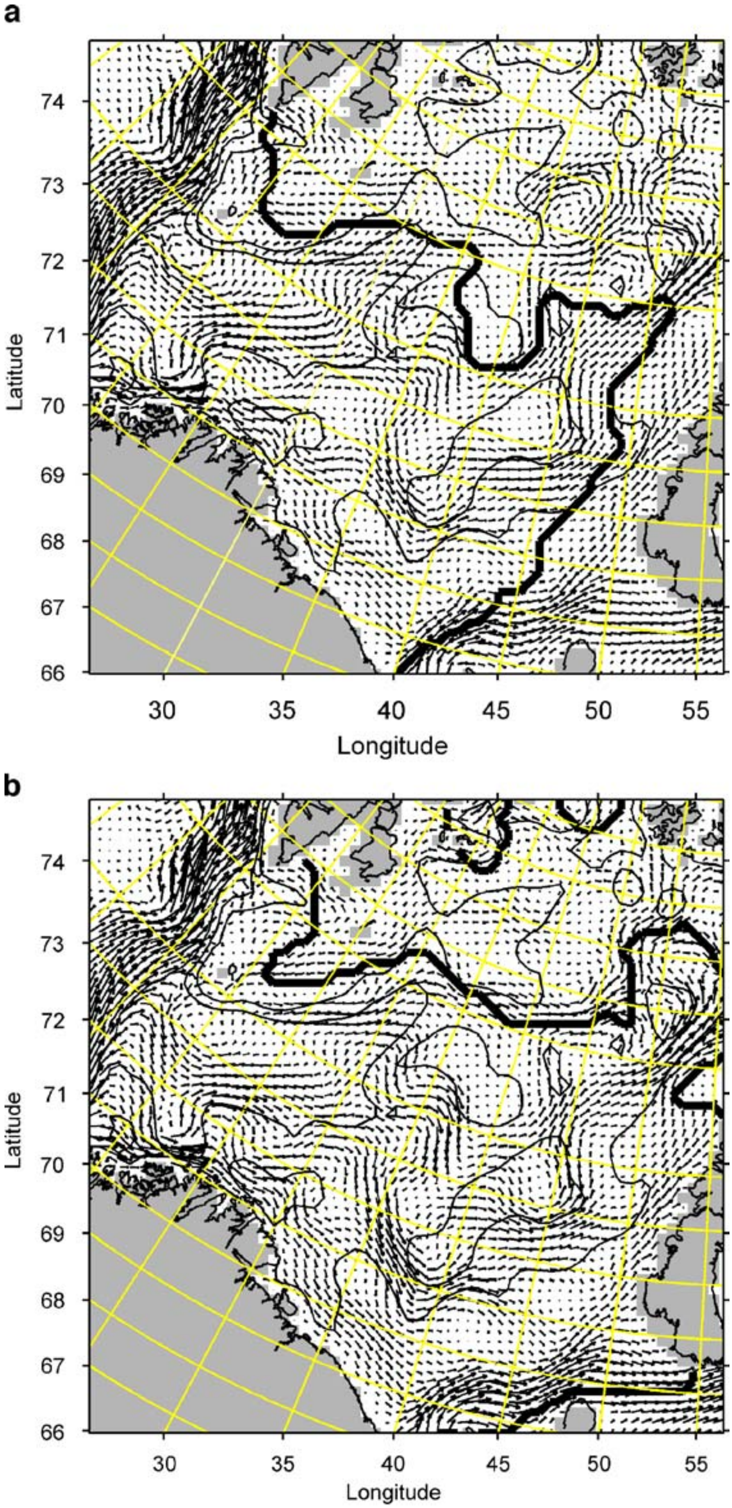
The model was started on 1 January. The initiation ranges for the traits on the strategy vector were [−1,1] (Strand et al. 2002) for the ANN weights and [1,180] for spawning day. The values for the strategy vectors were chosen randomly from a uniform distribution, separately for each individual. The population was initiated with a realistic age structure with identical attributes for all super-individuals within an age group. Individuals were initiated randomly in the central Barents Sea.

2.7 Submodels

2.7.1 The biophysical model

The hydrodynamic model is based on the Navier–Stokes primitive equations and solved by a finite difference scheme (Slagstad and McClimans 2005). The ice model is based on the elastic-viscous-plastic rheology described by Hibler (1979) and Hunke and Dukowicz (1997). The model system is forced by atmospheric data from a hydrostatic regional climate model, REMO that has been run for the ECHAM4/OPYC3 IPCC-SPRES B2 scenario by the Max-Planck-Institute for Meteorolgy, Hamburg (Göttel et al. 2008). The ecological model (Wassmann et al. 2006) contains state variables for nitrate, ammonium, silicate, diatoms, flagellates, microzooplankton, dissolved organic carbon, heterotrophic flagellates, bacteria and two groups of mesozooplankton representing the Arctic and Atlantic species. The vertical export of carbon is represented using two state variables, fast and slow sinking detritus. This model is run online with the hydrodynamic model using a time step of 1,800 s. The model 3D fields were saved on monthly and bimonthly time steps for physics and plankton respectively. The fields were converted to daily fields through linear interpolation.

The model domain encompasses the Nordic Seas and the Arctic Sea and uses a horizontal grid point distance of 20 km (Fig. 4). The model uses 25 fixed vertical levels. On the open boundaries in the North Atlantic and the Arctic Ocean, the current velocities are specified (Slagstad and Wassmann 1997).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◀ **Fig. 4** Mean annual currents at 50 m depth for model year 2000 (**a**) and model year 2047 (**b**). The *thick black line* indicates the position of the Polar Front. The *thin black lines* show the bottom topography

Four tidal components (M_2, S_2, K_1 and N_2) are imposed by specifying the various components at the open boundaries of the large-scale model. Data were taken from TPXO 6.2 (http://www.coas.oregonstate.edu/research/po/research/tide/index.html).

Initial values of temperature and salinity are taken from NODC World Ocean Atlas 1998 data (also known as the Levitus data base) provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA, from their web site at http://www.cdc.noaa.gov/. The model has been run from 1990 until 2059, whereof the first 5 years is considered to be a spin-up period.

2.7.2 Mortality

Egg mortality in Barents Sea capelin has not been investigated thoroughly, but some studies suggest that it is rather low (Dragesund et al. 1973; Bakke and Bjørke 1973), and it was here set to a constant rate of 0.5% day^{-1}. Daily larval fish mortality (μ_l) was here regarded to be dependent on size (Peterson and Wroblewski 1984; McGurk 1986; Bailey and Houde 1989), and was calculated by:

$$\mu_l = a_l \cdot L^{b_l} \tag{1}$$

where L is body length and a_l and b_l are constants (Table 1, Fiksen et al. 2002).

The main predators of adult capelin are cod, harp seals (*Pagophilus groenlandicus)* and minke whales (*Balaenoptera acutorostrata*) (Mehl 1989; Mehl and Sunnanå 1991; Bogstad et al. 2000), of which cod is by far the most important (Bogstad et al. 2000). Cod tend to be distributed in waters warmer than −0.5°C (Rose and Leggett 1990; Ottersen et al. 1998), and cod abundance was assumed to be distributed as linearly increasing with increasing temperature above this lower threshold (Fiksen et al. 1995). Marine mammals were distributed homogenously over the Barents Sea. Predation risk was calculated by considering the encounters (e) with the main predators of capelin (Evans 1989; Fiksen et al. 1995):

$$e = \pi r_c^2 \sqrt{u^2 + v_c^2}C + \pi r_m^2 \sqrt{u^2 + v_m^2}M \tag{2}$$

where r_c and r_m are the reaction distance of cod and marine mammals respectively, u, v_c and v_m are the swimming speed of capelin, cod and marine mammals (Table 1), and C and M are the local abundance of cod and marine mammals. Daily predation risk (μ_p) is then calculated using:

$$\mu_p = 1 - \exp^{(-e)} \tag{3}$$

Super-individuals are penalised with 0.5% daily starvation mortality if their relative energy density (ed/ed$_t$, Table 1) falls below 60% and terminated if it falls below 40%. The internal number of super-individuals is reduced from mortality and if the internal number gets below one the entire super-individual dies.

Table 1 List of parameters applied

Parameter	Value	Unit	Description	Source
a_1	0.01	dl	Larval mortality parameter	(Fiksen et al. 2002)
a_2	2,550	dl	Fecundity parameter	(Huse and Gjøsæter 1997)
b_1	−1.3	dl	Larval mortality parameter	(Fiksen et al. 2002)
b_2	0.57	dl	Fecundity parameter	(Huse and Gjøsæter 1997)
c	200,000	tonnes	Carrying capacity of a square	
d	50, 90	dl	Feeding parameter (larvae, adults)	
f	1,600	egg g^{-1}	Fecundity parameter	
hs	20	dl	Half saturation parameter	
r_c	0.4	m	Visual range of cod	(Fiksen et al. 1995)
r_m	0.5	m	Visual range of marine mammals	(Fiksen et al. 1995)
v_c	0.2	ms^{-1}	Swimming velocity of cod	(Fiksen et al. 1995)
v_m	0.5	ms^{-1}	Swimming velocity of marine mammals	(Fiksen et al. 1995)
ed_t	5.5	KJ g^{-1}	Energy density threshold	(dos Santos and Jobling 1995)

dl dimensionless.

2.7.3 Growth

Larval growth is calculated as a function of temperature and ingestion (Kiorboe et al. 1987; Fiksen and Folkvord 1999) using equation 14 in Fiksen and Folkvord (1999), where the ingestion rate F is given as a Michaelis–Menton like equation with a half saturation term (*hs*, Table 1):

$$F = \frac{d \cdot P}{hs + P} \tag{4}$$

where d is a constant (Table 1) and P is the local phytoplankton density, which indicates the productivity of the area although it does not represent the food utilised by capelin directly. The growth of adult capelin was calculated using a well documented bioenergetics model (Hewett and Johnson 1992). Within this model growth is the net difference between the energy consumed and the costs of metabolism, activity, excretion and egestion (Hewett and Johnson 1992). Since we lack a proper parameterisation of capelin bioenergetics, we used a herring bioenergetics model (Hewett and Johnson 1992; Fiksen et al. 1995). Herring co-occurs with the capelin in the Barents Sea and the two species have similar planktivorous life styles. While the expenditure of energy can be explained through fairly well known temperature dependent physiological relationships, consumption results from a range of complex ecological processes. We used Eq. 4 to give the ingestion rate (feeding level) that is needed in the bioenergetics model. Density dependence seems to be an important factor in motivating capelin movement (Hassel et al. 1991). It is not possible to provide feedback into the prey fields since these are produced in previous simulations using the biophysical ocean model. Instead density dependence (*DD*) was included as a reduction in the ingestion rate of capelin (F) dependent on the biomass of capelin (L) present in a square relative to a carrying capacity (c, Table 1):

$$DD = \exp^{-\frac{L}{c}} \tag{5}$$

All other growth parameters and equations are given in Hewett and Johnson (1992).

For adults the growth process is modelled using structural weight and energy density (Rosland and Giske 1994), where structural weight equates to wet weight. Growth occurs if the energy density is above the threshold level ed_t (Table 1). Structural weight is irreversible, but the total amount of energy is reduced if the net energy budget is negative during a time step. After a period of negative growth, the energy density has to be rebuilt and increased beyond the threshold value before structural growth can take place.

2.7.4 Movement

For larval fish, movement is calculated using the velocities from the ocean circulation by the Euler-forward scheme with random walk in the same manner as Ådlandsvik and Sundby (1994).

Adults are displaced by the current, but in addition they have directed movement that is determined by using the individual based neural network genetic algorithm approach (ING, Huse and Giske 1998; Huse et al. 1999; Strand et al. 2002). This method uses an ANN to calculate movement along the x and y axes from input information and inherited weights that are given on the strategy vector of the individuals. The ANN used here had seven input nodes, 15 hidden nodes and two output nodes. The input information used to calculate movement was: temperature (T), plankton density (P), longitude (E), latitude (N), day length (D), day number in relation to spawning date (S), and relative capelin density (DD, Eq. 5, Fig. 3). Since cod was distributed in proportion to temperature and marine mammals were assumed to be homogeneously distributed, no specific input on predator density was included. The calculations proceed sequentially from the input, via the hidden layer to the output layer (Fig. 3). The input data are standardised to be maximally 1, and then multiplied by the weights between the input and hidden layers:

$$N_h = \sum\nolimits_{i-1}^{n} IW_{ih} \cdot I_i \tag{6}$$

where I_i is the input data of input node i, IW_{ih} is the connection weight between input data i and hidden node h, N_h is the sum of the weighted input data of hidden node h, and n is the number of input nodes. At the hidden node, values are transformed using the standard sigmoid transformation:

$$TN_h = \frac{1}{\left(1 + e^{-(N_h + B_h)/R_h}\right)} \tag{7}$$

where TN_h is the transformed value and B_h is the bias (van Rooij et al. 1996) of hidden node h. The bias B_h is similar to an intercept value in a regression model. R_h determines the shape of the function, and large values make the curve flatter while small values makes it relatively steeper (Gurney 1997). Next the output values are calculated by adding together the sums of the transformed hidden node values multiplied by the output weights (OW_{ho}):

$$O_o = \sum\nolimits_{h=1}^{m} OW_{ho} \cdot TN_h \tag{8}$$

where O is the value of output node o, and m is the number of hidden nodes. The output values are then transformed:

$$TO_o = \frac{1}{\left(1 + e^{-O_o/OR_o}\right)} \tag{9}$$

The two output values are scaled from values in the range [0,1] to values in the range [−1,1] to allow symmetric movement along the horizontal axes. The output nodes give the relative swimming velocity along each horizontal dimension, and swimming speed is maximally one body length per second.

2.7.5 Spawning

The capelin were all assumed to be females. If the conditions for spawning are met, the female produces one batch of eggs (f) as a function of the internal number (n), the structural weight (w) and the relative energy density (ed/ed$_t$) of the super-individual:

$$f = \left(\frac{\mathrm{ed}}{\mathrm{ed}_t}\right) n \cdot a_2 \cdot w^{b_2} \tag{10}$$

where a_2 and b_2 are constants (Table 1). The batch was divided among 1–10 offspring super-individuals depending on the batch size f.

Offspring are equipped with strategy vectors that are clones of their mothers, with mutations occurring with probability of 0.06 per ANN weight or trait. Given a mutation the character value is changed randomly by maximally ±25% of the trait value.

The eggs hatch after a number of days (55–5T days) that depend on the local temperature T at spawning (Jangaard 1974; Reed and Balchen 1982). This expression disregards changes in temperature during the egg stage, and was chosen in order to simplify the model. The dynamics in temperature are generally minor during this stage and the discrepancies associated with this approximation are therefore likely to be small. At the time of hatching the larvae are 0.5 mg (Folkvord et al. 1996), with a length of 7.5 mm (Gjøsæter and Gjøsæter 1986).

3 Results

3.1 Physics and plankton

Figure 2 displays the mean annual primary production from the Barents Sea simulated for the ECHAM4/OPYC3 IPCC-SPRES B2 scenario from 1995 to 2059 (Ellingsen et al. 2008). The primary production increases with about 8% during this 65 year period. This increase in primary production is linked to changes in the physical environment of the Barents Sea. Figure 2b shows that the fraction of water with $T > 1°\mathrm{C}$ increases. Ellingsen et al. (2008) show that the simulated warming of the Barents Sea water results from a significant increase in the temperature of the water flowing into the shelf sea from the west. The warm water melts the ice from beneath and this partly explains why the ice cover decreases during the simulation (Fig. 2c). Even though there is a general warming of the Barents Sea, the inter-annual and multidecadal variations are substantial. The variability in the primary production in Fig. 2a is closely linked with changes in proportion of warm water and ice cover (Fig. 2b and c). This climate variability affects the ecological system of the Barents Sea.

Due to the large variability of the Barents Sea climate, a particular year near the end of the simulation might very well be characterised as colder than a year closer to the present time. A more correct approach will therefore be to compare similar situations. Figure 4 shows the annual mean current and the position of the polar front in a) a year of minimum ice cover in the decade 1995–2004 and in b) for a year of minimum ice in the decade 2040–2049.

The currents at 50 m depth show the mean circulation of the surface layer in the Barents Sea. Generally, the circulation patterns in Fig. 4a and b are similar. The position of the Polar Front in these two selected years differs significantly in the eastern and north-eastern Barents Sea. The position in the west is strongly influenced by bottom topography and less influenced by climate change. More details of how the physical and biological conditions in the Barents Sea changes during the IPYC-SPRES2 scenario are found in Ellingsen et al. (2008).

3.2 Capelin life history and distribution

In all the simulations the majority of the spawning took place in the Finnmark and Murman spawning areas (Fig. 5). But in simulation 2, spawning was shifted north-eastwards, and Novaya Zemlya became equally important to the Finnmark area. Simulation 3 produced a distribution of spawning area use in between simulation 1 and 2 (Fig. 5). There were notable cycles in the usage of spawning areas over time in all three simulations (Fig. 6). These were partly related to temperature, and in simulation 1 and 3 there were significant negative relationships (linear regression, $p<0.001$) between the proportion of fish spawning in the Finnmark area and the average temperature in the Barents Sea. In simulation 2 there was a negative, but non-significant relationship. This shows a tendency for westerly spawning in cold years.

The capelin biomass was about 30% higher in simulation 1 than in simulation 2, with simulation 3 having intermediate biomass (Fig. 7). The inter annual variation in number of recruits was considerable (Fig. 7a), with a standard deviation twice as high as for the adult abundance (Fig. 7b). The different spawning areas varied in recruitment success among the simulations. In simulation 1, only the usage of the Murman area was positively correlated with recruitment, whereas the usage of all the other spawning areas was negatively correlated with recruitment (Fig. 8). In particular the north and eastern areas had rather large negative correlation with recruitment. The usage of the Murman area was also positively related to recruitment strength in simulation 2, but here Novaya Zemlya had the strongest relationship (Fig. 8). In simulation 3, the Finnmark area was the overall most productive area in terms of recruitment, but the Murman area also had a positive slope in this simulation.

The evolved spawning day was on average earlier in simulation 2 than in simulation 1 and 3 (Fig. 9). However, there was some variation between the replicates in simulation 2, with two replicates spawning early and two spawning late as indicated by the relatively larger confidence intervals in simulation 2 compared with the other simulations.

The adult capelin was predicted to be distributed further to the east and north in simulation 2 compared with simulation 1 (Fig. 10). The different spawning components can be seen in Fig. 10 aligning along shore in the Murman (simulation 1) and Novaya Zemlya areas (simulation 2) in April.

4 Discussion

4.1 Life cycle modelling

The present study includes explicit modelling of all the life stages of the Barents Sea capelin including egg, larval, juvenile and adult stages. Although there have been previous studies modelling evolution of spawning areas of fish stocks (e.g. Mullon et al. 2002), the

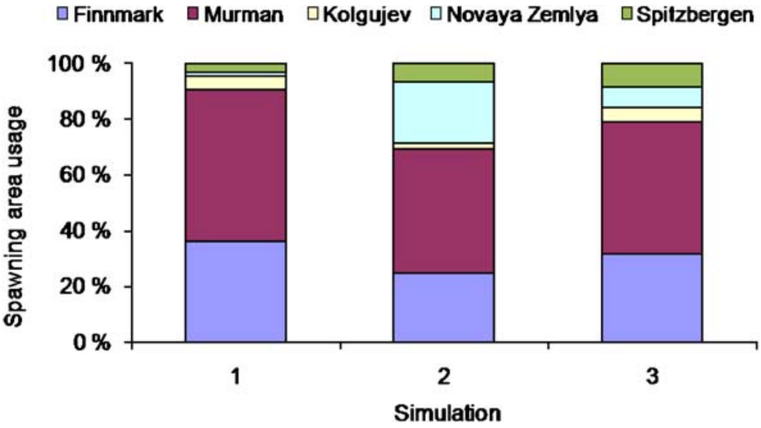

Fig. 5 Usage of spawning areas in simulations 1 (**a**), 2 (**b**) and (3), all replicates included. The locations of the spawning areas are indicated in Fig. 1

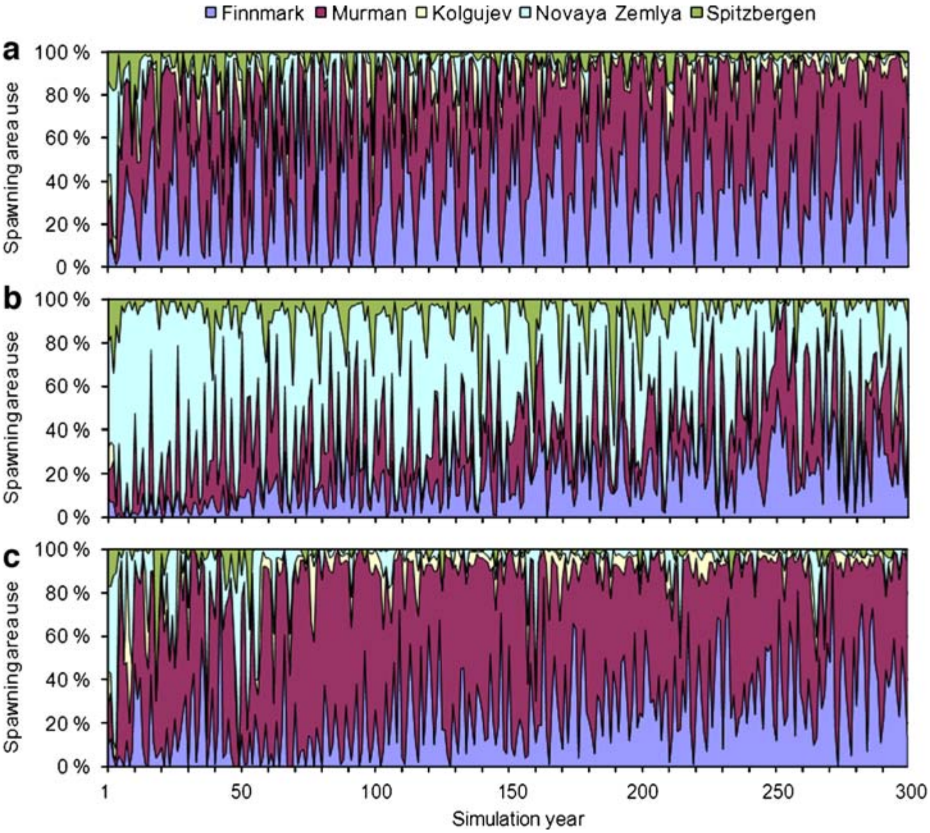

Fig. 6 Usage of spawning areas in arbitrarily chosen replicates of simulation 1 (**a**), 2 (**b**) and 3 (**c**)

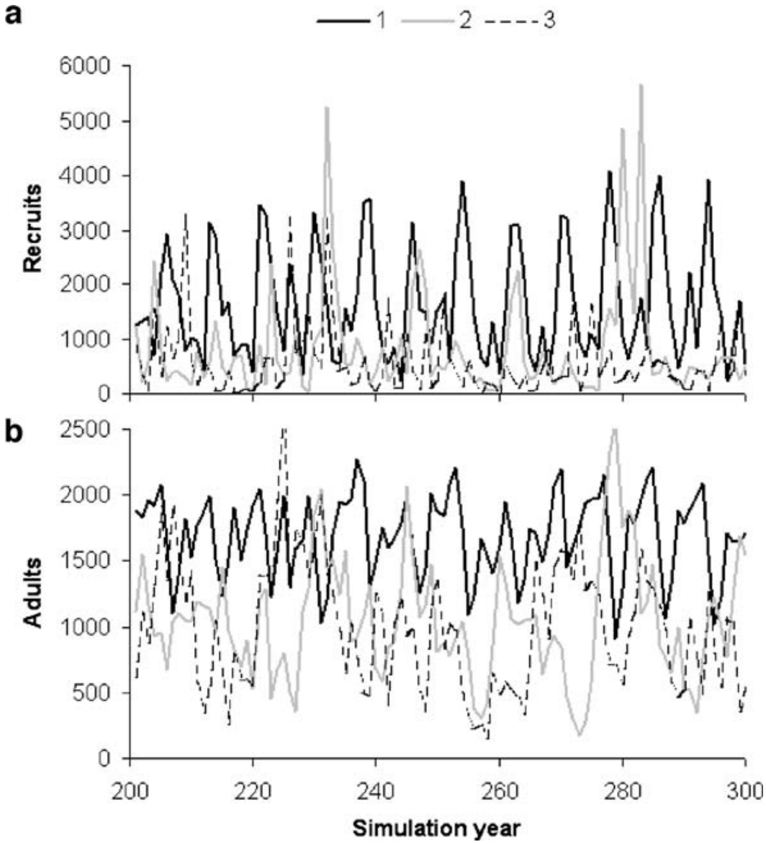

Fig. 7 Number of super-individuals of recruits (**a**) and adults (**b**) at the end of the year in the last 100 years of replicate 4 in simulations 1, 2 and 3

approach taken here is novel in its explicit simulation of capelin life history with behavioural and life history strategies evolved independent of restrictive assumptions. Furthermore the model at the same time yields population dynamics of capelin, and produces plausible capelin responses to global warming. Growth and survival are important

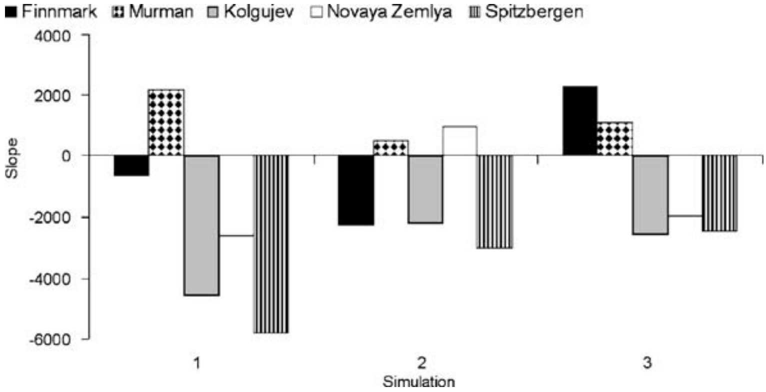

Fig. 8 Slope between spawning area use and number of recruits produced in simulations 1, 2 and 3

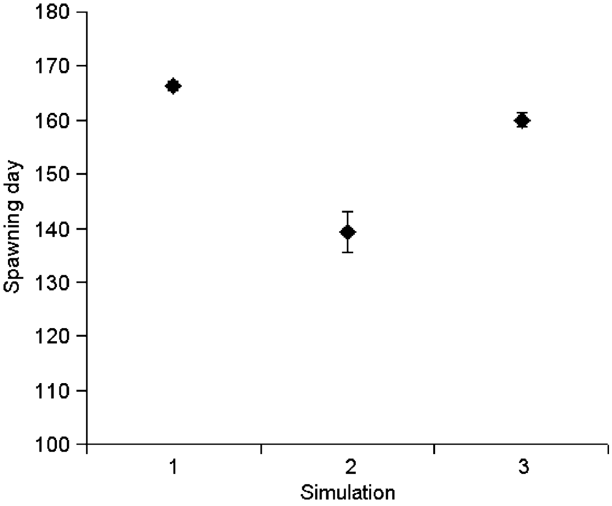

Fig. 9 Average evolved spawning day (±95% confidence intervals) in the three different simulations

adaptive features of horizontal migrations (Leggett 1977), but migration in fishes is also evolved to optimise spawning location. In order to analyse spatial distribution in migratory fishes the establishment and maintenance of spawning areas should therefore be addressed. Even though we do not present an exhaustive analysis of capelin migrations here, the approach in general can be useful for investigating likely effects of climate change on fish or other animal populations.

The usage of ANNs for calculating movements of fish has been shown to work well both for horizontal and vertical migrations (Huse and Giske 1998; Huse et al. 1999; Strand et al. 2002). The present simulations confirmed that this approach can be useful for climate change simulations as well. However, the key aspect of our modelling approach was not the usage of the ANN for calculating movement per se, but rather the evolution of robust strategies in variable environments. An alternative modelling approach based on optimality methods such as stochastic dynamic programming (Mangel and Clark 1988) could have been feasible. In this case the best place to spawn in any given year could have been found, which would have been an interesting additional analysis. However, it would not capture the linkage between cohorts and the episodic establishment of spawning areas often seen in fish stocks (Sinclair 1988) and also seen in the present simulations.

4.2 Spawning area dynamics

The spawning area is a key feature in defining the life cycle of fish since distribution during the subsequent stages are made relative to the spawning area. Climate change was predicted to impact on the capelin distribution. In particular simulation 2, where the capelin was adapted to a particularly warm scenario, produced a pronounced northeastwards shift in spawning location compared with present day climate in simulation 1. A smaller tendency for easterly spawning was seen in simulation 3 as well. We also found that spawning took place earlier in the warm scenario than in the cold. However, there was some variation among the replicates in the warm scenario (simulation 2) with regards to spawning day, which indicates that the selective pressure for early spawning was not very strong. In other stocks, such as Norwegian spring spawning herring, spawning has been moved forwards during the present warm period, and now occurs earlier than before. This is similar to our

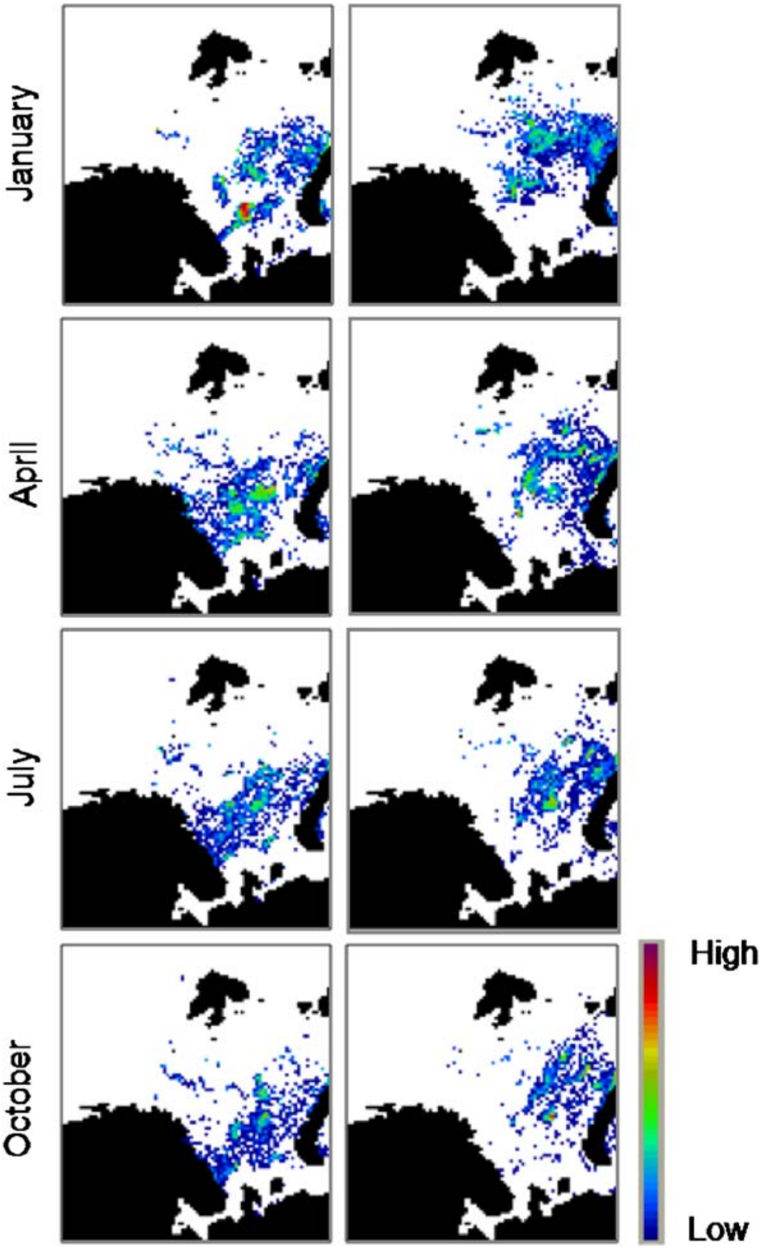

Fig. 10 The distribution of 1 year and older fish in four different months for simulations 1 and 2. The *colour bar* indicates density of 1 year and older fish

predictions for capelin. The optimal timing of spawning also depends on the location for spawning and thus the timing of plankton blooms etc, but we did not find any consistent relationship between spawning area and timing of spawning within the simulations.

The model predicted considerable inter-annual variation in population- and spatial dynamics in a cyclic pattern. There also tended to be separation in the populations where parts of the population spawned at Novaya Zemlya and other parts of the population spawned in Finnmark or Murman areas. The spawning location of the Barents Sea capelin varies, depending on the temperature regime. In warm years spawning is easterly, and further west during cold years (Ozhigin and Luka 1985). A similar inter-annual variation in spawning was seen in the simulations, particularly in simulation 3, which covered a great range of environmental states (Fig. 2), and therefore made it profitable to individuals to evolve climate dependent strategies. The Finnmark spawning area also stood out as the most productive spawning area in terms of capelin recruitment in simulation 3 (Fig. 8). In simulation 1 and 2 with more restricted environmental variation, the evolved strategies of capelin were more specialised for cold and warm situations respectively.

The spatial distribution in simulation 1 reproduced the main features of the migration pattern of the Barents Sea capelin (Gjøsæter 1995) with spawning on the coast of Northern Norway and Murman, and larval drift towards the east and north. However, the entire life cycle appeared to be shifted eastwards compared to observations on capelin (Gjøsæter 1998). This is partly attributed to the biophysical model which due to a rather course resolution has problems in recreating the current pattern near the coast. Westerly spawning, is therefore in the model associated with a high probability of being transported to the west side of Spitzbergen, and thus outside the most productive areas for capelin. In addition our “cold” period 1996–2005 is not really cold compared to other periods such as the early 1980s, and consequently one should not expect a strong tendency for westerly spawning.

4.3 Alternative capelin responses to climatic change

There are obviously several plausible scenarios for capelin migrations in face of the likely increase in available habitat induced by climate change and these are discussed in more detail in Roderfeld et al. (2008). The capelin may establish new spawning areas with a temperature span that resembles historic spawning areas, as found in this study. The Barents Sea capelin is presently associated with the marginal ice zone during summer. If the ice edge is withdrawn substantially deeper into the Arctic, capelin may give up the association with the marginal ice zone and rather feed in warmer waters. This might increase capelin growth, which is positively related to temperature (Gjøsæter and Loeng 1987), but may also increase predation mortality from cod. Since the predation risk from fish predators was assumed to be a linear function of temperature, it was implicitly assumed that the abundance of predator fish increased in proportion to the temperature in the Barents Sea. Both recruitment and growth of cod, which is the main predator of capelin (Bogstad et al. 1997; Bogstad et al. 2000) is positively related to temperature (Nakken and Raknes 1987; Sætersdal and Loeng 1987; Ottersen et al. 1994; Ottersen et al. 1998) so that this assumption seems reasonable. The increased predation risk from fish predators associated with the warming resulted in a reduction in capelin biomass in simulation 2 compared with simulation 1.

Predation by juvenile herring is in many years an important component in the larval mortality of the Barents Sea capelin (Hamre 1994; Gjøsæter and Bogstad 1998; Huse and Toresen 2000; Godiksen et al. 2006). However, this predation was not included in the present model since the biomass of juvenile herring in the Barents Sea is irregular and depends on herring recruitment. Herring recruitment is climate dependent and is favoured by inflow of warm water to the Barents Sea (Stephens and Krebs 1986; Sætersdal and Loeng 1987; Hamre 1994; Toresen and Østvedt 2000; Sætre et al. 2002).

4.4 Conclusions

Even though the biophysical model predicted rather modest changes in the climate and plankton production of the Barents Sea (Ellingsen et al. 2008), these changes were nevertheless sufficient to produce responses in capelin abundance, spawning area and adult distribution. Whether capelin will take up spawning at Novaya Zemlya as predicted by the model remains an open question, but there is anecdotal evidence for such spawning to have taken place in the past (Are Dommasnes pers. comm.). Whether capelin will take up spawning at Novaya Zemlya as predicted by the model remains an open question, but there is some evidence for such easterly spawning to have taken place in the past (see Gjøsæter 1998).

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