

A SPATIAL LIFE HISTORY MODEL OF THE BARENTS SEA CAPELIN

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ABSTRACT

Huse, G. A spatial life history model of the Barents Sea capelin. A spatial life history model of the Barents Sea capelin (*Mallotus villosus*) is presented which incorporates the entire life cycle of the fish. Horizontal movement is modelled by a drift algorithm for the larvae and by an artificial neural network with weights evolved by a genetic algorithm for the adults. A physical model creates temperature fields from which mortality risk and zooplankton production is calculated, and growth is modelled using a bioenergetic model. Several life history traits including size at maturity, energy allocation, and number of spawning trials are modelled explicitly along with spawning time and location. The genetic algorithm adapts life history traits and behaviour through evolution by natural selection among competing individuals.

The evolved spawning areas and timing of reproduction resemble those of the Barents Sea capelin. The seasonal distribution of the fish reproduces the general migration pattern of the Barents Sea capelin. A simulation with inter-annual variation in juvenile and adult mortality evolves sex dimorphism in size at maturity and life history strategy with large semelparous males and small iteroparous females. This latter result supports former findings of sex specific life history strategies in capelin.

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INTRODUCTION

The integration of full life cycle in spatial models of animal distribution is a challenging task. Especially so if the animal under consideration moves around according to its own will. Most fishes have larval stages where horizontal movement is controlled mainly by ocean currents. As the larvae metamorphose and become larger it takes control of its own positioning, and what previously has been mostly a passive physical process now becomes a complex array of movement decisions. These two situations are usually studied separately where the former is commonly referred to as early life history (e.g. BLAXTER 1974). Although this distinction is practical in some cases with regard to experiments and field studies, it may be fruitful to merge these disciplines in models. Current habitat occupied by an animal depends upon where it was previously. Consequently, spatial distribution at any time may be understood better if the entire life cycle is implemented in the model, rather than looking at each ontogenetic stage in isolation. This is especially important for the macro scale distribution (FERNØ & al. 1998) of migratory fishes whose life cycle is optimised to accommodate growth, mortality and reproduction (NORTHCOTE 1978). Passive dispersal of larval fish as particles in physical models of ocean currents has been extensively studied (BARTSCH & al. 1989; WERNER & al. 1993; BERNTSEN & al. 1994; DEYOUNG & al. 1994; ÅDLANDSVIK & SUNDBY 1994). These models contain little larval behaviour although vertical migration is implemented in some of them (BARTSCH & al. 1989; WERNER & al. 1993). As the larvae become larger they may actively choose their location. A common approach is to model habitat choice as a process that maximises a measure of Darwinian fitness (see reviews by TYLER & ROSE 1994; GISKE & al. 1998). This approach is applied in the ideal free distribution (IFD, FRETWELL & LUCAS 1970), optimal foraging theory (CHARNOV 1976), life history theory (WERNER & GILLIAM 1984; AKSNES & GISKE 1990), and in models based on stochastic dynamic programming (SDP, MANGEL & CLARK 1988).

The Barents Sea is a shelf sea north of Norway and Russia, with influx of Atlantic and coastal water from the south-west. The main current systems and water masses are indicated in Fig. 1. The capelin (*Mallotus villosus*) is a small, abundant planktivorous fish. It has an important ecological role in the Barents Sea where it is a predator of many species of zooplankton (HASSEL & al. 1991), and prey for a number of fishes, birds and marine mammals (MEHL 1989, 1991; HAUG & al. 1996; NORDØY & al. 1996). Historically the capelin has been a valuable resource (OLSEN 1968), but due to a short life span it is difficult to manage the capelin stock using conventional methods (GISKE & al. 1992). Currently a target escapement management strategy is

applied which involves setting a lower size for the spawning stock (TJELMELAND 1997). The lack of management tools for short-lived species such as the capelin has led to the launch of alternative modelling projects using spatial distribution. Balchen and colleagues initiated this modelling effort on capelin (BALCHEN 1976; REED & BALCHEN 1982), and the work was continued by GISKE & al. (1992), FIKSEN & al. (1995) and HUSE & GISKE (1998).

The capelin is known to decimate the abundance of its prey during summer (HASSEL & al. 1991), and has to change habitat in response to this depletion. The life history of the capelin is constrained by high adult mortality (MEHL 1989, 1991) and occasional years with high larval mortality due to predation from abundant immature herring (HAMRE 1991; FOSSUM 1992; HUSE & TORESEN 1995). Such stochastic elements in environmental factors are likely to have life history strategy implications (COHEN 1966; TULJAPURKAR 1990; YOSHIMURA & CLARK 1993). The problems mentioned above regarding full lifecycle enclosure, trophic links, and stochastic environments are difficult to solve using conventional methods in ecological modelling such as IFD and SDP. Also, these are situations in which common fitness measures such as the intrinsic rate of increase r and the net reproductive rate R_0 become invalid (e.g. ROFF 1992; STEARNS 1992). A discussion of the pros and cons of the various spatial models can be found in Giske & al. (1998).

A different approach to studying spatial distribution is to use evolutionary systems with endogenous fitness (ACKLEY & LITTMAN 1992; MITCHELL & FORREST 1995; MENCZER & BELEW 1996). In such systems, fitness is defined indirectly through interactions between individuals and the environment. Criteria are set for reproduction and the fittest organisms will, by definition, be those that are able to reproduce more, relative to the other individuals, under the set conditions. This approach is common in artificial life (A-life), a field that among other things simulates "life" in computer programs (LANGTON 1989). Many A-life studies apply artificial neural networks (ANN, ROSENBLATT 1958; RUMMELHART & al. 1986) and genetic algorithms (GA, HOLLAND 1975). These techniques are powerful in calculating behavioural actions and simulating evolution by natural selection, respectively. By combining these techniques a robust concept for evolving movement behaviour emerges (PARISI & al. 1990; ACKLEY & LITTMAN 1992; MENCZER & BELEW 1996; DAGORN & al. 1997). HUSE & GISKE (1998) used this evolutionary modelling approach to develop a method for modelling fish migrations, named the ING concept (see below).

The objective of the present study is to apply the ING concept in a spatial life history model of the Barents Sea capelin where all stages of the life cycle are

modelled explicitly. Properties of the life history cycle such as spawning time and location, are evolved. The reason for emphasising the link between spatial and life history models is the dependence of habitat characteristics on processes such as growth and mortality that affects life history strategies. The effect of variable mortality rates on life history strategies and spatial dynamics of the Barents Sea capelin, is assessed.

THE MODEL

The ING concept

ING stands for individual based neural network genetic algorithm, and a schematic outline of the concept is provided in Fig. 2. The concept was developed by HUSE & GISKE (1998) for studying fish migration, and integrates the individual based model paradigm (e.g. DEANGELIS & GROSS 1992) with two common computer techniques. The GA is a technique that applies the principle of evolution by recombinations, mutations, and natural selection in a gene pool in search for optimal solutions to a problem (HOLLAND 1975). For an introduction to GAs see GOLDBERG (1989) and MITCHELL (1996). Most optimisation problems can be solved using the GA, although its efficiency and suitability depends upon the specific problem. ANNs use neurobiological principles of synaptic brain-activity to weight input differentially and calculate output (ROSENBLATT & al. 1958; RUMMELHART & al. 1986). Here a simple feed forward network (ANDERSON 1995) is applied with input, hidden, and output layers. The nodes are associated with matrices of weights that are adapted through evolution by "natural selection" using the GA (MONTANA & DAVIS 1989; ROOIJ & al. 1996). To avoid confusion between biological genetics and GA "genetics" the GA terminology suggested by GOLDBERG (1989) is adopted, hence the analogy of a chromosome is termed "string" and gene is termed "character". Real value strings were used to encode the GA (DAVIS 1991; ROOIJ & al. 1996). Each character hence consists of one real number instead of several bits as in the previous version of the model (HUSE & GISKE in press.), and the strings are consequently shorter.

Since the model is individual based and each individual is handled explicitly, the computing time increases linearly with the number of individuals. Fish stocks may contain hundreds of billions of individuals, and can not be simulated individually. In order to be able to maintain an individual based structure and still simulate problems at the ecosystem level, "siblings" were introduced. Each modelled individual is represented as millions of siblings which act and grow synchronously. When predation acts, it reduces the number of siblings. All interactions between the

individual and the environment are done in this scaled up version. An individual here represents a strategy and these terms are used interchangeably. The number of siblings is the number of clones of a strategy.

Individual movement

The model area consists of a lattice of 60 by 60 squares of 20 km sides with land contours for the Barents Sea (Fig. 3). At the start of a computer run a population of individuals equipped with strings of random numbers are placed in a square in central areas of the lattice. Here they feed, grow, and may die. At the end of each time step the spatial position of each individual is updated. For larval fish, movement is determined in a probabilistic manner, with a certain probability for movement in each direction determined by ocean currents. In a former study it was found that the distinction into reactive and predictive movement was productive when modelling long distance migration (HUSE & GISKE in press.). Reactive movement relates to local search for the best habitat, whereas predictive behaviour is movement towards areas that are expected to contain certain features (such as high food abundance or good spawning substrate). It was found that reactive movement was applied throughout most of the life cycle of the fish, and that predictive movement was only used during migration towards the spawning ground (HUSE & GISKE in press.). The present movement control is based on these findings where predictive movement was found to be used one month prior to spawning and during the spawning month. Thus one month prior to spawning and during the spawning month predictive movement is applied; otherwise movement is calculated using the reactive network. When predictive control is applied, fish movement is calculated as the shortest route to the spawning area, and the square closest to the spawning area is consequently chosen. When the fish is at the spawning area it stays there until spawning commences. This mimics the well-known homing to birthplace of many fishes (e.g. QUINN & DITTMAN 1992). Reactive movement is calculated using an ANN from information on present and past growth, temperature, and mortality (Fig. 4). The value coming into hidden node h (n_h) is calculated as:

$$n_h = \sum_{i=1}^6 I_i \cdot W_{ih} \quad (1)$$

where I_i is the stimuli coming out of (equal to input value since no transformations are used) input node i , and W_{ih} is the weight between input node i and hidden node h .

Directions of movement upon firing of specific nodes are indicated in the grid at the right of the figure (Fig. 4). For each hidden node the input values are added together and transformed using the standard sigmoid equation (e.g. ANDERSON 1995):

$$F(n_h) = \frac{1}{(1 + e^{-n_h})} \quad (2)$$

where $F(n_h)$ is the transformed node value. If the node value ($F(n_h)$) is above a threshold value V_t (Table 1), the node H_h fires:

$$H_h = \begin{cases} 0 & \text{if } F(n_h) \leq V_t \\ 1 & \text{if } F(n_h) > V_t \end{cases} \quad (3)$$

The threshold value is set so that about 10% of the nodes fire at the start of the simulation when the weights are random. The same procedure is carried out at the output node, but only one of the output nodes, the one with the highest value is excited (Fig. 4). The individual consequently moves to the square which has been excited, or stays if node 5 is excited (Fig. 4).

Energetic costs depend on temperature and swimming speed. Swimming speed is set to 0.06 ms^{-1} when an individual stays within the same square as in the previous time step. If it moves the swimming speed is equal to the distance travelled divided by the time it has used (one time step). The distance is calculated as minimum distance between the centre of the squares. This may underestimate the actual swimming cost since it assumes that the fish swim in straight lines over long distances.

Several life history traits are evolved in the model along with the weights of the ANN (Table 2). Individuals are born with these traits and keep them throughout their lives. The consequences of a semelparous strategy (Table 2) here is that the individual dies when its spawning month is over. The advantage of a semelparous strategy is the potential for males to mate several times during their spawning month. Females are, however, limited by the number of eggs they can carry and may only mate once a year (HUSE 1998). Allocation of energy is here restricted to females, and males are simply assumed to invest all their energy into soma (HUSE 1998).

Growth

Where possible, parameter values and equations are taken from studies of the Barents Sea capelin. Otherwise, values from fishes with a similar life style and spatial distribution to capelin, such as herring, are applied. A physical model of the Barents Sea (SLAGSTAD 1981, 1987; SLAGSTAD & al. 1989; STØLE-HANSEN & SLAGSTAD 1991) is used to create monthly temperature fields (Fig. 5). The temperatures are averaged values of the upper 100 m. The larvae feed on copepod eggs and nauplia, which have a peak production in the Barents Sea in May (TANDE 1991). Larval growth is calculated as a function of temperature and relative abundance of copepod eggs and nauplia:

$$G_i = W_i \cdot (T_{jkt} + 3) \cdot N(t) \quad (4)$$

where G_i is the absolute weight gain per time step of individual i , W_i is structural weight (see below) of individual i , $N(t)$ is the relative abundance of copepod eggs and nauplia at time t (Fig. 6), and T_{jkt} is the temperature in location jk at time t (Fig. 5). $N(t)$ is implemented through a normal distribution with a peak at the end of May (Table 1, TANDE 1991). The growth is scaled so that the maximum attainable growth rate is about 10% d⁻¹ (MOKSNESS 1982). Beyond the larval stage the fish feed on copepodites (LUND 1981; HUSE & TORESEN 1996). To simplify, all the copepodites have the same size (Table 1). Zooplankton dynamics can be described by the following relationship:

$$Z_{jkt} = Z_{jkt-1} + R_{jkt} - \left(\mu \cdot Z_{jkt-1} + \sum_{i=1}^m P_{ijkt} \cdot A_i \right) \quad (5)$$

where Z_{jkt} is the zooplankton abundance in square jk at time t , R_{jkt} is the zooplankton abundance added in square jk at time t , μ is mortality in zooplankton from other causes than fish predation (Table 1), P_{ijkt} is the number of zooplankton eaten by one sibling of fish number i in square jk at time t , A_i is the number of siblings of fish i , and m is the number of adult individuals in square jk . A temperature dependent and seasonal ($S(t)$) production of zooplankton is added at the start of each time step during the productive season (Fig. 6):

$$R_{jkt} = S(t) \cdot T_{jkt} \cdot C_1 \quad (6)$$

where C_7 is a constant (Table 1). $S(t)$ is implemented through a normal distribution with a peak at the end of July (Table 1, TANDE 1991). After each individual feeding the copepod abundance is updated (Eq. 5). In frontal areas the production is enhanced during June-August to mimic the increased production in such areas due to the receding ice edge (REY & al. 1987). Fronts are here defined as areas in the central Barents Sea within the temperature range 0-1.8°C (HASSEL & al. 1991) and the production (R_{ykt}) here is increased by a factor of 10 during June-August. After November 1, the zooplankton abundance decreases abruptly to simulate the downward migration of copepods which takes place during fall (e.g. HIRCHE 1996).

Adult growth is modelled using the HEWETT & JOHNSON bioenergetic model with parameter values for herring (HEWETT & JOHNSON 1992). The bioenergetic model is modified to allow trophic level interaction (HUSE & GISKE in press.). Hence food consumption is estimated from the concentration of zooplankton in the volume searched rather than by a temperature dependent function. Search volume is a function of distance covered during a time step multiplied by the search radius. In order to implement seasonal variation in light conditions, the search radius r (Table 1) is varied over the year using functions for surface light at 76° N (Fig. 7, see ROSLAND & GISKE 1994 for the surface light model), with a maximum during mid summer (Table 1). The implementation of visual feeding is hence rather coarse since the vertical axis, which affects light level and hence visual feeding (AKSNES & GISKE 1993; ROSLAND & GISKE 1994; AKSNES & UTNE 1997), is left out. Vertical gradients in light and zooplankton concentration are thus not taken into account, but rather it is assumed that zooplankton production and grazing is homogeneously distributed in the upper 100 m. The stomach is assumed to be empty at the start of each day and feeding is limited by stomach capacity (Table 1, GISKE & AKSNES 1992).

The growth process was modelled as in ROSLAND & GISKE (1997) using the distinction between structural weight and energy reserve, where structural weight equates to wet weight. Each structural weight has a corresponding amount of energy, and if growth is to occur the total energy level has to be above that of the current structural weight. The energy amount needed for structural growth (q_b) is listed in 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. Following periods of negative growth the energy level has to be rebuilt and increased beyond the level corresponding to the current structural weight before structural growth can take place. An individual dies if its energy reserves fall below 10% of the energy level corresponding to its structural weight.

Predation risk

Egg mortality in Barents Sea capelin has not been investigated thoroughly, but some studies suggest that it can be up to 10.2% over the egg stage (DRAGESUND & al. 1973; BAKKE & BJØRKE 1973). Based on this estimate, egg mortality was set to a constant rate of 0.3% day⁻¹. Larval fish mortality is generally a decreasing function of body size (PETERSON & WROBLEWSKI 1984), and was estimated as (MCGURK 1986):

$$M_i = C_2 \cdot \exp^{(-0.7-0.38 \ln(W_i))} \quad (7)$$

where M_i is the mortality of individual i during a time step, C_2 is a constant (Table 1) and W_i is the structural weight of individual i . The main predators of capelin are cod, harp seals and minke whales (MEHL 1989, 1991; HAUG & al. 1996; NORDØY & al. 1996). Of these predators the cod stock is by far the most important (BOGSTAD & al. 1998). As capelin may adjust visual mortality risk by vertical migration, predation risk is calculated as a function of temperature, season, and bottom depth:

$$M_{jkt} = \frac{|T_{jkt}| \cdot L_t \cdot \exp^{-D_{jk}}}{C_3} + C_4 \quad (8)$$

where M_{jkt} is the predation risk at location jk at time t , L_t is the relative surface light intensity at day t , D_{jk} is the relative (to 300 m) bottom depth at location jk , and C_3 and C_4 are constants (Table 1). The number of siblings (A_i) is updated each day:

$$A_i = A_i \cdot (1 - M_{jkt}) \quad (9)$$

When $A_i < 1$ the strategy dies.

Spawning

During spawning, pairs of individuals produce a number of eggs in proportion to the body weight of the female, and the relationship between body size and number of offspring is:

$$E_i = \frac{g_i}{\alpha \cdot W_i \cdot q_e} \cdot F \cdot W_i^{0.61} \quad (10)$$

where E_i is the number of eggs laid by female i , g_i is the energy invested into reproduction by individual i , α is the maximum allowed energy investment into gonads (Table 1), and q_e is the energy density of eggs (Table 1). The fraction in Eq. 10 is limited upwards to 1 at which the full potential for reproduction is achieved, and allocation to gonads beyond this does not increase the number of offspring produced. The recruitment success parameter F is constant in deterministic runs (Table 1) and varies inter-annually in stochastic runs. The exponential term in Eq. 10 is obtained from field samples (HUSE & GJØSÆTER 1997). Fecundity is hence the result of the size specific relationship and the amount of energy invested into reproduction (Eq. 10). If reproduction is to occur, the individual has to be above its size at maturity, in its spawning month, at its spawning area and it has to be virile (it cannot be spent). In addition it has to find a partner at its current location. If these criteria are not met, spawning cannot take place. Partners are selected as the largest individual of the opposite sex to match the criteria for reproduction listed above, and a lower size at maturity is set at 8 g. Offspring are equipped with strings that through recombinations are a mix of the two parents (Fig. 2). Further string variability may be added through changes in character value using (Fig. 2). Mutations occur with a low probability ($P=0.001$) and change the character value by a randomly chosen value, but maximally 20% (creep mutations, DAVIS 1991). The sex of new individuals is given randomly with equal probability of becoming either sex. The individuals that manage to reproduce will by definition be those that are more fit for life in the present environment. The selection scheme is hence similar to the way natural selection work, and this fitness definition is referred to as endogenous fitness (MITCHELL & FORREST 1995; MENCZER & BELEW 1996). By repeating this procedure over and over, the population will consist of increasingly fit members (HOLLAND 1975).

The eggs hatch after a number of days (d) depending upon the temperature (T_{jkt}) at the location where the eggs are laid (JANGAARD 1974; REED & BALCHEN 1982):

$$d = 55 - 5 \cdot T_{jkt} \quad (11)$$

At the time of hatching the larvae are $5 \cdot 10^{-4}$ g (FOLKVORD & al. 1996), and after reaching a size of 0.1 g, the drift phase is over and the fish maintain position. Upon reaching a size of 1 g, the fish start to actively choose their habitat and are simulated in the adult domain as described above.

Many stimuli, including olfactory, visual, geomagnetic, water current, and temperature have been used to explain orientation of fishes during migrations (e.g.

Harden Jones 1968; Quinn & Dittman 1992). An organ for magnetic sense that is used for orientation has recently been recognised in rainbow trout (*Oncorhynchus mykiss*) (WALKER & al. 1997). Here it is simply assumed that capelin has a similar sense and that it can orient itself and sense its position using the magnetic fields of the earth. In addition, it is assumed that the fish can sense the ambient temperature and assess food availability and predation risk (see review by FERNØ & al. 1998).

Simulations

Two simulations were carried out: a run where mortality rates were constant, referred to as the “deterministic run”, and a run where the mortality rates varied between years, referred to as the “stochastic run”. The simulations were run over 200 years, and were initiated with a population size of 14000 strategies and population size was limited upwards to 15000 strategies. Each of the strategies at birth contained 2×10^{11} siblings. Variability in recruitment was simulated using a time series of larval capelin survival (HUSE 1998). The number of offspring (individuals) produced during the stochastic run depends on the annual value of F in Eq. 10, but the larval mortality acting on the siblings is constant. Adult mortality in the stochastic run is varied using a time series of cod abundance (ANON. 1998), and scales M_{jkt} in Eq. 8 by a relative value with average 1. For each year in the stochastic run, a value of mortality from each of the two time series is drawn, and each year of the time series has an equal probability of being selected.

To avoid problems with population crashes early in computer runs, the training of the ANN is decomposed by starting with a relatively “benign environment” which is gradually made more difficult to live in (GOMEZ & MIIKKULAINEN 1997). The model is run for 100 years after the final parameter values (Table 1) are initialised.

RESULTS

Evolution of timing and location of spawning

Timing of reproduction converges towards spawning from March to May (Table 3). Initially there is a lot of scatter, but successful reproduction is quickly limited to the three months. With an egg developmental time of one to two months there is a pronounced match between larval hatching and peak production of larval food (Fig. 6). The evolution of spawning area shows a similar trend to timing of reproduction with spawning areas spread out over the entire lattice at the start of the simulation (Table 4). After a small number of generations, however, most of the spawning is

limited to an area located close to the Norwegian-Russian shore. The same spawning area was evolved in the stochastic simulation.

Life history strategies

Females matured at a slightly higher size and age than males in the deterministic run (Table 5). In the stochastic run, however, size at maturity was considerable higher in males than in females. In the deterministic run, both the sexes were iteroparous, whereas males were semelparous and females were iteroparous in the stochastic run. Males had a higher average size than females in the deterministic run, but in the stochastic run both average size and energy level was higher in the females (Table 6). The average energy level was about 80% of that corresponding to the structural weights in the deterministic run, and about 70% in the stochastic run. Timing of reproduction showed some variation between the simulations, and spawning occurred earlier in the stochastic than in the deterministic run (Table 5). A common feature was that the simulated fish spawned prior to or at the time of the peak production of larval food as illustrated in Table 5. In general the variation around the average was quite small for most of the life history traits, and the degree of variation did not differ between the two simulations. However, some characters such as the timing of and location for spawning, varied somewhat (Tables 3 and 4).

Life cycle and migration

The simulated fish distribution pattern from the deterministic run is shown in Fig. 8. Larval drift and counter current migration dominate the life cycle of the fish. It congregates at the spawning ground in March-May and in the following months the fish distribution is dominated by larval drift (Fig. 8). An interesting feature is the association of the spawning area and consequent larval drift with a warm water tongue that reaches out from the coast of Russia towards Novaya Zemlya (Fig. 5). This warm water area is particularly distinct during the larval drift period in late spring and early summer (Fig. 8). During summer the juvenile and adult fish move north-east along the edge of the Polar front as this retracts. When winter approaches the fish starts to migrate in a south-east direction, and approaches the coast of Northern Norway and Russia. Most of the fish distribution outside of the spawning season is associated with the 0°C isotherm, which ensures high production during summer as well as a low predation risk (Eq. 8). There was a tendency for the age groups to occupy different areas (Fig. 9). The 0-group are shown during the drift phase in June. The immature 1-group occupies cold waters mostly along the central parts of the Barents Sea and along the coast of Novaya Zemlya. The older age groups are

generally found concentrated along the Polar front with a tendency for the oldest age groups to have the southernmost distribution (Fig 8). Although it is not recognised in the figures, the fish moved quite markedly in an east-west direction around the frontal zone as determined from an animation of fish movement over sequential time steps. During summer, food intake was mostly limited by stomach capacity whereas during winter it was limited by food availability (Fig. 10).

Population dynamics

The population biomass varied extensively between years (Fig. 11). After about 160 years the population biomass in the deterministic run climbed to a relatively stable level between 5 and 6 mill tonnes (Fig. 11). In the stochastic run the biomass was only about 1/6 of the biomass in the deterministic run, and the biomass varied relatively vigorously throughout the period. As a result of the variable population abundance, the age structure is far from stable in the stochastic run (Fig. 12), the strength of age groups depending on the past and present mortality level. The deterministic run had a more stable age structure than the stochastic run (Fig. 12). The number of siblings of the different age groups shows a consistent reduction (Fig. 12 A). For individuals, however, this consistent trend is missing (Fig. 12 B). Due to the skewed sex ratio among the five-year-olds (Fig. 13), average age of females was higher than for males in the stochastic run (Table 6). In the deterministic run the sex ratio was even.

DISCUSSION

The present study integrates the entire life cycle of the Barents Sea capelin in a 2 D spatial setting where all stages of the capelin life cycle are modelled explicitly. Since many aspects of capelin ecology were evolved, the process of stock formation can be studied. A general finding was that spawning only occurred within a limited area and that reproduction was restricted to a few months during spring. Migration cycles were consequently defined relative to and in the vicinity of the spawning area. The inclusion of the entire life cycle increases the applicability of the approach by allowing life history strategies and behavioural strategies to be evolved within the same framework. Another advantage of using full life cycle is the possibility of applying so-called endogenous fitness (ACKLEY & LITTMAN; MITCHELL & FORREST 1996; MENCZER & BELEW 1996). As opposed to exogenous fitness models where a measure of Darwinian fitness is maximised, fitness in the present model is determined by interactions between the individuals and their environment. The individuals that

manage to reproduce more copies of themselves, will become more and more common in the "gene pool" and after a long time period of simulations, these individuals will tend to dominate in the population. The advantage of the endogenous approach is that problems related to conventional fitness measures are avoided. Such problems are associated with stochasticity and density dependence (ROFF 1992; STEARNS 1992). By using the current methodology, stochastic environments are handled just as easily as deterministic ones.

Life history strategies

The present results support earlier predictions that capelin has sex specific life history strategies as a result of variable rates in juvenile mortality and high or variable adult mortality (HUSE 1998). Hence female capelin seem to be iteroparous while males are semelparous. Also the size at maturity was higher in males than in females in the stochastic run, which corresponds to observed capelin size dimorphism (OLSEN 1968). Despite this size dimorphism, the age at actual reproduction did not vary. This is probably attributed to the building of female ovaries that must be finished prior to spawning if reproductive potential is to be realised. Since allocation to gonad building in females was only allowed after maturity was initiated, females matured at a smaller size. Consequently the males had a lower average age at spawning. The investment into gonad building was higher and age at spawning was lower in the stochastic simulation compared with the deterministic one. According to life history theory, reproductive effort of which gonad investment is a major constituent, is generally higher in semelparous strategies than in iteroparous strategies (ROFF 1992). Although no females had semelparous strategies, variable adult mortality tends to favour a semelparous strategy, which supports the lower age at spawning and higher allocations to gonads observed in the stochastic run. Hence more emphasis is put on the first reproduction when prospects for future reproductions are uncertain. The greater average size of females compared with males in the stochastic run is explained by the lower average age of the males. The lower age was due to the post spawning mortality associated with the semelparous male strategy, as illustrated by the dominance of females in the oldest age group. A similar skewed sex distribution in the older age groups is observed for the capelin at Newfoundland (SHACKELL & al. 1994) and Iceland (VILHJÁLMSSON 1994), but has not been recognised for the Barents Sea capelin (GJØSÆTER 1995).

The difference in life history strategy between the two simulations emphasises the importance of implementing stochasticity in ecological simulations. If only the

deterministic run were carried out, the predictions would be completely different compared with the ones currently presented.

Migration

Fish migrations have traditionally been viewed as an adaptation towards abundance; there may not be enough food at the spawning ground to maintain the stock throughout the year (NIKOLSKY 1963; Harden Jones 1968). Vertical migration theory has improved substantially during the last decades through a combination of experiments, fieldwork, and theoretical work. It is now generally accepted that vertical migration is a trade off between growth and mortality (e.g. ZARET & SUFFERN 1976; CLARK & LEVY 1988; OHMAN 1990; ROSLAND & GISKE 1994,1997). Vertical and horizontal migration should be understood from common principles. Outside the spawning season, horizontal distribution of fishes should therefore be analysed as a trade off between growth and mortality. The importance of including mortality risk as a factor in fish distribution is illustrated in Fig. 14 where cod abundance is plotted against average ambient temperature in areas occupied by capelin during summer and fall. There is a clear trend towards capelin occupying colder waters when cod is abundant. Cod rarely enter waters of temperatures below -0.5°C (ROSE & LEGGETT 1988, 1990) and hence waters colder than this act as refuges from cod predation (ROSE & LEGGETT 1990). Mortality risk is therefore important when trying to predict capelin distribution. There was a strong tendency for the fish to seek the predation minimum at the 0°C isotherm throughout the year rather than the zooplankton production maximum further south-west. This supports the argument that predation avoidance is an important component of the motivation for staying in the Polar front area during summer.

Growth and survival are important adaptive features of horizontal migrations, but migration in fishes is also evolved to optimise spawning location. In order to analyse spatial distribution in migratory fishes the evolution of spawning area should therefore be addressed. The current study is to my knowledge the first example of evolving the life cycle of a fish including spawning, larval and adult distribution areas. The spawning area was the most important feature in defining the life cycle since distribution during the subsequent stages was made relative to the spawning area. The simulated spatial distribution contained the main features of the migration pattern of the Barents Sea capelin (Gjøsæter 1995). No quantitative comparisons were made against observed distributions of the capelin, as any conclusions would have been meaningless given the simple environmental description of the present model. Larval drift was associated with a tongue of warm water, which stretched from west to east

in the model area. Since larval growth and indirectly mortality was linked to temperature, the adaptive value of drifting in this warm water may be high. The evolved spawning area was hence situated upstream from the warm water tongue, in the outskirts of the range for capelin spawning (Sætre & Gjørseter 1975). It seems likely that the convergence of spawning area was due to the good conditions associated with larval drift in relatively warm waters, as the same spawning area was evolved in both the computer runs. Since the same environment was presented over and over again, such oceanographic features could be adapted to within the framework of the model. In the sea, the weighted average conditions must be adapted to, or else a conditional strategy, where spawning location differs between years depending on the state of the environment should be applied. The spawning location of the capelin varies, depending on the temperature regime. In warm years spawning is easterly, and further west during cold years (OZHIGIN & LUKA 1985). Since spawning location was evolved as a fixed trait here, it could be thought of as adapting to a specific climatic situation in which case it should not matter whether choice of spawning area is conditional or not.

Population dynamics

The abundance of the Barents Sea capelin varies tremendously. The effect of a very low abundance was experienced a decade ago when a large number of seals invaded the Norwegian coast in search for food (HAUG & NILSSEN 1995). The present stochastic simulation showed a similar trend in abundance variation, which illustrates the vulnerability of populations that inhabit environments with stochastic larval and adult survival. In the deterministic run, there were extensive fluctuations in abundance in the initial 160 years. These fluctuations were not environmentally driven. Rather they seemed to result from poor adaptation among the individuals, as determined from the relative stability achieved in the last 40 years of the deterministic run. During the this latter period the population seemed to be better adapted and maintained a much higher abundance than in the stochastic run.

Future work

The Barents Sea is an ecosystem of relatively low species diversity and complexity compared with lower latitude systems such as the North Sea, and it is therefore ideal for model development and testing. A long-term goal of the modelling effort on capelin distribution, is to achieve a spatial model that can be used as a tool in fisheries assessment. The ING concept has the potential of becoming such a tool. If a direction for future work is to be pointed out, there is a need for developing dynamic

agent based multispecies models to account for the importance of predator-prey interactions on spatial distribution and inter-annual variation in population abundance.

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Table 1. List of parameters applied.

Parameter	Value	unit	Description	Source
V_t	0.87	-	threshold value for node firing	
r	0.6	m	maximum search radius	BRECK & GITTER 1983
CW	2.5E-4	g	copepod weight	AKSNES & BLINDHEIM 1996
SC	5	%	daily stomach capacity	VESIN & al. 1981
W_m	1	g	size at metamorphosis	
X_z	210	Julian days	day for peak zooplankton production	TANDE 1991
V_z	120	days	variance in zooplankton production	
X_n	150	Julian days	day for peak nauplia abundance	TANDE 1991
V_n	60	days	variance in nauplia production	
C_1	1E+11	-	zooplankton production constant	
q_b	9600	J g ⁻¹	energy density in structural weight	NORDØY & al. 1996
q_e	4700	J g ⁻¹	energy density in eggs	IKEDA 1996
C_2	0.1	-	larval mortality constant	
C_3	50	-	adult mortality constant	
C_4	0.02	-	adult mortality constant	
F	20	-	fecundity parameter	
t_l	3	days	length of time steps	
α	0.15	-	maximum investment into gonads	
μ	0.1	-	zooplankton mortality constant	

Table 2. Life history and behavioural traits implemented in the GA.

Trait	Comment
Size at maturity	weight below which spawning is not allowed
Semelparity	on/off mechanism, iteroparous if off
Spawning month	month during which spawning is allowed
Spawning area	position ± 4 squares at which spawning is allowed
Allocation of energy	fraction of surplus energy diverted between somatic and gonadal growth
Weights of the ANN	used in the ANN to calculate movement behaviour

Table 5. Average sex specific life history traits evolved in the simulations. "Age at spawning" refers to the average age of spawning individuals in the last ten years of the simulation. In the "Parity" row I stands for iteroparity and S stands for semelparity. "Allocation" is investment into female gonads relative to somatic growth.

Life history trait	Simulation			
	Deterministic		Stochastic	
	♂	♀	♂	♀
Size at maturity (g)	15.8	16.6	16.0	11.1
Age at spawning (years)	4.65	4.83	4.02	4.02
Parity	I	I	S	I
Spawning month	3.6	3.6	2	2
Allocation	-	0.36	-	0.56

Table 6. Average state variables in the simulations. "Age" indicate average ages of the two sexes. "Numbers" indicate the number of individuals of each sex.

State variable	Simulation			
	Deterministic		Stochastic	
	♂	♀	♂	♀
Weight (g)	7.6	4.8	3.5	5.1
Energy (kJ)	57.7	36.7	23.0	35.9
Age (years)	2.53	2.49	2.45	2.66
Numbers	4597	4694	1672	1856



Figure 1. The Barents Sea with main currents and water masses. Redrawn from Loeng (1991).

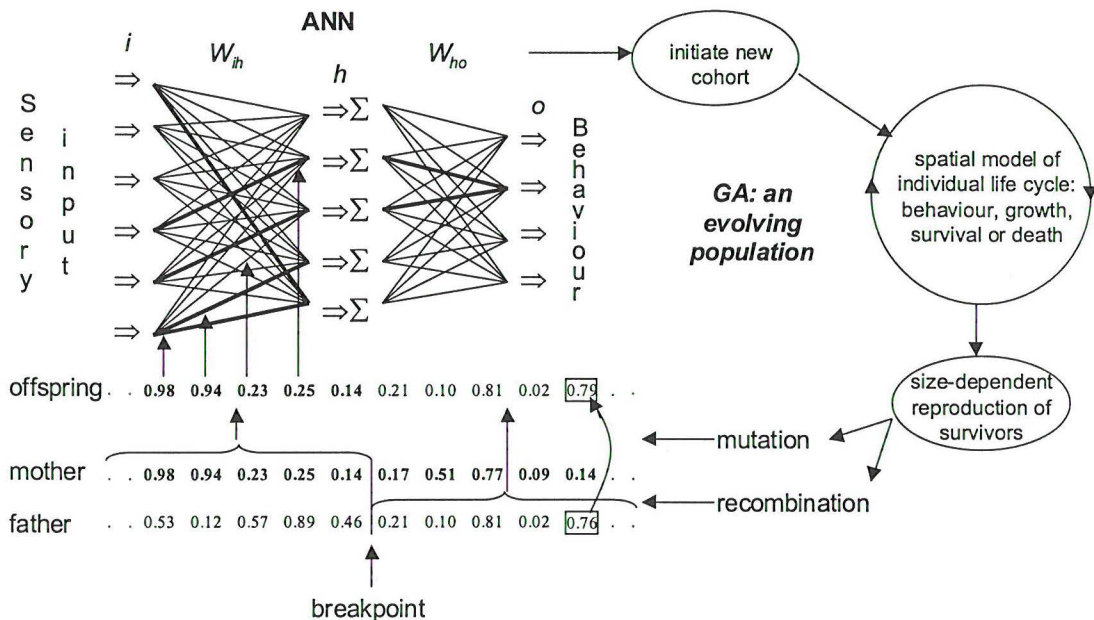


Figure 2. The ING concept with ANN based behaviour and GA based evolution in an individual-based setting. A cohort of individuals with randomly set strings which code for the weighting of the ANN, is initiated in the first time step. The individual's life cycle is simulated, and when maturity is reached, individuals reproduce and new recombined, possibly mutated individuals emerge. Differences between the strings are expressed through differences in weights of the ANN, which leads to behavioural differences. The i , h , and o refer to input-, hidden-, and output layers respectively. The input layer consists of internal (states) or environmental cues. A node fires if the value is above the threshold value. Each of the nodes in the i -layer are connected to all the nodes in the h -layer which again are connected to all the nodes in the o -layer. W_{ih} and W_{ho} are the weight matrices of connection strengths between the nodes. Modified from GISKE & al. 1998.

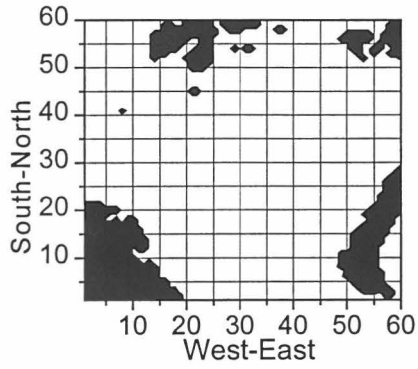


Figure 3. The model area with the lattice structure illustrated in a cruder resolution than applied in the model.

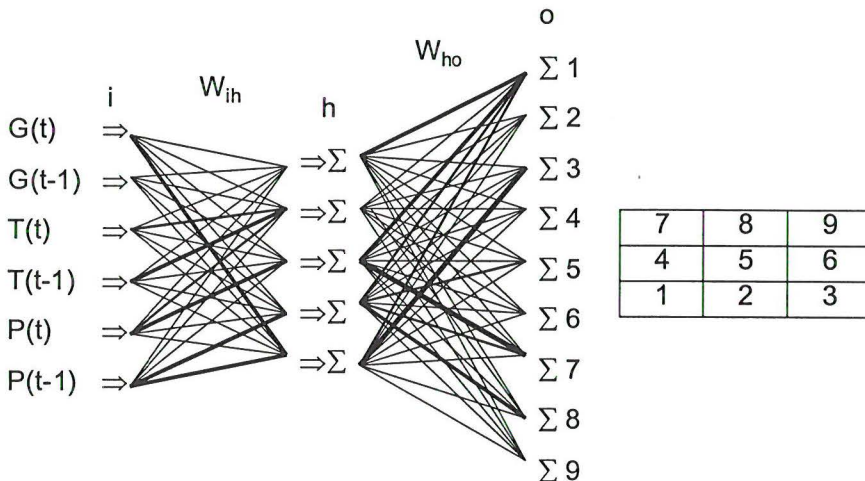


Figure 4. The reactive network where $G(t)$, $T(t)$, and $P(t)$ are growth, temperature and predation risk at time t . The input values are multiplied by a set of weights between the input (W_{ih}) and hidden (W_{ho}) layers. At the hidden layer the sum of the weights and the input values at each node (n_h) is transformed by the sigmoidal function (Eq. 2). If the transformed value is above a threshold the node is excited and takes the value 1, else the value is 0 (Eq. 3). This value is then passed on through another set of weights to the output layer where the transformation is carried out once more to produce the output value. The output nodes fire in a “winner takes all” manner where the node that has the highest value is excited. Each node codes for movement in one of the eight possible directions and node 5 codes for staying. The grid numbered from 1-9 at the right indicates the direction of movement upon firing of the respective nodes for an individual presently staying in cell 5.

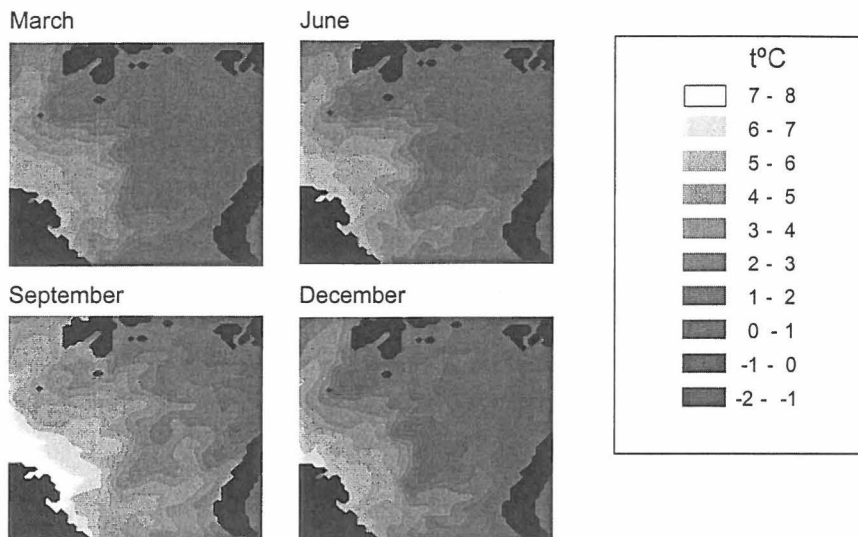


Figure 5. Modelled temperature distribution at different times of the year.

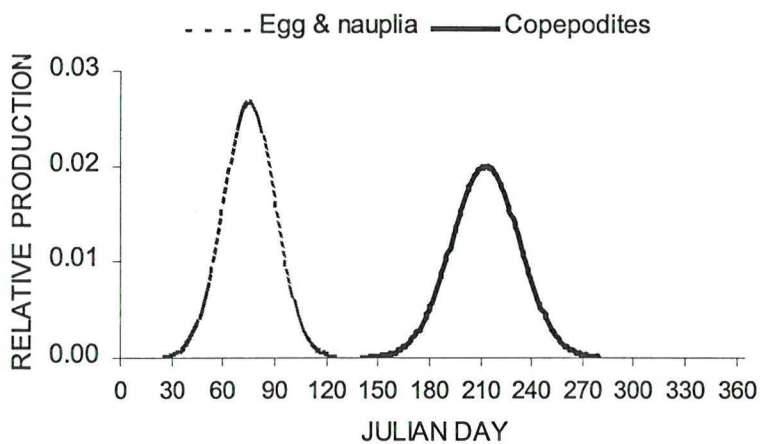


Figure 6. Seasonal distribution of abundance of copepod eggs and nauplia and production of copepodites.

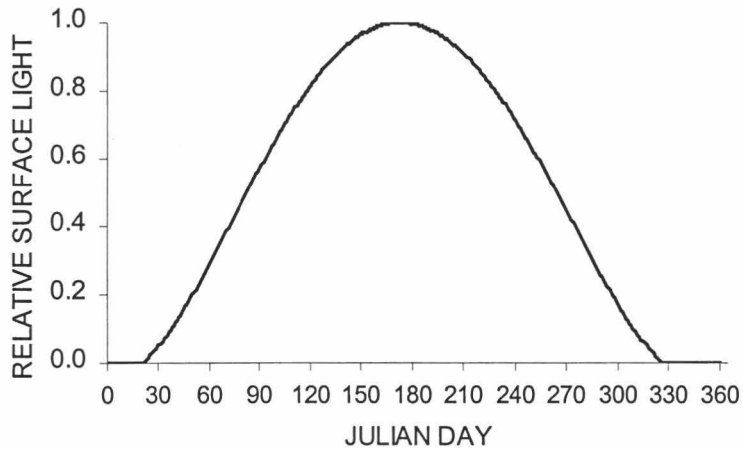


Figure 7. Relative distribution of surface light at 76° N over the year, according to the model by SKARTVEIT & OLSETH (1988).

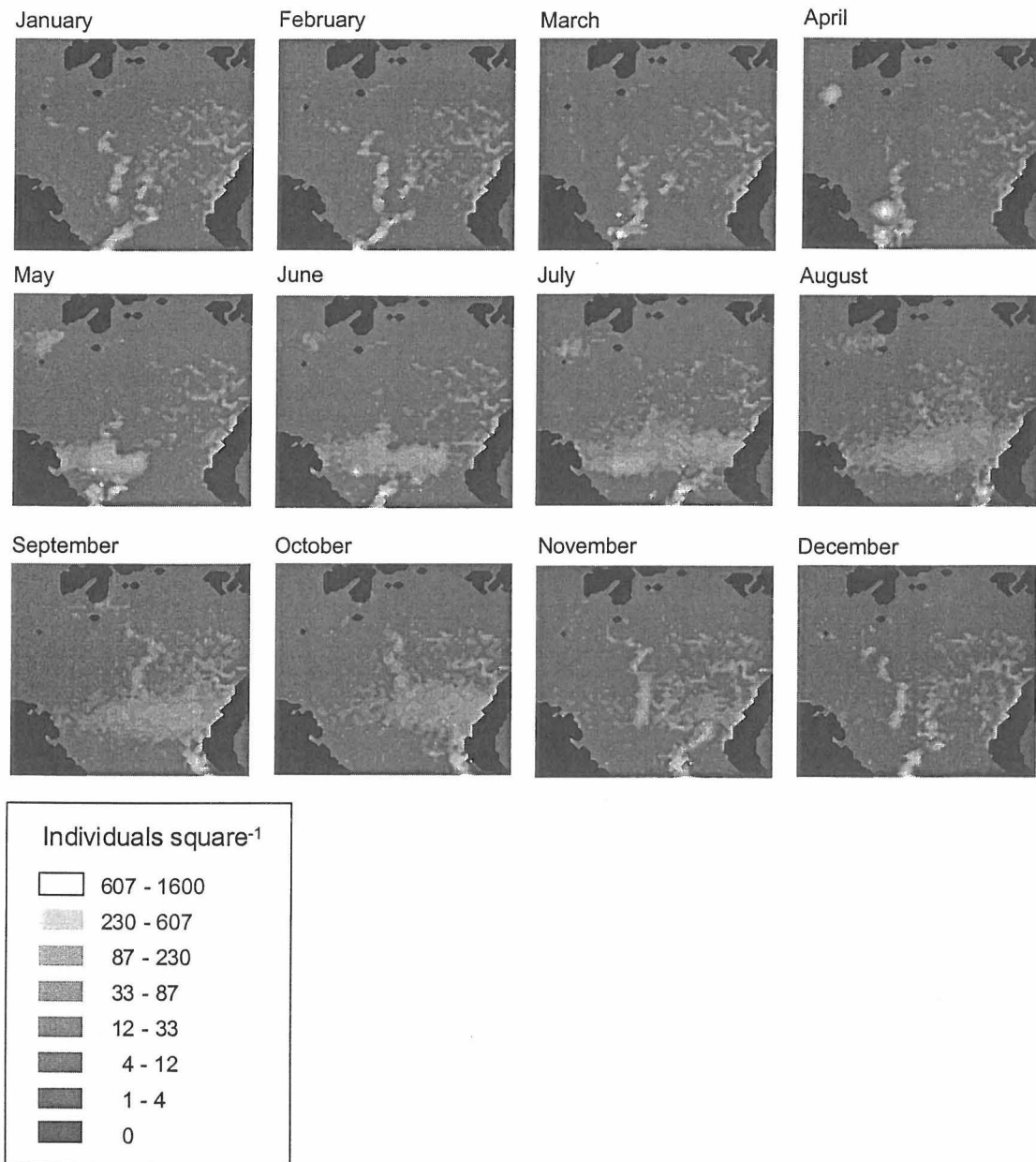


Figure 8. Distribution of the capelin throughout the year combined for all age groups in the deterministic run in year 200. Land contours of the Barents Sea are drawn in.

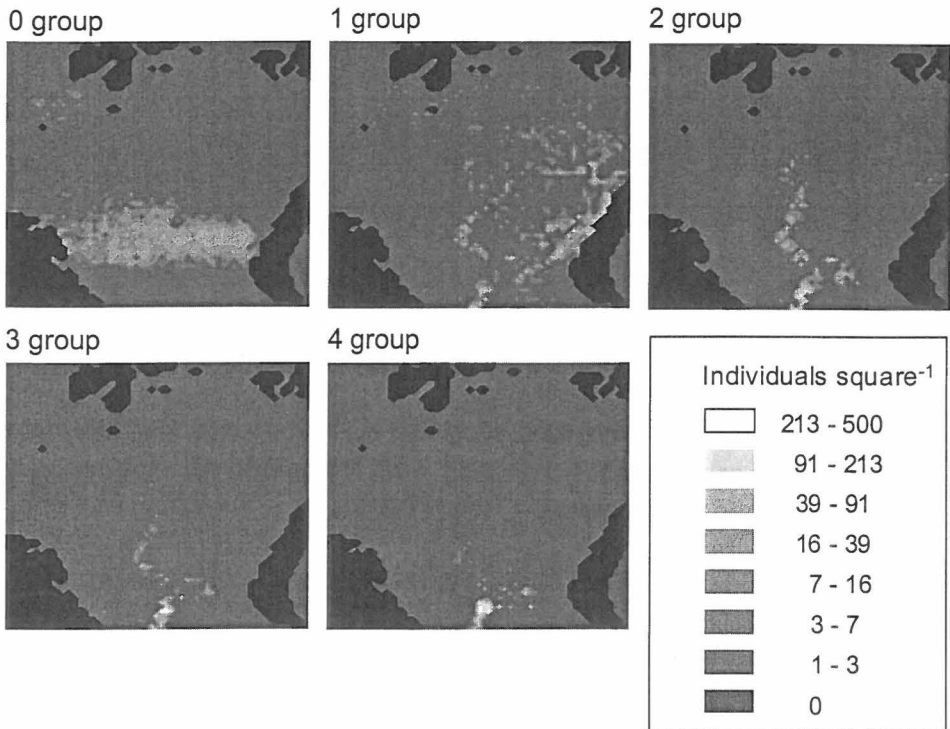


Figure 9. Distribution of the different age groups during June in the deterministic run in year 200.



Figure 10. Proportion of feeding bouts where individuals are limited by their stomach capacity and food availability respectively in the deterministic run. Only one feeding bout is carried out per time step.

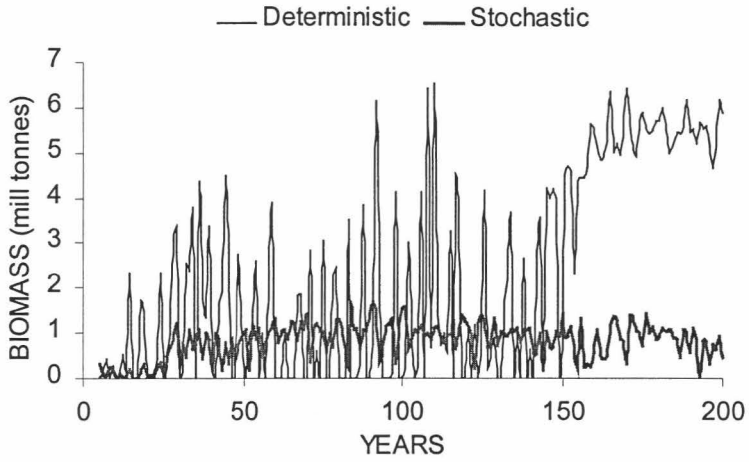


Figure 11. Total biomass of the two simulations during the computer runs.

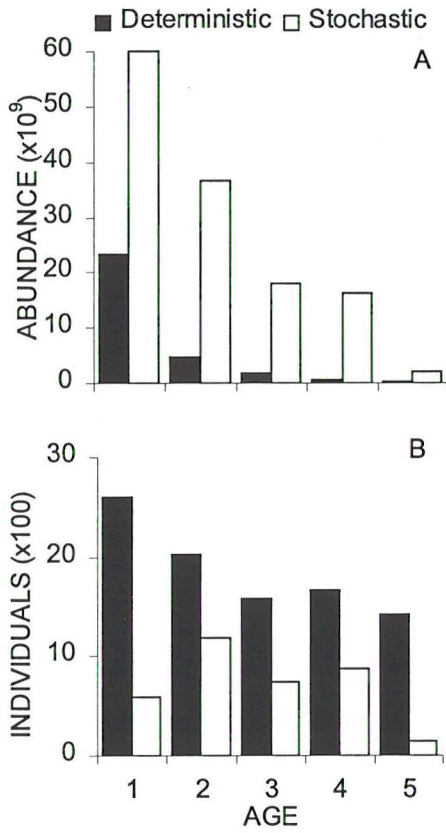


Figure 12. Age structure at the end the simulations given as stock size (total number of siblings) at each age (A) and number of individuals (B).

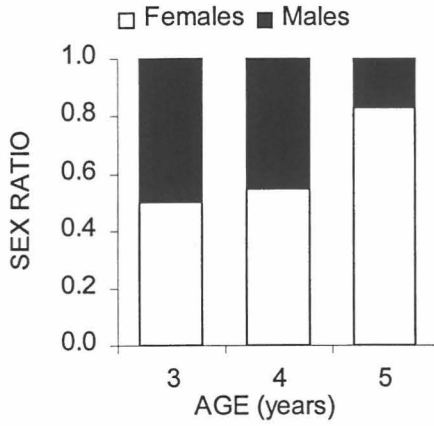


Figure 13. Sex ratio in the Stochastic run for the oldest age groups.

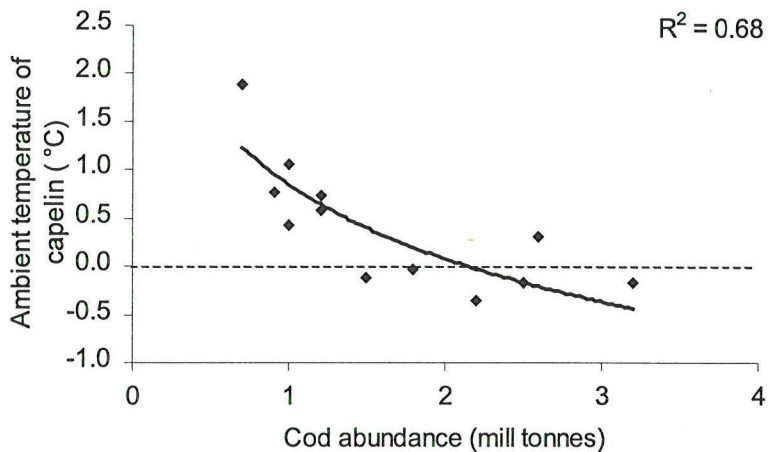


Figure 14. Abundance of cod plotted against the average ambient temperature of areas occupied by two and three year old capelin during fall. Capelin data are taken from GJØSÆTER & LOENG (1987) and the cod data from ANON. (1998).