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Individual based spatial models with evolved fish behaviour

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Abstract

Due to spatial heterogeneity, the survival and growth of fishes depend upon their habitat. For mobile pelagic fishes, it hence becomes important to analyse the factors responsible for spatial dynamics in order to understand population dynamics better. The current work is an attempt to approach fisheries assessment from a theoretical ecological perspective. We here present individual based single species and multispecies models where spatial behaviour and life history strategies are evolved. Spatial movement for each fish is calculated using an artificial neural network with weights evolved by a genetic algorithm. Behaviour relies on sensory information about food, temperature, light and predators. A concept for modelling life history strategies and migration in fish using this method is presented along with an application of this concept for the Barents Sea capelin. A predator-prey model based on the same principle is also presented. Potential areas of application for these kinds of models are discussed.

Keywords: genetic algorithm, artificial neural network, spatial, distribution, predator, prey.

Introduction

Fish-fish and fish-environment models

Due to spatial heterogeneity, the survival and growth of fishes depends upon their habitat, both due to environmental impact on growth and survival, and to environmental impact on fish-fish interactions. It is therefore important to consider spatial aspects when trying to understand the forces governing population dynamics.

Most of the fisheries management in the ICES area is based on single-species approaches, such as the VPA (Virtual population analysis, Gulland 1965). This is a demographic tool that, by assuming stability in some vital rates (i.e. assuming no variation in the fish-environment interactions), can be used to assess the age structure of a stock. For the North Sea, the VPA is elaborated into a multispecies VPA (MSVPA, Gislason and Sparre 1987), where survival (but not growth) is modelled as a density-dependent process. A different class of multispecies (MS) models are used in the Barents Sea and in Icelandic waters. In these models, MULTSPEC (Tjelmeland and Bogstad 1998 a, b) and BORMICON (Stefánsson and Pálsson 1997), both growth and survival are calculated from fish-fish and fish-environment interactions. All these three MS models also have a spatial resolution by

dividing the seas into a few sectors where interactions occur (Magnusson 1995). Fish migrations are performed by pre-described (static) movement vectors, and there is no behavioural component linked to the present ecological situation in the sea or in the vicinity of the fish.

Current limitations

The process of individual habitat choice in fish is central to the understanding of how fish-fish and fish-environment interactions can be scaled up to the population level. Habitat choice is commonly considered as a process that maximises the Darwinian fitness of an individual (for fish, see reviews by Tyler and Rose 1994; Giske *et al.* 1998). In ecology, several methods have appeared over the past 30 years to solve these problems. Basically, these methods can be divided into two approaches, based on optimality or game theory.

Optimisation in ecology started with optimal foraging theory (OFT) in 1966. This tool is able to solve short term decision problems related to feeding, but cannot find optimal solutions when mortality risk also varies (Table 1). Such trade-offs can be studied by methods that contain the whole life cycle of the organism. Therefore, life history theory (LHT) was developed from demography as a tool for predicting optimal behavioural decisions and life history choices. Recently, this method has been used to study life history responses to fishing in commercially exploited stocks (Stokes *et al.* 1991). However, LHT, particularly by the use of the Euler-Lotka equation, describes individuals by their age alone. This restricts severely the predictions possible by this method, and has been used as argument in favour of stochastic dynamic programming (SDP, Mangel and Clark 1988). This method will allow individuals to be characterised both by their age and by one or several "states", e.g. their hunger level, fat reserves, sex, body mass. Hence, SDP is able to yield far more precise predictions for behaviour related to fish-environment interactions. But this ability comes with a price: it is practically impossible to model density-dependent situations, e.g. fish behaviour that in turn will impact their own resources or their predators. Optimal density- or frequency-dependent decisions must be sought for by game theoretic methods.

Dynamic games

Game theory (in the form of the evolutionary stable strategy, ESS) was introduced to ecology from economy by Maynard Smith (Maynard Smith and Price 1973, Maynard Smith 1974, 1982), although a version of it, the ideal free distribution (IFD) had already been used (Fretwell and Lucas 1970). Situations where the profitability of behaviours of one actor depends on the behaviour of other actors are referred to as games. Games can yield very complex population and spatial dynamics, especially if both actors are allowed to relocate (Sih 1984). Since spatial overlap is inevitable for predation to occur, spatial dynamics are of paramount importance to the understanding of predator-prey relationships. Predators tend to aggregate in areas where prey are abundant (Hassell 1978; Sih 1984) or easily caught, whereas prey on the other hand tend to avoid predators (Stein and Magnuson 1976; Sih 1984). However, both the two game theoretical methods, the ESS and the IFD, will require some stability in order to find a solution to the game. And as the possible interactions increase very rapidly with system complexity, they are also both best suited for problems of low complexity. Such, it is in practice not possible to combine spatial heterogeneity, temporal variation and individual state variation in these classical game theoretical approaches. A new method is wanted, that may combine the best of state- and density-dependencies in a variable environment.

A discipline of interest in this respect is artificial life (A-life). A-life is a new field of science that emerged during the late 1980s inspired by evolution and life in general.

It is concerned with synthetic (man-made) life in hardware (robots), wetware (chemistry) and software (computer programs): "life as it could be" (Langton 1989). Although many issues of A-life are rather abstract to biologists, some of the methods applied in this field are of interest to ecological modelling. For example some studies simulate "animats" (artificial animals, Wilson 1991) that inhabit and interact with an environment (Ackley and Littman 1992, Holland 1995, Menciaer and Belew 1996). Such simulations bear resemblance to ecological systems, and correspondingly these A-life methods may be applicable in ecology. Here we provide an introduction to some A-life inspired fish migration models and discuss the possible use of such models in fisheries ecology.

By combining the neurobiological method artificial neural networks (ANN) for information-based decision-making, and the adaptation-based genetic algorithm (GA) for finding improved solutions, a new class of ecological models emerges. Opposite to LHT and SDP, here is no *a priori* assumption of optimality, but a process of adaptation (the GA) that evolves near-optimal solutions to ecological trade-offs. Opposite to classical game theory, there is no function to control the game, but the result is (extinction or) a dynamic and fluctuation interplay between the ecological players, including predation and intra- and interspecific competition. Hence, dynamic game methods are able to cope with several trophic levels as well as state- and density-dependencies. We have called this combination the Individual-based Neural network Genetic algorithm (ING), and we believe that analysing such dynamic games may be useful for ecosystem understanding and fisheries assessment.

Table 1. A comparison of tools for functional modelling (modified from Giske *et al.* 1998).

Approach Property/method	Demo- graphy		Optimality		
	VPA	MS	OFT	LHT (Euler-Lotka equation)	SDP
Individually variable motivation	No		Feeding state	Age-dependent ("static" motivation)	Age-, time- and state-dependent
Density-dependent growth and survival	No		Only through feeding	No	Possible only for very simple scenarios
State- dependent growth and survival	No		Only through feeding	No	This is what SDP is best at
Morphological and physiological plasticity	No		No, OFT covers shorter intervals	No	Phenotype characterized by states
Individual behaviour at several trophic levels	No		No	Static	Only as dynamic game
Dynamic behaviour and life history strategy	No		Does not cover the whole life, concentrates on feeding situations	Only in stochastic LHT	Of one actor in a specified environment
Find optimal strategies	No		To simple problems without predation risk	Yes	Will find global optimum
Learning	No		Yes	No	Yes
Ecosystem-modelling	No	Trophic interactions in MS models	No	The environment is described implicitly in the l_x and m_x vectors	Scenario-modelling or dynamic games
Heterogeneous and temporally variable environment	No	VPA assumes stability, MS models can include some variation	Only through feeding	Assumes conditions equal for each generation, genetic foresightedness	Unrealistic adaptation due to perfect foresightedness
Fitness measure	No		Partial: feeding rate and growth	Analytical, rate maximisation (or a derivative)	Full or partial, derived from analytical
Used in assessment	Yes		No	No	No
References	31, 32, 33, 34		2, 3, 16, 22, 28	5, 18, 21, 24, 27, 28, 30	8, 12, 13, 14, 17, 18, 23, 28

Table 1 (continued). A comparison of tools for functional modelling.

Approach	Game theory		
	ESS	IFD	ING
Individually variable motivation	No	In despotic IFD	Age-, time- and state-dependent
Density-dependent growth and survival	Yes, and frequency-dependent	Yes	Yes
State-dependent growth and survival	No	Very computer-intensive	Yes
Morphological and physiological plasticity	No	No	Probably possible, not yet done
Individual behaviour at several trophic levels	Find optimal strategies	Dynamic games	Two trophic levels presented in this paper
Dynamic behaviour and life history strategy	Frequency-dependent solutions	Density-dependent solutions	Will evolve according to environment
Find optimal strategies	Equilibrium analysis, requires simple system	Equilibrium analysis, requires simple system	May get stuck at local optima
Learning	No	No	Yes
Ecosystem-modelling	Can search for equilibrium	Predator-prey equilibrium	Not granted that global optimum or stability will be found
Heterogeneous and temporally variable environment	No: equilibrium analysis	Computer-intensive, in practice impossible	Variation at all scales possible, genetic foresightedness
Fitness measure	Any, but frequency-dependent	Usually partial (feeding or growth)	Endogenous (implicit) fitness function
Used in assessment	No	No	Not yet
References	9, 11, 15	6, 7, 9, 26	1, 4, 10, 19, 20, 25, 29

1: Ackley and Littman 1992; 2: Charnov 1976; 3: Clark and Mangel 1986; 4: Dagorn *et al.* 1995; 5: Fisher 1930; 6: Fretwell and Lucas 1970; 7: Giske *et al.* 1997; 8: Houston *et al.* 1988; 9: Hugie and Dill 1994; 10: Huse and Giske 1998; 11: Iwasa 1982; 12: Katz 1974; 13: Mangel and Clark 1986; 14: Mangel and Clark 1988; 15: Maynard Smith 1982; 16: McNamara and Houston 1985; 17: McNamara and Houston 1986; 18: McNamara and Houston 1996; 19: Menczer and Belew 1996; 20: Nolfi *et al.* 1994; 21: Roff 1992; 22: Schoener 1987; 23: Sibly and McFarland 1976; 24: Stearns 1992; 25: Terzopoulos *et al.* 1995; 26: Tregenza 1995; 27: Tuljapurkar and Caswell 1997; 28: Tyler and Rose 1994; 29: van Rooij *et al.* 1996; 30: Werner and Gilliam 1984; 31: Magusson 1995; 32: Rødseth 1998; 33: Tjelmeland and Bogstad 1998b; 34: Stefánsson and Pálsson 1997.

The model

Model outline

The model approach is inspired both by spatially explicit individual based models (IBMs Tyler and Rose 1994) and A-Life (Langton 1989). The technique is based on applying a genetic algorithm (GA, Holland 1975) to evolve the weights in an artificial neural network (ANN, Rosenblatt *et al.* 1958; Rummelhart *et al.* 1986; Montana and Davis 1989). The GA is a heuristic technique that applies the principle of evolution by recombinations, mutations, and natural selection to search for improved solutions to a problem (Holland 1975; Goldberg 1989; Mitchell 1996). Most optimisation problems can be solved using the GA, although its efficiency and suitability depends upon the specific problem (Davis 1991). ANNs apply a model of how the human brain works (sensory-based information processing and decision making) to weight input and calculate a behavioural output. Nodes in an ANN are linked together in the same way that brain cells are connected by synapses. ANNs can thus be applied to perform

tasks from input data and weights that are modified to accommodate certain goals. Presently a simple feed forward network (Anderson 1995) is applied with input, hidden, and output layers. The layers are connected by matrices of weights. In order to avoid confusion between biological genetics and GA "genetics" we adopt the GA terminology suggested by Goldberg (1989), hence the analogy of a chromosome will be termed string and gene will be termed character. The strings consist of real values (Davis 1991; van Rooij *et al.* 1996) rather than binary digits as in the original version of the GA (Holland 1975).

A schematic outline of the ING concept is shown in Fig. 1. A geographical lattice of squares (2 D or 3 D) confines the spatial setting of the ING concept. At the start of a computer run each individual is equipped with strings of random numbers and is placed in a randomly chosen square. Here it feeds, grows, and it may die. At the end of each time step the individual decides whether to stay at its present location or move to one of the surrounding squares. Movement is calculated using the ANN from information about the presence of food and predators in the immediate vicinity of the individual (Fig. 1). Movement is determined in a "winner takes all" fashion where the output node that gets the highest output value is excited and the individual consequently moves in this direction or stay.

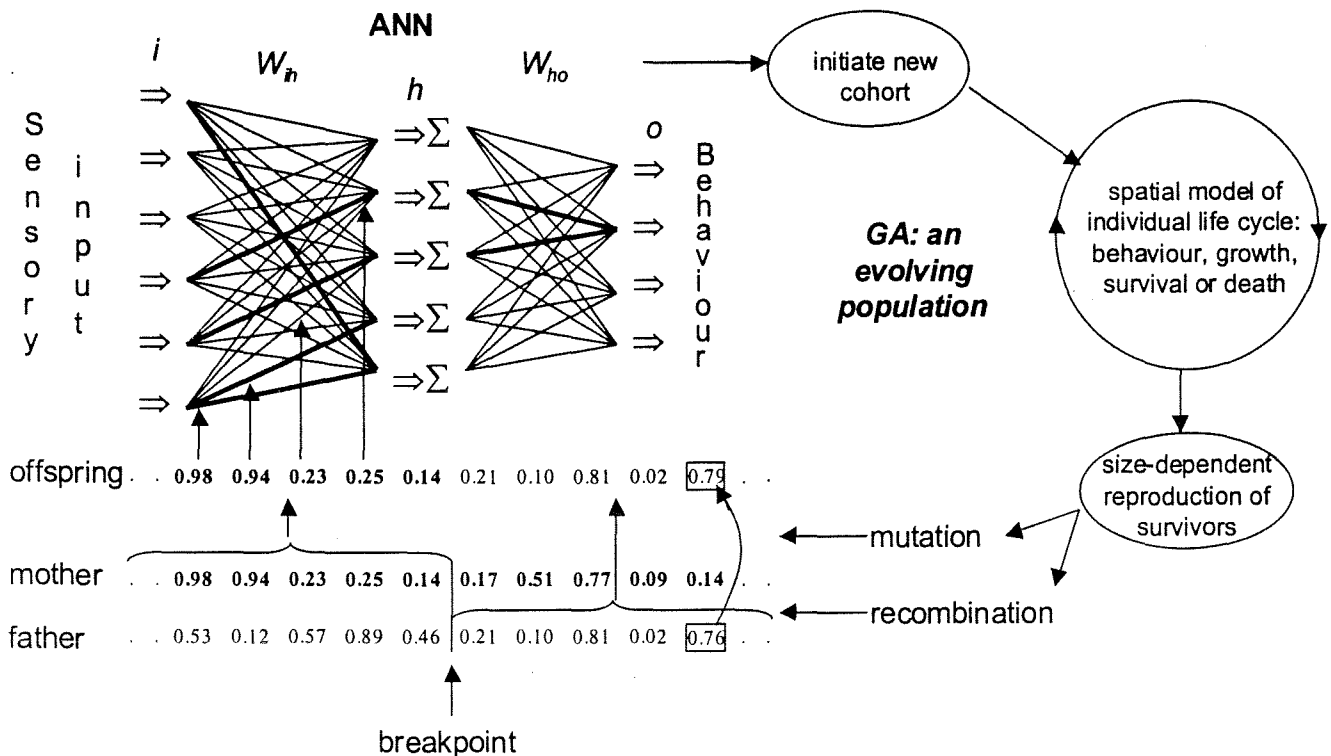


Figure 1. The ING concept with ANN based behaviour and GA based evolution in an individual-based setting. A cohort of individuals with randomly set strings which code for the weighting of the ANN, is initiated in the first time step. The individual's life cycle is simulated, and when maturity is reached, individuals reproduce and new recombined, possibly mutated individuals emerge. The breakpoints are randomly selected. 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 *et al.* 1998 and Huse (1998a).

When an individual fulfils certain criteria it can reproduce its fecundity which is dependent upon the body size of the individuals. The string of offspring is a mix of the parent individual and a randomly chosen individual, and simulates crossing over (Fig.1). Further string variability may be added through changes in character value using creep mutations (Davis 1991). These occur with probability ($P=0.001$) and change the cell value by a randomly chosen value (maximum 20%). The individuals who manage to reproduce will by definition be those which are more fit for life in the present environment. By repeating this procedure over and over the population will consist of increasingly fit members (Holland 1975).

This is the basic outline of the model, and the various applications shown below apply a model based on this scheme, but with specific alterations for the different tasks. For a more thorough description of the ING concept see Huse and Giske (1998) and Huse (1998a).

Results and Discussion

Predator-prey model

The first example of application of the ING concept is a small scale predator-prey model where the prey move about to find food and avoid being eaten, and the predator feed on the prey. As shown in Fig. 2 there was a typical cyclic pattern in the abundance of the predator and prey. Following an increase in abundance of the prey was an increase in predator abundance. Also with increasing prey abundance there was an increase in number of cells with overlap between predator and prey (Fig. 2). The peak abundance of the predator is typically somewhat later than that of the prey. The degree of spatial overlap (number of cells containing both predators and prey) shows a similar variation with a peak in between the peak in the prey and predator populations.

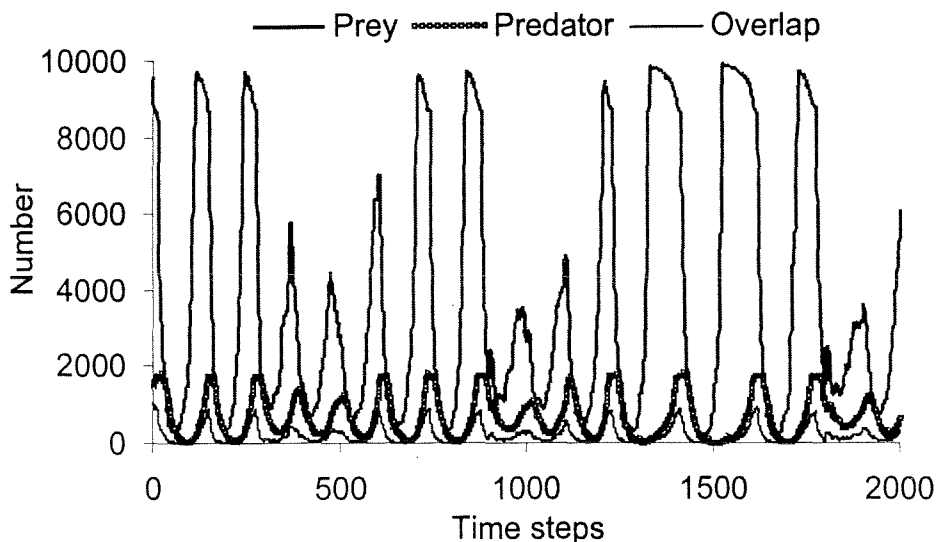


Figure 2. Population dynamics. Predator and prey abundance and the number of squares occupied by both trophic levels (overlap).

There was a spatial game between the predator and prey as illustrated in Fig. 3, which show the average position of predators and prey at each time step. This indicates that there was a consistent race between the predator and prey, and that there was adaptation involved in the interaction between the two actors. Initially there

were rather large differences in average spatial position between the predator and prey. After some time steps of simulation, however, the predator managed to follow the prey more closely (Fig. 3). Typically the prey move in one direction is followed by the predators responding by moving in the same direction. The prey then changes its direction and some time steps later the predator responds by following the prey (Fig. 3). There is hence a time lag in spatial position between the two. Whereas the predator in the beginning of the simulation responds slowly to changes in prey position the response is much faster towards the end of the simulation (Fig. 3). This illustrates that the adaptation of the predator increases throughout the simulation.

Although this simulation refers to a general predator and prey, such relationships are very common in the sea, and it exists for example between capelin and cod. By making the model more realistic through describing the environment or the constraints in a more detail the model could be applied to investigate how environmental variation or behavioural constraints influence on the predator prey relationship and consequently the population dynamics.

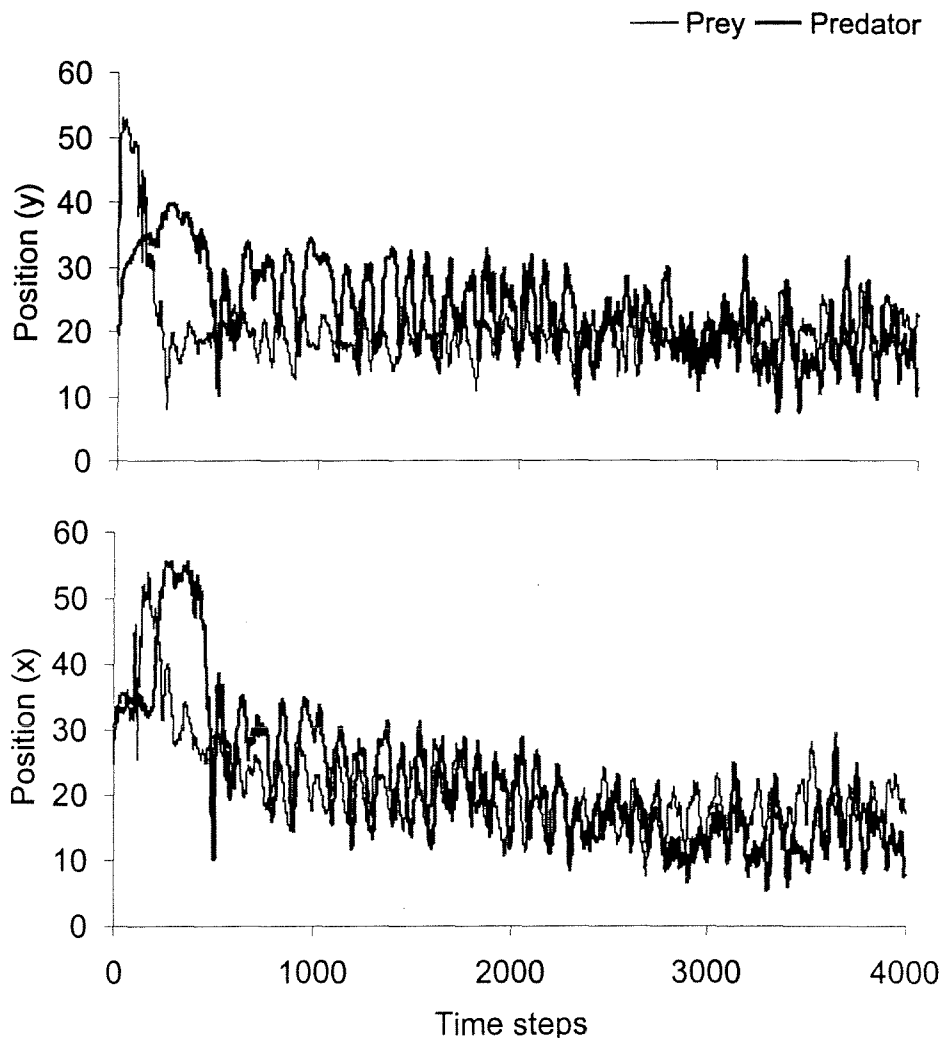


Figure 3. Average position of predator and prey during a computer run. The adaptation of the GA is seen in more close interplay after 1000 time steps.

Migration model

The migration model was implemented for the Barents Sea capelin in a model where both behaviour and life history strategies were evolved simultaneously. As illustrated

in Fig. 1 the model was initiated with a random population that evolved over successive generations to become well adapted to the environment. Timing and location of reproduction were evolved in the model. Initially spawning was widespread, but soon became restricted to a few areas in the southern part of the Barents Sea (Table 2). The evolved spawning area hence corresponds fairly well to the spawning area of the Barents Sea capelin. Evolution of timing of reproduction followed a similar pattern with an initially widespread timing that was restricted to the period March-May after 200 years of simulation. This is the period at which capelin spawning takes place.

Table 2. Evolution of spawning area at given years in the initial 200 years of simulation (deterministic run). Data for eastern column number (geographical position) are listed (see Fig. 6 where there is a total of 60 columns). Since no successful spawnings were made east of column 35, the data are limited eastwards by this square. The number of successfully spawning pairs in each column is given.

Square	Years												
	1	4	8	15	30	50	75	100	125	150	175	200	
1													
2	2												
3	4												
4													
5	34	9											
6	4	1											
7	8												
8	54	15											
9	11												
10	9	4	10										
11	9	2											
12	22	9	10										
13	22	1											
14	8	8											
15	15	9											
16	2	1											
17	5	5				1							
18	4	1										1	
19	3	1											1
20	2	7	8			2	12	18		4	2		10
21	4	3	3				3	3	12	10	20		9
22	8		6	4	11	9	9	2	15	11	8		4
23	2		6	24	4	3	3	5	2	4	1		69
24	3		6	20	15	6	6	7	3	5	9		1
25	2		6	6	2	4	34	32	6	18	46		
26	3		19	16	3	12	0			1			
27	2		6		10	13							
28	3				2								
29	8												
30													
31	1												
32													
33		1											
34	1												
35	1												

In the same manner that spawning area and timing of reproduction was evolved, life history strategies were evolved. Two different computer runs were carried out with deterministic and stochastic mortality respectively. Females matured at a slightly higher size and age than males in the deterministic run (Table 3). 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. In a former study (Huse 1998b) it was suggested that male and female capelin have different life history strategies under the mortality regime of the Barents Sea. The differences is due to the possibility of males to mate with several females during a spawning season, whereas females are limited by the number of eggs that they can carry to the

spawning ground. The current results hence support the former findings that in a stochastic environment sex specific life history strategies could emerge.

Table 3. 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

Modelled temperature field for the Barents Sea and simulated fish distribution pattern from the deterministic run are shown in Figs. 4 and 5 respectively. 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. 5). 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. 4). This warm water area is particularly distinct during the larval drift period in late spring and early summer (Fig. 5). 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. There was a tendency for the age groups to occupy different areas.

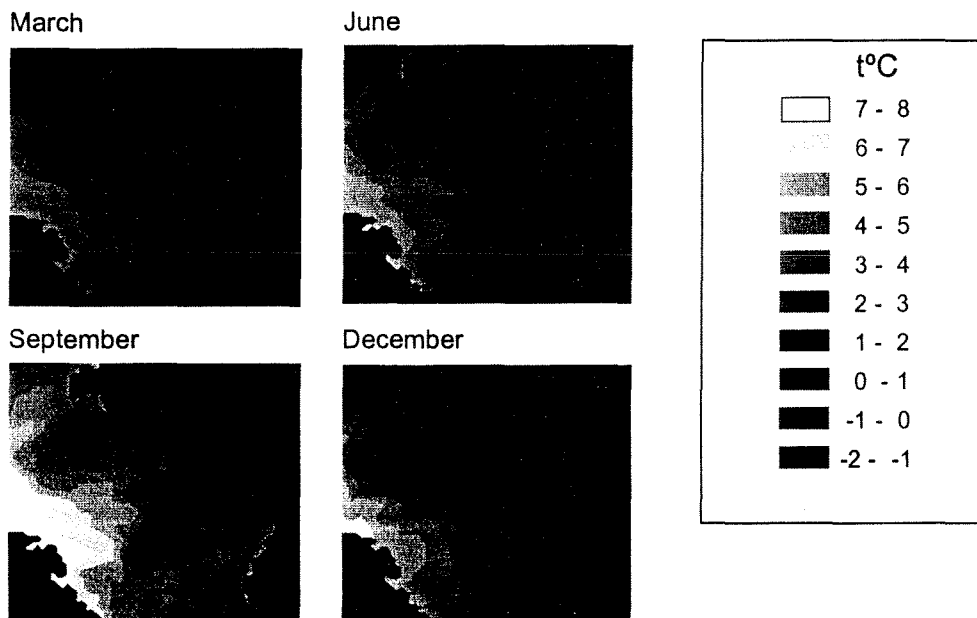


Figure 4. Modelled temperature distribution for the Barents Sea at different times of the year.

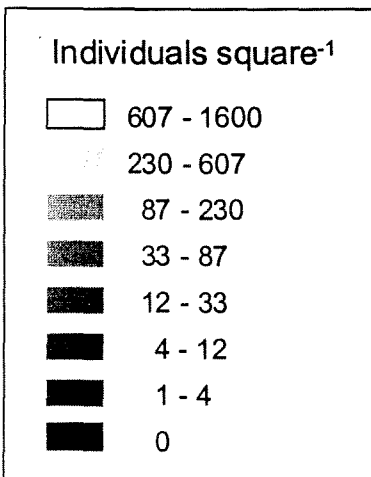
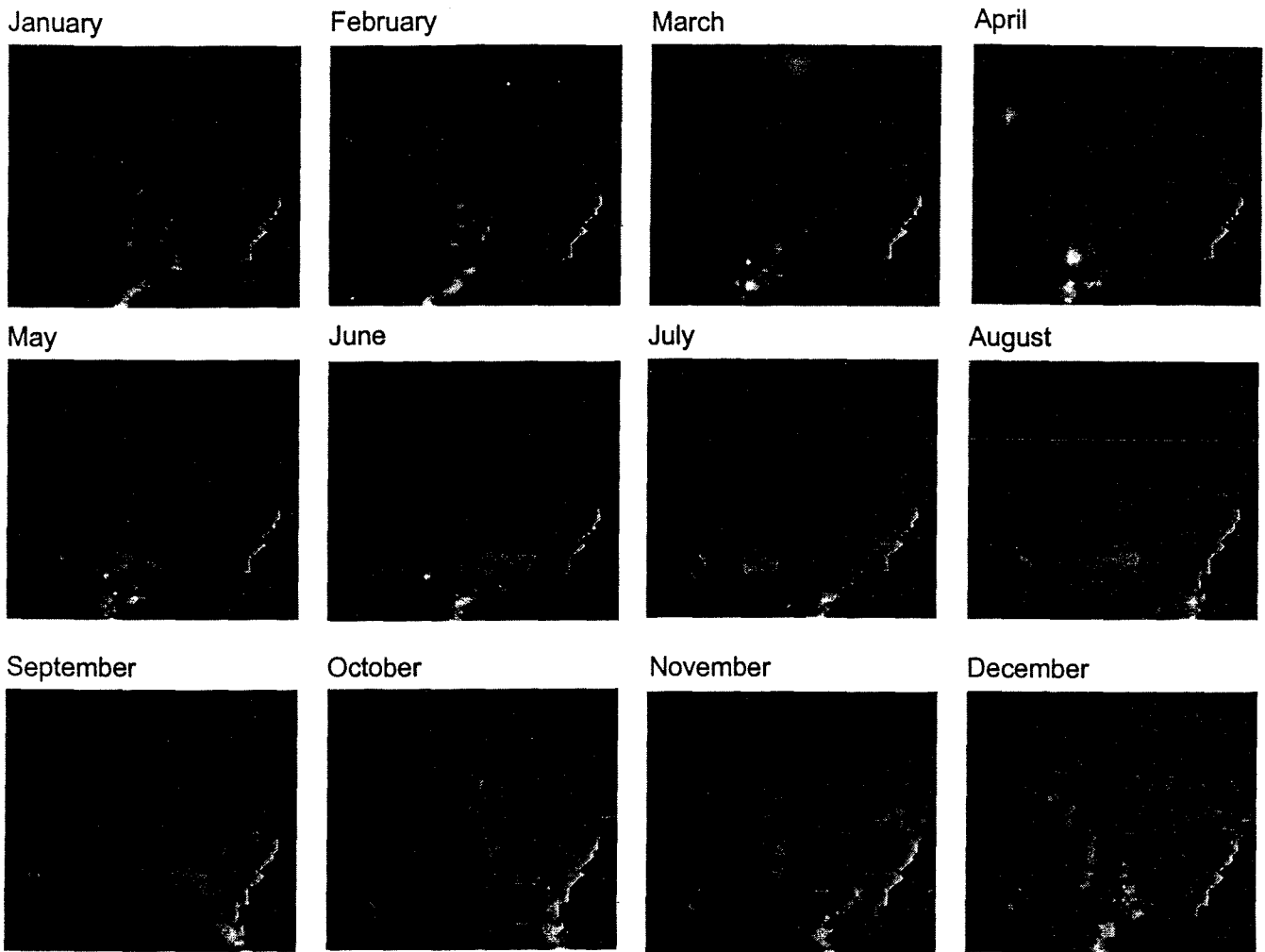


Figure 5. Distribution of the capelin throughout the year combined for all age groups in the deterministic run in year 200. Land contours of the Barents Sea are drawn in.

The population biomass varied extensively between years (Fig. 6). After about 160 years the population biomass in the deterministic run climbed to a relatively stable level between 5 and 6 mill tonnes (Fig. 6). 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.

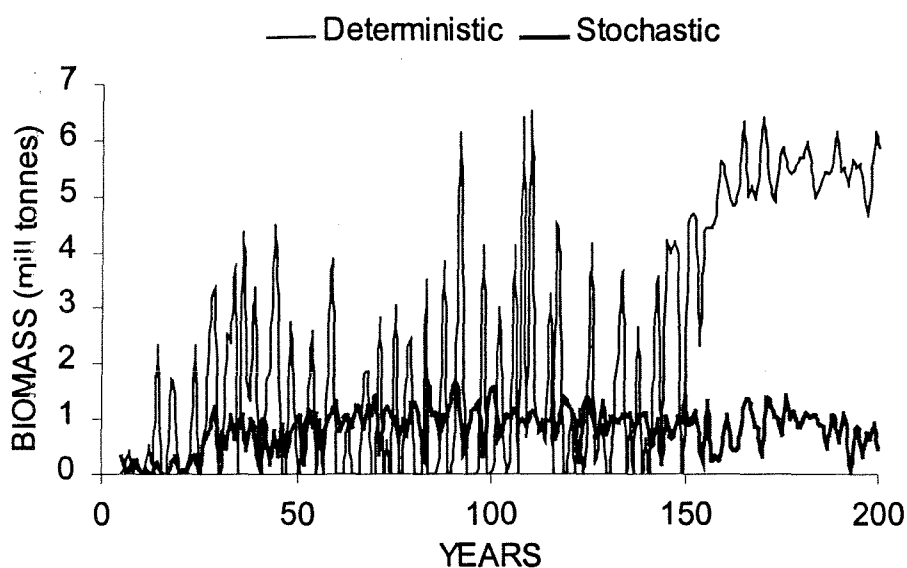


Figure 6. Total biomass of the two simulations during the computer runs.

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 and Littman 1992; Mitchell and Forrest 1995; Menczer and 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.

Conclusions

The ING concept is a fruitful way to study how spatial processes can affect population dynamics. It is a dynamic game tool of a very general nature and is here applied in two specific applications. By using such evolutionary systems, an increased understanding of how different processes interact to produce population dynamics which is a key element in fisheries biology. In general fisheries management uses little information about the environment when making estimations about future stock development. The approach taken here may be applied to increase our understanding of fish-environment and fish-fish interactions which are important processes underlying population dynamics.

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