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Ecology in Mare Pentium: an individual-based spatio-temporal model for fish with adapted behaviour

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Abstract

A conceptual approach to study spatial movements of fish using an individual-based neural network genetic algorithm model is presented. Artificial neural networks, where the weights are adapted using a genetic algorithm, are applied to evolve individual movement behaviour in a spatially heterogeneous and seasonal environment. A 2D physical model (for the Barents Sea) creates monthly temperature fields, which again are used to calculate zooplankton production and predation pressure. Daily fish movement is controlled by reactive or predictive mechanisms. Reactive movement governs search for local optimal habitats, whereas predictive control enables adaptation to seasonal changes. Levels of growth and predation pressure at the time of decision are used to assess whether to apply reactive or predictive movement control. To make the model realistic on a large scale, each of the individuals are scaled up to represent a clone of one million siblings acting and growing synchronously. The fish lives for up to two years, and may reproduce in its second year. In order to spawn it has to be at the designated spawning area in the south-western part of the lattice in January. During spawning it produces a number of offspring in proportion to its body size. The “genetic constitution” of offspring (the weights of the synapses in the neural networks) is a mix of their “mother’s” and a randomly picked member of the population.

The model is able to solve the problem of navigating in a heterogeneous and seasonal environment. The movement of the artificial fish follows a seasonal pattern, typical for migrating pelagic fish stocks. During summer and autumn the distribution is widespread whereas during spring it is more concentrated. When trophic feedback is removed (i.e. zooplankton survival is independent of fish predation) the distribution of the fish is less dispersed which shows that the model allows for density dependent behaviour. Large-scale migration is an interplay between reactive and predictive movement control and when only one of these is allowed, the individuals are unable to adapt properly. Throughout most of its life the fish relies heavily on reactive movement, but during the spawning migration predictive movement control is applied almost exclusively. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Fish; Genetic algorithms; Neural networks; Spatial; Movement; Distribution

1. Introduction

Fisheries scientists have for long been intrigued by the tremendous seasonal migrations exhibited by

many fish species (Roule, 1933; Harden Jones, 1968). Salmon and eels as well as herring, mackerel, and capelin are among the Atlantic species that undertake such migrations. Extensive fieldwork has been carried out in order to establish the routes of fish movements for fisheries and fisheries assessment purposes (Harden Jones, 1968). This has led to a very

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thorough knowledge of the seasonal distribution pattern of important commercial species like herring and capelin (e.g. Dragesund et al., 1980; Dommasnes and Røttingen, 1985; Ozhigin and Luka, 1985; Fernø et al., 1998). Less effort has, however, been put into understanding the underlying principles for movement of fishes, i.e. what basic cues does a fish use to navigate in a heterogeneous space (Harden Jones, 1968; Tyler and Rose, 1994)? Furthermore how and when does it make use of the different cues? It has been shown that biological factors like food availability and predation pressure are important (Thomas, 1974; Fiksen et al., 1995) as well as physical factors like temperature, salinity and currents (Weighs, 1978; Ozhigin and Luka, 1985; Nøttestad et al., 1996). Also the fish would have to consider internal states such as its size and maturity state and factors such as present habitat and time of year which will influence where to move next (Fiksen et al., 1995; Rosland and Giske, 1997). These factors have a great impact on the ultimate components of life such as survival and growth (reproduction) which motivate migration in the first place. Eventually there are proximate signals such as the sun, currents, and geomagnetic fields which the fish may use as directional cues (Harden Jones, 1968; Walker et al., 1984, 1997; Moore et al., 1990).

1.1. Reactive vs. predictive movement control

In order to model fish movement it is important to consider how fish find their way about. In a heterogeneous and seasonal large-scale habitat it seems unlikely that a fish at the decision point has “perfect knowledge” of its immediate surroundings. It rather seems plausible that over the generations, individuals in a population have become increasingly more adapted to their environment by inheriting rules for movement and the ability to learn from actions.

Distributional mechanisms may be categorised into reactive and predictive processes (Neill, 1979; Fernø et al., 1998). Reactive processes are undirected movements where the behaviour is biased by previous experiences (Neill, 1979). During feeding periods movement is dominated by turning at the presence of food patches or moving away from empty patches (Thomas, 1974), and it can be predicted that this is governed by reactive movement control (RMC). Even

though an environment is spatially and temporally variable it usually contains some predictable cues like seasonal changes in day length, temperature, and zooplankton production. Through evolutionary adaptation and learning the fish may use these predictable features to control its movement (Fernø et al., 1998). It seems plausible that such predictive movement control (PMC) could be applied during directed migrations. Thus there are two distinct problems that a fish must cope with in order to navigate in a best possible way through a heterogeneous and seasonal landscape (a clear parallel is evident in migratory birds). Assuming that movement can be modelled using this dichotomy, internal and environmental information can be categorised as input to RMC or PMC, respectively. For RMC important cues should be environmental factors that can be compared relatively with previous experiences like food availability, predation pressure, and temperature. Features such as time of year, age, size and present location on the other hand could govern PMC.

1.2. Model composition

Early attempts to model large-scale fish movement were carried out by Balchen and co-workers (Slagstad et al., 1975; Balchen, 1976; Reed and Balchen, 1982) who used comfort functions to move capelin about in the Barents Sea. Fiksen et al. (1995) applied dynamic programming to model capelin migrations by linking individual physiology to fitness. However, dynamic programming cannot easily handle trophic interactions and density dependencies in growth and survival. The latter is possible by using the ideal free distribution (Fretwell and Lucas, 1970; Hugie and Dill, 1994; Giske et al., 1997), but at the expense of ecosystem dynamics and individual variability in physiology. Lately, Dagorn et al. (1997), Le Page and Cury (1996), and Menczer and Belew (1996) have applied artificial life techniques to simulate fish-like behaviour. Artificial life, which is the study of life “as it could be” (Langton, 1989) rather than “as it is” (biology), enables a synthetic approach to ecology. Presently we adopt this synthetic approach to the problem of fish movement by combining two common computer techniques: artificial neural networks (ANNs; Hopfield, 1982; Kohonen, 1984) and genetic algorithms (GAs; Holland, 1992). Our objective is

to develop a framework in which spatial processes can be studied by incorporating a range of important ecological factors into one model. As distinct to much traditional ecology based on optimisation, the present model does not rely on optimising a constructed fitness measure. Instead the basic characteristics of the model determine the fitness of individuals through offspring production and natural selection. We investigate the following hypotheses: that complex population behaviour can be modelled by individually driven motivation, that individuals are more dispersed when the model is run with trophic feedback than without, that both predictive and reactive mechanisms are necessary to achieve large-scale migration patterns, and that reactive movement control dominates during feeding whereas predictive movement is principally applied during migrations. Our test organism is an artificial pelagic fish, which inhabits an artificial boreal ecosystem called “Mare Pentium”.

2. Physical model: “Mare Pentium”

2.1. Coupled 2D physical–biological model

Monthly temperature fields were gathered from a physical model of the Barents Sea (Slagstad,

1981, 1987; Slagstad et al., 1989; Støle-Hansen and Slagstad, 1991), which was also used by Fiksen et al. (1995) for studying capelin migrations. The model area consists of a lattice of 60×60 squares with sides of 20 km, and four of the monthly temperature fields from this model are shown in Fig. 1. The individuals are numbered and fed each day according to this number, starting with the lowest number. Essentially this means that the oldest fish consistently feed first. After each individual feeding the zooplankton abundance is updated (Eq. (1)). To make the model more realistic on a large scale each individual represents a clone of one million siblings. The zooplankton ingested by one individual is therefore scaled up by one million to represent the feeding of all the siblings. A daily temperature dependent production of zooplankton is added at the start of each day and zooplankton is continuously removed by fish feeding

$$Z_{jkt} = Z_{jkt-1} + R(T_{jkt}) - \sum_{i=1}^{\text{pop}} P_{ijkt}, \quad (1)$$

where Z_{jkt} is the zooplankton abundance in cell jk at the end of day t , $R(T_{jkt})$ the temperature dependent production of new zooplankton, P_{ijkt} the number of zooplankton eaten by the siblings of individual number i in cell jk during day t , and pop is the population size. The zooplankton here consists of one size group

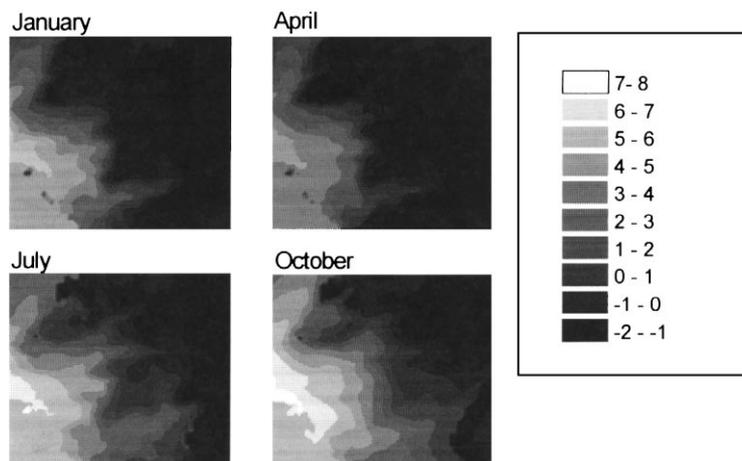


Fig. 1. Temperature ($^{\circ}\text{C}$) distribution at the beginning of quarterly intervals throughout the year. The top of the figure is north, and east is to the right.

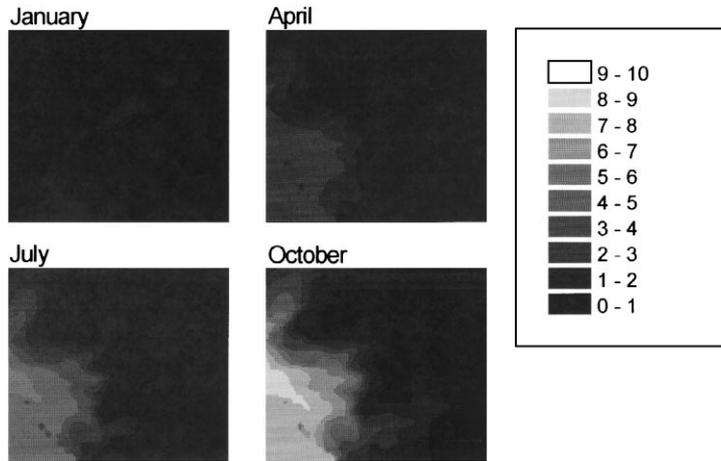


Fig. 2. Zooplankton distribution ($\times 10^{13}$ cell $^{-1}$) at the beginning of quarterly intervals throughout the year.

only (weighing 0.7 mg). Quarterly distributions of zooplankton are shown in Fig. 2.

2.2. Mortality risk

Daily predation risk on the fish ($M(T_{jkt})$) is assumed to be temperature dependent (Fiksen et al., 1995), as if predators were more active, efficient, or abundant in warmer waters (Fig. 3):

$$M(T_{jkt}) = \frac{T_{jkt}^2}{500}, \tag{2}$$

where T_{jkt} is the temperature in cell jk at day t . The

daily predation risk varies between 0 and 0.128 over the temperature range. Mortality is also a function of individual body weight ($M(W_i)$):

$$M(W_i) = e^{-\ln W_i \cdot 2.5}, \tag{3}$$

where W_i is the weight of individual i . This size-dependent mortality decreases from 1 to 0.0005 day $^{-1}$ when weight increases from 1 to 20 g. Whether an individual (and all siblings) dies during a day is determined by Monte Carlo simulations in the following manner: IF random number $< M(T_{jkt})$ OR random number $< M(W_i)$ THEN the clone is dead.

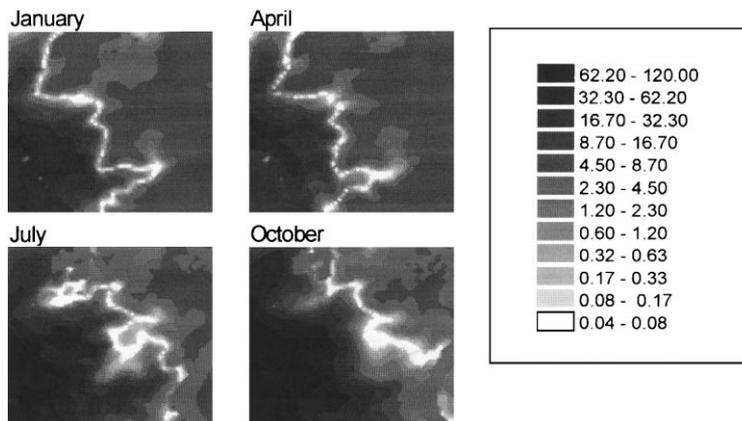


Fig. 3. Distribution of daily predation risk (log scale, $\times 1.0^{-3}$) at the beginning of each quarterly interval throughout the year.

3. Behavioural model: individual-based neural network genetic algorithm (ING-concept)

The behavioural model is founded on an individual-based approach (e.g. DeAngelis and Gross, 1992). The individuals move about according to decision variables that are implemented as weights in an ANN, and are monitored using state variables such as size, age, and position in the lattice.

3.1. GAs and ANNs

The GA is a heuristic technique that uses the principles of evolution by recombinations, mutations, and natural selection to search for optimal solutions to a problem (Holland, 1992). For an introduction to GAs, see Goldberg (1989); Mitchell (1996). Most optimisation problems can be solved using a GA, although its efficiency and suitability depend upon the specific problem. GAs are good at finding solutions when the solution space becomes too large for optimal control theory (where every possible solution is calculated, e.g. the dynamic programming models by Fiksen et al. (1995), Rosland and Giske (1994, 1997)) to be feasible. There are many ways of setting up a GA (e.g. Goldberg, 1989; Koza, 1992; Fogel, 1995) and we will concentrate on how it was implemented here.

Like the GA simulates evolution by natural selection, ANNs use the neurobiological principles of brain activity to perform complicated decisions. In the same way that brain cells are connected by synapses, an ANN is made up of clusters of nodes. These clusters learn by adjusting the weights between them so that input can be processed and proper output can be performed (firing or not firing of output nodes). The ANN consists of an input layer, an output layer and from zero to several hidden layers (Anderson, 1996). The weights of the ANN are presently evolved using the GA (see below, Montana and Davis, 1989; van Rooij et al., 1996). As with GAs there is a range of different ways to employ an ANN and reviews of these have been given by Hopfield (1982), Kohonen (1984), Alexander and Norton (1990), Hallam et al. (1994) and Anderson (1996). We choose a feed forward network structure for the present study with an input, one hidden, and an output layer. The reason for not using a simpler network structure is the poorer

adaptability of such networks compared with three-layer networks (Anderson, 1996). This was confirmed by test runs with a two-layer network that proved to be less adaptive.

3.2. The ING-concept

In order to avoid confusion between biological genetics and GA “genetics” we adopt the GA terminology suggested by Goldberg (1989), hence a “chromosome” will be termed string, a “gene” will be termed character, and “allele” will be termed character value. An important aspect of the GA is the representation of solutions as matrices of binary digits. Each individual has a string of binary digits with a length of 516 bits, each of which has the value 0 or 1. This string is divided into characters of 5 bits each. Character values are calculated relative to the poten-

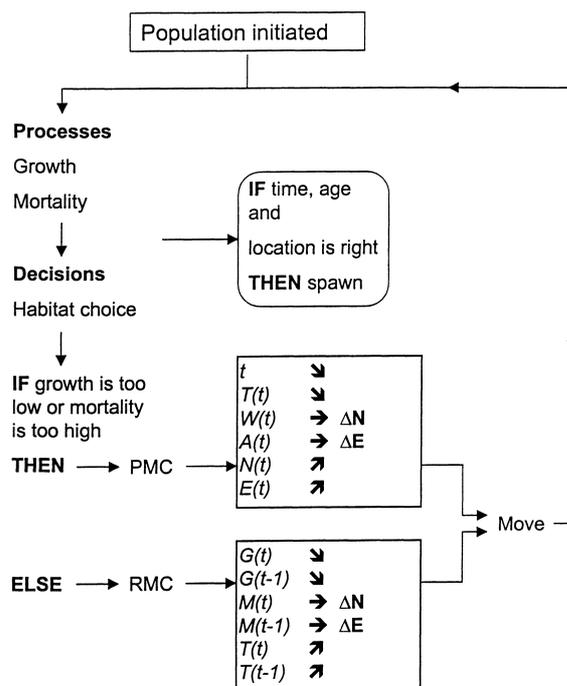


Fig. 4. Flow chart of the daily activities of the fish where t is Julian day, $T(t)$ is temperature, and $W(t)$, $A(t)$, $N(t)$, $E(t)$, $G(t)$, and $M(t)$ are weight, age, northerly position, easterly position, daily growth, and daily mortality risk at day t , respectively. Individuals die after spawning.

tial maximum value using the binary digit system. For example the value of the character 01010 is calculated as $0^0+2^1+0^2+2^3+0^4=10$, which is then divided by the maximum value (all 1's) of 31 to give a character value of 0.322. The character values were used as weights in the ANN and as threshold values for switching between RMC and PMC (as described below). At the start of each computer run the strings of 0's and 1's are initiated randomly.

The flow chart in Fig. 4 outlines the activities that the fish goes through each day. Initially each individual is placed randomly in a cell of the lattice. Here it feeds, grows, and it may die. At the end of each day it decides whether it should stay at its present location or move to one of the eight surrounding cells. Individuals are restricted from moving beyond the outer boundaries of the lattice. Movement is determined in a rather intricate manner. First the fish has to “decide” whether to use RMC or PMC. If a uniformly distributed random number is below an inherited threshold value, or if current growth is below a threshold value, or current predation risk is above a threshold value then PMC is applied (Fig. 4). Else RMC is applied. Habitat choice is then calculated by using the reactive or predictive ANN. This is implemented as two separate networks each of which receive different kinds of input. The reactive network receives input in the way of growth rate, predation risk, and temperature in its current cell and the cell it visited the previous day (Fig. 4). The predictive network receives input in the form of Julian day, age, size, temperature, and present position in the lattice. The input layer is connected to the hidden layer by a matrix of weights that gives the connection strength between them (Fig. 5). The hidden layer is further connected to the output layer by a second set of weights. Altogether 100 weights are applied in the two networks. The values coming into a node are added together (n_o):

$$n_o = \sum_{h=1}^5 W_{ho} L_h, \quad (4)$$

where L_h is the standardised value (see Eq. (5)) coming out of nodes in the hidden layer, and W_{ho} is the weight matrix between the hidden and output layers (Fig. 5). Before being passed on to the output nodes the values are converted using the standard sigmoid function (e.g. Anderson, 1996):

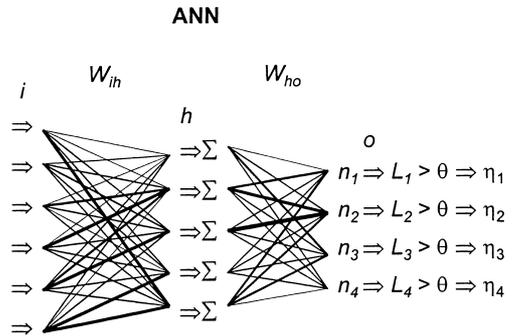


Fig. 5. Description of the ANN (RMC or PMC) applied in the present model. The i, h, and o refer to input-, hidden-, and output layers, respectively. The input layer consists of internal or environmental input that is different for RMC and PMC. The output nodes fire if the L_o value is above the threshold value ($\theta=0.91$). The lines indicate the relationship between the different layers. Each of the nodes in the i-layer are connected to all the nodes in the h-layer and each of the nodes in the h-layer 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 of the layers. Potential weight differences are indicated by the variation in line thickness of the connections.

$$L_o = \frac{1}{(1 + e^{-n_o})}. \quad (5)$$

This procedure is performed for the hidden layer as well, and is similar for both the reactive and predictive networks. There are four nodes in the output layer, each of which may be excited or not during a time step. An output node is excited if the standardised sum of weights and input values in the output layer (L_o , Eq. (5)) is above the level of excitation ($\theta=0.91$, Fig. 5). If an output node is excited it takes a value of 1 or else the value is 0. Each of the nodes has specific features upon firing, and node one and two work in the north–south direction whereas node three and four work along the east–west axis (Fig. 5). Change in habitat value along the north–south axis is denoted by the ΔN value and by the ΔE value along the east–west axis. If node one is excited the ΔN value is increased by 1 and if node two is excited the ΔN value is decreased by 1. The relative change in habitat is thus calculated simply by subtracting the value of node one from the value of node two

$$\Delta N = \eta_1 - \eta_2, \quad (6)$$

where η_1 and η_2 refer to output nodes number 1 and 2. Similarly the relative change in the east–west

extension is calculated by

$$\Delta E = \eta_3 - \eta_4. \tag{7}$$

It follows that if neither of the output nodes or both are excited, ΔE and/or ΔN will be zero. The individual will then move (or stay) relatively to its present location according to the ΔN and ΔE values in the next time step.

Reproduction can only take place for two-year olds and is confined to the area in the south-west corner ($N < 11, E < 11$) of the lattice during January. We assume that eggs and larvae drift passively north-eastwards as they grow and develop. This life history phase is not modelled here. Rather, we release the offspring randomly into the south-west part ($N < 41, E < 31$) of the lattice on 30 July with a size of 8 g. The mature individuals are ranked by size and spawn in descending order. Spawning commences when the carrying capacity (15 000) is reached, and smallest of the mature individuals may hence not reproduce. During reproduction an individual (Mum, Fig. 6) produces a number of offspring in proportion to its body weight (one offspring g^{-1} body weight). A partner (Mate) is selected randomly from the population (both age groups included), and the string of the offspring is a recombination of the strings of Mum and Mate (Fig. 6). The “crossing over” point can only occur between characters (van Rooij et al., 1996). Further string variability may be added through changes in bit value from 1 to 0 or 0 to 1 mimicking biological mutations. This is done by using Monte Carlo simulations and the probability for such “mutations” to take

Mum	Mate	Offspring	
1	1	1	
1	0	1	
0	1	0	←Character
1	0	1	
0	0	0	
0	1	1	←Break point
0	0	0	
1	1	1	←Character
1	0	0	
1	0	0	

Fig. 6. Example of how recombination and hence creation of new individuals is carried out. Mum is the individual who reproduces and Mate is a randomly drawn individual from the population. The string of offspring is a mix of “Mum” and “Mate”, and bits above and below the “crossing over” point are copied from “Mum” and “Mate”, respectively.

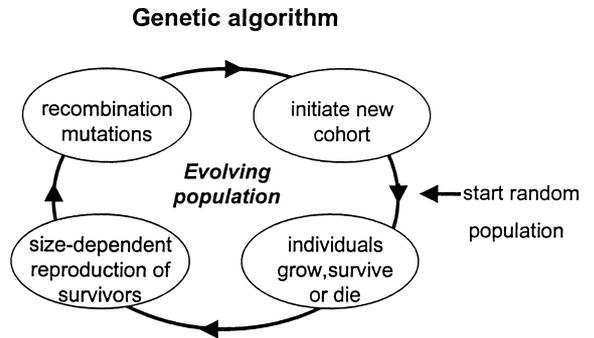


Fig. 7. Schematic outline of how the GA works.

place during reproduction is set to 0.001 for each bit. The individuals who manage to reproduce the most will by definition be those that are more fit for life in “Mare Pentium”. The selection scheme is hence very similar to the way in which natural selection (Darwin, 1859) acts. By repeating this procedure over and over the population will consist of increasingly fit members. A schematic outline of the present GA is shown in Fig. 7. Using the GA one is never certain that the optimal solution is found unless it has been calculated by other means. However, as the number of times the procedure is repeated increases, the probability of getting good, close to optimal solutions, increases. There are ways of setting up the GA so that it is less likely to get stuck on local optima (e.g. Sumida et al., 1990), which may be a problem when applying heuristic techniques. Since the present objective was to seek “good” rather than optimal solutions to the problem of navigating in a heterogeneous habitat, we accepted solutions that appeared reasonable after a large number of generations with a high population size.

A disadvantage of using the individual-based approach the way it is applied here is that one is dependent on having a non-extinct and reproducing population for the model not to terminate. This causes some obstacles in the initial phases of a model run when individuals are non-adapted, which often results in population crashes. To overcome this problem we decomposed the training of the ANNs by starting with low mortality rates and then increased the mortality in a stepwise manner to the desired level when the population had become sufficiently adapted to cope with it. Training decomposition was

also used to gradually restrict the geographic area for successful spawning. The model was always run for at least 200 years with its final configuration. We initiated the model with a population of 4000 individuals, and population size was limited upwards to 15 000 individuals to keep running time within reasonable limits.

3.3. Bioenergetic model

Since the model aims at studying spatial movement rather than realistic growth patterns, the representation of the growth process is not of paramount importance. Still, in order to provide a reasonable link to the zooplankton, we model growth by using a modified version of the bioenergetic model of Hewett and Johnson (1992). For reviews of bioenergetic models in fish biology, see Wootton (1990); Hansen et al. (1993). The modifications are done to allow for trophic level interactions. Hence food consumption is estimated from the concentration of food in the area searched rather than by some temperature dependent function. The volume searched is calculated as a function of distance covered during a day and search radius. In order to implement seasonal variation in light conditions the search radius is varied over the year by a normally distributed curve that peaks in June. We do not take vertical gradients in light and zooplankton concentration into account. Food intake is limited by a type II functional response (Holling, 1959; Aksnes and Giske, 1993), and at high prey concentrations an asymptotic level in feeding rate is achieved

$$\frac{\delta N}{\delta C} = \frac{\alpha C}{(1 + \alpha Ch)}, \quad (8)$$

where N is number of prey ingested, α is encounter rate, C is concentration of prey, and h is handling time (1 s). A further limitation on feeding rate is implemented by stomach capacity. If more food is encountered during a day than there is room for in the stomach, this extra food is not consumed (Giske and Aksnes, 1992). Daily stomach capacity is assumed to be 10% of the body weight, and at the start of each day the stomach is assumed to be empty. The model was parametrised for herring, which is a boreal species and hence adapted to the temperature regime of the physical model. The basic function of bioenergetic

models is

$$G = C - (R + S + F + U), \quad (9)$$

where G is growth, C is energy consumed, R is energy spent on respiration, S is energy spent on specific dynamic action, F is energy lost in egestion, and U is energy lost in excretion (Wootton, 1990). For further introduction to implementation of bioenergetic models to optimisation tools, readers are referred to Rosland and Giske (1994, 1997) and Fiksen et al. (1995). Swimming velocity is 0.1 m s^{-1} when the fish stays within the same cell as the previous day. If it moves the swimming speed is equal to the distance travelled divided by the time it has used (24 h). The distance is calculated as minimum distance between the centre of the cells in the lattice

$$d = D\sqrt{\Delta N^2 + \Delta E^2}, \quad (10)$$

where d is distance travelled, D is the length of a cell (20 km), and ΔN and ΔE are net movement in the north–south and east–west directions, respectively. Calculation of food intake is consistently done for the destination cell only. Eq. (10) underestimates the actual swimming costs, as fish normally does not swim in straight lines over long distances.

4. Results

The model was run over 300 years at which point the ANN seemed to have achieved a state of reasonable adaptation, as compared with runs over 600 years. A typical model run took about 4 h on a Cray Origin 2000. We believe that this can be decreased substantially by more efficient coding. The development in average character value similarity between the best individual (defined as the most fecund spawner) each year and the best individual at final year is shown in Fig. 8(A) and (B). PMC early achieves a high asymptotic level in similarity (Fig. 8(A)), whereas RMC has a slower increase and achieves a lower asymptotic level (Fig. 8(B)). Even after 300 years the string composition of the population seems to be fairly heterogeneous as determined from the variation in string composition of best individual. The development in survival probability from release (in July) to reproduction shows three distinct asymptotic increases interrupted by two abrupt changes in survi-

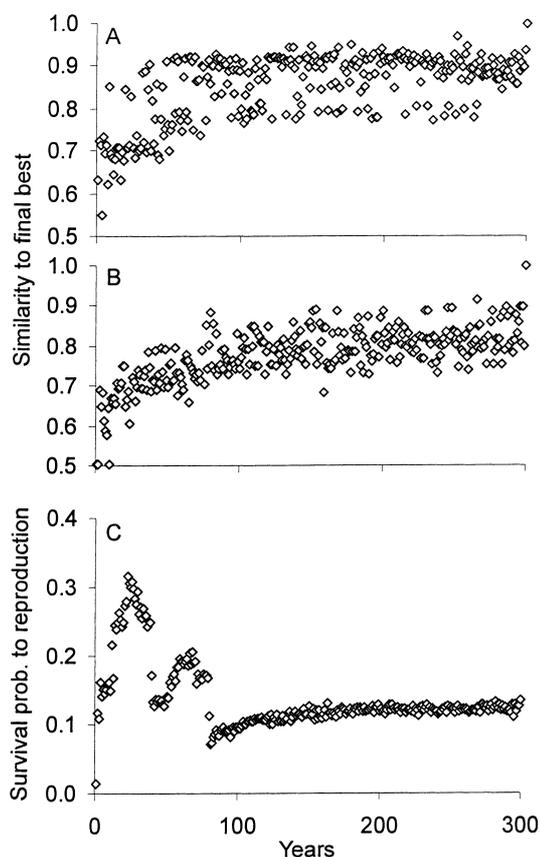


Fig. 8. Adaptation of predictive (A) and reactive (B) characters, and development in survival probability to reproduction (C). The character values of best individual each year is compared with the best individual at the horizon (A and B), where best is defined as the largest (most fecund) individual to spawn.

val (Fig. 8(C)). These crashes are caused by the step-wise increases in mortality during training decomposition. The final mortality level is reached after 80 years of simulation. At the end of the simulation the probability of surviving to reproduction is about 0.1 (Fig. 8(C)).

4.1. Reactive and predictive movement

The model was run with only RMC to test how this influences on movement adaptability, and the same was done for PMC. These results are shown in Fig. 9, and it is clear that there are extensive differences in adaptation between using only RMC or PMC compared with using both. A fourth network structure

Table 1

Average threshold values and their relative importance in inducing PMC

	PrPMC	Mthresh	Gthresh
Average	0.07	0.68	-0.30
SD	0.02	0.22	0.05
Use in inducing PMC (%)	75	0	25

Pr PMC is the inherited random probability of selecting PMC, Mthresh and Gthresh are the inherited mortality and growth thresholds, respectively, for inducing PMC.

where the RMC and PMC networks were coupled into one network with 12 input, eight hidden, and four output nodes (“two in one”) was tested. The “two in one” network also failed in showing sufficient adaptive behaviour. The results in Fig. 9 are from a run (50 years simulation) without training decomposition. When training decomposition was included, all model runs except the RMC+PMC crashed (all individuals died) as the area for successful spawning was restricted. This in itself is an indication of lack of adaptability in the single network settings for the present problem. The RMC+PMC structure was therefore applied in all the following runs.

Throughout most of its life span the fish uses RMC with a probability of about 0.93 (Fig. 10). This is controlled by the random probability of selecting PMC (Table 1). From 16 months onwards, however, the probability of choosing PMC shows a pronounced increase, reflecting the “spawning migration” (Fig. 11). This increase in use of PMC is promoted by a very low feeding rate during winter, which lowers the growth below the inherited growth threshold (Table 1). The mortality threshold was effectively turned off and never used to induce PMC (Table 1).

4.2. Distribution

The distribution of the fish follows a distinct seasonal pattern with a north-easterly distribution during late summer and autumn and a more south-westerly distribution associated with “wintering” (Fig. 11). In general the areas of high fish density co-occur with areas of low predation risk (Figs. 3 and 11). There are also large differences in the degree of dispersal between the seasons. During summer and fall the distribution is quite widespread whereas during winter

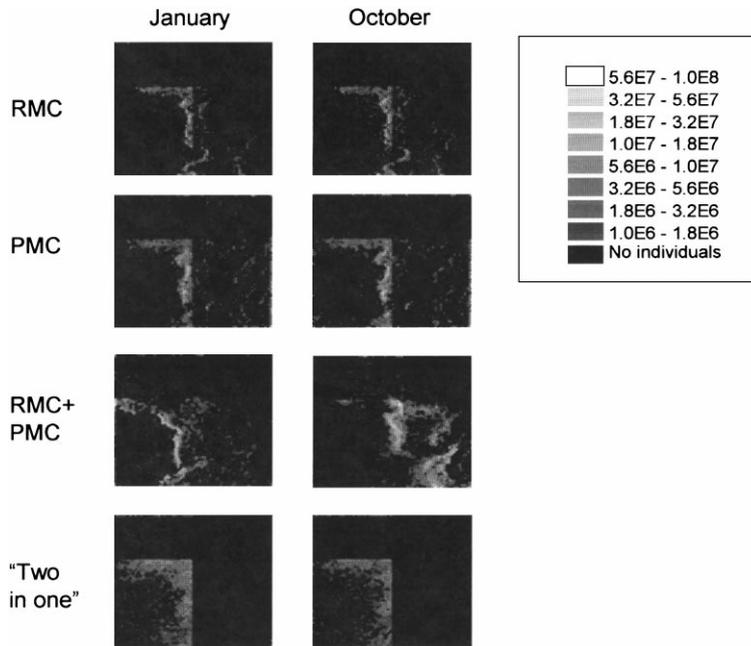


Fig. 9. Distribution (siblings cell⁻¹) of the artificial fish when using either RMC, PMC, RMC+PMC, or “Two in one”. Adaptation after 50 time steps without training decomposition is shown.

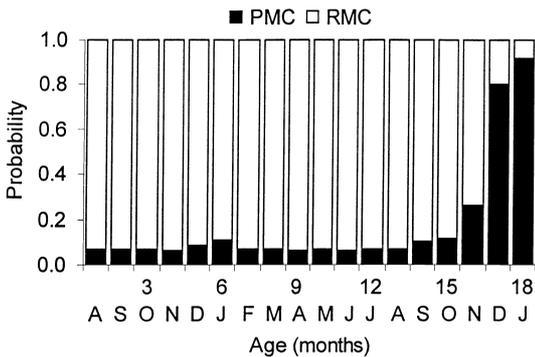


Fig. 10. Probability of using reactive (RMC) or predictive (PMC) movement control over the life span of a year class.

and spring, the fish stays closer together in narrow layers (Fig. 11). While mature (17 months old) individuals migrate towards the south-west corner in December, the immatures remain in the centrally located “wintering” area (Fig. 11). The “spawning migration” can be seen along the southernmost part of the lattice during November and December. The distribution in July shows the initiation of the new cohort in the south-west corner. The new cohort dominates

the distribution in July, but cannot be separated from the old one in August. The mortality is very high during the first month (Fig. 12) when the fish is small and occupies the warm, predator rich south-west corner. After this the mortality stabilises, before it drops off following spawning. In the computer run without trophic feedback (see below) the survival probability is higher from two months onwards. The seasonal component of the zooplankton production peaks in June. However, since this production is also temperature dependent there is a high production throughout the autumn (Fig. 2) due to the delayed warming of the sub-Arctic sea. The individual growth of the fish follows the zooplankton production and peaks during late summer and early autumn (Fig. 13). During winter there is a marked decrease in fish size (Fig. 13). Only minor differences in growth rate between the runs with and without trophic feedback are seen.

4.3. Density dependence

The model was run without trophic feedback to test the density dependent response of the fish. In such

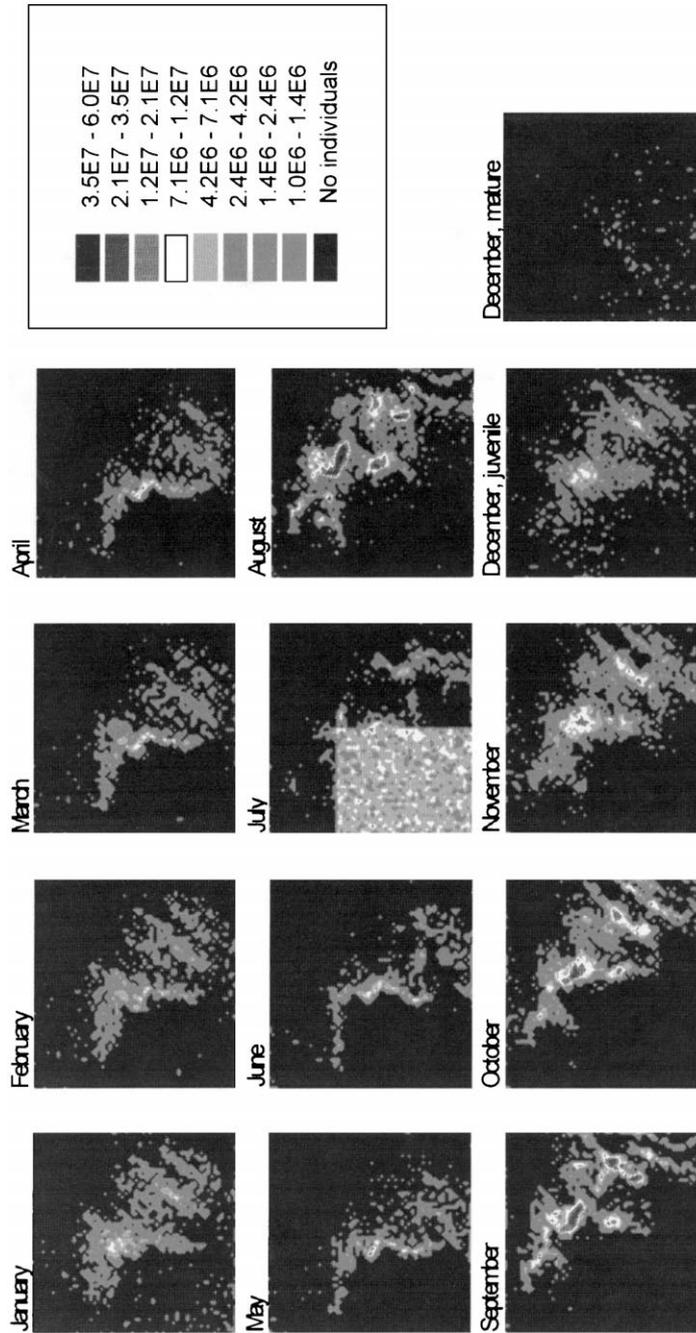


Fig. 11. The distribution of the fish at the end of each month.

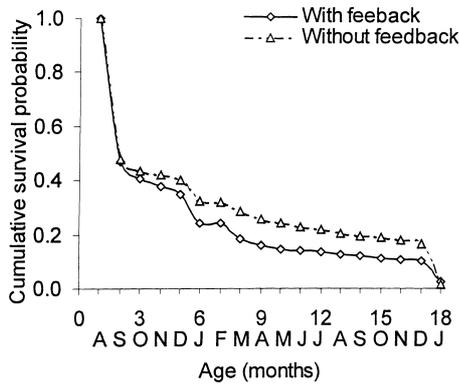


Fig. 12. Survival probability in computer runs with and without trophic feedback.

computer runs the zooplankton were hence not removed when eaten by the fish. To ensure that the density dependent behaviour is an inherent feature of the model, the individuals were not given the chance to adapt to the environment without trophic feedback. This was done by using a previously adapted population and expose it to an environment without trophic feedback. Average number of individuals cell⁻¹ was 2.9 and 5 for the runs with and without trophic feedback, respectively (Fig. 14). Although the distributions are not significantly different (Single factor ANOVA, *P*>0.05) there is a pronounced tendency for increased fish density when trophic feedback is removed.

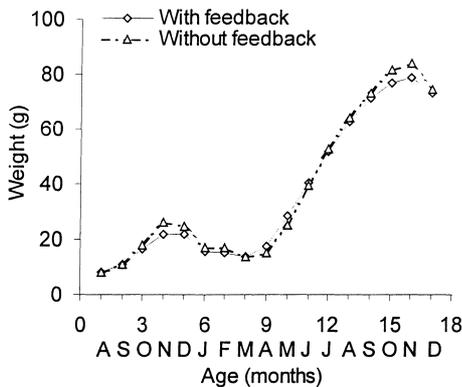


Fig. 13. Individual growth of best individual in computer runs with and without trophic feedback.

5. Discussion

The present contribution shows that by using a simple “sensory system” in the form of a reactive ANN and a “hormone system” in the form of a predictive ANN to assess the state of the environment and the organism, and a GA to evolve improved solutions, complex behavioural patterns can be achieved. Rather than saying that this is the way in which fish navigate in a heterogeneous space we conclude that it is possible to use this method to achieve spatial distribution patterns that look similar to the way real fish stocks are distributed. The present distribution, for example, looks similar to that of the Barents Sea capelin (Dommasnes and Røttingen, 1985).

The use of RMC and PMC to simulate fish decision making was inspired by recent work on herring migrations in the Norwegian Sea (Fernø et al., 1998). Our results show that this dichotomy in control of movement decisions enables large-scale migration. Interaction in movement control between RMC and PMC proved to be vital for the model to adapt properly, as determined from the lack of proper adaptation using the other network structures. It would probably be fruitful to investigate the effect on adaptation of using even more complicated network structures. RMC was applied much more extensively than PMC throughout most of the life span of the fish, but during the spawning migrations movement control was shifted towards PMC. RMC and PMC were hence applied in

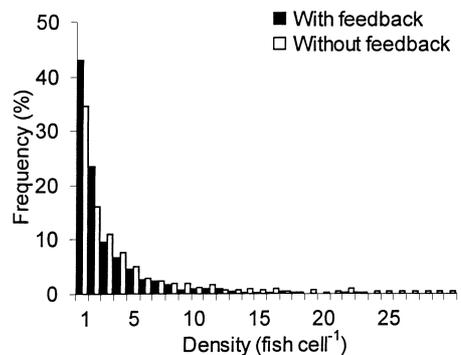


Fig. 14. Relative frequency distribution of number of individuals cell⁻¹ during October in computer runs with and without trophic feedback. Only cells containing individuals are included.

the predicted manner to control movement in feeding and migration, respectively. An interesting feature is that despite the dominating use of RMC, the characters of the predictive network converged more rapidly and towards a higher asymptotic level of character similarity (Fig. 8). This may be attributed to the spawning migration, where PMC is essential, and the vital role of reproduction in adaptive systems (Rose and Lauder, 1996).

As is usual in ecological optimisation theory, we have modelled ultimate selection forces, and just assumed that the fish has a way of sensing time (which can be done using day length as a cue) and direction (which they may obtain from geomagnetic fields, Walker et al., 1984, 1997; Moore et al., 1990). From this the weights of the ANN are evolved through the GA. Behaviour in the present model is carried out through firing or not firing movement nodes upon internal and environmental input. An important point is hence the shift from assuming a perfect habitat knowledge to stimuli based actions. This increases the realism in the actual knowledge that the animal has at the point of decision on whether and/or where to move. In the words of Wright (1994), we have modelled “adaptation executors” and not “fitness maximisers”.

During the adaptation of individuals the model is run for up to 600 years of simulations, which makes the computer runs very time consuming, despite the use of state of the art computers. Once a population of adapted individuals exists, however, the strings and state variables of this population can be saved and retrieved later for experiments. The trophic feedback experiment of the present study was carried out in this way which is much less computer demanding, and ensures that the adapted population is the same during the experiments.

5.1. Trophic feedback

One of the objectives of the present study was to compose a methodology where trophic feedback between fish and zooplankton could be implemented as an ecological factor affecting individual state. The dispersal of the fish varied seasonally, and when trophic feedback was removed the fish responded by stocking themselves at higher densities. This change in distribution pattern and in zooplankton

abundance did not change individual growth, which suggests that the fish were at least to some degree stomach limited. However, the survival probability increased when the trophic feedback was removed indicating that the fish occupied safer habitats when food depletion from feeding was removed as a factor. This illustrates the life history trade-off between growth and mortality (Werner and Gilliam, 1984). Trophic feedback is important when modelling ecosystems like the Barents Sea where the abundant capelin is able to graze down the zooplankton production at the polar front within short time intervals (Hassel et al., 1991). The capelin therefore continuously needs to move as a response to local food depletion. Models will not capture such density dependent features unless the prey density is decreased in response to predation. This is apparent when comparing the present results with those of Fiksen et al. (1995) who used dynamic programming to model capelin migrations in the Barents Sea. There are many similarities in the distributions, but the present fish distribution is much more dispersed, which corresponds to observed distributions of capelin during September–October (Dommasnes and Røttingen, 1985). This reflects the ability of the present approach and the inability of dynamic programming to include trophic feedback. An ideal free distribution based approach would redistribute the fish as prey were removed in the same manner as shown here. This difference between dynamic programming and ideal free distribution has been shown by Fiksen and Giske (1995) and Giske et al. (1997).

5.2. Fitness

As noted by Tyler and Rose (1994) one of the most troublesome problems in using process based spatial models is the choice of a proper Darwinian fitness measure. Using the ING-concept such problems are solved naturally as the fitness of individuals is determined from their offspring production. This endogenous fitness definition has been applied in many artificial life studies (Ackley and Littman, 1992; Holland, 1992; Menczer and Belew, 1996). We think that it also should have implications for fitness based ecology because of the generality of this approach in coping with processes such as density dependence and stochasticity. The application of endogenous fit-

ness may also solve the second problem posed by Tyler and Rose (1994, p. 115) which regards the quantitative influence of factors like predation risk and food availability on fitness. These relationships are state dependent and very complex. We ignore the analytical mathematical description of such relationships by evolving favourable strings using the principles of evolution through natural selection. There is hence no need to give “credits” for profitable behaviour at given situations since only reproduction counts.

5.3. Fisheries management implications

The present method could be applied in fisheries management initially as a test bed to investigate the effect on spatial distribution of fish given various management and fishing strategies. This is a large field in itself and we will only provide conceptual suggestions here. For example by concentrating the fishing effort in certain areas to avoid taking juvenile fish, one can investigate its effect on spatial distribution, population dynamics, and long term yields. Furthermore range collapses as observed for the Northern cod stock at Newfoundland (Kulka et al., 1995) could be predicted qualitatively from the present model as a population response to a decreased abundance. Another interesting point would be to take an initially adapted population, expose it to a fishery and let the population re-adapt to it. In this way the adaptive response of fish populations to fishing may be studied.

6. Conclusions

The present use of a GA to evolve weights in an ANN was first applied by Montana and Davis (1989). The method has also been applied in fisheries biology by Dagorn et al. (1997) who used it to predict tuna distributions in the Indian Ocean from remote sensing data. What is new in the present study is the way we have integrated the concept in an individual-based setting and modelled the full life history of a fish. As mentioned above artificial life is the study of the laws governing life in general. Our model may be classified as weak artificial life as opposed to strong artificial life where the complexity of the animats

(Wilson, 1985) is far greater than in the present model (Langton, 1989). We think artificial life approaches like the present are and will become increasingly more useful to ecology by representing an alternative way of modelling ecosystems. The use of simple artificial ecosystems and animats is fruitful during development of new tools when one needs to reduce the number of factors to a minimum in order to address the issue of tool making. The present contribution is the first in a process that later hopefully will enable us to simulate a realistic ecosystem.

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