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# Models for Multispecies Management

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## Ecological Modelling for Fisheries

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### HARVESTING A DYNAMIC ECOSYSTEM

#### Historical perspective

Large fluctuations in the fisheries have been a characteristic feature of great importance in the history of the Norwegian people. Herring periods have been times with large fisheries for herring spawning along the west coast of Norway, alternating with periods when the herring was gone. Herring periods and periods without herring appear to have been of cyclic nature with a periodicity of about a century (Devold 1963, Dragesund & al. 1980, Skjoldal 1990, Øiestad 1990). Towards the end of the last century, a common explanation for such fluctuations was that it reflected variable migration routes and therefore variable availability of perceived stable fish stocks to coastal fisheries. When ICES was established in 1902, a standing committee called the Migration Committee was created to deal with such issues (Sinclair & Solemdal 1988). However, in his classical book, Johan Hjort (1914) identified large fluctuations in stock size due to variable recruitment as a major source for fluctuations in the fisheries. Variable recruitment is an inherent property related to the reproductive mode of fishes with high fecundity and which produce a high number of larvae that are part of the planktonic system (Skjoldal & Melle 1989).

The large fluctuations in the fish stocks have caused many fishery crises that have focused the attention of the public, managers, and politicians on the need for better knowledge of the underlying causes. In the 1870s when herring had disappeared, G. O. Sars and H. Mohn were given the task to organise the "Vøringen" expeditions which explored the Norwegian Sea with the main motivation to search for the lost herring. Around the turn of the century there was a crisis in the cod fishery in northern Norway which coincided with massive seal invasions (Skjoldal 1990). Species interactions were considered to play an important part in current explanations for the crisis at that time. Fishermen believed that killer whales had large baleen whales and seals as their main prey. With the depletion of the stock of large whales by the whaling industry developed by Sven Foyn from the late 1860s, killer whales were believed to no longer frequent the area which then was open for seals to invade (Hjort 1902).

The events at the turn of the century took place during a cold climatic period. 1902 was a cold year with extensive ice cover during the winter. 1903 marked the peak in the fishery crisis with low catches in the cod fishery with small cod in poor condition,

massive seal invasion during winter, and large number of dead seabirds reported. From 1902 to 1904 there was a warming trend and in 1904 strong year classes of cod and herring were formed (Hjort 1914, Skjoldal 1990). The fishery crisis resulted in increased research effort. With the new research vessel "Michael Sars" built in 1900, systematic oceanographic and fishery investigations were carried out that resulted in benchmark publications (Helland-Hansen & Nansen 1909, Hjort 1914) during the "golden age" in Norwegian oceanographic research that ended during the first World war.

Nearly a century later, during the 1980s, events that resembled the events at the turn of the century, again took place in the Barents Sea. The capelin stock collapsed, the cod stock decreased and cod were small and in poor condition, there were seal invasions along the coasts of northern Norway, and there was heavy mortality in seabird colonies at Spitsbergen and in northern Norway (Skjoldal 1990, Blindheim & Skjoldal 1993). Due to an increasing awareness of the need to understand and take into account ecological relationships as a basis for management, the research program PRO MARE (Sakshaug & al. 1991, 1994) was run from 1984 to 1989 during the period of dramatic changes in the Barents Sea ecosystem. Along with results from routine fishery investigations, PRO MARE has provided us with a reasonable understanding of the main ecological features and causes for variability in the Barents Sea ecosystem (Skjoldal & Rey 1989, Sakshaug & Skjoldal 1989, Skjoldal 1990, Sakshaug & al. 1991, 1994).

The ecological events and the fishery crisis in the Barents Sea during the 1980s followed the longest and coldest period in the Barents Sea since the cold period at the turn of the century. The cold period from 1977 to 1981 coincided with the arrival of the "great salinity anomaly" which has been related to a large outflow of water from the Arctic Ocean through the East Greenland Current in the 1960s (Dickson & al. 1988). This anomaly affected or coincided with changes in fish stocks along its route of progress in the Nordic and adjoining seas (Blindheim & Skjoldal 1993). Bridging the two cold periods at the turn of the century and in the 1970/80s was a long-term climatic oscillation with a warm climate mode from about 1920 to the 1960s (Loeng & al. 1992) which also constituted the main part of the last herring period (Blindheim & Skjoldal 1993). The Barents Sea cod stock has also shown large changes over this time period from a small stock size dominated by first time spawners at the turn of the century, to a large stock size with multiple year classes in the spawning stock in the warm period, to the state in the late 1980s with again a small stock size with a young age composition (Hjort 1914, Jørgensen 1988, Godø & Skjoldal 1991). The lesson to be learned from a retrospective analysis of the history is that fish stocks show large changes in response to oscillations in the ocean climate. The challenge to fishery managers has been and will always be to regulate the fishing pressure on stocks against the background of large natural fluctuations (Skjoldal 1990).

Methods for monitoring and assessing the state of fish stocks have improved markedly over the last decades. Using echo sounders and trawls during scientific surveys as well as information from commercial catches, data are provided on size and age composition of stocks. This provides a basis for assessing the likely devel-

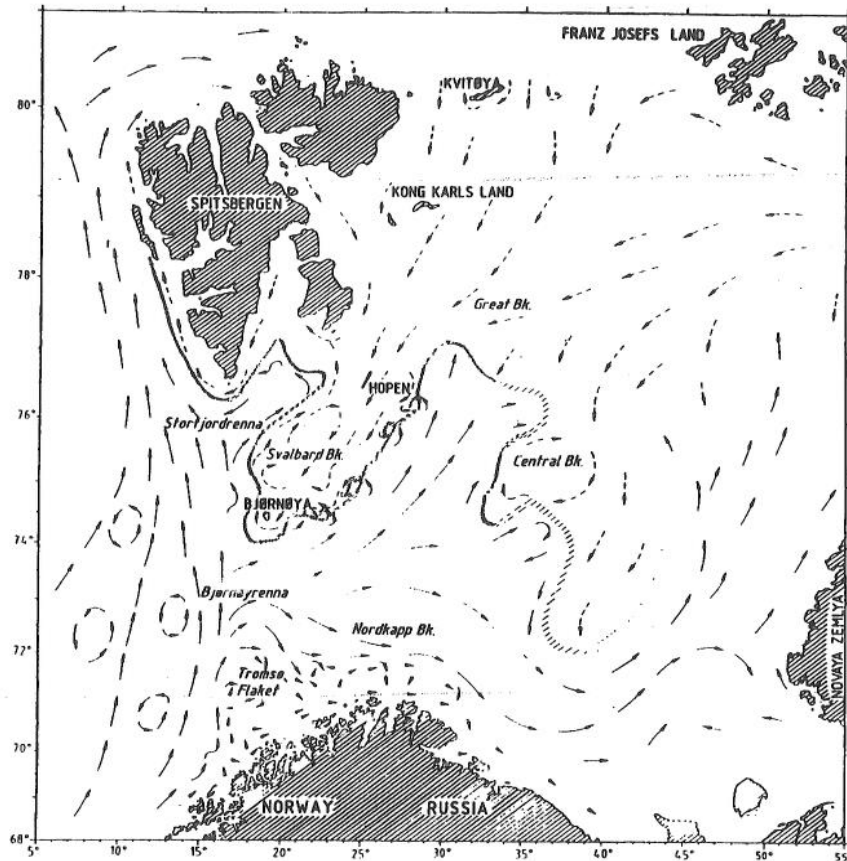
opment of stocks and for setting recommended catch quotas. Fisheries management has up to now been mainly single-species oriented. However, the need for taking species interactions into account has been recognised by fishery managers, and in 1990 a 5 years research program on Multispecies management was started in Norway with focus on the Barents Sea ecosystem. Major emphasis has been given to the development of a multispecies model, MULTSPEC, with capelin, cod and herring as key species (Bogstad & al. 1992, Tjelmeland & Bogstad 1997 (this book), Ulltang 1995). Environmental variability has also been considered in the Multispecies management program and development of ecological models has started. The aim has been to develop ecological models where the dynamics of main components of the ecosystem are linked to the physical driving forces and biological interactions which govern the variability of the ecosystem. Capelin is an important intermediate link in the pelagic food web in the Barents Sea, and it was chosen as the focal species for the initial development of ecological models (Giske et al. 1992a,b).

### The Barents Sea

The Barents Sea is a high latitude ecosystem located between 70 and 80°N. The main features of the physical and biological conditions of the ecosystem are presented in several recent reviews (Dragesund & Gjøsæter 1988; Loeng 1989a,b; Sakshaug & Skjoldal 1989; Skjoldal & Rey 1989, Sakshaug & al. 1991, 1992).

The water circulation is characterised by an inflow of relatively warm Atlantic water and coastal water from the west. The Atlantic water is separated from the cold Arctic water in the north by a sharp polar front in the western Barents Sea (Fig. 1) which is topographically determined. In the eastern Barents Sea there is extensive mixing and transformation of the inflowing water into Arctic water, and the polar front is less sharp and more variable in location (Loeng 1989a; Midttun 1989). There is large inter-annual variability in ocean climate related to variable strength of the Atlantic water inflow and exchange of cold Arctic water (Midttun 1985, 1989; Loeng 1989a,b; Ådlandsvik & Loeng 1991). This variability is cyclic with a dominant cycle length of about four years (Loeng & al. 1992). The year class strength of commercially and ecologically important fish species has been empirically related to these cyclic ocean climate changes (Helland-Hansen & Nansen 1909; Sætersdal & Loeng 1987; Loeng 1989b). Through trophic interactions, variable recruitment of one species affects populations of other species in the ecosystem (Skjoldal & Rey 1989; Hamre 1991). The variable ocean climate has also a direct effect on the lower trophic levels through the influence of ice on primary production. An ice edge phytoplankton bloom is generated when ice melts. This bloom sweeps across the sea as a band of high production as the ice retreats northwards during summer (Sakshaug & Skjoldal 1989). The ice edge bloom triggers reproduction and nourishes the new generation of zooplankton. The spring bloom in Atlantic water, not influenced by sea ice, is in contrast developing more slowly and is protracted in response to the seasonal thermocline formation (Rey & al. 1987; Skjoldal & al. 1987; Skjoldal & Rey 1989).

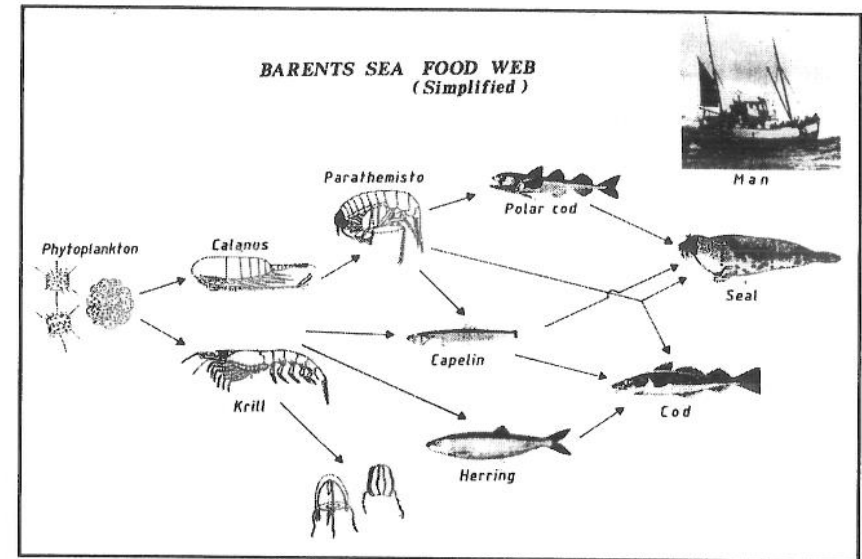
The transformation of inflowing Atlantic water into Arctic water makes the Barents



**Figure 1.** The dominant surface current system of the Barents Sea. Solid arrows: Atlantic currents; broken arrows: Arctic currents; dotted arrows: coastal currents. The polar front is indicated with a hatched line. Redrawn by Giske & al. (1992a) from Loeng (1989b).

Sea into a zoogeographical transition zone and into an ecosystem strongly dependent on plankton transport with incoming currents. The copepod *Calanus finmarchicus*, which is a key herbivore, performs a marked seasonal vertical migration in the Norwegian Sea (Østvedt 1955). During winter *C. finmarchicus* resides below the threshold depth at the entrance to the Barents Sea. Horizontal advective transport and seasonal vertical migration interact to produce large variability in standing stock of zooplankton in the western and central Barents Sea (Skjoldal & Rey 1989). Major inflows during winter will transport warmer Atlantic water but not copepods, while inflows during summer also will bring in food for the pelagic fishes (see section Inflow of *C. finmarchicus* from Norwegian Sea).

The food web of the Barents Sea ecosystem is relatively simple with a few domi-



**Figure 2.** Simplified food web of the Barents Sea.

nant species at each trophic level (Fig. 2). Diatoms and the colony-forming flagellate *Phaeocystis pouchetii* are dominant forms of phytoplankton during the annual spring bloom. Calanoid copepods (*Calanus finmarchicus* and *C. glacialis*) and krill (*Thysanoessa* spp.) are the dominant herbivores. Capelin (*Mallotus villosus*), herring (*Clupea harengus*) and polar cod (*Boreogadus saida*) are dominant planktivorous fish, while cod (*Gadus morhua*), sea mammals and seabirds are important piscivores (Dragesund & Gjøsæter 1988; Loeng 1989a).

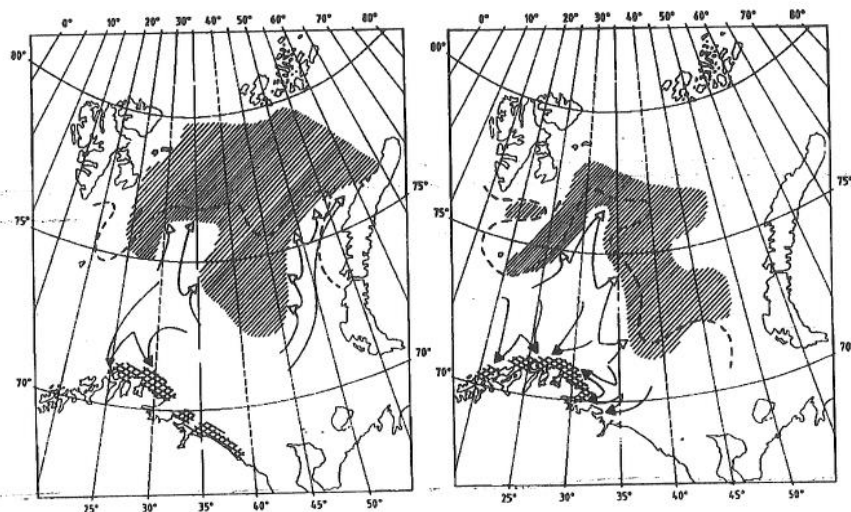
Amphipods (*Parathemisto* spp.) and gelatinous zooplankton (medusae and ctenophores) are important invertebrate predators.

#### Capelin

Capelin is of particular importance as an intermediate link in the food web. This species is a small salmonid fish with a short life span; the majority of individuals spawn only once (Hamre 1985, 1991, Vilhjálmsson 1994). The immature capelin performs a large scale feeding migration northwards in the Barents Sea during summer (Fig. 3). This migration can be viewed as an adaptation, whereby the fish follows the retreating ice edge with a time delay to exploit the ice edge phytoplankton production (Sakshaug & Skjoldal 1989; Skjoldal & Rey 1989). A large capelin stock needs a large feeding area to sustain its production, and the seasonal feeding migration is in this respect a necessary requirement (Skjoldal & Rey 1989).

The adult stage of capelin is characterised by reaching a minimum size rather than a minimum age (Forberg & Tjelmeland 1985; Hamre 1985, 1991). Growth is seasonal with large inter-annual variability in rate (Gjøsæter 1985; Gjøsæter & Loeng 1987;





**Figure 3.** Feeding distributions (hatched) and spawning grounds (double hatched) of Barents Sea capelin in warm (above) and cold (below) years. White arrows indicate feeding migrations, black arrows spawning migrations. Redrawn by Giske & al. (1992a) from Ozhigin & Luka (1985) and Loeng (1989b).

Loeng 1989b). Individuals which have reached a size of 14-15 cm in the autumn will mature and be part of the spawning stock which migrates to the coasts of northern Norway and Murman to spawn in late winter. The immatures overwinter in the polar front region from where they migrate northwards during the following summer (Fig. 3).

There are many spawning sites along the whole coastal stretch from Troms county to the Kola Peninsula (Fig. 3). The climatic fluctuations influence the spawning migration and choice of spawning sites, with trends towards a shift from westerly spawning grounds in cold periods to easterly spawning grounds in warm periods (Fig. 3; Ozhigin & Ushakov 1985; Ushakov & Ozhigin 1987). Following a relatively long incubation period in the sediments, the hatched larvae are released into the water in early summer (Alvheim 1985). From here they drift with the currents eastwards and northwards to the nursery and feeding grounds of the central Barents Sea. From easterly spawning grounds in warm periods larval transport tend to be towards the eastern Barents Sea, with a time-delayed shift towards more westerly distributions in cold periods (Ozhigin & Luka 1985; Ushakov & Ozhigin 1987; Loeng 1989b).

The geographic closure of the capelin life cycle is relatively loose in the sense that larvae drift from widely distributed spawning grounds along the coast of the southern Barents Sea to wide target areas in the central Barents Sea. Loss of recruits through vagrancy (Sinclair 1988) is therefore less likely for capelin than for species with more complex drift routes, such as the Norwegian spring spawning herring and the

Norwegian arctic cod.

Cod is the major predator on capelin, with a potentially high impact on the dynamics of capelin. Cod is mainly distributed in the southwestern (warmer) part of the Barents Sea, but young cod are known to migrate as far north as the Central Bank (Nakken & Raknes 1987). The spatial overlap between capelin and its major predator is thus largest in the spawning period, when capelin must pass this high risk area to come to the spawning grounds. In this period cod feeds almost exclusively on capelin.

Predation from juvenile herring appears to be an important factor for the recruitment success of capelin (Skjoldal & Rey 1989; Hamre 1991; Fossum 1992). Juvenile herring from strong year classes have their main nursery area in the southern Barents Sea. They are thus distributed in the area through which capelin larvae drift from the coastal spawning grounds to their nursery area in the central Barents Sea.

## STATE-OF-THE-ART IN ECOSYSTEM MODELLING

### Complexity and management

#### *Complexity*

The complexity of nature, and even of a relatively simple subset of it, is so overwhelming that it is impossible to describe it in detail, neither by words nor models. Our concepts are simplifications, and must be so to reveal understanding. However, this simplification has implications for predicting the future, as many processes and variables cannot be accounted for in verbal or mathematical models. And extensive inclusion of processes and variables need not improve the predictive power of a simulation model, as each new process and parameter also adds some uncertainty (Håkanson 1995). The benefit of mathematical modelling relative to a subjective judgement is that the mathematical language allows us to express current knowledge and assumptions in a precise form, and to compare the effects of forces and processes that may act on widely separated spatial and temporal scales. However, with the limitation of knowledge, the output from any model should be evaluated by the subjective judgement of an expert.

#### *Current fisheries management models*

Fisheries management in the Northeast Atlantic has for a long time been based on a combination of field investigations and modelling. The core of the common modelling concept, Virtual Population Analysis (VPA), is a cohort analysis of population dynamics. VPA models are based on catch data to calculate mortality rate of the fish population (Gulland 1965; Pope 1972, 1979). Population size and size frequencies are estimated from a data set on age composition, growth, fishing effort and recruitment. This technique is further developed to multispecies models (Magnússon 1995), where interactions between stocks (predation) are estimated from stomach analyses. VPA has proven to be a good tool for fisheries management. However, VPA has two limitations: 1) it assumes constant environment, and 2) since the pre-recruitment period in the life of the fish is not included, VPA is not suited for fish that lives only



for a short time after recruitment. In cases where the physical environment varies extensively over short intervals, and hence growth and survival prospects of the commercial fishes as well as of their prey (and predators), an approach where environmental variability is accounted for is needed. This is the situation in the Barents Sea. In addition, the planktivore in the Barents Sea, the capelin *Mallotus villosus*, lives only for 1-3 years after recruitment. For both these reasons the Institute of Marine Research has been developing a quite different set of models for the major fish species in the Barents Sea. The central tool, a multispecies fisheries model (MULTSPEC, see next chapter) includes predator prey relationships as well as food and temperature limitation in growth.

Since predictability of VPA based models relies on a statistical analysis of the years past, such models are far more capable of dealing with stable systems than with fluctuations and perturbations. Therefore, model predictions have not been good in years when stock sizes or environment have deviated from the normal. This has led to an interest for studying fish stock dynamics by means of other modelling concepts. Two properties are desirable: 1) feeding and growth to be dynamically coupled to food concentration (production and advection) and 2) migration and predator-prey relationships to be described in theoretical rather than empirical terms.

While a wide range of empirically tuned functions may produce fits with observations in stable systems, representation of the forcing functions and their influence in processes are crucial for the performance of theoretical models. Generally, a theoretical formulation of a process will demand a higher number of variables, constants and parameter values, many of which may not have been measured. This will probably lead to lower goodness-of-fit of any new theoretical model compared to existing empirical models. Quantification of the theoretically derived constants and variables is necessary for a theoretical model to reach the same level of goodness-of-fit as an empirical model, even in systems of some instability. The strength of theoretical models, however, is to handle unexperienced situations, which is when modelling is most valued.

Balchen and colleagues were the first in Norway to use theoretical models in studies of fish in ecosystems (Slagstad & al. 1975; Balchen 1976a,b). Not only have several new generations of computers passed since then, quantitative ecological theory has also evolved. Today, there are a number of dynamic models available covering water transportation, primary production and zooplankton (see Aksnes & Lie 1990, Aksnes & al. 1995), while fewer dynamic models of fish exist. The theoretical constraints has been the formal representations of mortality and of the biological forces that motivate the behaviour of the individuals. During recent years, spatial distributions have been studied by two methods: life history theory (Werner & Gilliam 1984; Aksnes & Giske 1990) and dynamic optimisation (Gilliam 1982; Clark & Levy 1988; Houston & al. 1988; Mangel & Clark 1988). Both rely on the assumption that fish behaviour can be understood from evolutionary forces. A prerequisite for applying them in natural habitats is that natural mortality rates can be calculated. This can be done by the method of Aksnes & Giske (1993) and Giske & al. (1994).

### *Goals of ecological modelling in the Multispecies Program*

Even in a high-latitude area as the Barents Sea, the overwhelming complexity of the ecosystem demands a focus on a few central factors in the modelling (Håkanson 1995). Therefore, and as the Barents Sea is an open area heavily influenced of the inflow of warm Atlantic water and zooplankton from the Norwegian Sea (Midttun 1985, 1989; Loeng 1989a,b; Ådlandsvik & Loeng 1991, Loeng & al. 1992, Sakshaug & al. 1991, 1992), modelling advection of zooplankton has been seen as a central task.

However, while several research groups have had considerable success in modelling the dynamics of nutrients and primary production (e.g. Aksnes & Lie 1990, Aksnes & al. 1995, Baretta & al. 1995), success in modelling higher trophic levels is still lacking, mainly due to the representation of the spatial processes. Successful representation of spatial dynamics of zooplankton and fish have been hindered by ignorance of, or low emphasis on, the role of advective transport (e.g. Giske & al. 1991 and Salvanes & al. 1992, vs. Salvanes & al. 1995), but often even more of the lack of understanding of how the internal motivation of the individual fish and zooplankton influence their behaviour and hence the dynamics of their population and the entire ecosystem.

Both for the force of advection and motivation, there is a big difference between phytoplankton and zooplankton (and fish). Phytoplankton drift passively with the currents, and are as such completely controlled by physical forces. However, their rate of multiplication under favourable local conditions may enable them to reproduce much faster than they are advected. Zooplankton, on the other hand, have generation times of weeks to years, and may not by reproduction counteract moderate currents. This was evident in the western Norwegian fjord Masfjorden (Aksnes & al. 1989, Giske & al. 1991), where the biomass of phytoplankton could be modelled from the local conditions, while understanding zooplankton dynamics required knowledge of the water transportation. Both this small fjord and the Barents Sea are open systems connected to the larger Norwegian Sea Large Marine Ecosystem (LME) (Blindheim & Skjoldal 1993, Sherman & al. 1993). But while phytoplankton are passively advected, zooplankton have the locomotory capacity to perform extensive vertical migrations on several time scales. Fish may even swim in opposite direction to currents, and hydrodynamics are poor indicators of horizontal distribution of all but the youngest individuals.

A major focus in this program has therefore been to model the motivation for behaviour of individuals. This has led us into complex models, with the hope one day to be able to synthesise the impact of these evolutionary and ecological forces into simpler expressions in later generations of ecosystem models. In the last part of this chapter we will demonstrate an attempt to model the distribution, growth and survival of capelin, as determined by natural selection (reproduction), ecological forces (food and predators) and the physical setting (hydrodynamics, temperature, bottom topography).

### **Hydrodynamics**

The Navier Stokes equation (Box 1) represents an excellent model of the hydrodynamical process in general. This equation is also widely used to calculate any flow of

liquid or gas and in models for weather forecasting. In contrast to biological processes, the model for hydrodynamical processes are well known. The main problem is how to simplify and represent the equation in a computer.

The forces that govern the circulation pattern may be different from one sea to another and will also depend on the season. It has been shown that wind, as in most other seas, is an important driving force for the circulation and inflow of Atlantic water into the Barents Sea (Ådlandsvik & Loeng 1991). Slagstad (1987) showed that it is necessary to include density variations in the models in order to obtain flow fields similar to what is observed. Density variations in the Barents Sea are caused by inflow of low saline water along the coast of Finnmark (continuation of the Norwegian Coastal current) and melting/freezing of ice in the northern Barents Sea. Since the Barents Sea has boundaries to other large Seas (Norwegian, Arctic and the Kara Seas), processes in these nearby areas also have a pronounced effect on the Barents Sea circulation pattern.

#### Baroclinic and barotropic currents

The pressure at a certain depth depends on the weight of the water column above and the atmospheric pressure. This weight is again a function of the water density. As the density depends on the temperature and salinity, the pressure will vary accordingly. An imaginary surface that connects all the points having the same pressure is called an isobaric surface. If temperature and salinity are not variable in space, this isobaric surface is parallel to the ocean surface.

In the same way one could make an imaginary surface by connecting all the points having the same density, isopycnal surfaces. When the isobaric and isopycnal surfaces are parallel to each other, we call this a barotropic field of mass. If the density varies horizontally, the isobaric and isopycnal surfaces may be inclined to each other and the mass field is baroclinic. The flow field driven by a baroclinic mass field is called baroclinic flow. The Barents Sea is characterised by large horizontal density gradients, which mean the baroclinic flow is important for this area.

When the flow is barotropic, the velocity will be the same in the whole water column, whereas one in the baroclinic case has currents which have a variable magnitude and direction with depth. Shelf seas at high latitude are often well mixed during the winter and spring. Many, so-called depth integrated circulation models, have been developed for this situation. It is only the central part of the Barents Sea, in the core of the inflowing Atlantic water, that can be regarded as well mixed during the winter and depth integrated models would not simulate the flow field with great realism. A hydrodynamical model of the Barents Sea must, therefore, be of baroclinic type having a vertical structure (3-dimensional).

There are several kinds of models that may be used for to simulate the baroclinic flow field of the Barents Sea. The most used models are of the so-called level type which mean that the vertical water column is divided in layers (or levels) each with a fixed thickness, independent of time. The level models may be divided into categories depending on how the vertical levels are divided. The  $\sigma$ -coordinate models divide the water column into a fixed number of levels, each occupying the same fraction of the water column. If a certain level represents 1 % of the water column, the depth of this

level will be 1 m if the depth is 100 m and 20 m if the depth is 2000 m. The main reason for using  $\sigma$ -coordinates is the ability to resolve some of the processes near the bottom which are important for the energy dissipation.

In the  $z$ -coordinate models the thickness of the levels is independent of the water depth except for the level that happens to be near the bottom which will change in thickness. However, the surface levels will have a fixed thickness, independent of the water depth.

Most models available today seem to handle the numerical in an acceptable way. Although improvements can be done, great progress can be achieved through a finer horizontal grid. Usually, grid point distance of 20 km has been used for the Barents Sea, but many important processes have a length scale which cannot be resolved by this grid. The lower limits of horizontal grid point distance is determined by the computer capacity (memory and computational speed). If the horizontal grid point distance is reduced by a factor of 2, the required memory capacity will increase by a factor of 4 and computational work by a factor of 8.

There are several models that have the potential to be usable for the Barents Sea, but the model should also be able to produce and melt ice in response to atmospheric forcing and water temperature. Most of the hydrodynamical simulations shown and used as input for biological simulations in this book are taken from a level model using  $z$ -coordinates.

#### Hydrodynamical model

In the ocean there are several forces connected to the movement of water masses. We may divide these forces into primary forces which produce water movements and secondary forces which are a result of water movements. The primary forces are horizontal pressure caused by variations in the density, sea surface elevation or air pressure, wind and tidal forces caused by variation in gravity forces from the moon and the sun. The secondary forces are the Coriolis force (which is due to the rotation of the Earth and acts on moving water with a force which is to the right of the direction of motion on the Northern hemisphere and to the left on the Southern hemisphere) and friction. Most models of ocean currents are dynamic (prognostic) which means that the forces acting on a certain water mass lead to acceleration according to Newton's 2. law of motion:

$$a = \frac{f}{m} \quad (1)$$

where  $a$  is the acceleration and  $f$  is the net force acting on the mass  $m$ . Integration in time of acceleration gives the velocity. Based on this equation and the equation of continuity (which states that water masses should be conserved) a set of partial differential equations can be developed.

The model described (Box 1) is a 3-dimensional, baroclinic, finite-difference "level model" that is defined by a sequence of fixed but permeable levels. Each level has a fixed thickness, except the level near the surface and the level that happens to be near the bottom. Thus, the number of levels will be a function of horizontal coordinates.

### Box 1: The equations of the hydrodynamical model

The equations describing the motion of incompressible water on a rotating earth, incorporating horizontal and vertical diffusion of momentum, can be written:

Acceleration in x-direction:

$$\frac{\partial u}{\partial t} = fv - u \frac{\partial u}{\partial x} - v \frac{\partial u}{\partial y} - w \frac{\partial u}{\partial z} - \frac{1}{\rho} \frac{\partial p}{\partial x} + A_v \nabla^2 u + \frac{\partial}{\partial z} A_v \frac{\partial u}{\partial z} \quad (2)$$

Acceleration in y-direction:

$$\frac{\partial v}{\partial t} = fu - v \frac{\partial v}{\partial x} - u \frac{\partial v}{\partial y} - w \frac{\partial v}{\partial z} - \frac{1}{\rho} \frac{\partial p}{\partial y} + A_h \nabla^2 v + \frac{\partial}{\partial z} A_v \frac{\partial v}{\partial z} \quad (3)$$

Vertical velocity is found from the equation of continuity:

$$\frac{\partial w}{\partial z} + \frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} = 0 \quad (4)$$

and surface elevation

$$h = \int w_t dt \quad (5)$$

where

- $u, v$  - horizontal velocity components in x- and y-direction, respectively
- $w$  - vertical velocity component
- $w_t$  - vertical velocity of surface elevation, i.e. upper layer
- $h$  - height of the free surface from the undisturbed mean
- $f$  - Coriolis parameter
- $\rho$  - density
- $A_h$  - horizontal eddy diffusion of momentum
- $A_v$  - vertical eddy diffusion of momentum
- $p$  - pressure found by the hydrostatic equation

$$p = \int_z^h \rho g dz + Pa \quad (6)$$

where  $Pa$  is the atmospheric pressure.

The space-time variations of water density  $\rho$  are found by the functional relationship

$$\rho = \rho(S, T) \quad (7)$$

where  $S$  and  $T$  are the salinity and temperature of the water, respectively. These scalar

fields can be modelled by a balance equation of the form

$$\frac{\partial c}{\partial t} = \frac{\partial}{\partial x}(uc) - \frac{\partial}{\partial y}(vc) - \frac{\partial}{\partial z}(wc) + K_h \nabla^2 c + \frac{\partial}{\partial z} \left( K_v \frac{\partial c}{\partial z} \right) + \delta_c \quad (8)$$

where

- $c$  -  $S$  or  $T$
- $K_h$  - horizontal eddy diffusion of salinity and temperature
- $K_v$  - vertical eddy diffusion of salinity and temperature
- $\delta_c$  - thermodynamic interaction between the upper layer and the atmosphere ( $c = T$ ) or supply of salt and fresh water during freezing of melting, respectively ( $c = S$ ) and the operator  $\nabla^2$  means

$$\nabla^2 \Theta = \frac{\partial^2 \Theta}{\partial x^2} + \frac{\partial^2 \Theta}{\partial y^2} \quad (9)$$

where  $\Theta$  is any function of  $x$  and  $y$ .

Vertical mixing is calculated as a function of the Richardsons number, wave height and parametrisation of tidal mixing in shallow areas.

### Phytoplankton dynamics

The phytoplankton model is based on nitrogen as the limiting nutrient and have two state variables: concentration of phytoplankton and nitrogen. The phytoplankton growth rate is a function of irradiance and the concentration of nitrogen. Loss of phytoplankton is due to respiration, sedimentation, and grazing from zooplankton. Model equations are given in Box 2. A recent review of phytoplankton modelling is given in Aksnes & al. (1995).

### Zooplankton dynamics

In the Barents Sea there are two dominating species of copepods which serve as food for fish larvae and planktivorous fish. In the Atlantic water (south of the Polar Front) we find *Calanus finmarchicus* whereas *C. glacialis* is found in water masses of Arctic origin. *C. finmarchicus* is regarded to have its core distribution area in the Norwegian Sea. Spawning starts in spring as soon as there are enough phytoplankton in the water column to sustain the energy needs for egg production. The new generation develops in the surface water in close relation to the phytoplankton bloom. Growth in size takes place through successive moulting, first through the six naupliar stages and then through six copepodite stages. Stage CV is the normal overwintering stage. North of Lofoten, there is only one generation a year, whereas further south



## Box 2: Phytoplankton model

The phytoplankton unit used in the model is: [mmol N m<sup>-3</sup>], but the results are presented in chlorophyll units [mg Chl a m<sup>-3</sup>] using a chlorophyll *a*:Carbon ratio of 6.3.

Transport and distribution of a scalar entity such as phytoplankton (P) or nitrogen (N) is governed by Eqs 2-4. Velocities and vertical mixing coefficients are taken from the hydrodynamical model. In the Barents Sea, ice is important for the light conditions in the water column. Ice cover is modelled by a ice model. The equations describing the growth of phytoplankton at a certain depth are:

$$\frac{dP}{dt} = PP_m^B \frac{Chl}{C} \left[ \min \left\{ 1 - \exp \left( \frac{-\alpha^B I_z}{P_m^B}, \frac{N}{k_N + N} \right) \right\} \right] - Pr - PS_{sed} \quad (10)$$

$$\frac{dN}{dt} = -PP_m^B \frac{Chl}{C} \left[ \min \left\{ 1 - \exp \left( \frac{-\alpha^B I_z}{P_m^B}, \frac{N}{k_N + N} \right) \right\} \right] + 0.5Pr \quad (11)$$

where  $P_m^B$  is the maximum photosynthetic rate [mg C (mg Chl)<sup>-1</sup> h<sup>-1</sup>],  $Chl/C$  is the chlorophyll *a*: carbon ratio,  $\alpha^B$  is the Chlorophyll *a* specific photosynthetic efficiency [mg C (mg Chl)<sup>-1</sup> h<sup>-1</sup> (μmol m<sup>-2</sup> s<sup>-1</sup>)<sup>-1</sup>],  $k_N$  [mmol N m<sup>-3</sup>] is the half saturation constant for uptake of nitrogen,  $r$  [h<sup>-1</sup>] is the respiration rate,  $I_z$  is the irradiance at depth  $z$  [μmol m<sup>-2</sup> s<sup>-1</sup>], and  $S_{sed}$  [h<sup>-1</sup>] is the sedimentation rate given by

$$S_{sed} = d_{mn} + (d_{mx} - d_{mn}) \exp \left\{ -\frac{N}{(k_N - N)/dg} \right\} \quad (12)$$

where  $d_{mn}$  [h<sup>-1</sup>] is the sedimentation rate at high nitrogen concentration,  $d_{mx}$  [h<sup>-1</sup>] is maximum sedimentation rate at low nutrient concentration and  $dg$  is a parameter which determines the functional relationship between sedimentation rate and concentration of nutrients.

The photosynthetic available irradiance (PAR) is calculated from the local height of the sun after a model by Bird (1984). Daily average cloud cover is interpolated from available meteorological stations in the Barents Sea. The depth variation of the irradiance is calculated after Kirk (1984):

$$I_z = \frac{I_0}{COSI} \exp \left\{ \int_z^0 \frac{1}{COSI} (k_w + f_{att}(Chl)) d\tau \right\} \quad (13)$$

where  $I_0$  is the irradiance at the surface,  $k_w$  is the attenuation coefficient of pure sea water [m<sup>-1</sup>],  $COSI$  is the average cosine of light in water and  $f_{att}(Chl)$  is a function that

calculates the attenuation due to chlorophyll in the water column (Parsons & al. 1983):

$$f_{att} = 0.0088Chl + 0.054Chl^{2/3} \quad (14)$$

For more information, see Slagstad & Stokke (1994) and Sakshaug & al. (1995).

part of the population may have two generations. In July, the first overwintering animals are found below 600 m. During the winter, moulting into the last stage (CVI) female or male, takes place. *C. finmarchicus* overwinters in the Norwegian Sea at temperatures below 0°C which usually are below 500 m. In the Barents Sea this depth is not found and we may find the overwintering stock at 200-300 m or even up to the surface (Pedersen & al. 1995).

*C. glacialis* is an Arctic species found in shelf areas which is seasonally covered by ice. The life cycle is similar to *C. finmarchicus*, but the generation time is two years.

### Zooplankton production

Attempts to model growth and secondary production have usually been performed as an investigation of the productivity of an area based on food availability (primary production), temperature and mortality due to predation. Such models have been used for the Barents Sea, but were not able to explain the variability in *Calanus* biomass that were observed in the 1980s (Slagstad & Støle-Hansen 1991). Model sensitivity analyses indicated, however, that the variability in the overwintering stock of *Calanus* would be an important factor determining the total production the following spring and summer (Slagstad 1981a, Slagstad & Støle-Hansen 1991). This has also been suggested in other studies (Colebrook 1985, Aksnes et al. 1989). Looking at a shelf ocean such as the Barents Sea, these would mean that there is a strong feedback from planktivorous fish to the secondary production. One of the major hypotheses drawn up after the PRO MARE was that import of *Calanus* from the Norwegian Sea could give an important contribution to the Barents Sea *Calanus* spawning stock.

Growth of a population (biomass formation) depends on the growth rate of each individual. Since weight specific growth and respiration rates of *Calanus* depend on the stage of development, the population structure (stage structure) should be a part of any model that intend to calculate population growth. The vertical distribution which is important for ocean-shelf transport and mortality rate, is also dependant on developmental stage. The *Calanus* model used here, therefore, consists of three parts: (1) a population model that calculates the stage distribution as a result of spawning time, developmental rate and advection (2) a physiological part that calculates hunger, growth rate and egg production rate as a function of temperature and concentration of phytoplankton and (3) a vertical migration model which computes

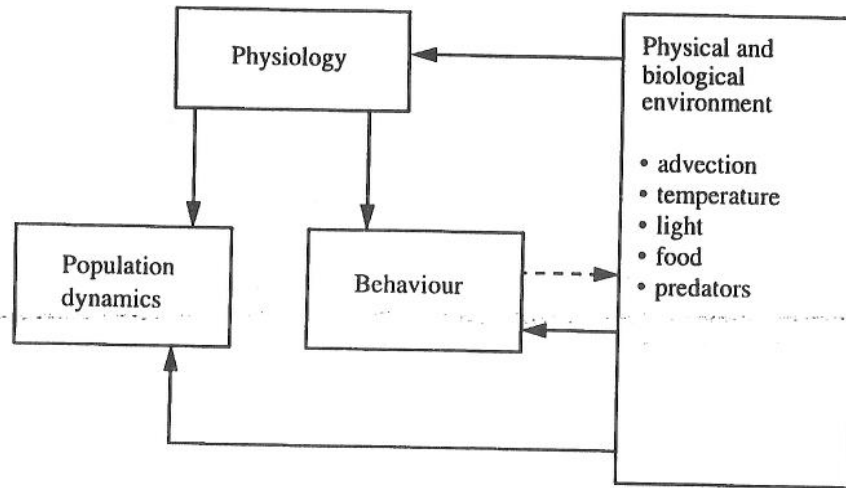


Figure 4. Interaction between physiology, vertical migration, population and environment in the *Calanus finmarchicus* model.

the vertical distribution as a dynamic function of light intensity and hunger. These three submodels interact with each other and the environment (Fig. 4).

#### Population sub-model

The population model consists of one part which produces a stage distribution of nauplii and one part which produces a weight distribution of the copepodites. An empirical relationship is used between stage and weight. The recruitment to the nauplii model is egg production from spawning of *Calanus* females. When the last nauplius stage is reached, the nauplii enters the copepodite model as CI. The copepodite model calculates the change in weight distribution as a function of growth rate, recruitment from the nauplii model and mortality according to the equation

$$\frac{\partial \eta(w)}{\partial t} + g(w) \frac{\partial \eta(w)}{\partial w} = R(w_0) - m(w) \quad (15)$$

where  $w$  is weight,  $\eta(w)$  is number of individuals having weight  $w$ ,  $g$  is growth rate for an individual of weight  $w$ ,  $R(w_0)$  is recruitment rate from the nauplii model and  $m(w)$  is the weight dependent mortality rate. Growth rate is taken from the physiological sub-model. The mortality rate has a fixed value, depending on developmental the stage, only. This mean that longer time spent in a stage due to low temperature would increase the mortality. The equation is solved by a finite difference method, which for numerical reasons makes it necessary to divide each stage into several weight classes. A similar equation is used for the nauplii model.

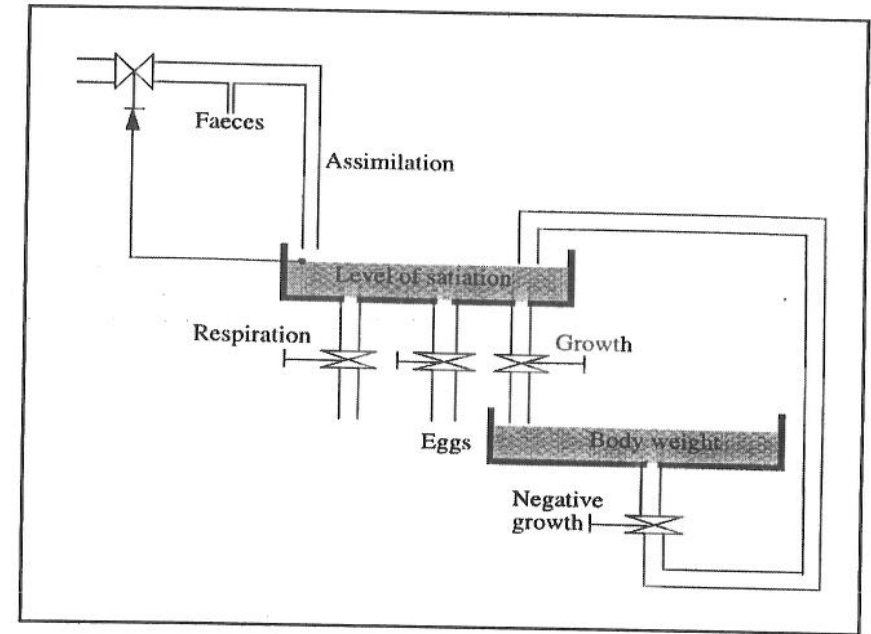


Figure 5. Illustration of the physiological model of *Calanus finmarchicus*.

#### Physiological sub-model

The physiological model has two state variables which are energy stores (Fig. 5). The first is simply energy stored in body structures and the fat droplet and is associated with energy which is not easily mobilised when energy is needed. The second state variable is associated with the energy store which is mobilised when energy is needed such as the pool of wax ester. The energy content of this store will determine the state of hunger and will affect the ability to migrate into the upper part of the water column even if the light intensity is higher than acceptable from a mortality point of view. This state variable (called the level of satiation,  $s$ ) which is the inverse of hunger, will control both the filtering rate, growth and egg production rate. The state variables are governed by the equations

$$\frac{dw}{dt} = g = f(s, w, T) \quad (16)$$

$$\frac{ds}{dt} = \frac{[A(s, P) - g(s, w, T) - E(w, s) - R(w, T)]}{S_v} \quad (17)$$

where  $A$  is the rate of assimilation,  $g$  is the growth rate,  $E$  is the egg production rate,

$R$  is the respiration rate,  $f$  is a function that gives the growth rate as a function of the level of satiation ( $s$ ), weight ( $w$ ) and temperature ( $T$ ).  $P$  is the concentration of phytoplankton at the depth of the animal. The level of satiation is a relative measure for the energy content in this store as we divide by its maximum size  $S_v$ .

#### Vertical migration behaviour model based on physiological state

Copepodite stages of *Calanus* are able to choose its vertical position in the water column. This is important for the advection process from oceanic to shelf areas. Since the depth of overwintering in oceanic water is below 500 m, advection into shelf water must take place in the spring and summer. Since currents may have directions depending of depth, the vertical position in the water column is important for calculating the transport. Predation rate from visual predators may also be affected by the depth distribution (see the "Static optimisation" section and Box 5).

It may be argued that the largest copepodite stages should stay deep (and dark) enough to avoid being eaten by visual predators (see the "Age- and size-dependent variation in motivation" section). On the other hand, if this depth is below the phytoplankton layer, animals will not be able to sustain maximum growth rate and may not be able to reach the stage CV with sufficient energy reserves to make it through the winter. The optimal choice can be calculated by a procedure for dynamic optimisation (Fiksen & Giske 1995, "State dependency dynamic optimisation" section). One may, however, also argue that *Calanus* does not know anything about dynamic optimisation, but will through its sensory apparatus perceive the environment and combine this by its perception of its internal state (e.g. hunger) to decide what to do. The weighing of different sensory inputs (e.g. light intensity, predator level, concentration of phytoplankton etc.) will be a result of evolutionary processes which seek to maximise the reproductive output (cfr. the "Natural selection and maximisation of fitness" section). In the following, we will describe a vertical migration model which is based on physiological state and environmental variables.

The nauplii are assumed to be randomly distributed in the upper 40 m. The copepodites have an internal light reference level which will adjust their vertical position throughout the day. When the level of satiation is low, the light reference level is increased and animals move upward in the water column to search for food (i.e. they will tolerate higher mortality risk when hungry). After the level of satiation is filled up again, the light reference level is reduced and, depending on the ambient light intensity, the downward migration start. For a vertical migrating animal, the energy content in  $s$  will fluctuate, but the growth rate will only be affected when the level of satiation becomes too low

$$\frac{dz}{dt} = f_z(I_r, I_z) \quad (18)$$

$$\frac{dI_r}{dt} = f_{Iref}(s) \quad (19)$$

where  $z$  is the depth in the water column,  $f_z$  is a function that calculates the vertical velocity from the difference in light reference level ( $I_r$ ) and the ambient light at depth  $z$  ( $I_z$ ),  $f_{Iref}$  is a function that calculates the rate of change in the light reference level as a function of  $s$ . In this version of the model, the concentration of visual predators is not taken into account, but it can be included in equation (19). More details about this model and parameter used can be found in Slagstad (1981b), Slagstad & Tande (1990) and Tande & Slagstad (1992).

#### Animal behaviour and life cycles

##### Proximate cues and ultimate forces

Both animals and plants react to environmental stimuli. That is why they have sense organs. Fishes have a wide variety of differentiated and specialised sense organs, making them capable of detecting changes in temperature, pressure, sounds, odours, light etc. In the study of the behavioural responses to the external environment, one can ask both *how* individuals sense and respond and *why* they do so. These are quite different questions: The *how* question will reveal which environmental factors triggers which behavioural response, i.e. the proximate cause of a response. The *why* question will reveal the ultimate cause of the sensitivity to the different environmental factors, i.e. why it is important to respond and which environmental factors one should expect the individual to have sensors to detect. To understand the ultimate *why*, one must focus on how evolution has formed the species.

##### Natural selection and maximisation of fitness

Natural selection is a genuine biological force operating with necessity when two conditions are fulfilled (e.g. Parkin 1979): 1) there is differential reproduction, i.e. not all individuals in a population produce the same number of offspring, and 2) the differences are heritable, or have a heritable component. After several generations in a habitat, natural selection will tend to make the individuals in a population similar in reproductive ability, manifested in local adaptations in body size, life history, reproductive capacity and behaviour. Evolution is therefore a good foundation for understanding characteristics of present living natural populations.

The force of natural selection has lately been demonstrated by the extensive use of genetic algorithms to solve complex numerical problems in science and engineering. The genetic algorithm kernel (GAK, Holland 1975, 1992) is a way of improving a "population" of suggestions for solutions to a complex problem by allowing small or large random changes in existing solutions ("mutations"), and to make new solutions by combining existing ("reproduction with recombination"). The performance of all suggested solutions are then evaluated, whereupon "natural selection" eliminates the poorest and reproduces the best, under a certain risk of mutations to allow for new ideas to come up. Thus, GAK will tend to improve solutions based on the existing alternatives, but will not necessarily find the globally best solution.

While natural selection will lead to the selection against inadequate responses, it is also necessary to show that behaviour to be selected for does exist in nature. This



has been done in several laboratory investigations, where fish have been shown to be capable of performing optimisations in relevant situations (see Milinski (1986) for a review). The life history of a population, and not our suppositions, sets the limitations on what behaviour can be expected of an animal. Thus, Milinski (1979) showed that sticklebacks are able to assess feeding rates at different feeding locations, and respond optimal to experimental manipulations of feeding regime. Milinski (1985) showed that preferred feeding locations are influenced by physiological status and predation risk. Magurran & al. (1985) have shown that feeding or escape, i.e. the trade-off between predation avoidance versus feeding is influenced by shoal size. Utne & Aksnes (1994) have shown that the risk-willingness also depends on age — i.e. on the life-history stage of the individual.

The degree of adaptation to the environment, and the animal's ability to spread its genes to future generations, is the core of the fitness concept. Fitness can be defined as an individual's contribution to the next generation, relative to other individuals, and can be estimated by the difference in instantaneous reproductive rate of the individual ( $\rho$ ) and the population ( $r$ ):

$$\Phi = \rho - r \quad (20)$$

(Giske & al. 1993). To maximise  $\Phi$ , an individual cannot do better than to maximise  $\rho$ , which therefore itself is a measure of optimal behaviour.

The development of biological optimality models started in 1966 by MacArthur & Pianka (1966) and Emlen (1966), who initiated the era of the "optimal foraging theory" (OFT, Schoener 1987). Laboratory investigations have generally supported OFT when animals were faced with simple set-ups (Stephens & Krebs 1986; Schoener 1987). OFT assumes that there exists a (linear) relationship between feeding rate and fitness (Calow & Townsend 1981). Implicitly, it was assumed that feeding could influence birth rate without also affecting death rate. Mangel & Clark (1986), however, showed that feeding alone cannot explain spatial distributions in general. By the use of dynamic optimisation, they showed that all fitness-related aspects of life could be combined in a common expression. At the same time, Life History Theory (LHT) developed from a descriptive to a predictive tool available to optimality studies (Stearns & Crandall 1984, Werner & Gilliam 1984, Sibly & Calow 1986).

#### *Life history theory and static optimisations*

Natural selection pushes a population towards better and better adaptations to the local environment, since the fittest individuals on average leave more and better offspring than the rest of the population in each generation. Such, natural selection acts to make all living beings into efficient "replicators", i.e. that individuals of any species who devote the most of their time and energy on leaving offspring will pass on this behavioural trait to coming generations. We can therefore assume that anatomy, physiology, life cycles and behaviour of organisms now occurring in their natural habitats are well adapted to this. And we can further assume that the characters of the individuals in an area are those that on average leave the most offspring. Hence, the

"meaning of life" for any living creature is to maximise  $\rho$  in Eq. 20. But how should they then live?

The instantaneous reproductive rate  $\rho$  can be decomposed to three factors: 1) *fecundity*, the number of offspring produced by an individual, 2) *survival*, and 3) *time* (age). The reproductive rate can be expressed by the Euler-Lotka equation:

$$1 = \sum_{Y=1}^{\omega} m_Y l_Y \exp(-\rho Y) \quad (21a)$$

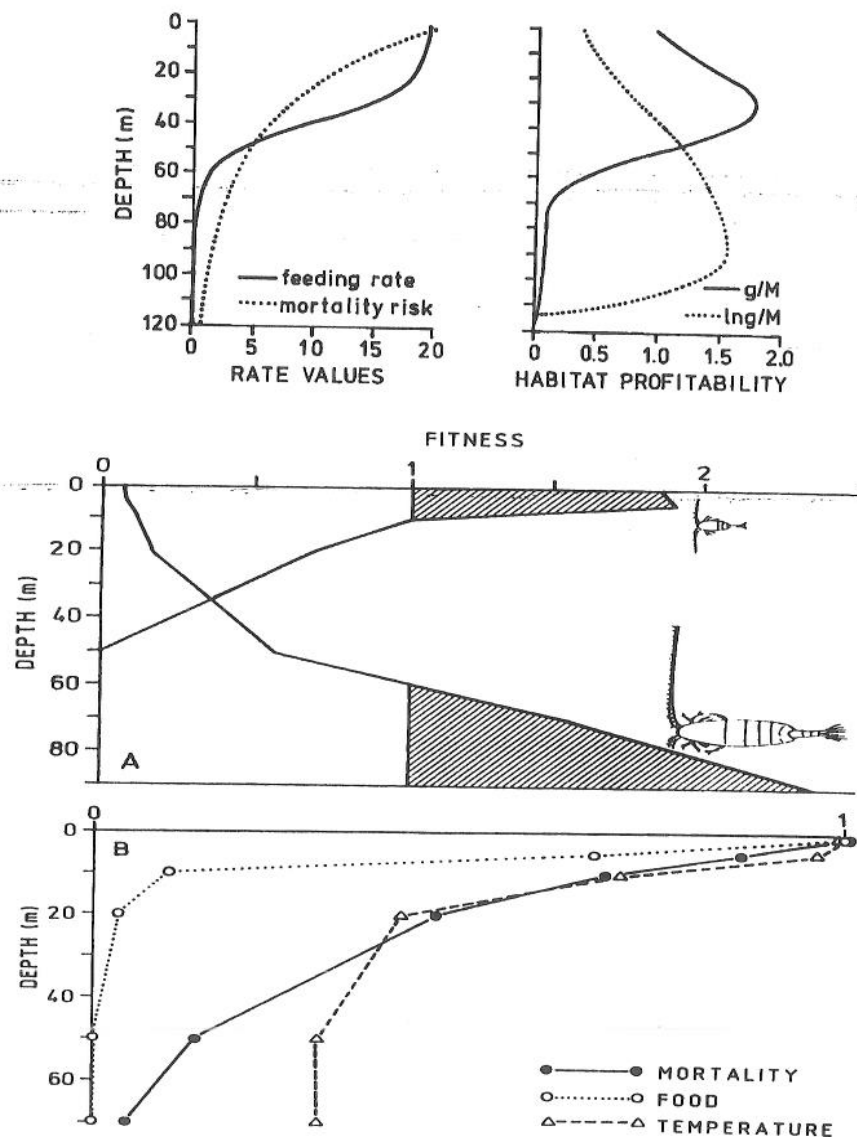
(Euler 1760, Lotka 1907) where  $m_Y$  is fecundity at age  $Y$ ,  $l_Y$  survivorship from birth up to age  $Y$  and  $\omega$  is last age of reproduction. Generally, fecundity and survivorship are interdependent. Early fecundity will be at expense of increased body mass and possibilities for even larger fecundity later in life. High food intake rate, which is needed to start reproduction at a minimum age, will often have a cost of larger exposure to predators. Natural selection will then work to optimise food intake, growth, fecundity and mortality exposure so that the resulting expected lifetime reproductive rate  $\rho$  is maximised. Repeated reproduction (several spawning periods) will develop when it does not pay to invest all reproductive capacity in the first attempt. For the case that an individual only reproduces once in a lifetime, the Euler-Lotka equation (21a) is simplified to

$$\rho = \frac{\ln(l \cdot m)}{T} \quad (21b)$$

where  $T$  is the generation time (age at reproduction).

If we can express how different environmental factors influence the life history variables  $l_Y$  and  $m_Y$ , then we may calculate the optimal behaviour of the individuals. From Eq. 21b we see that a favourable habitat is characterised by a potential for a high fecundity, a short generation time, and a low mortality rate. And although such a place is seldom found (and occupied if found), Eq. 21b shows how an optimal trade-off between these three factors should be performed to find the best of all available habitats. We see that factors influencing generation time has higher impact on fitness than factors influencing fecundity, due to the log-suppression of fecundity.

Werner & Gilliam (1984), Aksnes & Giske (1990) and Salvanes & al. (1994) have by different methods shown that an individual that may shorten its generation time by increased growth rate, should live as to maximise the ratio between somatic growth rate  $g$  and mortality risk  $M$  (maximise  $g/M$ ). This is often the case for juvenile fish, while adults, which by definition already have reached the onset of reproduction, only can use extra food to increase their fecundity. For such individuals, the optimal trade-off between searching for food and hiding from predators shifts towards a more vigilant life. Giske & Aksnes (1992) showed that the optimum trade-off was to maximise  $\ln g/M$ , i.e. less emphasis on growth relative to mortality risk (see Fig. 6a). For many other aquatic animals, e.g. in major zooplankton groups, the major trade-off may be of mortality risk versus temperature (as high temperature is only found in the dangerous well-illuminated surface waters). This is illustrated in Fig. 6b, where the vertical distri-



**Figure 6.** Top: Habitat profitability of fish. Juveniles may use extra growth to shorten time to maturation. Adults can only use extra food intake to increase fecundity. With typical vertical profiles of feeding rate and mortality risk (left), optimal depth will be shallower for juveniles (maximising  $g/M$ ) than for adults (maximising  $\ln g/M$ ). Center: fitness value of depth differ for the small copepod *Paracalanus parvus* that may use warm water to shorten generation time than for the large *Calanus finmarchicus* that has only one generation per year. The environment is the same for both species and is shown below. From Giske & Aksnes (1991).

bution of two zooplankton species is explained by their different fitness value of growth versus survival, and by the impact of temperature upon generation time.

### Dynamic optimisation

The attractiveness of life history based models lies in their simple deduction from fitness and in their high degree of intuitive value. A problem is their coarse time scale; they will not resolve events on a short time scale. They may give average optimal solutions for juveniles and adults, and optimal solutions before and after spawning, but will not describe optimal trade-offs for hungry versus well fed animals or for adaptations to temporal and seasonal variability. Dynamic optimisation (or dynamic programming) is a method by which several time scales may be included, as well as the energetic status of the organism. This method is therefore far more computer-demanding than life history based models.

Dynamic optimisation has over the last decade been used in studies of optimal fisheries regulations and fisheries economy (e.g. Clark 1976, Charles 1983, Bjørndal 1988, Flåten 1988, Bjørndal & al. 1993, Hanneson 1993). State variables are used to examine the consequences of an action in fitness-related terms in order to model optimal behaviour (Houston & al. 1988; Mangel & Clark 1988). A decision variable (e.g. optimal habitat) is made dependent on the internal state variables (e.g. physiological state) and external time-dependent variables (e.g. food availability, predation risk and spawning season). Dynamic optimisation is a three step process. First, optimal decisions for all states at all times are found by backwards iteration from a fitness-related function of the state variable at the end of the modelled period. Secondly, the ultimate state distribution of the population is found from an initial distribution, assuming optimal behaviour of all individuals. Finally, the fraction of the population adopting a particular behaviour is found by combining steps 1 and 2. (See Box 3 for technical details.)

The dynamic optimisation model will generate mortality rates for animals adopting the optimal strategy, and feeding and growth rates of the population can also be calculated in the last part of the three-step process. Since fisheries contribute heavily to mortality of capelin in the Barents Sea, geography, intensity and timing of fisheries could be included in the mortality risk (c.f. Law & Grey 1989; Sutherland 1990; Jensen 1991). This has not been done so far.

### Box 3: Dynamic Programming

Finding optimal distributions by backward iteration proceeds as follows: relative fitness is first determined for each possible energetic state at the end of the simulated period, e.g. by a life history related function. Generally, these fitness values are termed  $F(x, t, T)$ , where  $x$  is the value of the state variable,  $t$  is current time step number and  $T$  is total number of time steps.

During a time step, an animal may choose among several habitats. Predation risk ( $p$ ), probability of finding food ( $e$ ), the energetic value of the food ( $f$ ) and metabolic costs ( $c$ ) may differ among habitats. (For simplicity of presentation, we here assume

that all prey in a habitat are equal and that one or no item can be caught in a period.) In a period (from  $t$  to  $t+1$ ) an animal of state  $x$  ( $x, t$ ) either finds food and changes its state to  $(x-c+f, t+1)$ , or does not find food, and then changes to  $(x-c, t+1)$ . The average new state ( $x'_{t+1}$ ) for an animal of state  $x_t$  in a habitat is therefore

$$x'_{t+1} = e(xt-c+f) + (1-e)(xt-c) \quad (22)$$

and the probability of surviving the time step is  $(1-p)$ . The fitness value of the states  $x-c+f$  and  $x-c$  at final time ( $t = T$ ) is now already found, and fitness of state  $x$  in habitat  $h$  at  $t = T-1$  is

$$F(x, h, t=T-1) = (1-p) [eF(x-c+f, T) + (1-e)F(x-c, T)] \quad (23a)$$

$F(x, h, t=T-1)$  is then calculated for all habitats, and the optimal habitat is where  $F(x, h, t)$  is maximal. In this optimal location [ $h(x, T-1)$ ] the fitness value of animals of state  $(x, T-1)$  is

$$F(x, T-1) = (1-p^*) [e^*F(x-c^*+f^*, T) + (1-e^*)F(x-c^*, T)] \quad (23b)$$

where  $*$  refers to environmental values in the optimal habitat. Having found  $F(x, T-1)$  and  $h(x, T-1)$  for all  $x$ , calculation of fitness values and the corresponding optimal locations for all states at  $t = T-2$  proceeds according to the general equation

$$F(x, t) = (1-p^*) [e^*F(x-c^*+f^*, t+1) + (1-e^*)F(x-c^*, t+1)] \quad (23c)$$

#### Density dependency: Ideal Free Distribution

The models referred to above describe optimal trade-off for the individual, since the individual is the unit of selection. The value of a habitat for an individual does however depend on the presence of other individuals, as demonstrated by Magurran & al. (1985). Group size will influence both feeding (Clark & Mangel 1986) and mortality (Milinski 1986; Jakobsen & Johnsen 1988). Schooling and shoaling may increase individual feeding opportunities as the search volume of the group is larger than of the individual. Where food is patchy distributed, and especially if patches are ephemeral, the benefits of group searching will outweigh the costs of resource sharing (Clark & Mangel 1986). Under other circumstances, e.g. with overlapping search fields at low prey densities or for bad positioned individuals, flocking may reduce individual feeding rates. The fact that shoaling and schooling still are maintained, suggests that flocking has other functions than just to increase feeding. If predators feed by eating single food items, prey patching may reduce prey mortality risk both by dilution (Milinski 1977) and confusion (Milinski 1984). These effects also allow schools of fish to feed in areas where mortality risk for single individuals would be too high. Each individual in a school may also spend less time and attention on predator avoidance, and schools will generally discover a predator earlier than solitary individuals. Due to confusion costs, planktivores feeding in dense zooplankton swarms have a lower ability to locate their own predators (Milinski 1986). Unless they are very hungry, planktivorous fish therefore tend to feed at the edge of swarms,

where feeding rate, confusion costs, and mortality risk is lower (Milinski 1977; Godin & Smith 1988).

So, while dynamic optimisation increases realism in behavioural models by including internal state and variable motivation, the method treats interactions between individuals in a static manner. A different concept is the density-dependent life-history based model, where habitat quality is directly linked to competitor density. Group-size dependent optimal distributions within and among feeding sites have been studied using the Ideal Free Distribution (IFD) concept (Fretwell & Lucas 1970; Fretwell 1972). It is called 'free' because all individuals are assumed free to relocate at no cost, and it is 'ideal' because each individual is supposed to move to the site where its gain will be highest. The original IFD was based on four assumptions: 1) a number of equal competitors are found in a habitat, 2) within the habitat there are several different patches of food available to the competitors, 3) the competitors can move freely at no cost among these patches, and 4) each individual will go where its expected gain is highest. The competition was further assumed to be 'scramble', without any contest or combat between the competitors. The theory of Ideal Free Distributions (IFD) has been used by MacCall (1990) to distribute fish optimally among unequal patches. IFD was developed in the era of optimal foraging theory, and although Fretwell & Lucas (1970) stated that food was but one component of fitness, IFD assumed a direct relationship between feeding rate ('gain') and fitness. We have been interested in IFD as an alternative to dynamic programming, as the latter focus on internal state as basis for motivation, and then cannot easily include effects of competitors. [Some dynamic programming models investigate optimal groups size, but then at the expense of physiological state (Mangel 1990)].

For our purpose, the IFD had to include density-dependent effects of predation risk, also. To incorporate also mortality risk, the second assumption may be restated: 2) 'Within the habitat there are available to the competitors a continuous range of localities differing with respect to expected fitness gain'. (See Box 4 for technical details.)

The assumption of 'free' travel between patches may hold for small distances. However, Tyler & Gilliam (1995) showed that swimming costs had to be considered for the distribution of stream fish. Even more will such costs apply to long-distance horizontal migrators. Also the assumption of 'ideal' individuals with perfect knowledge is questionable, both for use in IFD models and elsewhere. Several authors have found that perceptual constraints may reduce the ability of the fishes to assess the quality of their habitat so that the spatial distribution was more random and less ideal (Abrahams 1986, Utne & al. 1993, Gray & Kennedy 1994, Tyler & Clapp 1995).

#### Box 4: Ideal Free Distribution

Under Ideal Free Distribution with equal competitors, the total number of individuals distribute among the habitats so that the gain of an individual is equal in all habitats. In the classical version of the model, food was the resource, and the individual gain



( $S_i$ ) in a habitat ( $i$ ) declined from a density-independent maximum  $B_i$  by a habitat-specific function of competitor density  $d_i$

$$S_i = B_i - f_i(d_i), i = 1, 2, \dots, L \text{ (habitats)} \quad (24)$$

and the IFD is achieved when individual gain is equal among habitats

$$S_1 = S_2 = \dots = S_i \quad (25a)$$

and total number in the  $K \leq L$  occupied habitat match population size  $N_T$

$$N_1 + N_2 + \dots + N_K = N_T \quad (25b)$$

For zooplankton and fish in a natural environment it is not to be expected that food gradients alone shall cause an IFD, for three reasons: 1) there are combinations of low competitor density and high food production where individual feeding rate will not be influenced by a (minor) increase in competitor density, and more important, 2) one of the main resources for development and fitness for aquatic organisms may be environmental temperature and 3) predation risk will affect fitness in a density-dependent manner. Habitat profitability may then be expressed directly in terms of the habitats' expected contribution to the fitness ( $\Phi$ ) of the animal (Eq. 20), and ideal free individuals will distribute so that

$$\Phi_1 = \Phi_2 = \dots = \Phi_i \leftrightarrow \rho_1 = \rho_2 = \dots = \rho_i \quad (26a)$$

[as  $r$  is a population parameter constant for all habitats (and is the average of all  $\rho_i$ 's)]. In a situation where feeding will be sufficient for growth and where reproduction may occur unhindered by e.g. seasonal constraints, fitness is proportional to the life-history trade-off  $g/M$ , as shown above. Then we may write

$$\Phi_1 = \Phi_2 = \dots = \Phi_i \leftrightarrow g_1/M_1 = g_2/M_2 = \dots = g_i/M_i \quad (26b)$$

(Giske *et al.* 1997). In IFD terms we will find the relation between the optimum number in each habitat, so that gain is equalised by competition and predation risk dilution. Fecundity, growth and survival will be derived from mechanistical equations of the environment and density-dependent responses. The ideal free distribution — where no individual could increase its fitness by moving — is obtained when competitor density in each available habitat is adjusted so that the ratio  $g/M$  is equalised.

## ECOLOGICAL MODELLING OF THE BARENTS SEA

### Physical oceanography

The first attempt to develop a 3-dimensional (3D) hydrodynamical model for the Barents Sea took place in 1975 when the OCEAN-BIO\_MODELS research program started (Slagstad *et al.* 1975, Balchen 1980, Berntsen *et al.* 1981). The model was not completed with open boundaries. Parallel to this work, a 1-D (vertical direction) was used to simulate primary and secondary production in different water masses (Slagstad

& Tande 1990, Slagstad & Støle-Hansen 1991). This model used measured sea surface values of temperatures and ice covers combined with the general seasonal knowledge of seasonal variation to calculate vertical mixing coefficients.

In 1987 the first 3D-model using the main driving forces was applied for the Barents Sea (Slagstad 1987). The model was used to calculate the hydrodynamical environment (flow field, vertical mixing coefficients and ice cover) to be used in a 3D phytoplankton model (Slagstad & Støle-Hansen 1991, Støle-Hansen & Slagstad 1991). This work was a part of PRO MARE and has also continued during the Multispecies program (Slagstad & Stokke 1994).

Other models have been used to study variations in wind driven inflow of Atlantic water into the Barents Sea (Ådlandsvik & Loeng 1991) and drift of fish larvae from the spawning grounds along the Norwegian Coast to the Barents Sea. At The Norwegian Meteorological institute, a 3D model is running operationally. Study of heavy deep water formation in the Barents Sea has been performed by a so-called plume model by Harms (1994).

The circulation pattern in a shelf ocean like the Barents Sea are governed by the prevailing wind, flux through the boundaries and the density field. Ådlandsvik & Loeng (1991) showed that the variations in the inflow through the Fugløy-Bear Island section was mainly due to the wind. Easterly wind tends to slow down the transport from the Norwegian Sea whereas westerly wind increases the inflow.

Vertical mixing is important for the primary production. In the spring, the deep winter mixing brings nutrients into the surface water, but the average light intensity in the water column is too low to allow any net phytoplankton growth. In oceanic waters away from the coast or other sources of fresh water influx, the water column has to be stabilised by thermal heating of the surface layer by solar input or heat transfer from the atmosphere. Wind tends to break down the stabilisation, especially wind from north which usually is cold and thereby decreases the vertical stability by vertical convection in addition to the mechanical steering. If fresh water is added to the sea surface, stabilisation may take place independent of the heat flux from the atmosphere. Large areas of the Barents Sea are dominated by fresh water input from various sources. Along the ice border melt water is formed when the ice comes in contact with warm Atlantic water. Since most of the salinity contained in the water is rejected during the formation of the ice, fresh water is released when the ice melts. This creates a thin stable layer of low salinity water along the ice border. Along the coast, the Norwegian Coastal Current and freshwater run-off from land create a layer of low saline water which stabilises the water column.

### Model set up

The hydrodynamical model (Box 1) is implemented for an area from SW Norway to the Kara Sea (Fig. 7). Horizontal grid point distance is 20 km. The vertical column is divided into 20 levels (layers) of different thicknesses; from surface and down: 10 m, 6 x 5 m; 10 m; 6 x 25 m, 2 x 50 m; 100 m, 200 m, 400 m and 1000 m. The initial density field for an autumn situation was taken from the Climatological Atlas of the World Ocean produced by the National Oceanographic Data Centre (NODC) in USA (Levitus 1982). In the Barents Sea this field has been improved by measurements performed by the

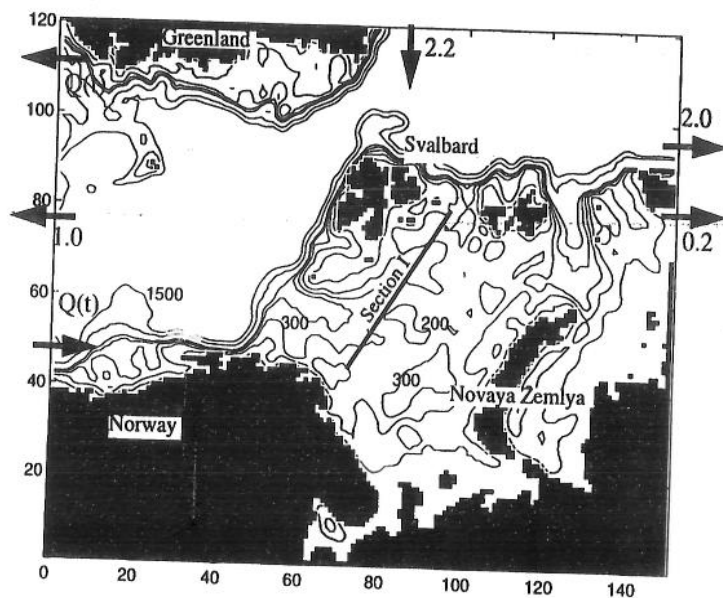


Figure 7. Model area and specified flux through the open boundaries in Sverdrups ( $10^6 \text{ m}^3 \text{ s}^{-1}$ ). Isobaths are shown for 100, 200, 300, 400, 500, 1000, and 1500 m. "Section I" indicates a transect from where data in Figs 10 and 12 are presented.

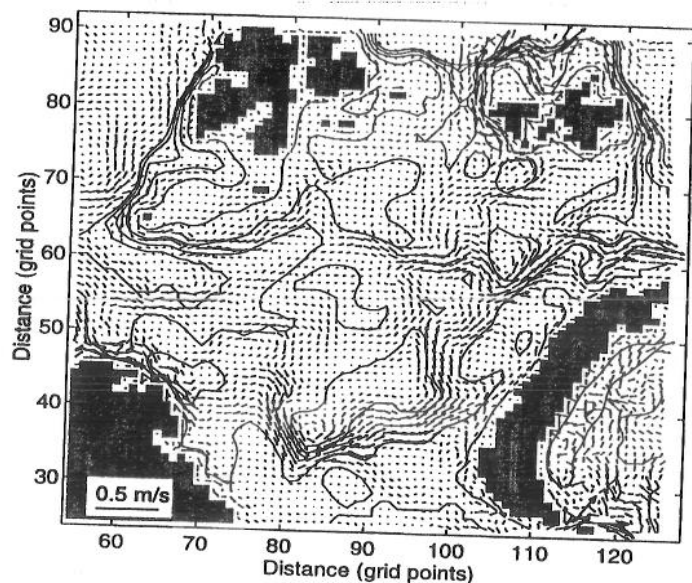


Figure 8. Simulated average surface currents for June 1984.

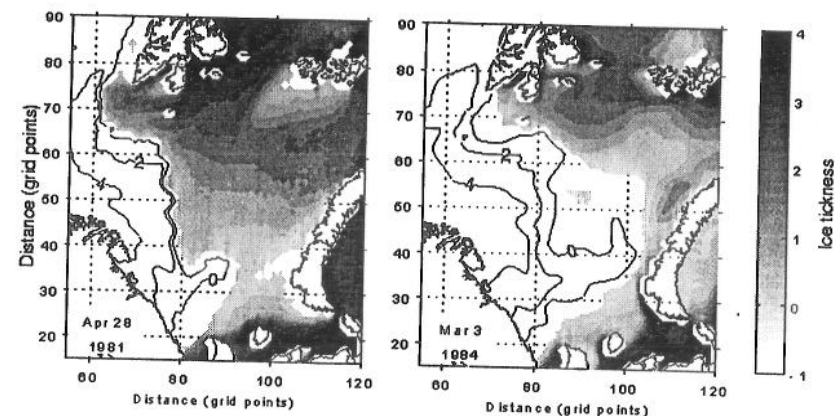


Figure 9. Simulated maximum ice cover and surface temperature for the "cold" year 1981 and the "warm" year 1984.

Institute of Marine Research in Bergen. The flux along the Norwegian Coast ( $Q(t)$ ) is calculated according to an algorithm by McClimans (1993). More information about the model and the model parameters used can be found in Slagstad (1987) and Slagstad & Stokke (1994).

### Results

When the effect of wind and tidal forces are smoothed out by averaging the flow field over a period of one month, we observe that the water movements tend to follow the depth isolines (isobaths) (Fig. 8). This mechanism, often referred to as topographic steering, often dominates the average flow pattern on shelf areas with strong variations in the bottom topography.

Extensive hydrographical data collection are usually performed in the Barents Sea each autumn. In winter and spring the available hydrographical data are more scattered especially in the ice covered areas. In order to create an environment which can be used in connection with the biological model runs, simulations have been initiated with a measured distribution of temperature and salinity. This field was advected from autumn to the spring using meteorological forcing (wind, air pressure, air temperature, humidity and cloud cover). The daily average flow field was stored and used for advection scenarios shown in this paper. Simulated maximum ice concentration in late winter is shown in Fig. 9 both for a cold year with heavy ice cover in the southeastern Barents Sea and for a warm year with much less ice cover.

The simulated hydrographical sections show the same vertical structure as the data (Fig. 10). Along the ice border, the melting ice creates a zone of high vertical stability. This stability is also found during the summer behind the ice border. South of the ice border, the water column is well mixed in April, but the depth of the vertical mixing is gradually reduced due to reduction in thermal heating and wind speed.

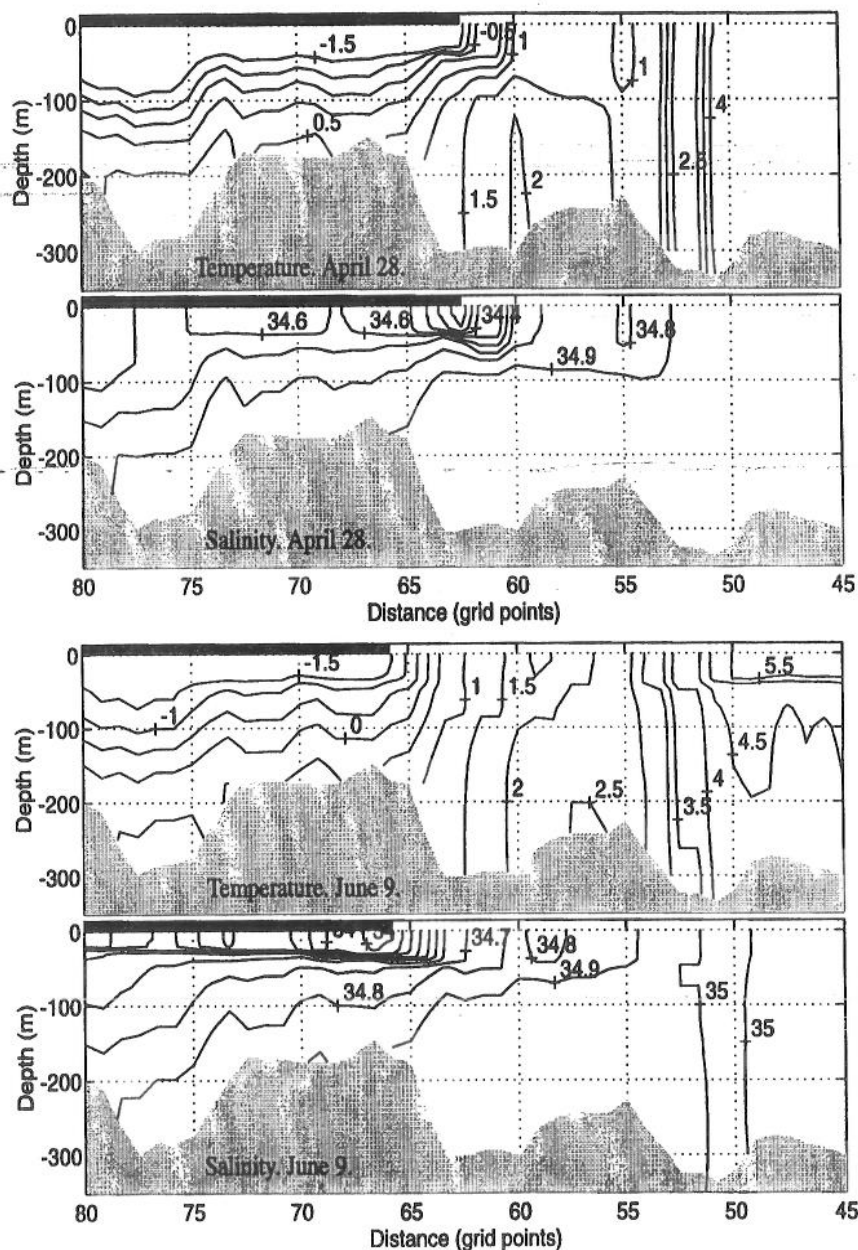


Figure 10. Simulated vertical distribution of temperature and salinity along "Section I" in 1984 after a simulation period of 210 days (upper) and 252 days (lower). The position of the section is shown in Fig. 7.

### Primary production

The simulation start for phytoplankton is March 1st, driven by the data from the hydrodynamical model. These data were: daily average of three velocity components, vertical mixing, temperature, ice thickness and ice concentration. The initial concentration of phytoplankton and nitrogen (nitrate) were  $0.2 \text{ mg Chl m}^{-3}$  and  $11 \text{ mmol N m}^{-3}$ , respectively, in the whole model domain.

Simulated surface concentration of chlorophyll for the warm year 1984 is shown in Fig. 11. In the beginning of May the concentration of chlorophyll is rapidly increasing, especially along the ice border. The south eastern Barents Sea has the earliest bloom due to meltwater input which stabilise the water column. In late May most of the ice-free areas now has a bloom, except for the Bear Island Trench, where the bloom does not start until June. This pattern is similar from year to year. After the nutrients in the surface are depleted, further primary production will take place deeper in the water column. In the northern areas a surface bloom will take place as soon as the ice concentration is low enough to permit light to penetrate into the water column.

### Effect of ice on primary production

To illustrate the difference in primary production between a warm and a cold year, the primary production for the cold year 1981, with extensive ice cover during the late winter has been simulated. The annual primary production along "Section I" was much higher in 1984 than in 1981 (Fig. 7). The greatest difference was found in the Atlantic water, west of the Central Bank. The 1981 production here is less than half the production of 1984 (Fig. 12). The simulated total primary production for the Barents Sea was about 30% higher in the warm year 1984 than in year 1981 (Fig. 13). Most of this difference is due to the extent of the ice cover. Areas covered by ice in the late winter will have a very stable water column the following spring and summer, inhibiting nutrients to enter the euphotic zone by vertical eddy diffusion.

### Zooplankton dynamics

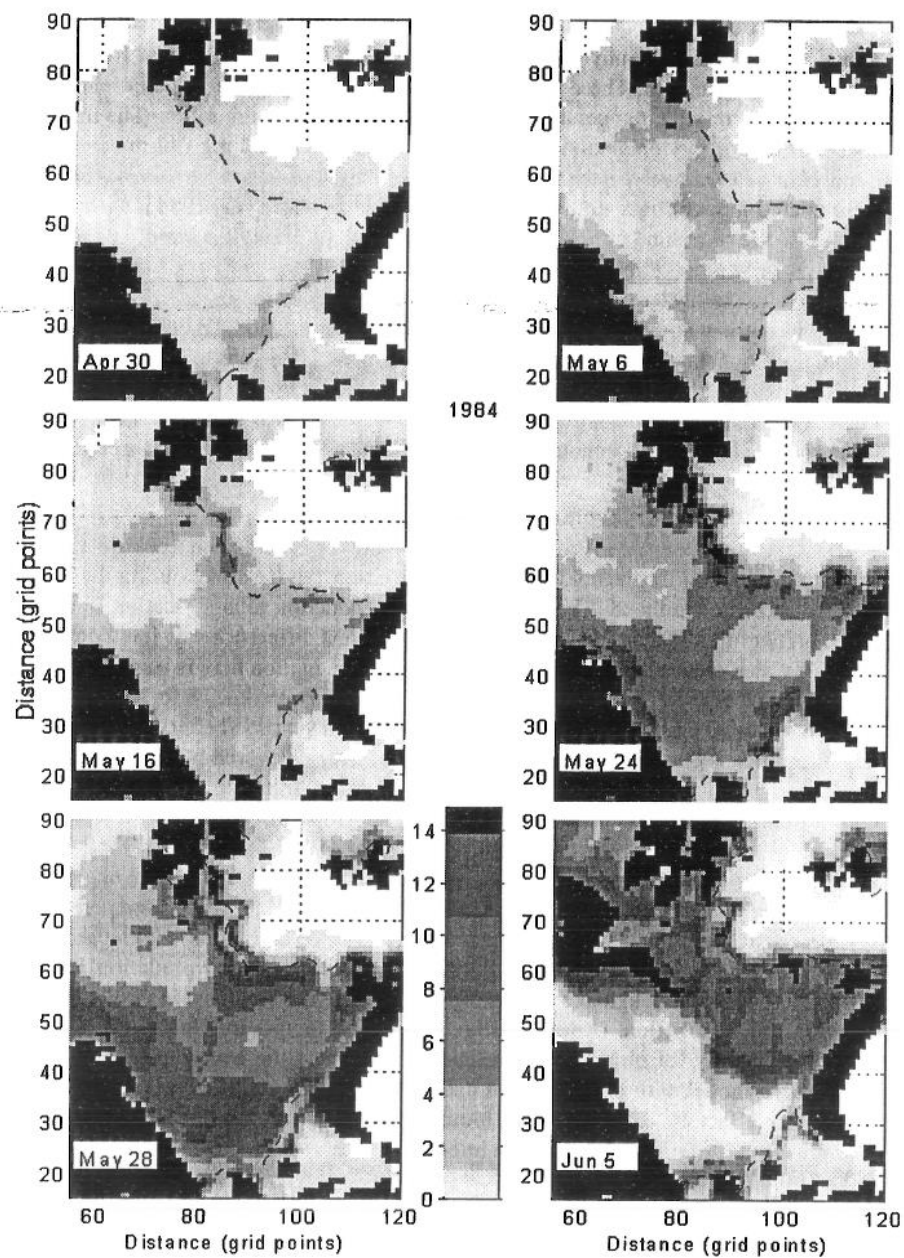
The ultimate goal of a coupled *Calanus* model is to simulate horizontal (and perhaps vertical) distribution and stage distribution which can be compared with measurements. Knowledge or estimates of future physical forcing and predation from planktivorous fish should make us able to predict future development in the *Calanus* biomass and distribution. However, more spatial and temporary resolved data are needed especially for obtaining an initial distribution of the overwintering stock. However, a model without such input data can be a useful tool to investigate the factors that affect the distribution and biomass formation of *Calanus*. Here we shall examine possible consequences of the import of *Calanus* from the Norwegian Sea.

### Inflow of *C. finmarchicus* from the Norwegian Sea

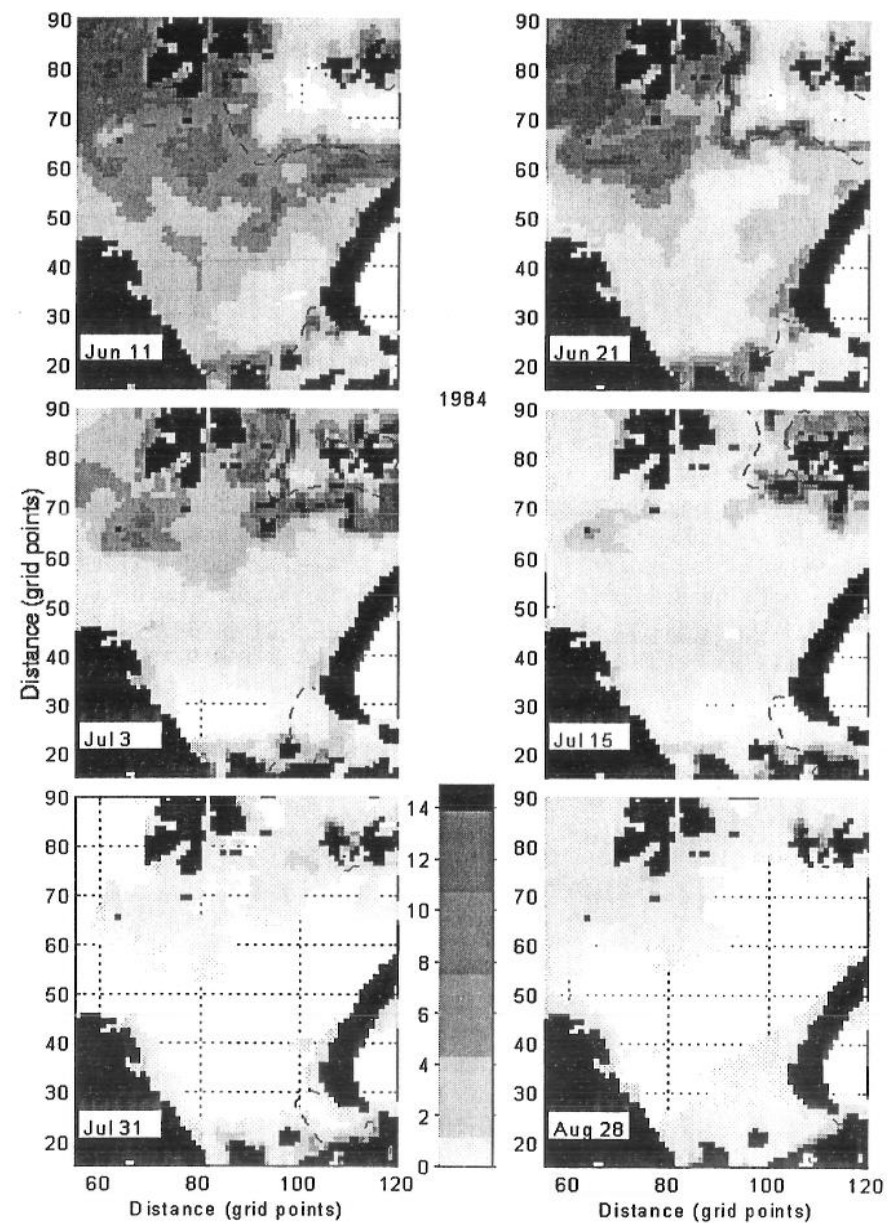
To investigate the effect of the inflow from the Norwegian Sea we have made two model runs, one with an initial stock of females only on the Barents Sea shelf and one with an even initial distribution of females in the whole model domain.

The ontogenetic migration behaviour is such that females ascend to about 250 m in the first half of March and stay there until the concentration of phytoplankton is high





**Figure 11.** Simulated concentration of chlorophyll ( $\text{mg Chl m}^{-3}$ ) at the surface at selected dates spring and summer 1984. (The figure continues on the next page).



**Figure 11** continued from previous page.

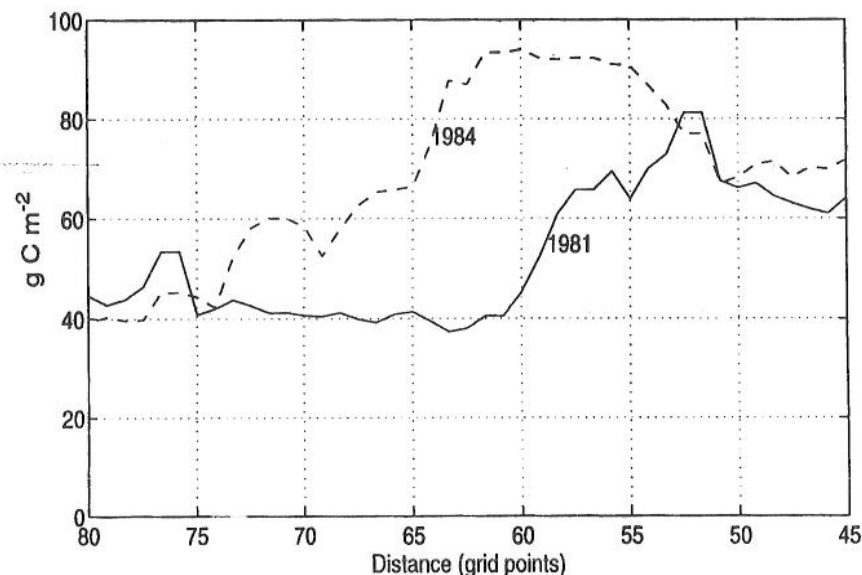


Figure 12. Simulated annual primary production along "Section I" for the years 1981 and 1984. The position of the section is shown in Fig. 7.

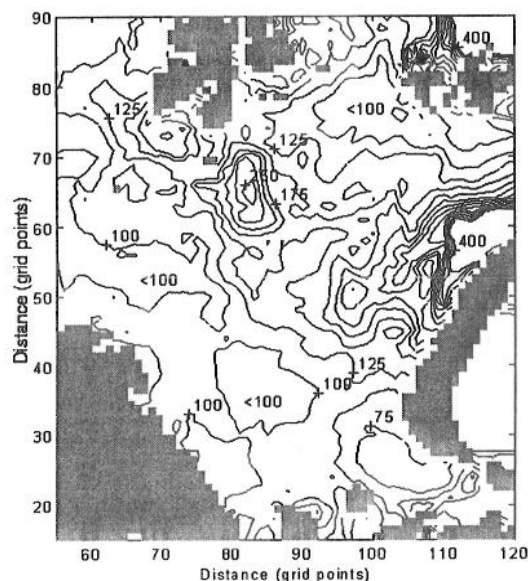


Figure 13. Relative annual primary production in 1984 in percent of the production in 1981.

enough to sustain egg production after which the females enter the surface layer. The vertical migration behaviour of the copepodites are calculated according to Eqs 18-19. When the last weight class within the Stage CV is reached, downward migration to 500 m is assumed. If such depth is not found, the CV's migrate towards the bottom.

In the first model run, we assume no *Calanus* in the inflowing water. The average overwintering stock is 2000 females  $\text{m}^{-2}$ . The physical forcing is from the relatively warm year of 1984. The new generation develops fast in the South and shifts gradually northwards as a result of the decreasing temperature to the North (Fig. 14). Stage CV are first seen at the end of June East of Vardø. At the end of August, the CV are found in the South East basin and in the deep areas South East of Nordkappbanken. Very few stage CV are found north of the Polar Front. The average concentration of Stage CV on the Barents Sea shelf in late August was 700 ind.  $\text{m}^{-2}$ .

In the second run we assume 2000 females  $\text{m}^{-2}$  in the whole model domain (Fig. 15). The first CI are seen on Tromsøflaket at the end of April. These animals are born in the Lofoten area. In late May CI is found in the whole South Western Barents Sea (Fig. 15a). In June the first overwintering stages tend to concentrate in deep areas, west of Tromsøflaket and Ingøydjupet. This is emphasised later in the summer (Fig. 15c). The average concentration of CV in late August was 7960 ind.  $\text{m}^{-2}$ .

A third simulation starting with initial distribution of females only in the oceanic Norwegian Sea produced an average concentration of 2760 ind.  $\text{m}^{-2}$ . Thus, import from the oceanic regions of the Norwegian Sea alone produces 4 times the biomass of CV in the Barents Sea in August compared with the nonimport case. When the initial distribution of females were placed in the whole model domain, the biomass of CV was 11 times the nonimport case. The reason for this high number is the production on the Mid Norwegian shelf. Copepodite stages from this area are transported north with the Norwegian Coastal Current. The animals that have reached the overwintering stage will tend to be trapped west of Tromsøflaket when they descend to depths below 500 m, but those who are still in their growth phase and most of the time near the surface, will be advected into the Barents Sea.

The processes that dominates the amount of *C. finmarchicus* found in the Barents Sea seem to be:

1. The strength of the physical transport from Norwegian Sea (Lofoten Basin).
2. Size of the overwintering stock along the North Norwegian shelf break.
3. Spawning and survival success south of Lofoten (on the Mid Norwegian shelf and along the shelf break).

## Models of motivation and behaviour

### Static optimisation

In the following three examples on the applicability of static optimisation will be provided. The central assumption for all models is that the general Life History Theory can account for the optimal trade-off between opposing forces: growth versus survival or current versus future reproduction.

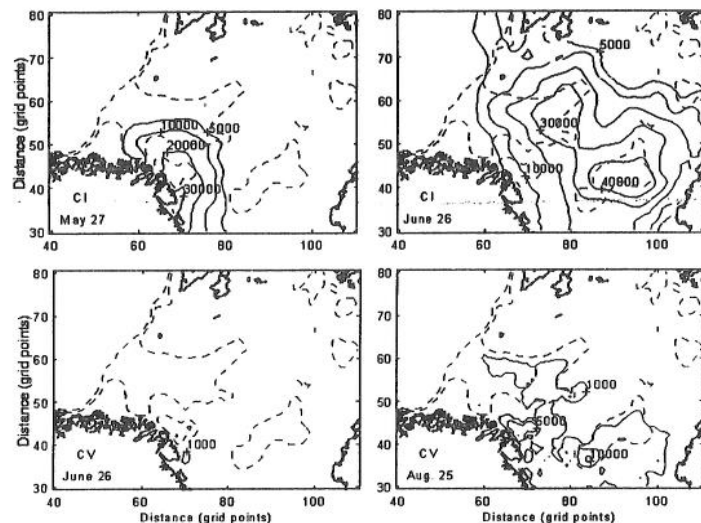


Figure 14. Simulated distribution of *Calanus finmarchicus* when the initial concentration of females are found in Barents Sea, only. A and B: Stage I (1000 individuals  $m^{-2}$ ) on May 26th. and June 26th. and C and D: Stage V on June 11th. and August 25th.

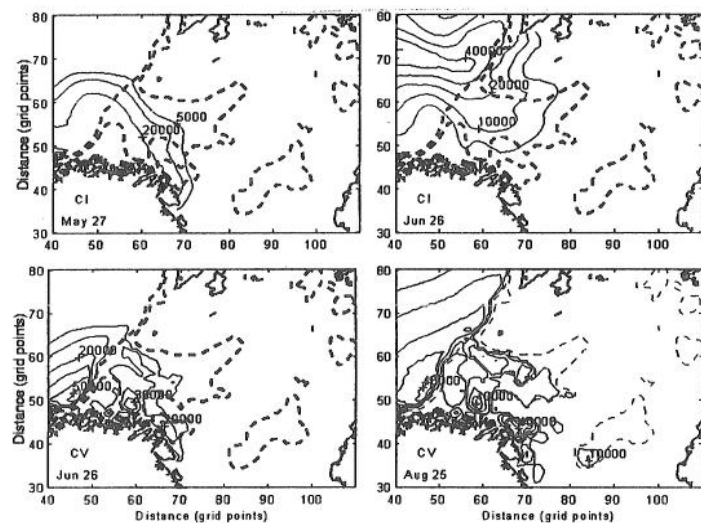


Figure 15. Simulated distribution of *Calanus finmarchicus* when the initial concentration of females are found in the whole model domain. A and B: Simulated distribution of *C. finmarchicus* stage I (1000 individuals  $m^{-2}$ ) on May 26th. and June 26th. and C and D: Stage V on June 11th. and August 25th.

### Life cycles of herring and capelin

The two major planktivores in the Barents Sea are capelin and juvenile herring. Capelin spends its entire life in the Barents Sea, while herring eggs are spawned at the west coast of southern Norway, the larvae drift into the Barents Sea, and adults live in the Norwegian Sea. The life cycles of these species are quite different. Capelin reproduces once, while herring may survive 15-20 reproductive seasons. Why is it so?

One can argue (Eq. 21b) that the optimal habitat for any organism is where the generation time is at a minimum, which at these highly seasonal latitudes is one year for fish. If this is achieved, the next goal is to maximise survival probability until the spawning season. In this life history strategy, fecundity is not of great importance, and egg numbers will count hundreds rather than millions. Due to the vertical correlation between feeding opportunity and mortality risk through the exponential decay of light (see explanation in Box 5), they will often be found deep in the water most of the year and the individual production of such animals will be low. Many fishes in the mesopelagic assemblage fit into this category. However, the Barents Sea is not a good environment for mesopelagic fish, as the bottom depth is too shallow to keep survival rate high, and because the long period with continuous daylight also enables predators to maintain continuous high activity.

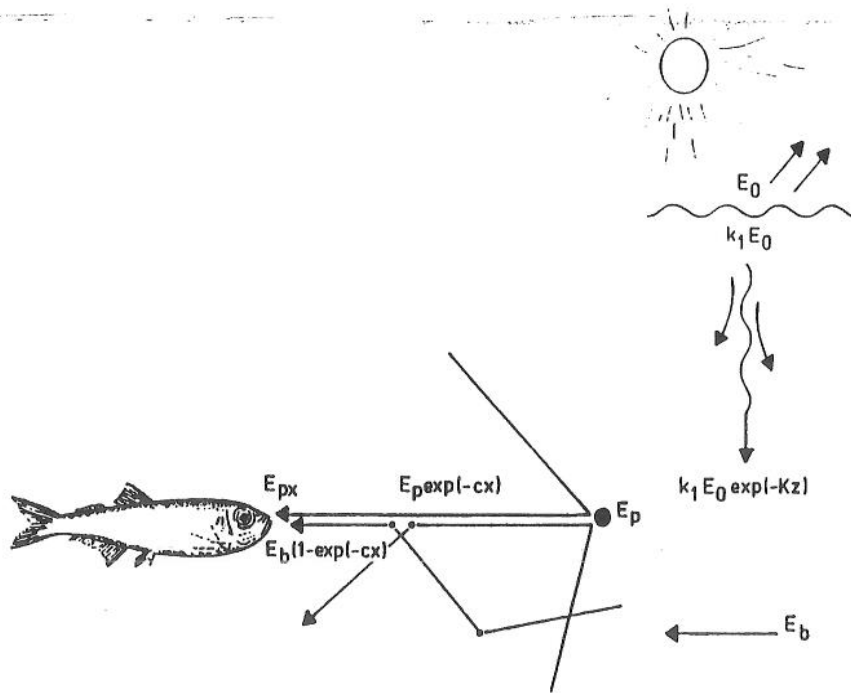
Another life cycle with a higher age at maturity, lower juvenile survival and higher fecundity is common among long-distance migrants. Long-distance migration is very costly for small-bodied forms, and this life style thus requires a rapid juvenile growth. A large body size is also needed to have a potential for a high fecundity. Such animals will generally have high individual growth rate and potentially a high population biomass. Fishes in this life style are valuable resources to man, and include all the large stocks exploited in the Nordic Seas. This distinction between the mesopelagic, short-lived, low-fecundity life form and the horizontally migrating, high fecundity life form with multiple spawning seasons corresponds to the life history types Ia and Ib of Kawasaki (1980, 1983). Both types are typical in boreal waters. Kawasaki (1980, 1983) argues that both types are evolutionary adaptations to variable and unpredictable environments. Type Ia is adapted to irregular variation in environment and fecundity by a potential high per capita reproductive rate  $p$ , while type Ib is an adaptation to long-period variation, by high longevity and high adult survival. Capelin does not fit into any of these simple categories, as it is a long-distance migrator with only a small fraction of the population having more than one spawning season.

Life histories with drifting planktonic larvae which are susceptible to fluctuations in currents and feeding conditions, are likely to experience large fluctuation in juvenile survival. Most of this mortality takes place in the first week after hatching, in relation to start-feeding (Miller & al. 1988, Bailey & Houde 1989). This is related to the reproductive strategy of producing many small offspring. To counter the effect of variable juvenile survival the fish may spread the risk over several spawning seasons (iteroparity) and spread the eggs over a prolonged period (batch spawning) (Armstrong & Shelton 1990). Murphy (1968) and Kawasaki (1980, 1983) concluded that high fecundity, iteroparity and delayed maturation would increase juvenile survival in environments with variable juvenile mortality. Nevertheless, there are typically large



### Box 5: Light as forcing for feeding and predation risk

Light does not only influence the ecosystem through primary production, but makes also a direct and instantaneous effect at higher trophic levels. Traditionally, prey concentrations have been regarded as the central variable for feeding opportunities. Visual predation is an important feeding mode for pelagic fish, and the highly variable surface light, the exponential attenuation in water, and its dependence on the variable scattering and absorbance properties of the water, makes the feeding process and thereby the mortality risk highly dependent on the light regime. Light intensity will thus influence the growth, mortality and spatial distribution of zooplankton, planktivores and fish-eaters in the Barents Sea. As many of the examples given in this section are vertical models, we will illustrate how light influences prey detection (Aksnes & Giske 1993).



**Figure 16.** Simplified aspects of fish vision (after Skjoldal & al. 1993). Surface light in the air ( $E_0$ ) is reflected and absorbed at the air-sea interface (p). Downwelling light is reflected and scattered ( $K$ ) so that light at depth  $z$  [ $E_b = p E_0 \exp(-Kz)$ ] is diffuse. Irradiance reaching the fish eye has two sources: image-forming light from the prey [ $E_p \exp(-cx)$ ] where  $c$  is the beam attenuation coefficient and  $x$  is the horizontal distance, and scattered light [ $E_b (1 - \exp(-cx))$ ] that disturbs the image.

fluctuations in year class strength of 0-group fish.

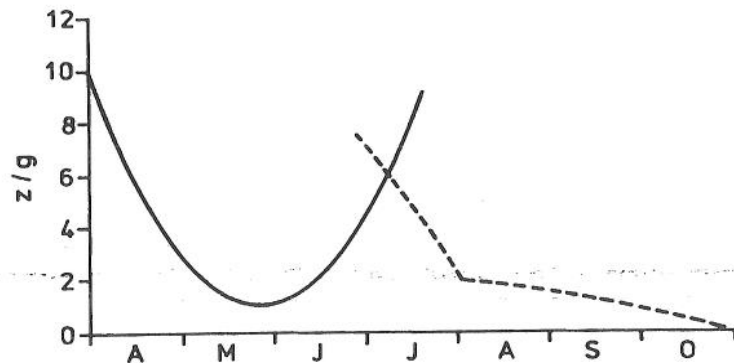
The life cycle of herring fits well with the scheme of Kawasaki (1980, 1983), while capelin does not. The difference between these two planktivores is probably most pronounced in their spawning areas. Capelin spawns along the southern shores of the Barents Sea, where the adults have to swim through the cod stock in order to cross from the feeding areas to the spawning grounds. In this period, capelin is the dominant prey for cod and mortality of adult capelin is high. If adults should reproduce two seasons in stead of one, they would have to cross this dangerous zone three times in stead of one. If they reproduce only once, they may also allocate more of their body reserves into reproduction, as they do not need to save energy for the return. So this is the trade-off for a coastal spawner having reached the southern shores of the Barents Sea: reproduce once with all available energy ( $m$  eggs), or save some grams [ $m(1-q)$  eggs] with a probability of  $p^2$  to be able to survive two more crossings (assuming all adult mortality risk is associated with the probability  $p$  of surviving a crossing through the cod belt). Reproduction twice gives a higher number of offspring than a single reproductive event only if

$$m < m(1-q) + mp^2 \Leftrightarrow q < p^2 \quad (27)$$

According to Eq. 27, semelparous (big-bang) reproduction is optimal at high mortality risk, while low fecundity loss ( $q$ ) associated with saving energy for survival will favour iteroparity (repeated reproduction). Mortality risk during migration depends both on the sizes of the cod stock and the capelin spawning stocks and fecundity loss  $q$  will depend on the body size of the capelin. Hence, the proportion of individuals attempting multiple spawning may vary interannually and with condition. However, if spawning capelin can anticipate the stocks of capelin and cod one year in advance with some accuracy, they are far better qualified than the fisheries biologists.

#### Timing of habitat shifts

In the process of development from newly hatched larvae to adults, fish undergo substantial changes in anatomy and increases in size by several orders of magnitude. During this growth, the individuals also have to change to new diets, and in most cases growth also leads to changes in preference for place to live. These habitat shifts may be motivated by increased mouth opening that in turn enables the fish to expand its diet, or that larger body reduces risk of predation from one group of predators, while perhaps increasing the risk from other predators. Salvanes & al. (1994) studied the optimal timing for the switch from pelagic to benthic habitat for young cod. They showed that for juveniles, the optimal balance between growth rate ( $g$ ) and mortality risk ( $M$ ) was attained by minimising  $M/g$  (c.f. Werner & Gilliam 1984, Werner & Hall 1988). Early in life and in the pelagic habitat, mortality rate is extremely high but diminishing (with size and age). As a result there is a period where the ratio  $M/g$  is improving, indicating an increased quality of the pelagic habitat for cod larvae. However, the growth rate will eventually be reduced as the cod grows, leading to a decline in profitability of the pelagic habitat later in spring. The benthic habitat is



**Figure 17.** Statistical optimization: optimal timing for settling of cod can be predicted at the intersection between the pelagic and benthic habitat profitability curves. Conditions are initially best in the pelagic habitat (left curve), but through June this habitat is becoming poorer as cod grows; and in the beginning of July conditions are better in the benthic habitat. Redrawn from Salvanes & al. (1994).

extremely poor for newborn cod, mainly due to the food particle size and concentration. However, as cod grow and increases its feeding capacity, a diet shift to larger benthic prey is profitable. Over the same period, the larger codlings becomes more visible to their predators, and shelter becomes important in the habitat quality assessment. Based on data on growth and mortality from different areas, Salvanes & al. (1994) predicted that the settling of cod should take place at midsummer (Fig. 17).

#### Diet versus depth

In optimal foraging theory, much attention has been put into predicting the diet selection of fish (Townsend & Winfield 1985, Schoener 1987, Gilliam 1990). Giske & Salvanes (1995) showed that the model commonly used is based on the assumption that the time budget of the optimal individual may be divided into separate bouts of feeding and hiding. This is relevant for nearshore and most freshwater fish, but does not apply to open ocean pelagic fish. They then showed that the extra gain in growth achieved by a selective diet in the pelagic could not balance the increased mortality risk associated with staying in so illuminated water that food selection was possible. Rather than be diet-selective, pelagic planktivores should be depth-selective in order to maximise their fitness (see also Box 5). This result may simplify the construction of coupled trophic models of pelagic systems.

#### *Seasonal variation in motivation*

Life history theory can be used to predict differences in risk-willingness associated with feeding for juvenile and adult fish. Giske & Aksnes (1992) showed that juveniles that may utilise ingested food to shorten their generation time, benefit more from hazardous feeding than do adults that by feeding only may enhance their egg production. While the optimal trade-off for juveniles is to minimise  $g/M$ , adults should

minimise  $\ln g/M$  (Fig. 6a).

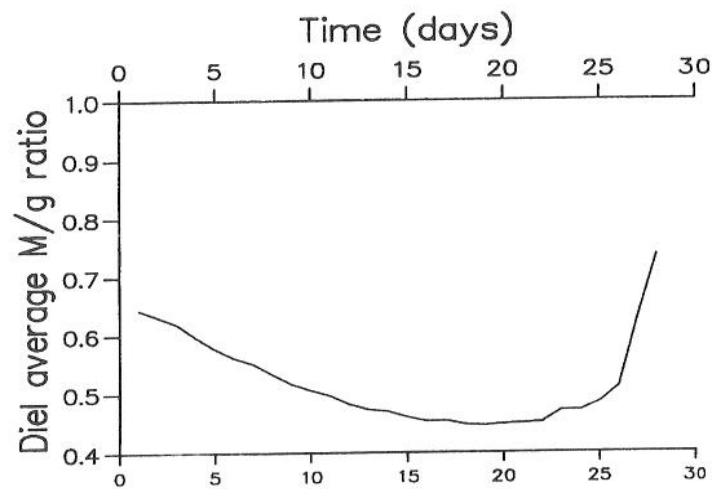
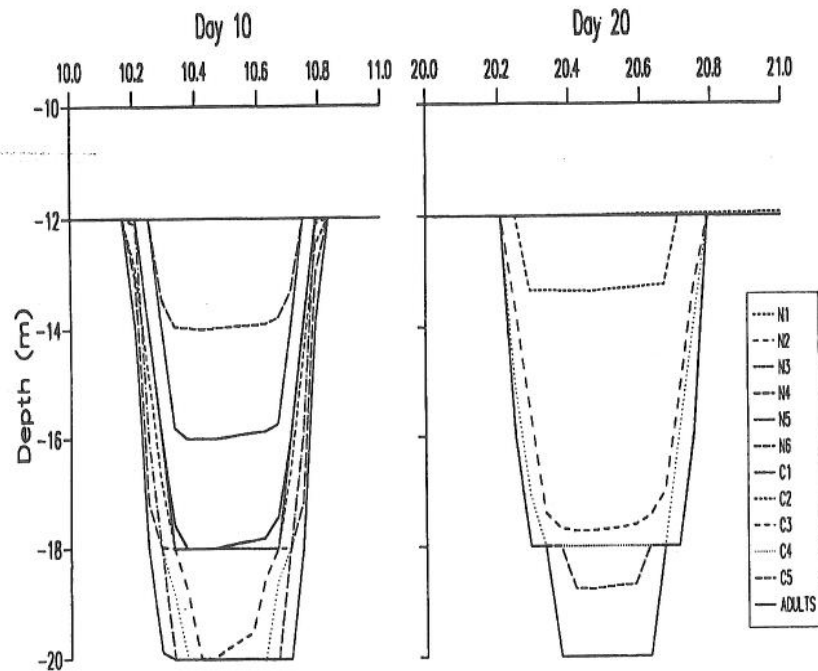
However, when testing this hypothesis on the mesopelagic planktivore *Maurolicus muelleri* in Masfjorden in winter, they found that adults had so low feeding rate that their growth rate was negative. This is not compatible with any life history model, as an average negative growth rate cannot produce offspring. The negative growth was not associated with poor feeding conditions, as the calculated growth rate of juveniles was very high. (The two age groups separated into two different sound scattering layers, Giske & al. 1990). Adults seemed rather to maximise probability of overwintering survival, which is also observed in dynamic optimisation studies of the life cycle of this planktivore.

Rosland & Giske (1994) modelled the diel vertical distribution of *M. muelleri* during winter by dynamic optimisation. The two age groups were offered the same environment (although visual predation would impact the larger adults far more than juveniles), but the fitness functions, i.e. the relationship between growth over 24 h and fitness gain differed: juveniles were given a high premium for growth, while the reward for adults were almost equal as long as they did not risk short-term starvation. These differences then made the model predict two vertically separated age-groups, very much as observed in the fjord. They also found that the vertical range of each age group, as observed by echo sounder (Giske & al. 1990), corresponded with differences in optimal depth between hungry and satiated individuals. Hence, seasonal variability could explain the overall patterns, while state differences could explain the immediate variability.

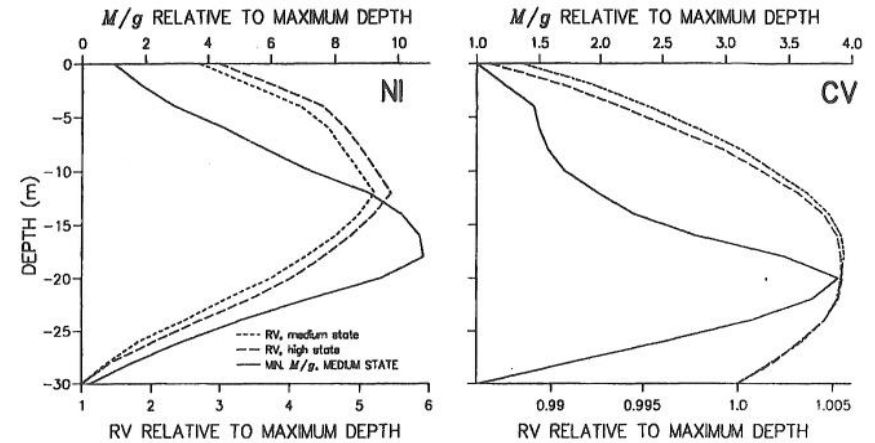
#### *Age- and state-dependent motivation*

The negative growth rate of adult *Maurolicus muelleri* in winter is an example of the impact of the external environment on motivation and behaviour. From life history theory we also know that motivation will change during the life of an individual, according to the potential fitness value of an action (Giske & Aksnes 1992). This has been studied for the life cycle of a copepod cohort by Fiksen & Giske (1995) by the use of dynamic programming. The environment modelled was constant through time, so the only effect of changes in motivation and behaviour (depth selection) is due to potential changes in growth rate and mortality risk due to the size development of the individual, and to the allocation of assimilated energy to either body growth or egg production. The modelled vertical distribution of the cohort is given in Fig. 18a. The optimal depth of the developmental stages differed, in that larger individuals migrated deeper during daytime to avoid visual predation. However, they overcompensated for predation risk, showing that optimal risk-willingness is reduced as the acquired resources and the probability of survival until first reproduction ("pay day") increases (Fig. 18b).

Also the physiological state (stomach fullness) impacts the short-term motivation and risk-willingness of individuals. Fig. 19 shows that optimal depth is shallower for hungry than for satiated individuals, and that the life-history derived optimum (minimise  $M/g$ ) applies to neither of them.



**Figure 18.** Dynamic optimization: A. The development of the vertical distribution of the copepod cohort. B. Dynamic changes in risk-willingness given as the average mortality risk : growth rate ratio. Redrawn from Fiksen & Giske (1995).



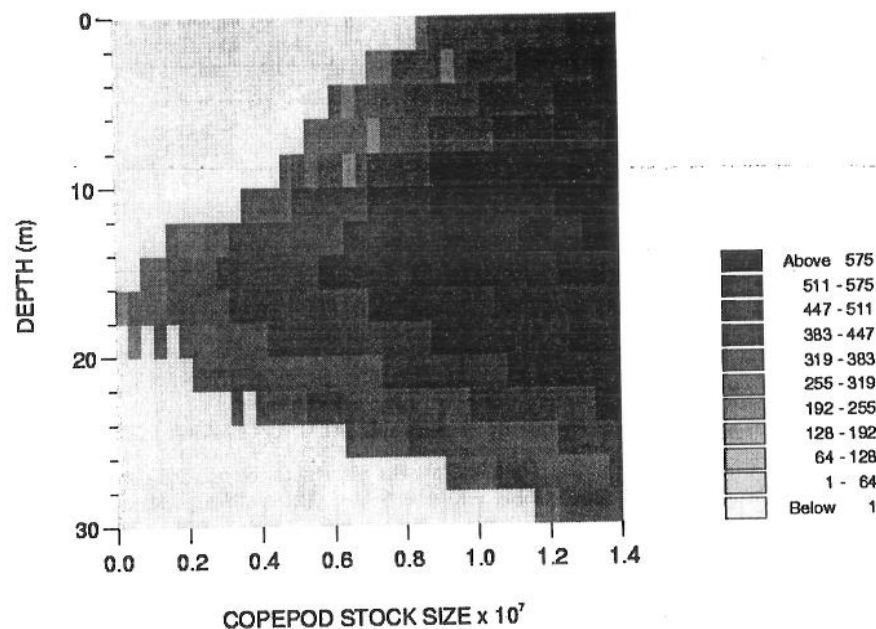
**Figure 19.** Dynamic optimization: physiological state influences the optimal depth of the copepods. The dotted lines show habitat profitability for NI and CV-individuals of low, medium and high internal state. The solid line depicts habitat profitability as measured by the "minimise  $M/g$ " rule, which does not account for internal state. Redrawn from Fiksen (1994).

#### *Effect of density-dependent profitability on copepod distribution*

The combination of age-, (size-) and state-dependent motivation of the copepods described above gave a diel range in vertical distribution of 8 meters (11-19 m) with the environmental parameters used. From a constant distribution of the smallest nauplia, diel vertical migration became gradually more emphasised. Later in life the copepods stayed at 17-19 m during daylight hours and at 11-13 m during daytime. Being a dynamic programming approach, the density of copepods was assumed so low that their feeding did not interfere with the dynamics of the food source (phytoplankton). This is a necessary condition for running dynamic programming models over extended time periods. In many practical situation, we are concerned with large populations influencing on their predators and prey, and SDP can then only be used over time scales where these important processes have not had opportunity to affect the environment. These two limitations reduce their value of SDP for practical purposes. Rosland & al. (ms) have therefore studied how density of potential competitors may influence habitat profitability and spatial distributions. An Ideal Free Distribution model was formulated, incorporating 1) dilution of predation risk whenever "competitor" density was high enough to satiate predators, 2) temperature-limited growth rate in absence of competition, but 3) reduction of growth rate when zooplankton community feeding rate exceeded phytoplankton production rate, and finally 4) habitat profitability expressed by the static model of minimise mortality risk per growth rate  $M/g$ . This may be a valid assumption during the spring and summer growth season, but does not fit with an overwintering phase (for which dynamic programming would find seasonally adjusted motivations).

There is no diel variability (e.g. in light intensity) in the model, so it does not



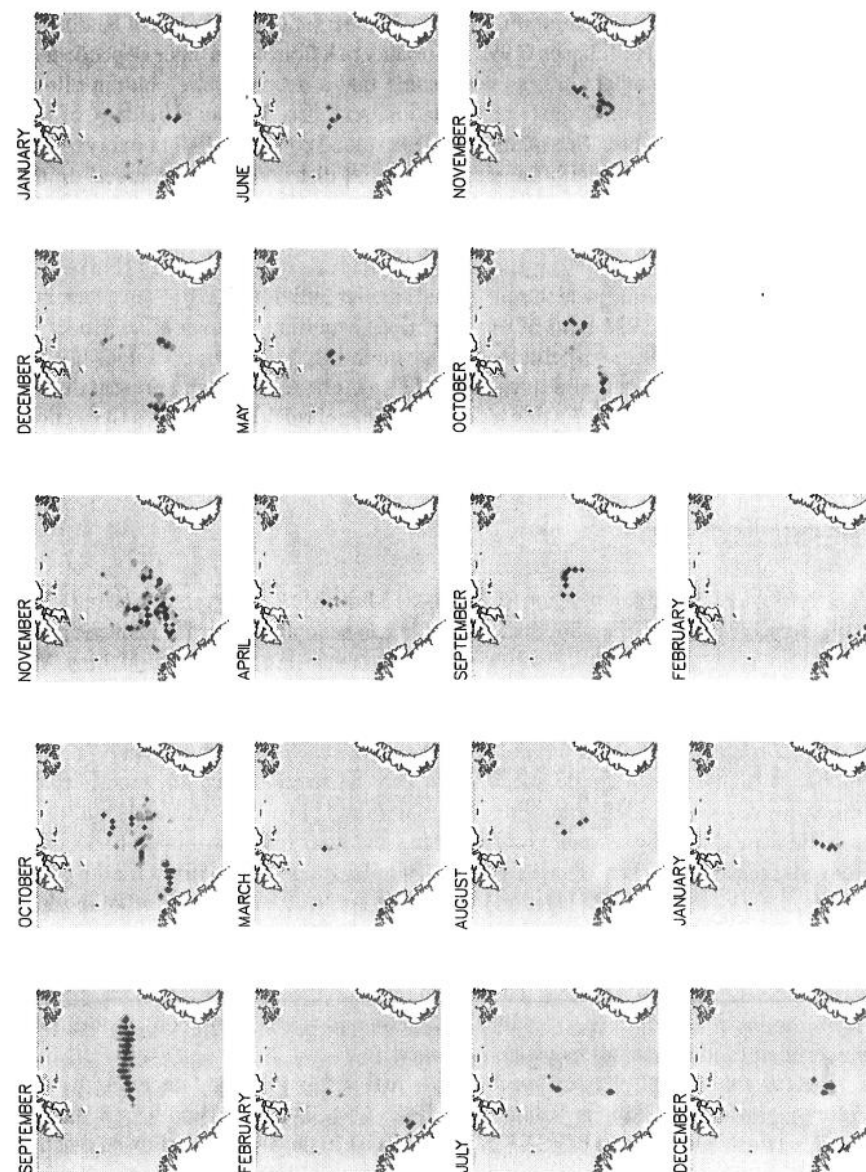


**Figure 20.** Ideal Free Distribution: optimal vertical distribution depends on the presence of other individuals. As density increases, more depths are utilised, and an increasingly higher fraction of the population seeks shallower depths. Redrawn from Giske & al. 1997.

account for vertical migration. Rather, a optimal daytime distribution is described, dependent on competitor density. With the same environmental data as in Fiksen & Giske (1995), the IFD model finds optimal depth at 12-14 m at very low densities (Fig. 20). With increasing competition, the whole water column (0-30 m) is gradually exploited. As competition increases, the population's vertical distribution will converge towards the profile of the resource input rate. Thus it is evident that optimal distributions should also account for density-dependent factors.

#### A coupled model for capelin distribution

As a first attempt to make a coupled model of hydrodynamics, zooplankton and fish in the Barents Sea, the model of hydrodynamics and zooplankton (Slagstad 1981a,b, 1987, Slagstad & al. 1989, Støle-Hansen & Slagstad 1991) has been used as input to a dynamic optimisation model of capelin spatial distribution, growth and survival (Fiksen & al. 1995). As there is no interactive link between fish and zooplankton, the model is obviously incomplete. The results from the three-dimensional hydrodynamics and copepod model are summed up to surface-integrated values of temperature and copepod biomass. The growth of capelin is made dependent on swimming costs,



**Figure 21.** Horizontal distribution of capelin from September 1979 to February 1981, modelled by dynamic programming with temperature, *Calanus* and predation risk as environmental forces. From Fiksen & al. (1995).

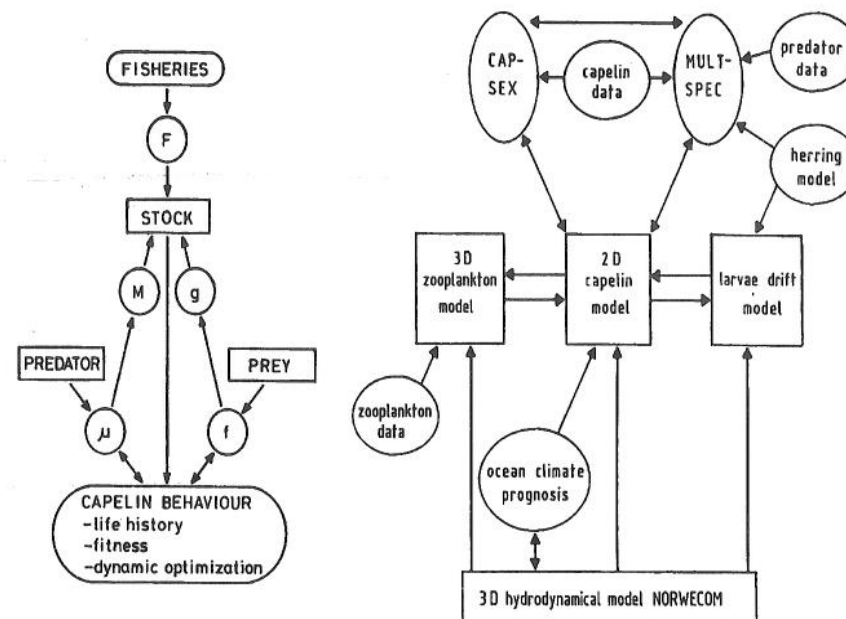
temperature and food concentration, using the bioenergetics framework of Kitchell & al. (1977) and Hewett & Johnson (1992). Mortality risk from cod is made dependent on bottom depth and temperature, as we assume that a deeper water column allows capelin some protection against cod predation, and also that the efficiency of cod decreases in colder water. Sea mammals are assumed equally efficient everywhere. The capelin is initialised with the size and spatial distribution as observed on the Institute of Marine Research autumn cruise in 1979, and the behaviour of the capelin is motivated by the fitness premium of spawning along the coast of Finnmark in January-March in either 1980 or 1981. Only individuals larger than 14 g (Forberg & Tjelmeland 1985) are allowed to spawn, and smaller individuals are given a terminal reward in February 1981 (end of model period) according to their size. Modelled monthly dynamics of the capelin stock is given in Fig. 21. The model does not account for the fate of eggs, and traces only the year classes that were present during the autumn cruise in 1979. As this model is quite preliminary and also a theoretical model, no emphasis has been put into tuning output data to observations.

## PERSPECTIVES

The ecological modelling performed during the Multispecies program has been rather single-species and process-oriented. And this has been necessary for achieving the long-term goals, given the current state-of-the-art in marine ecological modelling. We have focused on capelin, as a key component in the ecosystem. We will here sketch two ways of incorporating more ecosystem dynamics into the fisheries management.

Fig. 22a depicts a frame for an ecological model of capelin growth and survival. The model is focused on a single species, but ecosystem dynamics are incorporated through stock sizes and distributions of predators and prey. Growth and mortality of capelin is modelled by dynamic programming and ideal free distribution to account for state, season (SDP) and density (IFD). A similar frame may be used for the other actors, e.g. cod and juvenile herring. Fig. 22b depicts a more complex set of models where competition, predation, reproduction and drift of larvae can be run in concert. Here are also indicated direct links between the ecological models and the assessment tools. One of the problems with modelling an ecosystem is that so many processes are interdependent (e.g. feeding of capelin and survival of zooplankton) that integration of model components is necessary.

The current state of physical modelling is reasonably good and encouraging for future ecological applications. Validation of the ECOM-3D model (Blumberg & Mellor 1987) against data from the ICES SKAGEX exercise in the Skagerrak showed that the model reproduced many of the main features of the currents and hydrographic structures (Svendsen et al. 1996). However, it may be difficult to maintain correct descriptions of horizontal and vertical gradients in the density field in models, which may through feed-back have consequences for the modelled current fields. Increased spatial resolution will generally reduce such errors and improve the accuracy of physical models. This increases the model computations, and computing power sets a practical limitation on how far one can go in resolution in coupled physical-chemical-

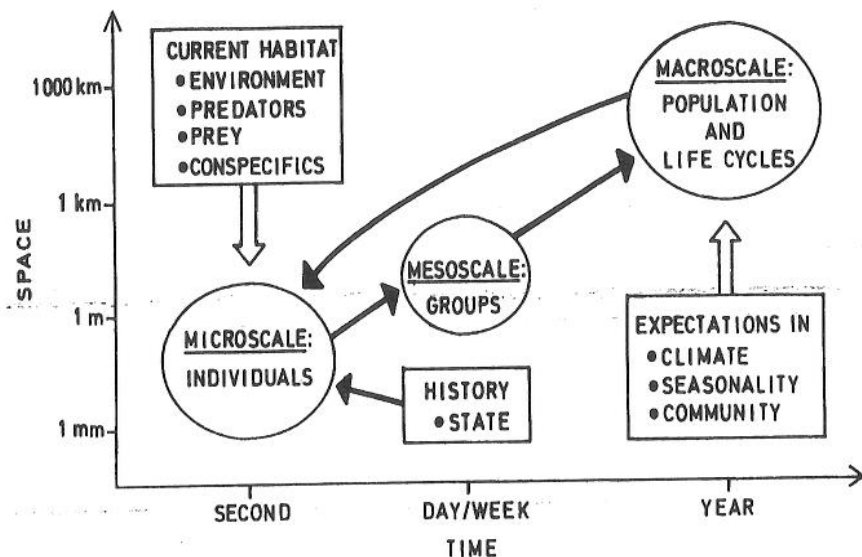


**Figure 22 A.** Suggested assessment model environment of capelin. Survival and growth of the stock is determined by fisheries (F), natural mortality (M) and individual growth rates (g). The biological stock assessment variables (M, g) result from the interplay between environmental variables (e.g. predator and prey density) and capelin behaviour. This behaviour is governed by internal fitness-related forcing, capelin stock size and also experienced mortality risks and feeding rates. **B.** Sketch of a coupled model family containing hydrodynamics, zooplankton and capelin, field data input and links to assessment models.

biological models. Major technical challenges lie in parametrisation of smaller-scale processes at a larger model scale, and in nesting finer-scale models within coarser scale.

Physical models have with some success been used to drive models of primary production and advection of zooplankton and fish larvae. Validation against experimental results and comparison with data from the field have shown reasonably good agreement between model and data (Ådlandsvik and Sundby 1994, Slagstad & Stokke 1994, Aksnes et al. 1995, Svendsen et al. 1995). Use of coupled physical-biological models holds great promise for wider use as integral parts of ecological models. Models of advection of fish larvae may provide important information on larval drift routes and geographical recruitment as input to multispecies models (Berntsen & al. 1994, Ådlandsvik & Sundby 1994, Svendsen et al. 1995).

In contrast to fish larvae which typically originate from known and limited spawning grounds, zooplankton spawn over most of their area of distribution (Skjoldal & Melle 1989). Realistic modelling of zooplankton production and advection is therefore dependent on data on the initial fields of zooplankton abundance (Slagstad &



**Figure 23.** Different methods may be suitable at different scales. Life history theory may give the overall aspects of life in order to understand the match with the physical and biological environment. Dynamic programming is suited to resolve individual differences according to internal state, temporal fluctuations and local environment. Dynamics of schools and shoals may be better studied by density dependent methods like ideal free distribution.

Tande 1996, c.f. see the "Inflow of *Calanus finmarchicus* from the Norwegian Sea" section). A minimum monitoring program of zooplankton in the Barents Sea has been established with the aim to produce data input to models of zooplankton production and advection (Hassel & al. 1993).

From the perspective of ecological modelling of higher trophic levels, the first challenge is to combine the benefits of season- and state-resolution of motivation (dynamic programming) with density dependent habitat profitability (ideal free distribution) into a truly coupled model of several trophic levels (Fig. 23). In this respect, there is also need for more attention to other components in the ecosystem (Fig. 2), both phytoplankton, other groups of zooplankton (krill, amphipods, *Calanus glacialis*) and competitors and predators (herring, cod). Altogether this is a huge task, but on the other side the Barents Sea is a simple ecosystem. There are few ecosystems — if any — of this size and economic interest that are more suited for this enterprise.

However, for the sake of predicting the future, we are still in trouble. If growth and survival of capelin depend on temperature and the distribution of zooplankton, and these depend on hydrodynamics which are heavily influenced by wind force, then we have a time horizon equal to the weather forecast of 4-7 days. Luckily, we are not that bad off. The ocean is not moving as fast as the atmosphere, and changes in the heat content and density structure of large water masses occur quite slowly over some

time. The heat and density properties of the ocean have feedback influences on the atmosphere and is likely to act to stabilise the meteorological driving forces. The high degree of regularity and periodicity in ocean climate revealed in oceanographic time series from the Nordic Seas offers some promise that we may be able in the future to forecast the development in ocean climate at time scales of weeks to months or even years. Such predictions may be based on statistical analyses of time series (Ottersen & al. 1994) or better, future insight into the mechanisms and quantitative relationships behind the climatic fluctuations. The current regional GLOBEC program MARE COGNITUM on the ecology of the Nordic Seas aims at providing such basic understanding and predictive capability regarding ocean climate (Skjoldal & al. 1993). Also, biological processes are quite slow, except perhaps for growth and survival in the early life phases. There are thus possibilities for creating qualified statements about the near future of plankton and fish stocks in the Barents Sea.

While this chapter has emphasised the large current uncertainties related to the selection of mathematical formulations, this is a problem that may be overcome with time and funding. However, data uncertainty will probably be the dominant source of error in future, mostly due to a strong chaotic element in weather formation. We may not be able to unify all the concepts described above into one model. Rather than constructing one all-encompassing model, we might therefore end up with a series of smaller and different models, each capable to describe one *what-if* question. In combination with statistical techniques to help find the most probable outcomes, the fisheries managers could compare the predictions of several models before making their final subjective decision. In 1995, this seems to us to be as far as ecological modelling can aid fisheries management.

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