A CONCEPTUAL MODEL OF DISTRIBUTION OF CAPELIN IN THE BARENTS SEA

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To support an assessment model, we propose a set of numerical models where distribution and growth of capelin (Mallotus villosus) is modelled by biological (evolutionary, ecological) and physical forces. The basics of a dynamic optimization fish distribution model is outlined. This model must be coupled to hydrodynamical/meteorological (temperature, ice conditions, light regime) and biological (plankton transport and production) models. While modelling capelin distribution is the short term aim, the ultimate goal is to develop management models where understanding (theory) rather than knowledge (empiricism) is the basis for prediction. This will enable sustainable management also in years deviating from past experience.

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INTRODUCTION

'Since all models are wrong, the scientist must be alert to what is importantly wrong' (Box 1976).

Management of fisheries in the Northeast Atlantic has over a period been based on a combination of field investigations and modelling. The common modelling concept, Virtual Population Analysis (VPA), is 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 statistical data set on age composition, growth, fishing effort and recruitment. This technique is further developed to multispecies models (e.g. MSVPA in the North Sea), where interactions between stocks (predation) are estimated from stomach analyses (e.g. BOGSTAD & TJELMELAND 1990).

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 transport, primary production and zooplankton (see AKSNES & LIE 1990), while fewer dynamic models of fish exist. The theoretical constraints has been the formal representations of mortality and of the forces leading to changes in distribution. During recent years, spatial distributions have been studied by two methods: life history theory (WERNER & GILLIAM 1984; AKSNES & GISKE 1990) and dynamic optimization (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 (in press).

Evolution and optimization

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.

Modelling of behaviour based on optimality criteria is grounded on the assumption that animals respond adequate to changes in their environment. Natural selection will lead to the selection against inadequate responses, but 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 optimizations in relevant situations (see MILINSKI (1986) for a review). MALONE & MCQUEEN (1983) stated that 'those who looked for non-random horizontal distributions in zooplankton, finds them'. This seems to be true for most behavioural responses. 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.

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 (r_d) and the population (r):

$$\Phi = r_d - r \qquad (1)$$

To maximize Φ, an individual cannot do better than to maximize r_d, which therefore itself is a valid fitness measure of optimal distribution.

Models of optimal spatial distributions

The development of theoretical biological models of optimal spatial distributions started in 1966 by MACARTHUR & PIANKA (1966) and EMLEN (1966), who started the era of optimal foraging theory (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 distributions in general. By the use of dynamic optimization, they showed that all fitness-related aspects of life could be combined in a common expression. Also by the use of dynamic optimization, GILLIAM (1982) found that a fish larvae would maximize its fitness by staying in the habitat where mortality risk per growth rate (μ/g) was minimal. This result is also deduced from life history theory (WERNER & GILLIAM 1984; AKSNES & GISKE 1990; LEONARDSSON 1991) and confirmed experimentally (GILLIAM & FRASER 1987). AKSNES & GISKE (1990) did, however, show that there exist several different optimal trade-offs, depending on life history pattern and ontogenetic status. For adult fish with annual reproduction μ/ln(g) applies, while for many aquatic animals the major trade-off may be of mortality risk versus temperature.

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). Flock 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 flock 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). Group-size dependent optimal distributions within and among feeding patches have been studied using the ideal free distribution concept (FRETWELL & LUCAS 1970; FRETWELL 1972), where individuals distribute so that all have the same feeding rate. Modifications of the theory allow for unequal competition, so that individuals may feed at different rates, but no individual can achieve higher rate by moving (PARKER & SUTHERLAND 1986). However, IFD does not consider mortality risk in its optimality criterion. IFD has been used by MACCALL (1990) to distribute fish optimally among unequal patches.

The attractivity of life history based models lies in their simple deduction from fitness (through RV, R_0 or r) 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 animals encountering a temporary higher mortality risk. These aspects are discussed (for birds) by CARACO (1980, 1981) and STEPHENS (1981). Ectothermal fish have lower metabolic rates than endothermal birds (e.g. PHILIPSON 1981), but short-term trade-offs will also be important for the survival of fish fry and larvae.

Dynamic optimization

Dynamic optimization (often but misleadingly called 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. It has over the last decade been used in studies of optimal fisheries regulations and fisheries economy (e.g. CHARLES 1983; KENNEDY & WATKINS 1986; Lane 1988). Dynamic optimization in behavioural ecology uses state variables to examine the consequences of an action in fitness-related terms in order to model optimal behaviour (McFARLAND & HOUSTON 1981; HOUSTON &

al. 1988; MANGEL & CLARK 1988; SARGENT 1990). 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 optimization 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.

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

$$x'_{t+1} = e(x_t-c+f) + (1-e)(x_t-c) \qquad (2)$$

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

$$F(x,h,t=T-1) = (1-p)$$
$$[eF(x-c+f,T) + (1-e)F(x-c,T)] \qquad (3)$$

$F(x,h,t=T-1)$ 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

$$F(x,T-1) = (1-p^*) \, [e^*F(x-c^*+f^*,T)$$
$$+ (1-e^*)F(x-c^*,T)] \qquad (4)$$

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

$$F(x,t) = (1-p^*) [e^*F(x-c^*+f^*,t+1) \\ + (1-e^*)F(x-c^*,t+1)] \quad (5)$$

Dynamic optimization is sensitive to time step length. To maintain biological realism, a time step should be so short that only well-fed individuals may fill their stomachs and that only energetical poor individuals may starve during one time interval. In order to maintain population variation, time step lengths (and feeding function) must be chosen so that both an increase and a decrease in state has a realistic probability. This could be done by finding encounter probabilities from a Poisson distribution

$$e(n) = (\lambda t)^n \exp(-\lambda t)/n! \quad (6)$$

where e(n) is probability of encountering n prey during a period of length t when mean encounter rate is λ (MANGEL & CLARK 1988).

The dynamic optimization 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 must be included in the mortality risk (cfr. LAW & GREY 1989; SUTHERLAND 1990; JENSEN 1991).

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).

The water circulation is characterized 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 of the inflowing water into Arctic water, and the polar front is less sharp an more variable in location (LOENG 1989a; MIDTTUN 1989). There is large interannual 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. in press). 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 Sea into a zoogeographical transition zone and into an ecosystem strongly dependent on plankton transport with incoming currents. *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 treshold 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).

The food web of the Barents Sea ecosystem is relatively simple with a few dominant species at each trophic level. 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).

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). The immature capelin performs a large scale feeding migration northwards in the Barents Sea during summer (Fig. 2). This migration can be viewed as an adaptation, whereby the fish follow the retreating ice edge with a time delay to exploit the ice edge phytoplankton production (SAKSHAUG &
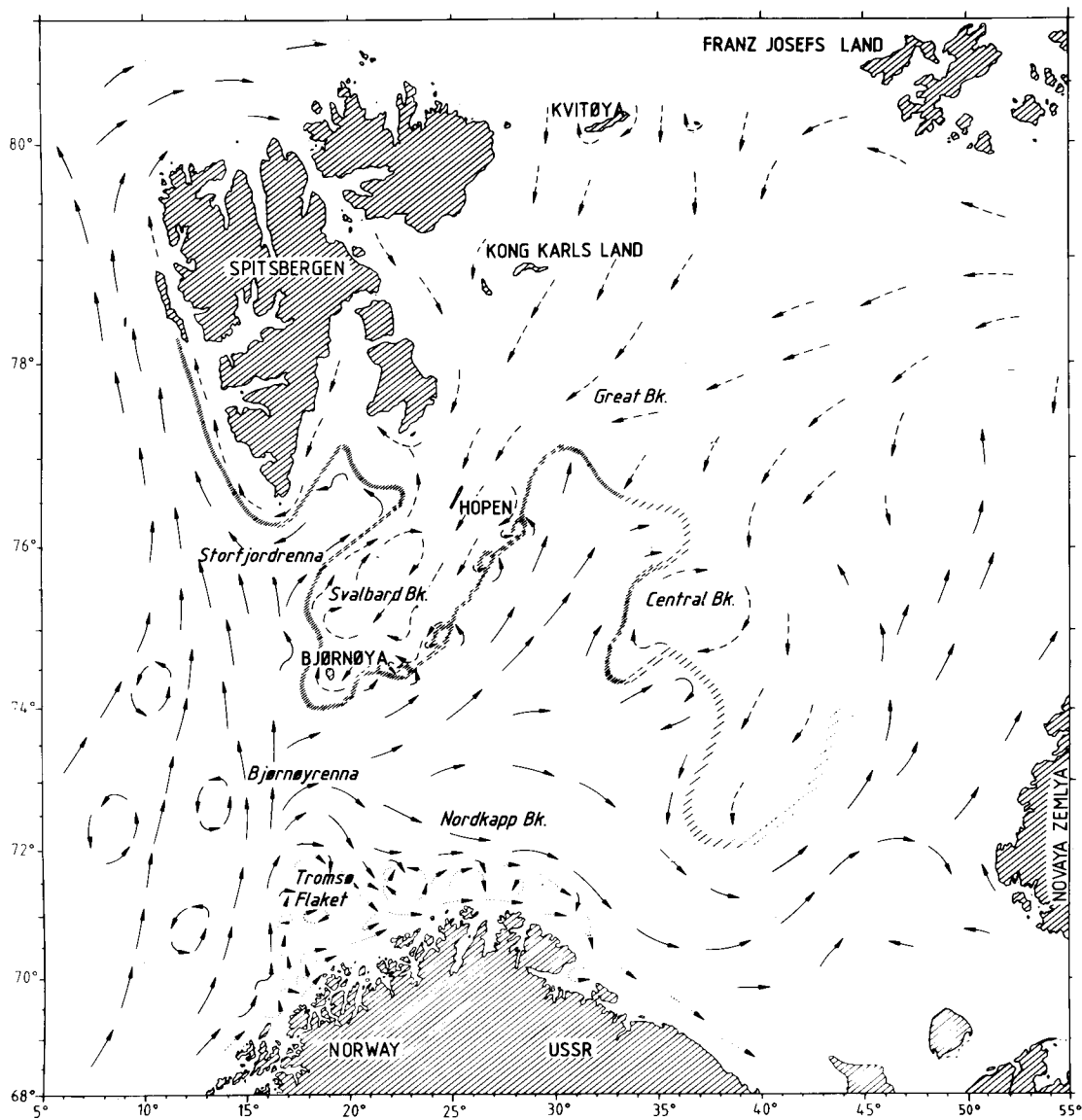
Fig. 1. The dominant surface current system of the Barents Sea. Solid arrows: Atlantic currents; broken arrows: Arctic currents; dotted arrows: coastal currents. The polar front is indicated by a hatched line. Redrawn from LOENG (1989b).

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 characterized 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; 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. 2).

Spawning takes place in relatively shallow water where the eggs are deposited on coarse sediments. There are many spawning sites along the whole coastal stretch from Troms county to the Kola Peninsula (Fig. 2). The climatic fluctuations influence
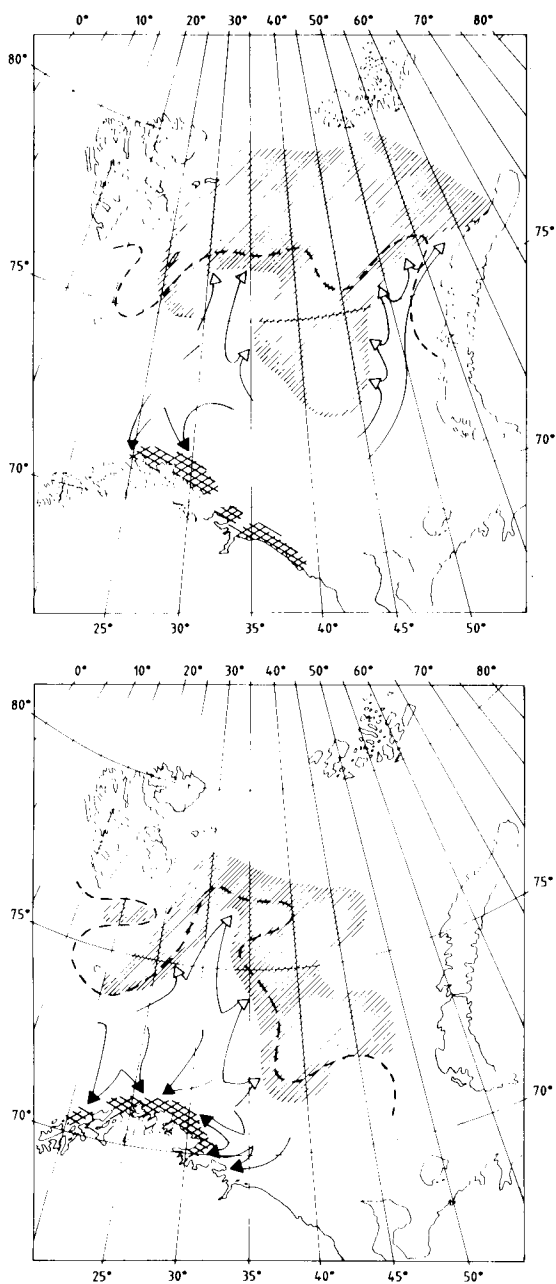
151

Fig. 2. 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 from Ozhigin & Luka (1985) and Loeng (1989b).

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. 2; Ozhigin &

Ushakov 1985; Ushakov & Ozhigin 1987). Following a relatively long incubation period, 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 & Oshigin 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.

Predation from juvenile herring appears to be an important factor for the recruitment success of capelin (Skjoldal & Rey 1989; Hamre 1991; Fossum in press). 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.

MODEL

Dynamic optimization capelin model

We see the need of not one but a set of models on which management should be based (Fig. 3). Meteorological-geophysical models are needed to predict large-scale ocean climate on an annual scale, and coupled water transport and plankton models will generate mesoscale drift routes for planktonic stages of fish and food for planktivores. Physical models of ice, temperature and light are also needed. Dynamic optimization models may find spawning places, fish distributions, growth and survival rates, which again can be utilized in population dynamic models and assessments.

A first modelling attempt may be to study migration of adult capelin females. The model will optimize habitat use over the year to maximize probability of offspring survival and drift into the summer feeding area the coming year (Bartsch & al. 1989). A backwards trajectory of advection of larvae, including feeding, growth and predation risk along this trajectory, will be used to find optimal spawning sites and times. Given these locations,

feeding and migration the previous season may be optimized in order to maximize spawning mass.

This model may be run for years differing in meteorological conditions, with varying drift routes, ice conditions, temperatures and also with different densities and distributions of predators and competitors. The large-scale annual geophysical model will be used to predict probable Barents Sea scenarios one year in advance.

Processes

For visual feeding planktivores, feeding rate and mortality risk are both dependent on light. For a single visual predator searching for prey while swimming, encounter rates with immobile prey is a function of visual range (AKSNES & GISKE in press): –

$$\lambda = e(r) = \pi(r \sin\Theta)^2 v n \qquad (7)$$

where e is encounter rate, r is visual range, Θ is visual angle, v is predator swimming speed (m/s) and n is prey density. Probability of encountering any number of prey items can then be found from Eq. 6. Alternative equations including both predator and prey swimming are given by ROTHSCHILD & OSBORN (1988). Maximum feeding rates for visual predators is (CLARK & LEVY 1988; AKSNES & GISKE in press)

$$f_n = \frac{h^{-1}n}{(h \pi (r \sin\Theta)^2 v)^{-1} + n} \qquad (8)$$

where f_n is individual feeding rate (ind ind^{-1} time^{-1}) and h is handling time of prey. Visual range is a complex function of light regime, underwater optics and predator and prey characteristics (AKSNES & GISKE in press). In Eq. 8 is assumed that all time is devoted to searching or handling prey. For a fish under predation risk, time to anti-predation activities should also be included. In exploited populations, mortality consist of a 'natural' and an exploitation (fisheries) mortality. We here describe the 'natural' part, as fisheries are not modelled. Mortality from fisheries must however be included to find optimal distributions. Individual mortality risk (μ) of prey due to fish predation is

$$\mu = f_n N/n \qquad (9)$$

where n is prey and N predator density. In Eq. 9, n also includes competitors and other alternative prey items. Predator preferences can be included according to optimal diet width theory (SCHOENER 1971; CHARNOV 1976). Competitors affect feeding (Eq. 8) by reducing food availability. These equations must be transformed for two situations: (1) stomach limitation on feeding of capelin and its
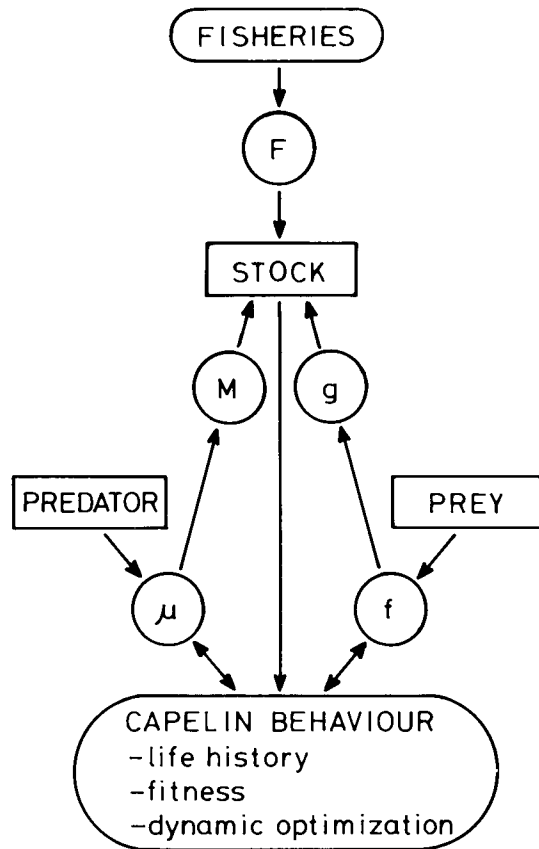

Fig. 3. Suggested assessment model environment. Survival and growth of the stock is determined by fisheries (F), natural mortality (M) and individual growth rates (g). The biological stock asessment variables (M, g) result from the interplay between environmental variables (e.g. predator and prey density) and capelin behaviour. This behaviour is governed by internal fitness-related forcing, capelin stock size and also experienced mortality risks and feeding rates.

predators and (2) patching of plankton and schooling of fish.

Feeding rate (g g^{-1} time^{-1}) is

$$f_w = f_n w/W \qquad (10)$$

where w is prey and W predator weight. Combined stomach and vision limited feeding in a period of length t can then be described by

$$ft = \min (f_w t, D) \qquad (11a)$$

$$D = D_{max} - D_r = D_{max} - D_s \exp(- td) \quad (11b)$$

where D is stomach capacity available for feeding, D_{max} is stomach capacity, D_s is stomach content in beginning of period, D_r is non-digested remains of D_s at end of period and d is digestion rate. Hand-

153

ling time, swimming speed and digestion rate are temperature-dependent functions.

The effect of group formation on feeding and mortality is not so trivial (Eggers 1976; Clark & Mangel 1984, 1986). From a feeding perspective, the optimal group size as viewed by its members is when each individual has maximal fitness, i.e. when $\Phi(n^*) = \max \Phi(n)$ (Clark & Mangel 1986). But if the fitness function is so that fitness of joining a group is higher than for solitary individuals, group size will increase beyond n^* until the equilibrium group size ($\bar{n}$) in reached, i.e. when $\Phi(\bar{n}) = \Phi(1)$ (Clark & Mangel 1986). Clark & Mangel (1986) have developed a set of models for feeding rate of schooling predators, including search, communication, learning, dominance, satiation and prey patching. They have also studied optimal group sizes at starvation-risk food concentrations. Shoaling and schooling greatly reduce swimming costs (Weihs 1973, 1975; Pitcher 1986), allowing higher travel speeds through areas of higher predation risk.

Growth rate can be calculated from feeding rate, assimilation efficiency and metabolic costs

$$g = af - m \qquad (12)$$

where a (according to Kiørboe & al. 1987) can be expressed by

$$a = K(1 - \exp(-\beta f))/f \qquad (13)$$

where K and β are constants. The growth rate of Eq. 12 includes both somatic growth and production of gonad tissue. Temperature-dependent metabolic costs including swimming can be expressed by

$$m = m_0 \exp(qT) \exp(bu) \qquad (14)$$

where m_0 is standard metabolism at 0 °C, q = $\ln(Q_{10})/10$, T is temperature, u is swimming speed (body lengths per second) and b is a species-specific constant ($0.2 < b < 0.5$; Priede 1985). For fast moving fish, swimming-related metabolic costs may be several times higher than standard metabolism (Priede 1985). Swimming speed being included both in f and m of Eq. 12, optimal swimming speed can be found from the relevant life-history trade-off (μ/g or μ/lng).

Problems: need for new insight

Theoretical models of the spatial distribution of capelin, or any other fish in an ocean, demands insight which currently does not exist. How do cod and other predators respond to changes in distribution of capelin? How do groups of capelin and predators form? How is the geographical distribution of predation risk? Answers can be found by applying dynamic optimization on several different as-

pects of optimal behaviour of predators and prey, and feed the main capelin dynamics model with the (numerical) solutions. In the biological world, where everything is interacting, the main objective is to reveal the dominant processes and forces.

Other than optimal trade-offs, analytical models, such as the energetical benefits of group swimming, feeding and predation risk in groups, and effect of vigilant behaviour on feeding rate, need to be developed.

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