

Life history strategies and spatial dynamics  
of the Barents Sea capelin (*Mallotus villosus*)

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**Preface**

First of all I am greatly indebted to my supervisor Jarl Giske for initially convincing me that programming is easy, and later, for very inspiring counselling and for always taking the time.

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A thank is due to Ketil Eiane who has been my roommate and with whom I have had numerous exciting scientific, and not so scientific discussions.

Jarl Giske, Paul J.B. Hart, Harald Gjøsæter, Ketil Eiane and David Kirby provided constructive criticism on a former version of the Synthesis, which I think improved it substantially.

I would like to thank friends and colleagues at the Department of Fisheries and Marine Biology for providing a nice working and social environment.

Acknowledgement is due to my father and colleague Ingvar Huse for many interesting discussions about fish and science through the years, and to the rest of the family for keeping up with us.

I would finally like to thank my wife Jane for enduring love and support.

Bergen, June 1998

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## Papers

- I      Fecundity of the Barents Sea capelin (*Mallotus villosus*).
- II     Sex-specific life history strategies in capelin (*Mallotus villosus*)?
- III    Ecology in Mare Pentium: An individual based spatio-temporal model for fish with adapted behaviour.
- IV    A spatial life history model of the Barents Sea capelin.

## Summary

This thesis consists of four papers on the life history strategy and spatial distribution of the Barents Sea capelin (*Mallotus villosus*). In the first two papers, sex specific aspects of capelin life history are investigated from a combination of field sampling and modelling. Paper III deals with the development of a concept for modelling spatial distribution of fish, and in Paper IV the concept is applied for the Barents Sea capelin.

Female capelin were found to invest much more energy into reproductive tissue than males. Capelin fecundity was found to depend upon body weight, and inter annual variation in fecundity is related to variation in body weight. A life history model (Paper II) predicts that males have a higher fitness associated with semelparity than females since males may fertilise many females, whereas female fitness is limited by her number of eggs. Given a high or variable adult mortality risk, it may be more profitable for males to be semelparous than iteroparous. Capelin is therefore predicted to have sex specific life history strategies with semelparous males and iteroparous females. This prediction is supported by literature on capelin ecology.

In Paper III a concept for modelling spatial distribution of fish is developed. The background for applying a new approach to studying fish distribution, is the lack of approaches for solving specific problems related to capelin ecology. The model is individual based and behaviour is calculated using an artificial neural network where weights are evolved using a genetic algorithm. Through simulating evolution by natural selection in a seasonal spatial model with life cycle, physiology, mortality, and reproduction, the individuals with the best "genetic weights" become increasingly more common in the population. Eventually the population consists of well-adapted individuals, which migrate back to spawning areas in winter, and grow and avoid being eaten throughout the rest of the year. The importance of separating between reactive and predictive behaviour in controlling local search and long distance migration respectively, is discussed. In Paper IV this model is elaborated to include: explicit representation of each stage in the life cycle of the Barents Sea capelin, larval drift, and evolution of spawning areas and timing of reproduction. Furthermore the model includes life history traits such as size at maturity, allocation of energy, and number of reproductive events. Larval drift was associated with a warm water area, and the evolved spawning ground was situated upstream from this, in the outskirts of the range for capelin spawning. The migration pattern follows the same general pattern as that of the Barents Sea capelin. In a simulation with stochastic mortality rates, sex specific life history strategies with semelparous males and iteroparous

females were evolved, which supports the predictions from Paper II.

The major achievement of this study is the development of an evolutionary system for fish migration, and the way this is applied to provide predictions about the life history and spatial dynamics of the Barents Sea capelin. Another important finding is the recognition that some aspects of capelin life history strategy are sex specific, with female iteroparity and male semelparity.

## List of papers

- Paper I:** Huse, G. & H. Gjøsæter 1997. Fecundity of the Barents Sea capelin (*Mallotus villosus*). *Marine Biology* 130:309-313.
- Paper II:** Huse, G. 1998. Sex-specific life history strategies in capelin (*Mallotus villosus*)? *Canadian Journal of Fisheries and Aquatic Sciences* 55:631-638.
- Paper III:** Huse, G. & J. Giske 1998. Ecology in Mare Pentium: An individual based spatio-temporal model for fish with adapted behaviour. *Fisheries Research* 37:00-00.
- Paper IV:** Huse, G. (Manuscript). A spatial life history model of the Barents Sea capelin.



## **Evolutionary modelling of life history strategies and spatial distribution**

### **Introduction**

Life history theory is ultimately the study of how fecundity and survival is maximised through various life history strategies (Fisher 1930, Wright 1931, Haldane 1932, Lack 1947, Andrewartha & Birch 1954, Cole 1954, Roff 1992, Stearns 1992). Life history strategies have been defined as "programs of decision rules where an individual chooses between available developmental or behavioural alternatives at critical control points" (Cohen 1993). The variety of life history strategies displayed in nature illustrates that there are many ways to solve the "general problem of life". This point is beautifully illustrated in a prologue by Stearns (1992) using examples from albatrosses, oak trees, reef fishes and the community on a rotting plum. Two approaches prevail in the analysis of life history evolution: the genetic approach and the optimisation approach (Roff 1992). Central to the genetic approach is finding equilibrium frequencies of alleles. The optimisation approach on the other hand is concerned with finding the most favourable combinations of life history traits such as size at maturity, reproductive effort, number of reproductive events, clutch size, and offspring size (Roff 1992, Stearns 1992). In this work life history strategies will be approached from an optimisation point of view.

Ecology can be defined as the study of interactions that determine the distribution and abundance of organisms (Krebs 1978), which puts spatial distribution at the core of ecology. Due to spatial heterogeneity, the vital rates of survival and fecundity will depend on the habitat. Many pelagic fishes consistently change location on a number of different scales varying temporally from seconds to months and spatially from centimetres to hundreds of kilometres. For highly mobile animals such as pelagic fishes, it hence becomes important to analyse the factors responsible for spatial dynamics in order to understand the population dynamics. Movement of organisms can generally be divided into migration and dispersal (Begon & al. 1990). Migration is mass directional movement of individuals from one location to another whereas dispersal refers to spreading of individuals away from others, and may involve active movement or passive transport. With regard to modelling spatial distribution, the distinction between active and passive dispersal as mentioned above is important.

Models of active dispersal rely upon behavioural algorithms whereas in passive dispersal, movement is a function of physical forces such as wind and ocean currents. Most aquatic studies have dealt with either active or passive dispersal, and very few have included both of them. 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 behaviour on the part of the larvae although vertical migration is implemented in some of them (Bartsch & al. 1989, Werner & al. 1993). A common approach to modelling habitat choice is to apply models based on maximisation of Darwinian fitness. As indicated above, life history theory relates directly to the theory of evolution by natural selection (Darwin 1859). The analysis of fitness consequences of life history strategies and actions is a powerful tool. Models based on measures of fitness have proved to be a fruitful way to study the spatial distribution of animals (see reviews by Tyler & Rose 1994 and Giske & al. 1998a). The "classic" spatial models are the ideal free distribution (IFD, Fretwell & Lucas 1970), and models based on optimal foraging theory (Charnov 1976) and life history theory (Werner & Gilliam 1984). Within the last decade, stochastic dynamic programming (SDP, Houston & al. 1988, Mangel & Clark 1988) has become extensively applied in behavioural ecology, with many applications in habitat choice (Clark & Levy 1988, Rosland & Giske 1994, Fiksen & al. 1995). Some studies have dealt with fish migration as a maximisation of comfort (or minimisation of pain) as in the models by Balchen and colleagues (Slagstad & al. 1975, Balchen 1976, Reed & Balchen 1982). Others again have provided statistically or empirically based models without explicit evolutionary motivation (Harden Jones 1965, Arnold & Holford 1995, Dat & al. 1995, Downing & Reed 1996, Vabø & Nøttestad 1997).

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 has been 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 population 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 (Slagstad & al. 1975, Balchen, 1976, Reed & Balchen 1982), and the work was continued by Giske & al. (1992) and Fiksen & al.

(1995). Despite a considerable effort on modelling the spatial distribution of capelin using state of the art techniques in ecological modelling, there are still several problems of importance to capelin biology that remains to be solved. The capelin is known to efficiently decimate the abundance of its prey during summer (Hassel & al. 1991), and has to change habitat in response to this depletion. Furthermore the life history of the capelin is constrained by the 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, Roff 1992, Stearns 1992). 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 & Lucas 1970, Hugie & Dill 1994, Giske & al. 1997), but at the expense of ecosystem dynamics and individual variability in physiology. None of these methods are able to fully include environmental stochasticity, and hence these general problems of specific importance to capelin ecology cannot be solved using conventional tools in ecological modelling. Also density dependence and stochasticity are situations in which common fitness measures used to evaluate actions, such as the instantaneous rate of increase  $r$  and the net reproductive rate  $R_0$ , become invalid (e.g. Roff 1992, Stearns 1992). Common to all optimisation techniques (where all solutions to a problem are calculated) is the "curse of dimensionality" (Bellman 1957) which limits the number of applicable dimensions (states) for which the optimal solution can be calculated. It may therefore be fruitful to search for other methods that can solve these problems. 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 & Littman 1992, Holland 1995, Menczer & Belew 1996). Such simulations bear resemblance to ecological systems, and correspondingly these A-life methods may be applicable in ecology.

## **Objectives**

The main objective of this work is to develop a spatial life history model for the Barents Sea capelin. The reason for emphasising the link between spatial and life history models is the close relationship between habitat characteristics and processes such as growth and mortality that have strong influence on life history strategies (Roff 1992, Stearns 1992). The first part of the study is focused upon life history features of the capelin while in the latter part the spatial life history model is developed. Now I will discuss some A-life approaches and compare these with conventional tools in ecological modelling.

## **Evolution**

Ever since Charles Darwin proposed the theory that evolution is the result of natural selection, we have been equipped with a powerful tool in the analysis of biology. The theory of evolution by natural selection in its current refined form is, in addition to being a theory for life on earth, a general principle which many fields of science have now adopted. A quick World Wide Web search reveals disciplines such as evolutionary psychiatry, evolutionary medicine, evolutionary psychology, evolutionary physics, and evolutionary economics. Cziko (1995) extends the principle of natural selection to a principle of universal selection in what he calls the "second Darwinian revolution", which captures the ongoing spread of evolutionary theory to other disciplines. The genetic algorithm (GA) developed by Holland (1975) is a technique that applies evolution by natural selection in computer programs to find optimal solutions to a problem by representing solutions in "genetic code". Although it was not the first attempt to use the principle of evolution by natural selection in computer programs, Holland's work has been the most influential of its kind. The GA has successfully been applied to problems within a large number of fields, such as engineering, physics, economics, medicine and biology (Goldberg 1989). The GA has also been applied extensively in A-life, and this method is here used in an evolutionary modelling concept. 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".

## Evolutionary modelling vs. optimisation techniques

There has been a continuous debate about the optimisation approach in ecology (Gould & Lewontin 1979, Pierce & Ollason 1987, Stearns & Schmid-Hempel 1987, Parker & Maynard Smith 1990, Orzack & Sober 1994). This controversy stems either from the idea that those who adopt the approach assume that animals are optimally adapted, or that they are trying to prove that animals are optimally adapted (Parker & Maynard Smith 1990). The optimisation approach originates from the apparently perfect adaptations achieved through the process of evolution by natural selection. Although adaptation is powerful it should not be viewed as a process whose result is perfection (Parker & Maynard Smith 1990). The aim of an optimality model is rather to provide predictions about specific adaptations that are evolved under the given boundary conditions (Stearns & Schmid-Hempel 1987). Optimisation in ecology hence refers to local adaptations of traits constrained by evolutionary history. Given an awareness of its restrictions and assumptions, the optimisation approach can be fruitful in ecology (Stearns & Schmid-Hempel 1987, Parker & Maynard Smith 1990).

Optimisation techniques are a collection of procedures for calculating all possible solutions to a problem and consequently selecting the best ones. An example of such a technique is SDP (Mangel & Clark 1988). Optimisation techniques are commonly applied in evolutionary biology, but should not be confused with the optimisation approach as discussed above. Both optimisation techniques and evolutionary modelling in ecology are based on the optimisation approach, but still there are some important differences between the two methods. By repeatedly exposing a population to certain situations, individuals can adapt through differential survival and reproduction and thus the population will tend to consist of individuals that are increasingly better adapted as the generations go by. This is the essence of evolutionary modelling. The general nature of evolutionary modelling enables us to tackle the problems posed towards the end of the Introduction, among other features listed below. This is not to say that this method is perfect, and the limitations of evolutionary modelling will be touched upon later. However, there are some new features that make evolutionary modelling worthwhile for a number of problems in contemporary ecology:

1) *Trophic links*: Since evolutionary modelling relies on a forward search procedure, links between individuals and the environment can be implemented. Environmental feedback can thus be allowed to impact on behavioural decisions.

II) *Games*: Games between a predator and prey or between individuals at the same trophic level can be seen as a special case of Point I. In such situations the behaviour (or strategy) of one individual affects the behaviour (or strategy) of other individuals at the same or different trophic levels. Games can be solved using evolutionary modelling (own unpublished data).

III) *Environmental stochasticity*: Evolutionary modelling allows robust strategies to be evolved in stochastic environments through exposure to a variety of different environments.

IV) *Endogenous fitness*: The assumptions of Darwinian fitness measures often restrict implementation of features such as density dependence and stochastic environments in ecological models (Roff 1992, Stearns 1992, Giske & al. 1993). Evolutionary models based on endogenous fitness (Mitchell & Forrest 1995, Menczer & Belew 1996), avoids problems related to fitness measures since fitness is defined indirectly by the interactions between individuals and the environment.

V) *Curse of dimensionality*: There are limits to the size of solution spaces that an optimisation technique can solve since all possible solutions have to be calculated. One type of problems that evolutionary modelling techniques have been applied to is complex combinatorial problems (Goldberg 1989, Reeves 1993). For such problems evolutionary modelling can provide answers by searching through solution space, whereas optimisation techniques will be inadequate.

VI) *Complete knowledge*: Complete knowledge of, for example, predation risk and food availability in surrounding habitats is commonly assumed in optimisation models. Although this is a good approach in many cases with small-scale problems it fails on a larger scale. Complete knowledge of patch profitability is assumed in the Ideal Free Distribution (Fretwell & Lucas 1970) and the Marginal Value Theorem (Charnov 1976). The validity of this assumption decreases with increasing patch size and interpatch distance. Evolved behaviours do not comprise assumptions about knowledge.

The features listed above contain those called for in the Introduction as well as some additional ones, and evolutionary modelling should therefore be a firm basis for establishing a new concept for spatial modelling.

## Merging A-life with B-life

As pointed out by Toquenaga & Wade (1996) there has been little interaction between A-life and conventional biology (B-life), due to sparse communication between the two fields. While biology is run by biologists, A-life had its origin among computer scientists and mathematicians (Levy 1992), and still the number of conventional biologists interested in A-life seems to be rather low (but see Belew & Mitchell 1996). In fact judging from my own limited sphere most biologists hardly know of its existence. Many A-life models simulate life processes of animats where variables define the state of the organism and rules to live by are supplied by a "genetic code" (string) that the animat possesses. According to Ray (1995), biologists have found parallel methods to the A-life approach in individual based models (IBMs, Łomnicki 1988, DeAngelis & Gross 1992, Uchmański & Grimm 1996). IBMs are currently popular among ecologists, and even though IBMs are good for solving a range of different problems, there is an important deficit: IBMs are really no more than a philosophy of modelling. A number of bookkeeping methods conform to this philosophy by enabling populations to be made up of individuals that differ rather than being identical in their characteristics. IBMs manage to solve some problems where models based on average individuals fail (Judson 1994), but IBMs have no way of motivating individuals for actions or calculating optimal life histories. Hence an important aspect is missing which can be found in many A-life models. By incorporating a GA into an IBM the evolutionary aspect can be provided, which makes the IBM a robust tool for calculating optimal life histories. If an IBM is to be used as a spatial model there is need for a formalised way to relate environmental variables and state variables to the behaviour of the animal. In SDP models this relationship emerges directly from the dynamic programming equation (Mangel & Clark 1988). In models where the solution space is large, however, a different way of relating environment and internal state to behaviour has to be used. A common way of doing this in A-life is to apply an artificial neural network (ANN). The ANN is a computing method inspired by a model of how the human brain functions. Neurons in the brain are interconnected by synapses; similarly layers of nodes in an ANN are linked together and pass signals between each other. The ANN paradigm was initiated by McCulloch & Pitts's (1943) theoretical outline of the two-state neurone. Since then there has been a considerable development in ANNs, and today a wide variety of ANN architectures are available (Rosenblatt 1958, Hopfield 1982, Kohonen 1984, Rummelhart & al. 1986, Montana & Davis 1989). The combination of GAs and ANNs has been applied in many A-life studies (e.g. Ackley & Littman 1992, Menczer

& Belew 1996), but in few ecological simulations (e.g. Dagorn & al. 1997). By combining the GA and ANN in an individual based setting the ING (individual based neural network genetic algorithm) concept emerges, and a schematic outline of this concept is provided in Fig. 1. Hence we have individuals that are equipped with a string that is used in an ANN to calculate behavioural actions. Profitable behavioural codes will be evolved as individuals reproduce and pass on their strings in new recombined versions (Fig. 1). This concept is here applied in spatial life history models of fish migration.

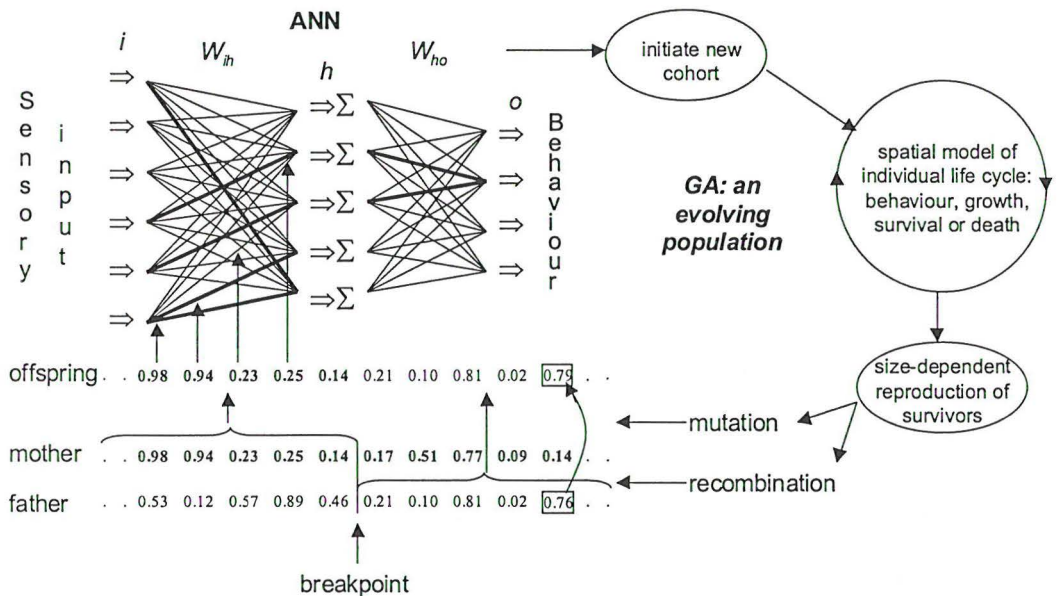


Figure 1. The ING concept with ANN based behaviour and GA based evolution in an individual-based setting. A cohort of individuals with randomly set strings which code for the weighting of the ANN, is initiated in the first time step. The individual's life cycle is simulated, and when maturity is reached, individuals reproduce and new recombined, possibly mutated individuals emerge. 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. Diagram is taken from Paper IV.



## The capelin

The capelin belongs to the family *Osmeridae* and has a circumpolar distribution in the Northern Hemisphere (Jangaard 1974). Four major capelin stocks prevail in the Atlantic: the Newfoundland-Labrador, the West Greenland, the Icelandic and the Barents Sea stocks (Jangaard 1974, Vilhjálmsson 1994). Despite many common features, the stocks differ with respect to life history traits such as spawning mode (beach or deep water), fecundity and egg size (Stergiou 1989). The capelin is exploited commercially and the Barents Sea stock, which historically is the largest, may reach abundances of up to 8 mill. tonnes (Gjøsæter 1995). During summer and fall the capelin preys heavily on copepods and krill (Lund 1981, Huse and Toresen 1996), and it serves as food for a number of fishes, seabirds, and marine mammals throughout the year (Jangaard 1974, Mehl 1989, Vilhjálmsson 1994, Haug & al. 1996, Nordøy & al. 1996). Maximum size of the Barents Sea capelin is about 50 g and 25 cm. The Barents Sea capelin matures at age 3-5 years, at a size of about 15 g and 14 cm. The life cycle of the Barents Sea capelin is illustrated in Fig. 2. The geographical distribution of the capelin is closely associated with the Polar front throughout most of the year. During summer the capelin follows the retracting front and preys on the secondary production in the rich waters (Hassel & al. 1991). As fall approaches, the capelin follow the Polar front southwards. The juveniles overwinter along the ice border (Fig. 2) whereas the mature fish migrate further south and overwinter closer to the coast of Northern Norway (Gjøsæter 1995). During spring the adults migrate to the coast of Northern Norway where they spawn (Fig. 2). During the spawning migration and on the spawning ground the adults are heavily preyed upon by cod (Mehl 1989, 1991). Spawning takes place on sand and gravel at depths of 10-100 m (Sætre & Gjøsæter 1975). During the spawning season the male capelin develops secondary sex characteristics as hairy spawning ridges of longitudinally enlarged scales and a swollen anal fin. Outside of the spawning season it is difficult to separate the two sexes by external examination (Vilhjálmsson 1994). Most males die following spawning, from exhaustion and injuries caused by the violent digging behaviour during reproduction (Bakke & Bjørke 1973, Friðgeirsson 1976). Females on the other hand, can survive to spawn in repeated spawning seasons (Friðgeirsson 1976, Shackell & al. 1994). The eggs are about 1.1 mm in diameter at hatching, which occurs after 1-2 months depending upon the temperature (Gjøsæter & Gjøsæter 1986). During May-July the larvae are widely distributed in the southern Barents Sea (Fossum 1992, Gundersen & Gjøsæter 1998). The mortality regime of

the larvae varies extensively between years, and this is an important factor in regulating capelin population abundance (Hamre 1991, Fossum 1992, Bogstad & Gjøsæter 1998). Juvenile herring spends the first 2-4 years in the southern Barents Sea where they may be very abundant following years of good recruitment. High larval capelin mortality is observed in years when herring is abundant in the Barents Sea (Hamre 1991, Fossum 1992, Bogstad & Gjøsæter 1998). It thus seems plausible that the high larval capelin mortality is caused by predation from the juvenile herring as indicated from stomach samples of herring (Huse & Toresen 1995).

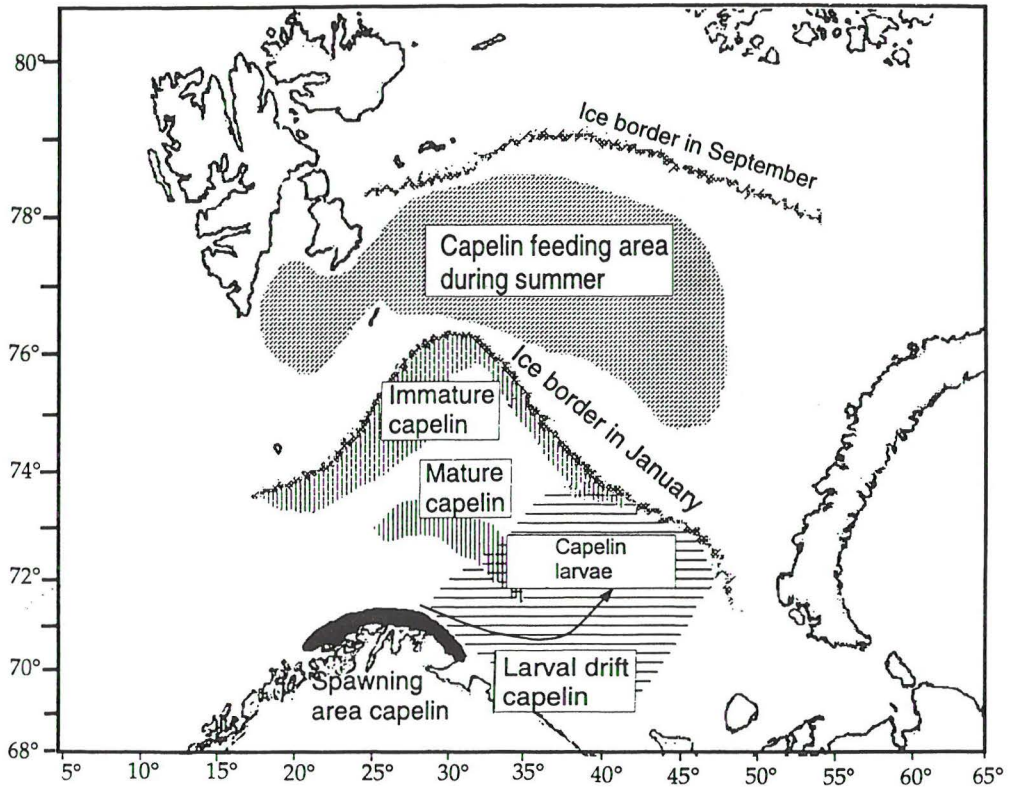


Figure 2. Distribution and migrations of the Barents Sea capelin stock. Redrawn from Gjøsæter (1995).

## The Papers

### *Paper I: Capelin fecundity*

A field investigation of capelin fecundity is presented. It is motivated from the fact that offspring production of females is ultimately limited by their fecundity. Fecundity data can hence be applied to improve stock recruitment models in fisheries assessment. In this thesis it is applied to study life history strategies in capelin and to estimate offspring production at female size in a spatial model.

The fecundity and oocyte diameter of 70 female capelin from different locations in the Barents Sea were investigated. An average fecundity of about 11 500 was found. The oocyte size was quite uniform within ovaries although there was a slight increase from anterior to posterior. The oocyte diameter as well as the fecundity increased with increasing weight and length of the female. It is suggested that the increase in oocyte diameter with increasing female size may affect recruitment so that higher larval survival associated with larger eggs could be expected in years with larger females. Inter-annual variation in capelin fecundity is large, but corresponds to individual differences in body weight.

### *Paper II: Capelin life history and the importance of sex*

This paper discusses the relative profitability of iteroparity and semelparity for male and female capelin based on the idea that the environment inhabited by capelin affects the sexes differently with regard to life history. Whereas males by mating with many females may increase their Darwinian fitness in an additive manner, the number of eggs a female can carry and spawn limits her potential fitness. Females may only increase their fitness by undertaking several spawning seasons with yearly intervals or through growing larger and becoming more fecund. Since the females for the most part lay all their eggs in one batch (Templeman 1948, Friðgeirsson 1976), males can get large fitness gains from each reproductive event. The adult mortality of capelin is very high (Mehl 1989, 1991) and to a large degree associated with migration through a belt of predacious cod. If the capelin spawns only once, it only passes through the cod area once, but if it is to spawn twice, it has to pass through the belt three times (Giske & al. 1998b). The high adult mortality risk is traded off against the "cost" of having all offspring produced within one season. This fitness "cost" may be quite high depending on the mortality of the larvae. In years when

juvenile herring is abundant in the Barents Sea the mortality of larval capelin is very high due to predation from herring (Hamre 1991, Fossum 1992, Huse & Toresen 1995). Energy for maintenance in females is traded off against investment in eggs. The amount of energy required for post spawning survival seems to be low in capelin since feeding can be initiated shortly after spawning and in the same area.

A life history simulation model which takes adult mortality and observed recruitment variability into account predicts that for females, iteroparity is more profitable than semelparity. For males, semelparity with several matings may be as profitable as iteroparity depending on the level of the adult mortality. These predictions are supported by: 1) reports of individual males mating with several females during a spawning season, 2) a lower gonadosomatic index in males than in females while males instead spend their energy on mating and somatic growth, 3) an observed higher mortality for males after spawning. It therefore seems plausible that the life history strategy of capelin is sex-specific with a semelparous batch-spawning male and an iteroparous female. However, even though the female follows an iteroparous strategy, the likelihood of repeat spawning is quite low due to the high predation risk, associated with spawning migration.

### ***Paper III: Ecology in Mare Pentium***

The aim of this paper was to develop a concept for modelling the spatial distribution and population dynamics of fish. An individual-based neural network genetic algorithm (ING) model inspired by recent developments in A-life was applied. The weights in the ANN are evolved using the GA and this concept produces individual movement behaviour in a spatially heterogeneous and seasonal environment referred to as "Mare Pentium". A 2-D physical model creates monthly temperature fields, which are used to calculate zooplankton production and predation risk. Fish movement could either be controlled by reactive or predictive mechanisms (Neill 1979, Fernø & al. 1998). Predictive movement is defined as movement directed towards areas that can be expected to possess certain qualities, for example a lot of food, conspecifics, etc. Reactive movement on the other hand relates to movement that is biased by recent experience (Neill 1979). Two ANNs relying on different input variables were used to represent this dichotomy. Each individual is scaled up to represent a clone of millions of siblings, which act and grow synchronously. In this way an individual based model can be used to simulate abundances similar to that of a pelagic fish stock. All interactions with the environment take place in this scaled up mode. During spawning, individuals produce a number of offspring in proportion to

body size. The strings of offspring are a mix of their "mother's" and a randomly picked member of the population.

The seasonal movement of the modelled fish follows a pattern typical for migratory pelagic fish stocks. During summer and autumn the distribution is widespread whereas during spring it is more concentrated. When trophic feedback between fish and zooplankton is removed, the fish is less dispersed which shows the importance of density dependent behaviour. The results indicate that fish movement is an interplay between reactive and predictive movement control, where the first is used during feeding and the latter during migrations. When only the reactive or the predictive network is allowed, the individuals were unable to adapt properly within the current framework. Neill (1979) applied the predictive/reactive dichotomy to movement of fish in relation to temperature optimisation, and Fernø & al. (1998) applied it to discuss migrations of Norwegian spring spawning herring. Also a similar type of control is often used in autonomous robots (Donnart & Meyer 1994) which are faced with many of the same problems that animals have. The division into reactive and predictive movement seems to be important for controlling behaviour, and it may even be profitable to increase the number of categories for classifying behaviour.

#### ***Paper IV: A spatial life history model of capelin***

The developments from Paper III are elaborated and applied in a more realistic setting to model the life history and spatial dynamics of the Barents Sea capelin. The physical model is similar to that in Paper III, but with the addition of land contours for the Barents Sea. Results from all of the previous papers are incorporated including: size fecundity relationships from Paper I, the importance of representing each sex explicitly when simulating life history strategies seen in Paper II, and the modelling concept developed in Paper III. Life history traits such as size at maturity, timing and the location of spawning, and allocation of energy, are evolved within the confines of the model. The entire life cycle of the capelin is modelled explicitly, including egg, larval, juvenile and adult stages. The eggs are demersal, but following hatching the larvae start to drift in a north east direction, and later they start to move around according to their own will. The predictive/reactive dichotomy is applied, but is implemented through a direct migration approach instead of the predictive ANN as used in Paper III.

Simulations with deterministic and stochastic environments are performed. The results show that both the evolution of timing of spawning and the choice of spawning area rapidly converge towards areas and times of capelin spawning. The problem of

finding mates in a large ocean is illustrated since only a few spawning areas are evolved. The spatial distribution of the simulated fish shows good resemblance to the general distribution pattern of the Barents Sea capelin (Fig. 2), with summer feeding in the north eastern part of the sea and spawning along the coast of Norway and Russia during spring. A simulation with inter-annual variation in juvenile and adult mortality evolves sex dimorphism in size and life history strategy, with large semelparous males and small iteroparous females. This latter result supports the findings in Paper II where it was suggested that capelin has sex specific life history strategies. In the stochastic run there is great variation in abundance and biomass which resemble the abundance variation observed in the Barents Sea capelin stock.

## **Discussion**

### **Life history strategies**

It was predicted in Paper II that capelin has sex specific life history strategies. This prediction is supported by the available literature on capelin and by the results in Paper IV where sex specific life history strategies emerged in the stochastic simulation. The mortality schedules applied in Paper IV are representative of those that constrain the evolution of capelin life history. Hence many indices suggest that male and female capelin have different optimal and actual life history strategies.

Size at maturity is generally considered to be a trade off between present vs. future offspring production (Roff 1992). In a growing population there is a strong selection pressure for maturing early due to the effect of compound interest of grandchildren (Sibly & Calow 1986, Giske & al. 1993). It has been hypothesised that the size at maturity in capelin is further constrained by the migration distance between the feeding area and the spawning ground (Nøttestad & al. in prep.). The Balsfjord capelin stock inhabits a fjord in Northern Norway, but the stock does not appear to be genetically isolated from the Barents Sea stock (Mork & Friis-Sørensen 1983). Size at maturity for females in the Balsfjord stock is about 11 cm (Nyholmen & Hopkins 1988) compared with 14 cm for the Barents Sea stock (Forberg & Tjelmeland 1985). Also the Balsfjord capelin matures mostly as two years olds, which is one to three years ahead of the Barents Sea stock (Olsen 1968). During most of the year the capelin resides in the deepest basin of the fjord, but prior to spawning it migrates to the head of the fjord, a distance of about 30 km (Nyholmen & Hopkins 1988). By comparison the Barents Sea stock usually undertakes a spawning

migration of at least 250 km (Paper II). The energy reserves of a capelin at 15 cm are approximately similar to the estimated energy expenditure of a typical capelin spawning migration (Paper II). The other oceanic capelin stocks, the Icelandic and Newfoundland stocks, have a size at maturity similar to that of the Barents Sea capelin (Templeman 1948, Vilhjálmsson 1994). The lower size at maturity in the Balsfjord capelin therefore supports the theory that maturation in Barents Sea capelin is constrained by the migration distance from wintering areas to the spawning ground. Below a length of 20 cm it becomes costly to swim due to increased drag (Ware 1978, Nøttestad & al. in prep.), and migratory fishes should be above this size. Repeat spawning in the Barents Sea stock may be constrained by its marginal body size both in terms of energy requirements (Paper II) and swimming-size efficiency (Nøttestad & al. in prep.) in addition to the mortality factors mentioned above. This idea is substantiated by the higher occurrence of iteroparity in Balsfjord capelin, the extent of which seems to be about 25% for females (Nyholmen & Hopkins 1988). For Balsfjord capelin to rebuild following spawning it only has to migrate 30 km back to its main residence area at a lower energetic cost and probably under a much lower exposure to predation risk than for the Barents Sea stock.

### **Population dynamics**

As well as being important constraints on the evolution of life histories, the high predation rates are responsible for some tremendous variations in abundance that are characteristic for the capelin. During the early larval phase, capelin is very vulnerable to predation and it seems unable to avoid predatory attacks from fish (Moksness & Øiestad 1987). Consequently recruitment failure is prominent in years when juvenile herring is abundant in the Barents Sea. Since most individuals only spawn once, the capelin abundance is particularly sensitive to recruitment failure. During the period 1984-1990 the stock went from an abundance of 3.0 mill tonnes down to 0.1 mill tonnes and back up to 5.8 mill tonnes (Gjøsæter & al. in press.). This shows that although the capelin is vulnerable to recruitment failure, it is able to rebuild rapidly following population crashes. By comparison, the rebuilding of the Norwegian spring spawning herring stock took almost 20 years following its collapse in the late 1960s (Dragesund & al. 1997). An analysis of anecdotal evidence ranging 300 years back in time suggests that the collapse-rebuild pattern observed during the 1980s and 90s is the rule rather than the exception (Øiestad 1992). In addition to the recruitment driven population crashes, an intrinsic feature tends to amplify the population dynamics. In years with high individual growth, a larger fraction of the

younger age groups will mature. This yields a greater spawning stock, but also a consequent drop in the post larval population abundance due to low survival of spawners (Hamre 1991, Gjøsæter 1995).

## 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, Fiksen 1997). Vertical and horizontal migration should be understood from common principles. Outside the spawning season the distribution of fishes should therefore be analysed as a trade off between growth and mortality (Werner & Gilliam 1984). The importance of including mortality risk as a factor in fish distribution is illustrated in Fig. 3 where cod abundance is plotted against average ambient temperature in areas occupied by capelin during summer and fall (Paper IV). There is a clear trend towards capelin occupying colder waters when cod is abundant. Cod rarely enter waters of temperatures below  $-0.5^{\circ}\text{C}$  (Rose & Leggett 1988, 1990) and hence waters colder than this act as refuges from cod predation (Rose & Leggett 1990). The somatic growth of capelin is generally higher in the warm south-west Barents Sea than in the relatively cold north-east area (Gjøsæter & Loeng 1987). Since opportunities for growth are better in the south, the northward migration of capelin seems to be partly motivated by predator avoidance (Fiksen 1995). In Paper IV there is a strong tendency for the fish to seek the predation minimum at the  $0^{\circ}\text{C}$  isotherm rather than the zooplankton production maximum further south-west. A similar trend is detected in Paper III as well, where the highest fish abundance is generally associated with areas of low mortality. This supports the argument that predation avoidance is an important component of the motivation for staying in the Polar front area during summer.



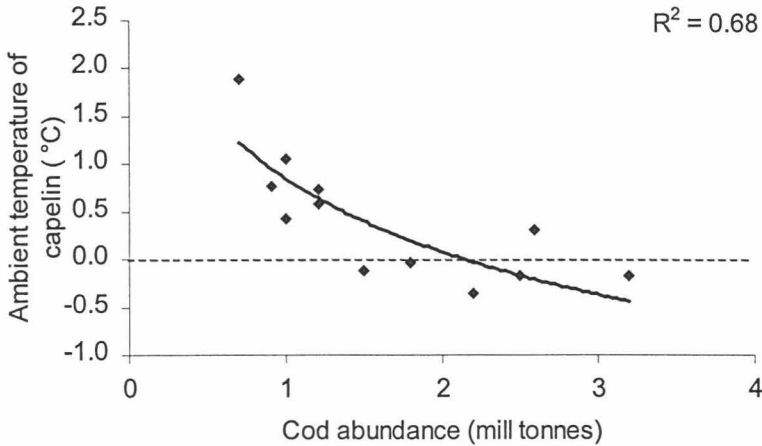


Figure 3. Abundance of cod plotted against the average ambient temperature of areas occupied by two and three year old capelin during fall. Capelin data are taken from Gjørseter & Loeng (1987) and the cod data from Anon. (1998). Taken from Paper IV.

Growth and survival are important adaptive features of horizontal migrations, but migration in fishes has also evolved to optimise spawning location. In order to analyse spatial distribution in migratory fishes the evolution of spawning area should therefore be addressed. Paper IV 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 subsequent stages was made relative to the spawning area. Slotte & Fiksen (in prep.) suggested that choice of spawning ground in Norwegian spring spawning herring depends upon the condition of the individual herring. Prior to spawning, the herring migrates in a southward direction, which means that the further south the spawners migrate, the warmer the water is going to be and the faster the larvae will grow in general. This is traded off against the migration costs, and the fish with the best condition migrates the furthest. The importance of warm water for larval growth was seen in Paper IV where larval drift was associated with a tongue of warm water that stretched from west to east in the southern part of the model area. Since larval growth, and indirectly mortality, was linked to temperature, the adaptive value of drifting in this warm water is apparent. 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, since the same spawning area was evolved in both the computer runs (Paper IV). In Paper IV it was shown that by starting with random individuals, highly synchronised populations emerged after a period of simulation. Simple animals hence carry out life in a similar fashion to the Barents Sea capelin. Iles & Sinclair (1982) proposed the member/vagrant hypothesis to explain stock formation and maintenance of Atlantic herring stocks. This theory suggests that population abundance is determined by the size of the larval retention area associated with spawning sites. An alternative view is metapopulation theory, which instead suggests that population dynamics are driven by local extinction and colonisation from the larger metapopulation (Levins 1969, Hanski 1996, McQuinn 1997). These theories provide a starting point for discussions regarding life cycle closure in fish stocks. Simulation models (Paper IV) provide a means to study the circumstances under which metapopulation or member/vagrant theory gives the best explanation for population dynamics. In the computer runs in Paper IV, especially during early stages, spawning often occurred on several separate spawning grounds. In a sense this can be thought of as sub populations in a larger metapopulation. However, since spawning only was allowed within a short distance of the inherited spawning position, there was only exchange of strings between neighbouring sub populations. Less rigid criteria for spawning would probably have increased the exchange.

### **Trophic links**

The rich production in the Polar front areas is ensured by an availability of nutrients for phytoplankton as the sea ice retreats throughout summer (Rey & Loeng 1985). During its northward migration the capelin feeds heavily and decimates the abundance of its prey (Hassel & al. 1991). In order for this depletion to affect habitat choice, prey abundance must be decreased in response to feeding. A more widespread distribution of individuals was found in Paper III when trophic feedback was included, which shows that the ING approach is able to implement this factor in behavioural decisions. Even though production in the Barents Sea is high, the individual growth of the capelin seems to be controlled by density dependent factors (Skjoldal & al. 1992), and the weight at age varies considerably between years (Anon. 1998). Trophic links are therefore of considerable importance in understanding the dynamics of the Barents Sea system. Although it is of particular importance to the capelin, many other animals manage to decimate their prey density and have to change location in response to local depletions. Simple patch dynamics can be implemented using IFD, which assumes that individuals select patches in

such a manner that all individuals receive the same pay off (Fretwell & Lucas 1970, Giske & al. 1997). Hence if patches are decimated, the individuals will respond by redistributing themselves. Some of the assumptions of the IFD distribution such as no movement cost between patches and complete knowledge of patch profitability make IFD unsuited for modelling large-scale habitat choice. In SDP models the fitness of all possible solutions are initially calculated in a backward procedure (Mangel & Clark 1988). This matrix of all the possible solutions can then be used in a forward routine by selecting optimal strategies from the matrix, given current state. This method has been applied extensively in calculating patch choice (e.g. Rosland & Giske 1994, 1997, Fiksen & al. 1995). If the prey abundance at a patch is reduced as a result of feeding, the matrix needs to be recalculated since the profitability of the patches is changed, which may change the optimal decision. This implies that environmental feedback is difficult to implement in SDP models.

## **Fitness**

It is common to compare the success of different behavioural or life history strategies by using a measure of Darwinian fitness (e.g. Roff 1992, Stearns 1992). The argument behind the application of fitness measures is that the particular feature or trait under investigation has become optimally adapted over evolutionary time under the given boundary conditions (Stearns & Schmid-Hempel 1987, Parker & Maynard Smith 1990). Although there is an ongoing debate of what is the ultimate definition of fitness (Stearns 1992, Giske & al. 1993, Yoshimura & Clark 1993, Mylius & Diekman 1995), there seem to be a consensus about the importance of including aspects of survival and fecundity into the fitness definition. The common fitness measures based on this assumption are the intrinsic rate of increase  $r$  and the net reproductive rate  $R_0$ . These fitness measures are hampered by strict assumptions: 1) no density dependence, 2) no stochasticity, 3) no frequency dependence, and 4) repeated vital rates for all offspring (Stearns 1992). The problems listed above limit the applicability of fitness measures in ecology. Fitness in stochastic environments can be calculated using stochastic demography (Cohen 1966, Tuljapurkar 1982, Tuljapurkar 1990, Yoshimura & Clark 1993), where assumptions about the magnitude of environmental stochasticity and degree of autocorrelation (correlation between consecutive values) are provided (Metz & al. 1992). Density dependent situations can be tackled using analysis of evolutionary stable strategies (Maynard Smith 1982, Metz & al. 1992, Mylius & Diekman 1995). Due to the complex mathematical analysis that is required, the latter two approaches are difficult to implement into coupled physical-biological

models.

The model in Paper II applied geometric mean fitness of individuals following a strategy with inter-annual variation in the vital rates. The fitness of the strategies was calculated for all the observed environmental conditions. Geometric mean finite rate of increase was then calculated for each strategy over 100 000 years of simulation given the frequency of the different observed years. In this manner stochasticity was allowed to impact on the fitness of different strategies.

Traditionally, fitness measures are applied to evaluate solutions in GAs, and it is common to select strings in proportion to their fitness (Goldberg 1989). GA fitness measures are parallel to fitness measures applied in behavioural ecology, and act as test criteria for specific tasks (Goldberg 1989). A new class of GAs works without an explicitly stated fitness measure, and instead applies an endogenous fitness criterion (Ackley & Littman 1992, Mitchell & Forrest 1995, Menczer & Belew 1996). In endogenous systems, no fitness measure to maximise is provided, but rather fitness emerges by interactions between the environment and the organism. 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. Such models come closer to the way in which evolution works: through "adaptation execution" rather than by "fitness maximisation" (Wright 1994). Many of the areas in which conventional fitness measures meet problems such as stochastic environments and density dependence are handled naturally through simulations using endogenous fitness (e.g. Menczer & Belew 1996). Since the resources provided in an endogenous system are finite, the system functions in a density dependent manner (Menczer & Belew 1996). Furthermore, the rate of food provision and the mortality rates may be varied inter-annually in a stochastic fashion. The benefit of endogenous fitness is the lack of constraints imposed through assumptions, and the general applicability of the approach in ecological simulations. A restriction set by this approach is the necessity of implementing the entire life cycle in order to simulate reproduction as part of the model. In ecological models that span over short periods of the life cycle, the endogenous fitness definition is not applicable. Since endogenous fitness is defined locally by the criteria set for growth, survival and reproduction, endogenous fitness cannot be wrong. This is due to the circularity of the fitness definition. However, the degree to which endogenous models provide similar predictions as models based on conventional fitness measures or to observations, is largely unexplored. The model in Paper IV was developed to mimic natural systems, and an emphasis was put on setting criteria for reproduction that were similar to the constraints found in nature. Under such circumstances

endogenous fitness represents the selection pressure found in nature and model predictions have a solid basis for comparisons with observations. Still the model in Paper IV has some discrepancies with how growth, mortality, and reproduction occur in a natural system. The number of new strategies and siblings produced during reproduction in Paper IV for example is constant and independent of how many siblings are left of the strategy. A different way to implement this would have been to let the number of siblings of each new strategy depend upon the number of siblings left in the parent strategies. Alternatively the number of new strategies could have depended upon the number of siblings left in the parent strategies. Such representations of the reproductive system would probably resemble nature in a better way, and they were tried initially. However, their use added a great deal of instability to the system and they were abandoned. When comparing different simulations carried out in endogenous systems, it is useful to apply a measure for comparison. In Paper IV this was done using population abundance (Menczer & Belew 1996).

The life history strategy predictions given in Paper IV were in accordance with observations as well as with predictions provided in Paper II. This shows that predictions made using endogenous fitness compare well with observations, but nevertheless comparative tests of predictions made by endogenous models and models based on conventional fitness measures should be undertaken.

## **ANNs & GAs**

A central theme in this thesis has been the application of ANNs and GAs. These methods are the topics of several symposia every year and have a wide sphere of application. They are young, but firmly established fields of science. Despite this manifestation there are pros and cons with these techniques as for most other methods. The GA has a potential problem of getting stuck at a local optima in multi-peaked fitness landscapes, a feature that is shared by its originator process – organic evolution (e.g. Parker & Maynard Smith 1990, Ridley 1993). There are ways to get past such problems. For example Sumida & al. (1990) proposed a method based on evolutionary shifting balance theory (Wright 1977) where the GA is made up of a set of sub-populations instead of one large one. The shifting balance method proved to be more efficient than the common version of the GA in solving the complex problems presented. In a different experiment using both the shifting balance GA and the standard GA, Sumida & al. (1990) showed that the optimal policy for singing in birds as previously found using dynamic programming, was

evolved using both the GAs. Despite some shortcomings, the GA thus usually finds near optimal solutions quite efficiently. A practical way of ensuring this may be to simply apply a large number of generations, large population size, or to use methods such as the one applied by Sumida & al. (1990). A problem associated with the current migration models (Papers III and IV) is the extensive computing time needed, which limits the number of years for which the model can be run. Ideally the model should have been run over more generations to test how the solution develops over many years. The association between larval drift and warm water areas in Paper IV is encouraging as it shows the ability of the model to find what appears to be adaptive peaks in the fitness landscape. A feature that mimics the shifting balance GA is the development of sub populations that may exchange “genetic” information (Paper IV). This bears resemblance to metapopulation theory and may be favourable for the efficiency of the GA.

Although I have only used the GA to evolve the weights of the ANN, learning could have been applied instead, or as a complimentary method, a technique that has proved effective in many A-life studies (Hinton & Nowlan 1987, Ackley & Littman 1992). It has been argued against ANNs that they are “black box” models whose behaviour is hard to interpret (Sharkey & al. 1994, Andrews & al. 1995). There may be ways around this “black box” nature of the ANNs if the weights can be analysed in a constructive manner to give biological meaning. Another potential problem with ANNs is the lack of formalisation in model development and therefore the empirical nature of network construction. I find this latter objection more troublesome, and it usually takes a lot of effort to find the best way to build the network by choosing the best number of nodes and hidden layers. For the present tasks it was not obvious which type of input data should be provided in order for the network to be most effective. This aspect of ANNs is more art than science, with a lot of “common sense” type decisions involved. The potential for formalised network compositions is there, but needs to be explored further along with tests of whether different network architectures give different adaptations. Despite these objections ANNs provide a general and efficient method to model actions and decisions in ecological models that should be explored further.

### **Artificiality vs. reality in ecology**

No theory, either verbal analytical or numerical, can explain everything that we consider as reality. In this sense theories describe artificial worlds, and this is made explicit in A-life. In this thesis, techniques that have been successful in A-life are

applied to simulate real life. A-life may directly provide conceptual understanding of how complex systems, such as Earth ecology, function and behave, through simulations of artificial systems that resemble the basic properties of an ecosystem.

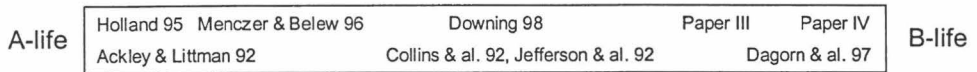


Figure 4. The spectrum between A-life and B-life with some central studies placed.

Fig. 4 shows the spectrum of studies between A-life and B-life. For example, the Echo project of Holland (1995) aims at building artificial ecosystems of great complexity as a tool to learn more about conventional biology. This is simulated at the very left of Fig. 4. It is common in A-life to apply “minimal models for an idea” (Roughgarden & al. 1996) where all unnecessary detail is avoided and the specific topic is focused upon. Ackley & Littman (1992) aim at studying the interaction between learning and evolution employing evolutionary reinforcement learning (ERL). Menczer & Belew (1996) investigate how complex environments affect behaviour in their latent energy environment (LEE) concept. These are examples where questions of importance to evolutionary ecology are studied using minimal models. The three models referred to above are at the very left of Fig. 4. One step closer to B-life is the Euzone simulator of Downing (1998) which model evolution of a specific ecosystem, namely plankton in the euphotic zone. Somewhat further to the right are the scent tracking ant model Genesys/Tracker (Jefferson & al. 1992) and the AntFarm model (Collins & al. 1992), which model co-operation in ants. These latter three models aim specifically at studying properties in artificial systems that resemble specific components of earth ecology. Studies situated in this part of the continuum in Fig. 4 may be productive in focusing on problems in biology, but still maintain a high degree of artificiality. At the right of the spectrum we find models such as the one in Paper IV, which rather than being classified as A-life, have adopted this approach to study a specific biological problem. Other models that conform to this latter category are the studies of Dagorn & al. (1995, 1997) on tuna schooling and migration. The model of Dagorn & al. (1997) did, however, not apply an endogenous fitness, and tuna movement was controlled solely by temperature data. The problem of fish migration was handled in this thesis by starting out with a general model in Paper III, which then was made more realistic in Paper IV. In general it may be productive to start out

at the left of the continuum with a minimal model (Roughgarden & al. 1996) and in consecutive steps move to the right by increasing the realism of the simulation.

### **Evolutionary systems and specific ecology**

It has been shown throughout this work that evolutionary systems have many advantages over conventional modelling approaches in biology with regard to stochasticity, fitness measures, dimensionality, generality, density dependence and other factors. One problem that was recognised here is the difficulty in simulating "realistic" ecology or rather implementing the ING technique into a simulation model of a species. This probably has its basis in the lack of constraints in the evolution of the life history and the spatial dynamics of the animals. If a realistic behaviour is to be expected, the model should be forced in a more restrictive manner in order to follow an evolution trajectory similar to that of the particular animal. By imposing such constraints, however, the model loses some of its explanatory power (Loehle 1983). The degree to which one should try to force the adaptive system in a specific direction should therefore depend on the nature of the problem one is trying to solve. If the model is to be applied as a calculation tool (Loehle 1983) in, for example, fisheries assessment, then the model could to a large degree be directed by constraining spawning and feeding areas in correspondence with those observed for the particular species rather than letting these features be evolved. Even though explanatory power is lost, such a model may be applied to calculate population dynamics and spatial patterns that are quite "realistic". A different approach is the one taken here where even though many parameters and some forcing functions were similar to those of the capelin and the Barents Sea, the evolution was unsupervised. Rather than expecting the ecology of the Barents Sea capelin to emerge from such a setting, what evolved here could be thought of as a possible route of evolution for a pelagic fish in the Barents Sea. An alternative to constraining evolution is to provide a more accurate description of environmental features. This would probably have improved the fit of the simulated fish distribution with observations in Paper IV. Model testing has been discussed extensively elsewhere (Loehle 1983, Jørgensen 1988, Orzack & Sober 1994, Hilborn & Mangel, Mangel & al. in press) and will not be pursued here. The models used here have been verified for internal logic, and for consistency with ecological theory. Finally, the predictions from the models have been evaluated by comparisons with observations as discussed above. Model evaluation has therefore followed the common procedure for testing theoretical models (Mangel & al. in press.).



## Epilogue

Among the limitations of the current work is the choice of spatial scale to study. I have only studied distribution on a macro scale, and in the analyses largely neglected the importance of the meso- and micro scales. This has been a conscious choice from the realisation that the macro scale is the most productive scale for the problems addressed here. As advocated by Fernø & al. (1998) an effort should be made to increasingly link the different scales in modelling studies.

Much emphasis in this thesis is put on methodological aspects (Papers III & IV) rather than on testing specific theories in ecology. The deficiencies of conventional models in ecology became apparent when the specific issues of capelin migration related to trophic links and stochastic environments were addressed. I therefore think that the need for new tools in ecological modelling justifies the skewness towards method development in the present contribution. The concept for fish migration that was developed in the latter two papers is the major achievement of this work and is likely to form a basis for future efforts in modelling spatial dynamics of fish (Giske & al. 1998). The recognition of sex specific life history strategies in capelin is another important finding. Areas in which the current modelling approach may be prosperous have been pointed out, and problem areas have been addressed. By taking in results from A-life this thesis provides a link to a young but promising field. Although the communication between ecology and A-life has been sparse (Toquenaga & Wade 1996), there are now some initiatives that may act to close the gap (Dagorn & al. 1995, 1997, Belew & Mitchell 1996, Le Page & Cury 1996, 1997, Menczer & Belew 1996, Paper III & IV). I think we will see an increasing interaction between A-life and ecology in the years to come - a connection that could be very fruitful for both fields of science. Mathematicians and computer scientists "took" the GA and the ANN from biology - perhaps it's time for biologists to take them back!

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