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## The challenge of the herring in the Norwegian Sea: making optimal collective spatial decisions

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### ABSTRACT

Herring are long-lived multiple spawners exhibiting strong variation in reproductive and recruitment success between years. They tend to adopt low-risk, preferred-conservative strategies; for example, shifts to alternative overwintering areas do not take place until there are large benefits. At the same time, herring is an extremely flexible species, displaying considerable plasticity in migratory behaviour.

Migration patterns of herring have been investigated over many years. Most studies are however, descriptive and little is published that analyses the factors and mechanisms that govern spatial dynamics. In this paper we try to interpret the existing observations from an ecological and evolutionary perspective, emphasising proximate mechanisms that restrict the extent to which herring are capable of attaining an optimal distribution. Focus is directed to observations and literature on the Norwegian spring spawning herring.

Our starting point is the assertion that the migratory behaviour of herring can be explained by an interplay of relatively few forces operating on behavioural mechanisms that are expressed at both the individual and collective level. Although the environment in the Norwegian Sea shows spatial and temporal variations with regard to temperature, currents and the abundance of food and predators, there are several consistent and predictable features, such as the distribution of water masses and timing of seasonal plankton production. Given incomplete information about the environment, herring may locate favourable habitats through the use of a combination of predictive and reactive orientation mechanisms. For example, changes in the inner motivational state such as increased hunger level, may release westwards feeding migration in the spring through predictive mechanisms based upon genetic factors and learning. This behaviour could then be modified by reactive mechanisms, such as memory-based state-space comparisons and orientation to gradients in the sea. The ability to keep within favourable areas may be achieved by alterations in swimming speed determined by a non-directional kinesis mechanism.

Observations of herring schools show that changes in density occur on micro-, meso- and macroscale. After reviewing the available information on school density, school size, school size adjustments (splitting and joining), synchronised behaviour patterns and swimming speed of both individual schools and school clusters, we attempt to form a link across scales to explain patterns in distribution. The dynamic behaviour exhibited by large schools does not necessarily reflect optimal decisions of individual fish. It is suggested that the resolution for the analysis of school dynamics should perhaps be directed to that of the school unit, as opposed to that of the individual.

*Key words: herring, migration, orientation mechanisms, scale, school dynamics*

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## INTRODUCTION

Since ancient times the migration of fish has interested man. Many human coastal societies have relied upon the harvesting of fish that come close to the shore on a seasonal basis. Sudden unforeseen changes in migration patterns constituted a serious threat to livelihoods. Even today, incomplete knowledge of the dynamics of the spatial distribution of fish sets restrictions for both fishing efficiency and accurate abundance estimation. Changes in fish distribution relative to fishery boundaries have great implications for the division of harvest quotas between nations.

During recent years, spatially partitioned fish population dynamics has been recognised as being essential for effective fisheries management. In the past, lack of spatial information has been identified as being responsible for unforeseen stock collapse (Walters and Maguire 1996). For example, retrospective spatial analysis of the trawl surveys of the Northern cod (*Gadus morhua*) stock in Newfoundland revealed symptoms that might have averted a catastrophic collapse; habitat occupied by fish became more patchy and concentrated during the fishery collapse (Hutchings 1996). For migratory schooling species like herring, following migration paths between feeding, overwintering and spawning areas, spatial information about the dynamics of growth, abundance and recruitment has been gathered for over a hundred years (Harden Jones 1968, Blaxter 1985). Yet, until recently such data were invariably pooled for assessment purposes.

Norwegian spring spawning herring (*Clupea harengus harengus* L.) makes long-distance migrations between spawning, feeding and overwintering areas (Johansen 1927, Runnstrøm 1941, Østvedt 1965, Devold 1968, Dragesund *et al.* 1980). Although there is sufficient regularity for us to recognise discrete spawning and overwintering grounds, the elements of the herrings migration paths are not constant from year to year. We do not understand the factors that bring about these shifts, nor are we able to predict them.

A research programme, *Mare Cognitum*, aiming to increase understanding of the ecosystem in the Norwegian Sea, has recently started (Skjoldal *et al.* 1993). This is taking place simultaneously with a rapid growth of the herring population accompanied by an extension of the feeding area into the Norwegian Sea (Røttingen 1992). The spawning population is estimated to be around four million tonnes (Foote and Røttingen 1995) compared with less than one hundred thousand tonnes when the stock had collapsed in the late 1960s (Dragesund 1970). The large herring stock has a major impact on the ecosystem in the Norwegian Sea, and an extended cruise programme now maps the distribution of herring in relation to the biotic and abiotic environment (Skjoldal *et al.* 1993). Studies on the spatial organisation of

herring schools (Misund *et al.* unpublished) and the behaviour of single schools (Pitcher *et al.* 1996) in addition to modelling studies on schooling behaviour have also been initiated.

This paper tries to summarise what is known about the distribution and migration of Norwegian spring spawning herring and to identify the main challenges for future research. Most publications regarding this subject tend to be descriptive. In contrast we take an evolutionary and ecological perspective. Our approach will try to form links to establish how the behaviour of single fish, collective decisions of schools and life history traits combine to determine the spatial distribution of the whole population. We assert that the spatial analysis of herring on the macroscale ( $> 1000$  m) has to be complemented by greater understanding at the meso- (100 m) and microscales (1 m). Mesoscale phenomena include the clustering of schools that respond to different ocean habitats with their shifting regimes of predators and food. Microscale phenomena are the intraschool behavioural dynamics that facilitate trade-offs between feeding, mitigation of attacks from predators and ensure efficient spawning. These dynamics are believed to be the result of individual fish decisions to feed, join a school, leave a school, stay within a school or mate in response to changes in local conditions. Our objective is to build a conceptual insight of the spatial dynamics of herring populations at the macro-, meso-, and microscales that is structured upon its life history, is in conformity with natural selection optimising herring biology and behaviour, and embeds the herring within its ecosystem. The aim is to allow those of us entrusted with planning the human harvest of this valuable resource, a more sustainable and responsible mode of operation.

## METHODS

Data on spatial dynamics of herring in the Norwegian Sea are collected by a number of methods. The distribution and behaviour of herring are investigated by acoustic methods. Analysis of echosounder and sonar data in conjunction with data from trawl sampling provides abundance estimates (MacLennan and Simmonds 1992, Misund *et al.* 1996). A modified pelagic trawl (Valdemarsen and Misund 1994) is used to take samples from close to the surface to 300-400 m deep. Multibeam sonar (Misund *et al.* 1995) is used to study spatial organisation, size, density and movements of schools.

Standard methods of the Institute of Marine Research are used to record long time series of biological data from herring such as length, weight, condition factor, age, stomach fullness and maturation status. Sub-samples of herring stomachs are taken from all trawl catches for diet composition analyses.

Depth profiles of environmental variables such as temperature, salinity, fluorescence and light are recorded by CTD -sondes equipped with fluorometers and photo cells. Nutrients and chlorophyll-*a* are determined from samples collected at a range of discrete depths. Along the ship track, continuous measurements are made of surface light level and temperature, salinity and fluorescence at a depth of 5 m. A multinet sampler (MOCNESS, Wiebe *et al.* 1976, 1985) and midwater trawl with small-meshed cod end are used to collect zooplankton and micronekton for determination of abundance and biomass (Fosså *et al.* 1994, Melle *et al.* 1994).

## MACROSCALE DISTRIBUTION AND MIGRATION

During its life cycle the Norwegian spring spawning herring inhabits at least four different water masses in the Nordic and Barents Seas (Figure 1 and 2). Larvae and juveniles are found in Norwegian Coastal and Atlantic water over the Norwegian shelf and in the Barents Sea (Dragesund 1970, Hamre 1988). Adolescent and adult herring occur in Atlantic, Norwegian Coastal, Arctic Intermediate and Arctic water during their feeding season in the Norwegian and Icelandic Sea, and wintering takes place at present in Atlantic and Coastal water in North Norwegian fjords (Dragesund 1970, Dragesund *et al.* 1980, Blindheim 1989, Røttingen 1990, 1992).

### The Nordic Seas - a partly predictable environment

The Atlantic water mass enters the Norwegian Sea from the south (Figure 1), mainly through the Faroe Island-Shetland channel (Blindheim 1989). When entering the Norwegian Sea temperatures in Atlantic water are usually above 8°C and salinities above 35.2‰. The main current of Atlantic water flows northwards along the Norwegian continental shelf, and is called the Norwegian Atlantic current. Between Bear Island and the Norwegian continental shelf an eastern branch of the Atlantic water enters the Barents Sea, the main current continues north into the Polar Ocean. A western branch extends towards Jan Mayen and meets the Arctic water over Mohns Ridge. On its way in the Norwegian Sea the Atlantic water mixes with Arctic water with reduced temperatures and salinities as a result.

The East Icelandic Current enters the Norwegian Sea from northwest between the shelves of Iceland and Jan Mayen, bringing Arctic water into the southern basin of the Norwegian Sea (Figure 1). This water mass is characterized by temperatures below 3°C and salinities between 34.7 and 34.9 ‰ (Blindheim 1989). In the frontal zone between Arctic and Atlantic water

masses in the southern Norwegian Sea, the heavier Arctic water spreads out towards north and east beneath Atlantic water as Arctic Intermediate water.

Over the Norwegian shelf Coastal water flows northwards, separated from Atlantic water to the west by a sharp front over the shelf break (Figure 1). The position of the front is relatively fixed over the shallower parts of the shelf break, while some fluctuations are seen over the deeper parts. The Arctic front in the northern Norwegian Sea is situated over a sea bottom ridge (Mohs Ridge) that goes from Jan Mayen towards Bear Island. Since the geographic location of the front is largely governed by bottom topography, there are only minor shifts in position with season or over the years. In the southern Norwegian Sea the position of the Arctic front between the Arctic Intermediate and Atlantic water masses is less dependent on bottom topography and varies with the volume of water carried by the two current systems involved.

The time for the onset of the phytoplankton spring bloom differs between the water masses of the Nordic Seas (Halldal 1953, Paasche 1960). Before the bloom can start the depth of the upper wind mixed layer must be limited relative to the euphotic zone by stabilisation of the water column or by shallow water depth (Sverdrup 1953, Sambrotto *et al.* 1986). There are different mechanisms involved in water column stratification, which leads to differences in timing of the bloom (Halldal 1953, Paasche 1960, Rey 1980a, b). In Norwegian Coastal water the bloom is early due to shallow water depths over the banks and permanent stratification in the front towards Atlantic water by a thin layer of Coastal water above the heavier Atlantic water. In Atlantic water stabilisation of the water column is caused by the formation of a thermocline due to atmospheric warming of the near surface layer. This is a slower process and the bloom occurs later than in Coastal water. Within the Atlantic water mass the bloom may occur later in the north and west due to the generally lower air temperatures. In Arctic water and in water masses of Arctic origin such as the East Icelandic Current, the bloom is even more delayed, except for some areas influenced by melt water during the spring (Rey & Loeng 1985).

During winter, the main prey of herring in the Norwegian Sea *Calanus finmarchicus*, *C. hyperboreus* and krill (euphausiids) hibernate in the Norwegian Sea deep water or at intermediate depth with reduced feeding (Østvedt 1955, Connover 1988, Dalpadado and Skjoldal 1991, in press, Ikeda and Dixon 1982). These zooplankton species reproduce for the first time and start their growth season at the onset of the spring bloom (Ruud 1932, Østvedt 1955, Mauchline 1959, Lindley 1978, 1980, Dalpadado and Skjoldal 1991, in press, Diel and Tande 1992, Hirche and Kattner 1993, Melle and Skjoldal 1994). The start of zooplankton production will therefore differ among the various water masses in the Nordic Seas. Although

there are year to year differences in timing and level of zooplankton production within water masses, the water masses will show the same sequence with respect to start of the production with generally delayed zooplankton development in the western Norwegian Sea.

Varying degrees of competition may exist between herring and other pelagic planktivorous species such as blue whiting, mackerel, horse mackerel and Atlantic salmon (Daan 1980, Holst and Iversen 1992). During the feeding season the migration of herring may be modified by feeding interactions with other species.

Norwegian spring spawning herring are predated upon by fish, marine mammals and sea birds. Although oceanic predators do not seem to be attracted to the coast to feed on herring (Høines *et al.* 1995), there are probably a higher predation pressure in coastal areas than in the Norwegian Sea. Fish predators like cod and saithe are abundant at the shelf and in behavioural studies of herring schools, a high occurrence of predatory attacks by cod and saithe was observed above the shelf (Pitcher *et al.* 1996). The most important bird predators like puffins have a restricted feeding range in Coastal waters (Anker-Nilsen and Barrett 1991, Ancker-Nilsen and Øyan 1995). Minke whales are abundant on the coast, but of minor importance as predators offshore in the Norwegian Sea (Øien *et al.* 1987, Haug *et al.* 1993, 1994) and seals are also most common at the coast (Wiig 1986, Bjørge 1991). However, the distribution of killer whales are closely related to the distribution of herring (Simulä and Christensen 1992, Simulä *et al.* 1996) and marine mammal predators could be abundant in the Norwegian Sea, especially at oceanic fronts (Christenssen *et al.* 1992, Haug *et al.* 1995).

As described, the environment in the Norwegian Sea shows consistent features with predictability in geographic location of oceanographic fronts, water mass distributions and timing of zooplankton production cycles. There are, however, variations in the timing of the plankton bloom within water masses and the location of the oceanographic fronts from year to year. These variations may be related to climate changes, to which the herring could respond to some extent. The environment with regard to food can be considered partly predictable, but with a stochastic element. Many features of the predation pressure are not known at present. The strong predation pressure by piscivores on the continental shelf may be predictable, and there are indications of significant pressure from predators at oceanographic fronts. However, for the large part, predation pressure could be unpredictable. From the perspective of herring, fishing pressure may occur as random events.

## Temporal changes in migration patterns

The migration pattern of adult herring has changed markedly during recent decades (Figure 2). In the 1950s a large stock with a spawning population of more than 10 million tonnes had feeding areas north and northeast of Iceland with overwintering grounds in the Norwegian Sea. Spawning took place along the Norwegian coast from Møre in the north to Karmøy in the south. This is described in detail by Dragesund *et al.* (1980). From the mid 1960s a gradual shift towards north was observed in both feeding and wintering area in the Norwegian Sea and spawning area along the Norwegian coast (Devold and Jakobsen 1968, Dragesund 1970).

After the late 1960s stock collapse, migration pattern changed radically. The herring now stayed within feeding areas close to the coast with no known migrations into the Norwegian Sea. Overwintering took place in two fjords in northwest Norway and spawning grounds were restricted to an area off western Norway (Røttingen 1992). As the stock size gradually increased in the 1980s and 1990s the feeding migration into the Norwegian Sea restarted and continued to extend over larger and larger areas. Spawning grounds were also expanded, and in 1996 herring spawned along substantial parts of the coast up to the Lofoten area. However, overwintering concentrations of herring were still restricted to fjords in contrast to the situation in the 1950s (Røttingen *et al.* 1994).

The change in migration pattern in connection with the collapse of Norwegian spring spawning herring strongly indicates a correlation between stock size and distribution. For many species, stock collapse is associated with a corresponding range collapse (Dragesund 1970, Pitcher 1996). A possible mechanism is that small populations may become concentrated in a range-limited optimal habitat. Population growth may result in being forced out of optimal habitat due to shortage of food and suitable spawning sites. This may explain the gradual expansion of feeding and spawning areas observed in Norwegian spring spawning herring. A behavioural mechanism controlling preferred school size and distance between schools (see later) could reinforce such effects.

## Catalysts of change - driving forces and motivation

An underlying assumption is that the migration pattern of herring reflects fitness maximisation, i.e. that migration leads to increased survival and growth and thereby reproductive output. Migrating herring may for example utilise regional and seasonal production cycles. In the absence of any specific driving force herring should remain in an

area since movements demand energy expenditure and could lead to increased risk of detection by predators with a resulting decrease in fitness.

Although the situation in the sea is complex, our hypothesis is that an interplay between relatively few key factors operating in conjunction with changes in the motivational state of the herring can explain the dynamics of spatial distribution. The major driving forces are believed to be food availability, abundance of predators, temperature regime and availability of suitable spawning sites. The first three of these factors may independently exhibit strong spatial and temporal variations.

Food is a major driving force. The amount of food available for herring is influenced by variations in the seasonal production cycles of zooplankton both with regard to the amount of zooplankton produced and to the timing of the production in relation to the herring feeding migration (Lie 1961, Østvedt 1965, Melle *et al.* 1994). Food shortage caused by competition in connection with increasing population size is believed to lie behind the gradual expansion of the feeding areas (Røttingen 1990, 1992). During the cold period from 1965 to 1971 giving rise to the mid-seventies anomaly, the abundance of *C. finmarchicus* in North Icelandic waters decreased (Ástthórrson *et al.* 1983) and this could also to some extent have influenced the migration pattern.

Fish do not simply try to maximise growth rate by maximising food intake. Studies on fish schools demonstrate trade-offs of growth with safety (Nonacs *et al.* 1994, Mangel 1994). Threat of being eaten is a strong driving force. Herring may modify their behavioural responses in the presence of different types of predators. Such changes may result in quite different spatial dynamics.

Temperature influences many physiological processes in fish as digestion rate and swimming capacity (He and Wardle 1988, Videler 1993). When food supply is limited, fish should feed in areas where ingestion rate is maximised and then move to areas where energetic costs are reduced (Jobling 1995). Although changes in temperature across oceanic fronts often coincide with changes in species, age and size composition of zooplankton (Østvedt 1965, Melle *et al.* 1994), temperature effects on the distribution of herring have been reported (Devold 1963). Herring seem to avoid water below 2°C and generally stop westwards migration when reaching the Arctic front (Østvedt 1965), in spite of higher zooplankton biomasses on the colder side of the front (Melle *et al.* 1994).

The availability of suitable spawning grounds is another important driving force governing spatial distribution. Spawning sites are in fixed positions from one year to the next. Herring



that have left a particular spawning site last year must migrate back to a suitable spawning site in time to reproduce again. Some time prior to spawning, changes in the relative contribution of each of the driving forces in conjunction with alterations of the motivational state of the fish will combine to result in a change of the spatial dynamics; the overall result being a tendency to migrate to the spawning grounds.

Water currents are an additional external factor that can have an important influence on the distribution of herring (Harden Jones 1968). Whilst migrating, herring can take advantage of favourable currents with regard to direction and speed (Nøttestad *et al.* 1996). Overall population abundance could effect the distribution of herring by influencing food abundance, predation pressure and availability of suitable spawning sites.

### **Vertical migration - dynamic adjustment to environmental factors**

Environmental conditions in the vertical plane usually show much stronger variations than in the horizontal plane. Vertical migrations are often observed in herring (Blaxter and Hunter 1982, Melle *et al.* 1994, Blaxter 1985). Making diurnal vertical movements, the herring can rapidly adjust to changes in critical environmental parameters. For example, downward migrations take the fish to a habitat with lower light levels and could thus decrease visually mediated predation (Aksnes and Giske 1990,1992). Deeper water may offer other advantages in addition to predator avoidance. The Norwegian Sea exhibits strong temperature gradients, water being significantly colder at great depths (Nansen and Helland Hansen 1909, Blindheim 1989). Herring may feed close to the surface at dawn and dusk then descend to deep colder water, saving energy during daytime. Observations of migrating herring in early spring show herring to swim deep both day and night (Melle *et al.* unpublished data). This may be explained by feeding opportunities, as wintering Calanus (a primary food source for the herring) are distributed at intermediate depth during this period (Østvedt 1955). Changes of vertical distribution may also be determined by the ability of herring to choose specific depth layers with favourable current direction and speed, thus saving energy (Nøttestad *et al.* 1996).

## **MESOSCALE DISTRIBUTION AND MIGRATION**

### **Spatial organisation of schools**

Reliable data about the three-dimensional distribution of schools can be achieved using sonar technology in conjunction with verification of target by fishing. Figure 3 shows a typical

picture of the distance between herring schools from a transect outside Northern Norway. The closest schools are only about 20 m apart and they seem to occur in clusters. The observed mean interschool distance was 300 m in the frontal region between coastal and Atlantic water and 600 m in Atlantic water (Misund *et al.* unpublished observations).

### **Regulation of school size - dynamics of splitting and joining**

Herring is an obligate schooling species (Breder 1976). Variations in school size, from several hundred to millions have been observed in the wild (Misund 1993). It is inevitable that such wide variations have a significant influence on the distribution of fish at the mesoscale.

It is assumed that school size in herring is an adaptation to the prevailing conditions, but the relationship is poorly understood. One exception is a study of schools on spawning grounds (Nøttestad *et al.* 1996). Large schools immigrating to the spawning area subsequently break into smaller units when searching for spawning substrate. Individuals within a school may inhabit different physiological states, leading to splitting of the school into smaller units with fish with similar gonadic index. After spawning, emigrating schools coalesce, increasing in size, but these schools were still smaller than pre-spawning immigrating schools. An explanation for these observations is the relatively rapid change in the relative influence of determinant factors governing school size. For immigrating schools avoiding predation may have the dominating influence and large schools may give the best protection against predators (Pitcher and Parrish 1993). Emigrating schools, preparing for feeding, may organise themselves in a school size that serves to achieve optimum feeding opportunities under prevailing conditions.

For herring during the feeding season, there should theoretically exist an optimal school size where the trade-off between feeding and avoiding predation is maximised. Since there is no mechanism to prevent animals joining groups, and thus animals may join until there is zero net benefit, the idea of optimum group size being an evolutionary stable strategy has been questioned (Pulliam and Caraco 1984). However, herring do generally not occur as isolated individuals. As already fish in small groups have some advantage of schooling, they should be less likely to join another school than single fish. For joining schools, an increase in fitness is only attained if the size of the joined school deviates less from the optimal value after joining than before. It is also possible that the school being joined could avoid the join by swimming away. In addition, disadvantages incurred as a result of deviations from an optimal school size are not necessarily symmetrical. If a school 50% larger than optimal splits in two equal parts, it will form two schools 25% smaller than optimal, but there may be higher costs associated

with being too small ( increased risk to predation) than too large (decreased feeding rate), since survival has a higher priority than feeding (Life-Dinner principle, Krebs and Davis 1986). Hence, It would seem likely that in reality, school size in herring may vary somewhere in between the optimal value and the value of zero net benefit.

Within specific locations, large variations in school size have been observed (Misund 1993, Nøttestad *et al.* 1996). Such an observation could be accounted for with two opposing explanations. The first would be that school size is not sensitive to the environmental conditions; the second argues that in fact the large variation is a direct result of the ability of schools to fine tune school size relative to minor fluctuations in environmental conditions. There are observations indicating that frequent group size adjustment takes place in herring schools under certain conditions (Pitcher *et al.* 1996).

For splitting and joining to take place it is required that fish have mechanisms to perceive deviations from optimal school size in addition to mechanisms to accomplish group size changes. School splitting can be initiated by increased hunger level leading to increased interfish distance (Robinson and Pitcher 1989). Tendency to join can be increased by a high perceived level of threat from predators. Performing splitting could be relatively complicated, since there may exist cohesive forces between the fish that depend on group size. A complete split may be unsuccessful, with for instance the smaller school rejoining. Splitting followed directly by joining has been observed in herring schools (Pitcher *et al.* 1996). Joining of schools may involve even greater difficulties, since joining requires coordinated movements of two originally independent units. Joining processes may also be restricted by the availability of nearby schools to join (Pitcher and Wyche 1983). In the study by Pitcher *et al.* (1996) the density of schools was high and joining was frequently observed, but this may not be possible in areas with fewer schools.

Given that the mechanisms involved in perceiving and compensating for changes in these conditions are sensitive enough, the result is a dynamic response of changes in school size with an associated time lag, but these mechanisms have probably serious constraints. Availability of other schools also restricts adaptive increases in school size. The great variations in school size observed in an area therefore probably reflect variations around a mean optimal, with a time lag before schools changing habitat are adapted, and the constant risk of a school of optimal size that it will be joined by another school with more to win than to lose by joining.

### **Movements of individual schools**

The swimming speed of herring determines how rapidly changes in spatial distribution can take place. Speed of migrating herring can vary. Schools immigrating to the spawning grounds swim faster than schools searching for suitable substrate and emigrating schools, whereas post spawned feeding schools had the lowest swimming speed (Nøttestad *et al.* 1996).

The swimming direction and pattern of herring schools can vary markedly. Figure 4 shows the swimming path of a herring school followed for one hour in the Norwegian Sea (Pitcher *et al.* 1996). Despite many intra- and inter-school events, the school swam in a relatively straight line. Sonar observations on schools disturbed by fishing vessels show more complicated patterns associated with an avoidance response (Misund 1994). Other sonar studies showed herring schools migrating to the spawning grounds swim on a straight course, whereas schools feeding after spawning show less directional swimming (Nøttestad *et al.* 1996).

### **MICROSCALE DISTRIBUTION AND MOVEMENTS**

The optimal distance between individual fish may be expected to vary according to the optimum distance required to perform feeding and avoid predators. The mode of feeding (filter or particulate, Gibson and Ezzi 1985) and perceptive distance to prey are important considerations. In contrast to what is the case for school size, school density could potentially be rapidly adjusted in response to external environmental factors. Possible restrictions to this may occur when for instance different hunger states exist. Marked density variations within herring schools have been observed and are believed to reflect the dynamics of a moving mass (Misund 1991, Misund 1993), rather than fine adjustments to environmental factors.

School density of adult herring can vary between 0.1 and 20 fish per  $m^3$ , but usually lies between 1 and 2 fish / $m^3$  (Misund 1993). During spawning season, herring schools searching for suitable spawning substrate have the highest density, followed by immigrating, emigrating and feeding schools (Nøttestad *et al.* 1996). This could be explained by changes in motivational state in conjunction with changes in the relative importance of spawning, feeding and avoiding predation. Laboratory experiments on herring show that density is decreased by starvation (Robinson and Pitcher 1989).

School shape influences the distribution of herring. Changes in school shape may also be associated with changes in motivational state. Herring schools migrating to spawning grounds were observed to be more elongated than spawning and feeding schools (Nøttestad *et al.*

1996). Microscale distribution is also influenced by coordinated movements of schools. Antipredator behaviour patterns such as clumping and deorganization (Pitcher *et al.* 1996) result in changes in local densities.

## THE MODEL APPROACH

Individual based modelling and simulations of fish schools has been reported by several authors (e.g. Anderson 1980, Okubo 1986, Swartzman 1990 Niwa 1994). However, most of them have been purely theoretical, with few practical applications. A few recent papers have, however, tried to include biological realism (Huth and Wissel 1994, Reuter and Brechling 1994). Techniques of Individual-Based Modelling (IBMs) which model the internal structure of populations and communities can be divided into two methodologies; 1) i-state distribution and 2) i-state configuration approach (DeAngelis and Rose, 1992). The i-state configuration models should give accurate descriptions of populations that are likely to have strong stochastic components and to be subject to highly localized interactions (DeAngelis and Rose, 1992). This model approach may be fruitful when considering the high interaction between members in a fish school. A class of models that are specifically designed to mimic systems with strong interactions like fish schools are Cellular Automata (CA). This approach has been employed to describe the polarised and synchronised behaviour of individuals within a school (Huth and Wissel 1992, 1994, Reuter and Brechling 1994). CA have the property that individual entities change from one state to the next through time in parallel or concurrently, which is true as well of entities in nature (Phipps 1992). In stochastic (or probabilistic) CA, the selection of a state at each time step, is done subject to a probability function (Lee *et al.* 1990). A simple CA model describing internal dynamics of herring schools including antipredator tactics in herring is under preparation (Vabø and Nøttestad, unpublished). This model are able to mimic highly complex and coordinated behaviour in herring schools as we observe them in nature, based on simple individual decision rules, interpreting realistic biological variables. This model visualises the fact that certain behaviour characteristics of whole schools can be explained by the action of the individual.

Another type of modelling approach; dynamic programming has lately been widely used in behavioural ecology (e.g. Mangel and Clark 1986, 1988, McNamara and Houston 1986; Houston *et al.* 1988, 1993, Rosland and Giske 1994, Fiksen *et al.* 1995). However, few papers have applied Stochastic Dynamic Programming (SDP) approach on schooling dynamics in pelagic planktivorous fish (but see Nonacs, 1994). The model approach makes it possible to predict optimal habitats (e.g. school density and size) over several time scales for animals trading off predation risk and growth. Density and size distributions in schooling fish in

dynamic optimization models not only depend on external physical or biological properties of the environment, but also on the internal or motivational state of the fish. The optimization criterion must be related to the Darwinian concept of maximization of fitness, established through the action of natural selection (Dawkins 1989). The method implies that animals behave optimally (i.e. maximise fitness). A mesoscale dynamic model on optimal school size and density, based on join, leave and stay decisions of individual herring, is under preparation (Nøttestad and Giske unpublished). This model will be developed through Stochastic Dynamic Programming (SDP, Mangel and Clark 1988, McNamara and Houston 1996). The physiological state of the herring and the environmental factors change with time, thus optimal behaviour changes with time. Input variables to the model will include realistic values for schooling parameters such as school density and fish size in addition to depth, prey density, temperature and light level. A preliminary quantification of feeding rate and mortality risk will also be included. A random influence parameter will be added to allow for stochastic nature of events.

#### **THE BOTTOM-UP APPROACH - FROM INDIVIDUAL FISH TO MACROSCALE DISTRIBUTION**

SDP models are based on individual fitness maximization and it ought to be possible to understand some features of the horizontal distribution of herring schools from an understanding of those factors that influence individual fish. For a species such as herring that typically exists in very large schools, school behaviour does not, however, directly reflect the need of the individual. Fish in a school are not identical, and if a fish is to keep within the school it has to make compromises. Although little is known about the dynamics of school movements, mechanisms of social facilitation and individual variations in feeding efficiency and risk-taking, it takes presumably many individuals with the same tendency to influence school behaviour.

Herring from the same school have been found to differ markedly in stomach contents (Dalpadado 1993). Presumably, a hungry herring should maintain a large distance from its neighbours to improve feeding conditions (Robinson and Pitcher 1989), however, the behaviour of other school members could modify this. As mentioned previously, to accomplish splitting or joining of schools appears to require an even stronger dependency of one fish with another.

School behaviour not only reflects a collection of individual behavioural decisions. There are conflicts between individuals and different fish may not have the same information.

Behaviour of individuals within the school may then to some extent be governed by neighbours. For example, by reacting to other fish moving in relation to environmental gradients (Kils 1986, Hurth and Wissel 1992, Wodemeyer and Kils 1996), the swimming direction of an individual is partly controlled by others. Reactions to predator attacks release evasive manoeuvres, the dynamics of which can be explained at both the school and individual unit. Thus, although natural selection works at the individual level and many observations on the behaviour of schools can be understood in terms of individual fitness maximisation (Pitcher and Parrish 1993), the school in many cases may constitute the functional unit appropriate to study.

The distribution of schools themselves constitutes another level of analysis. Herring schools seem to occur in patches (Misund *et al.* unpublished data). Such clusters of schools can be the result of attraction of schools to each other and not merely caused by aggregations to favourable areas. Clusters can decrease predator pressure through the dilution and abatement effect (Pitcher and Parrish 1993), although they may also attract predators. In addition, clusters constitute a pool for school size adjustments.

Modelling over a range from individuals to schools, populations and metapopulations may be done with nested models, each of which considers processes over a limited range of space and time scales (US. Globec 1995). For modellers to successfully address this "scale-transfer" issue will require coordination among empirists working at different scales and in scale interfaces.

## ORIENTATION MECHANISMS

In studies of fish distribution it is often assumed that fish have perfect knowledge about the environment and can distribute themselves according to some optimality criterion. However, a prerequisite is that the fish have proximate mechanisms enabling them to orientate towards the optimal area. Some candidate mechanisms and their limitations will be briefly discussed below.

### 1. Kineses

Using the case of temperature gradients, if the non-orientated activity level is proportional to the deviation from the preferred temperature, animals can concentrate in the area with the optimal temperature. Although individual fish through synchrokineses (Kils 1986) can react to

environmental gradients some distance away by following neighbours, the large distances and the dynamic nature of the temperature, food and predator fields in the Norwegian Sea would seem to make kinesis too imprecise to lead to an optimal distribution of herring.

## **2. Predictive mechanisms: Genetic factors and learning**

Disregarding the near field, animals use predictive mechanisms if they orientate towards where the habitat quality is predicted to be higher. Predictive mechanisms may be based on both genetically based tendencies to orientate and previous experience. Younger fish have been observed to follow larger fish during migrations (Harden Jones 1968, Hourston 1982, Rose 1993). Older fish would then follow known landmarks experienced and learned in previous years (Baker 1978). In herring, there is evidence that migration is controlled by both genetic factors and through learning processes (Corten 1993). The choice of spawning grounds is an example of a tradition that is passed on by one generation of herring to the next and learning may affect also the choice of feeding and overwintering area (Corten 1993). Directional cues may be acquired using the sun, currents and geomagnetic fields (Runnström 1936, Fredrikson 1944, Harden Jones 1968).

For predictive mechanisms to work, the environment should be predictable. Although variations exist, environmental factors in the Norwegian Sea show regular features with respect to water mass distributions and seasonal zooplankton cycles (see above). Therefore, orientated swimming based on predictive mechanisms could partly explain the observed westwards feeding migration of herring. The initiation of such migrations could depend on the inner motivational state of the fish, with westwards migrations only released when herring exceed a critical hunger level.

## **3. Reactive mechanisms: Response to near field and State - Space comparisons**

Near-field orientation demands that the fish can perceive gradients in the sea. Herring could detect a temperature difference of  $0.6^{\circ}\text{C}$  (Shelford and Powers 1915). Fish swimming  $1\text{m/s}$  could be able to react to temperature gradients of  $0.003^{\circ}\text{C per m}$  (Harden Jones 1968). Well defined gradients could exist in the Norwegian Sea at oceanic fronts. At the front between Atlantic water and polar water, the maximum temperature change in intervals of  $180\text{ m}$  was  $0.005^{\circ}\text{C per m}$  (Melle unpublished observations). Zooplankton in the Norwegian Sea is unevenly distributed at the large scale and shows marked changes in species and size distribution in connection with fronts between water masses (Wiborg 1955, Østvedt 1965, Pavshikovs & Timokhina 1972, Blindheim 1989, Melle *et al.* 1993, 1994). The mesoscale



distribution has not been studied in such detail, but based upon studies from other areas (Wiebe 1970, Steele 1978) it can be assumed that zooplankton is patchily distributed. Reactions to gradients in such patches are possible, although fish are generally believed to keep within patches because of non-directional changes in swimming speed and frequency plus angle of turning (Thomas 1974).

Fish can concentrate in the front area with higher zooplankton abundance due to the same mechanisms that enables them to find and stay in the highest concentration of a patch. Movements in a front should thus mainly be along the front and herring schools have been observed to swim along oceanographic fronts (Misund *et al.* 1996). Migrating herring do not swim in straight tracks but frequently make side-to-side movements, indicating search for directional gradients (Misund *et al.* unpublished data). Reactions to the near field may thus exist in connection with water fronts and in mesoscale.

There is another reactive mechanism herring can use to attain an optimal distribution. State-space comparisons allow fish to compare the habitat quality between different sites. If the new locality has higher quality than the locality the fish came from, the fish should stay in the new place and eventually proceed in the same direction. If not, the fish should return. In laboratory studies, such mechanisms based upon a memory of the previous patch have been shown to result in an ideal free distribution (Fretwell and Lucas 1970) with fish distributed according to the resource value of the patches (Dill 1983, Milinski 1984). A state-space comparison mechanism could be based on evaluation of the major driving forces.

There are some indications that herring use state-space comparisons. Herring schools tracked with sonar generally swam with a component westwards in the spring but the most western schools swam in an eastwards direction (Misund *et al.* unpublished). Temperature decreased towards the Arctic front in the west and the herring seemed to swim ahead of the preferred place, evaluate local conditions and turn.

### **Predictive and reactive mechanisms working together**

Since the herrings information about the environment is not perfect, the use of predictive mechanisms only would mean excessive distances may be covered during migration as a result of deviations due to the unpredictability of the environment. For example, an initial prediction that high food concentrations are found further west may be wrong, and when the fish return to the initial habitat the situation could have changed. On the other hand, using only reactive mechanisms can lead the fish into higher and higher food concentrations within

a particular location, but when food abundance becomes low in the whole area, the herring is left with no directional cues.

To solve such problems the herring could use a combination of predictive and reactive mechanisms. In birds, detailed orientation studies have demonstrated that they do not depend on a single factor for orientation, but that many different mechanisms are involved (Delius and Emmerton 1977). A single mechanism is not reliable in all circumstances, and when the situation changes, an alternative mechanism is activated.

Since information on orientation mechanisms in herring is scant, available evidence from other animals is used to support a proposed mechanism to account for the control of migration and distribution of Norwegian spring spawning herring (Figure 5). If herring has good feeding conditions, they seem to stay close to the coast in spite of a high predation pressure. Poor feeding conditions on the coast may release large-scale westwards migration based on the prediction of high food concentrations. This predictive mechanism may have a basis involving both genetic and learning mechanisms, the combination of which holds greater flexibility allowing herring to adapt to its variable environment. The observation that herring has taken many years to gradually resume the old migration pattern into the Norwegian Sea gives some support for learning mechanisms, although the simultaneous gradual increase in population size can also be involved. Oldest individuals, presumably with the greatest experience, migrate the longest distance to the west (Harden Jones 1968, Melle *et al.* 1994, Slotte and Johannesen 1996), although this can also be explained by large fish having higher swimming speed and large surplus energy reserves (Ware 1975, 1978).

Travelling west herring find the front between Atlantic water and the Arctic Intermediate water of the East Icelandic current in the Norwegian Sea. Although its position may vary, this frontal system may be considered stable and predictable. The mixed water of the frontal zone is richer in zooplankton than Atlantic water. West of the front high concentrations of zooplankton may still exist, but here the water is colder and possibly not suitable for the herring. It is likely that herring adjust to these local environmental features by finding a combination of rich plankton concentrations and favourable temperature.

Secondly, superimposed on the predictive migration mechanism could be a system involving state-space comparisons. If the initial prediction of high food concentrations is supported, the fish should continue to swim to the west, but if no food is found or the temperature decreases to a critical value, the fish can compare the state in the two habitats and turn back to the original habitat. Thirdly, herring may be able to record the strong gradient in oceanographic fronts which can enable orientated swimming in the fronts. Fourthly, reaction to food gradients

in patches may occur by use of kinesis mechanisms, food concentration influencing swimming speed and turning. Response to predators may be governed by reactive mechanisms.

## **FLEXIBILITY IN DIFFERENT LIFE STAGES AND STRATEGIES OF MINIMIZING RISK**

The extent of the westward feeding migrations into the Norwegian Sea of adolescent and adult herring in the spring seem to depend on population size, extended feeding migration being correlated with an increase of population size (Røttingen 1990, 1992). Norwegian spring spawning herring thus seem to adopt a flexible feeding migration strategy. Spatio-temporal variations in food abundance demands great flexibility.

Norwegian spring spawning herring always spawn near the coast on hard bottom. Herring has spawned in the Møre area in western Norway during the whole 20th century and after the stock collapse in the late 1960s this was the only spawning area (Røttingen 1990). As the population size increased, the herring again spawned at the grounds used before the collapse, first at the grounds in the Lofoten area and then eventually at those in southwestern Norway (Bergstad *et al.* 1993). Competition for space offers one explanation for the extension of spawning areas. In this respect, the changes in spawning and feeding areas show similar features. In both cases, it seems that when competition is low, herring have a preferred area with some variation, but with stronger competition the fish migrate to alternative habitats. The distribution may approach an ideal free distribution (Fretwell and Lucas 1970), with the fish distributed according to the density-dependent resource value of different habitats. Variations in spawning localities over time complicates, however, this picture.

Herring more than 3 years old may overwinter either in the Norwegian Sea or in fjords in northern Norway. In the 1950s when the population was large, the vast majority were found in the Norwegian Sea (Røttingen 1990). At present, the whole population overwinters in the fjords. It is tempting to speculate that there is a connection between choice of wintering area and how far west the herring migrate or how late in the autumn the fish turn east. Herring may reach a threshold where the energy costs or the time left until the onset of the winter prohibit return to the coast for hibernation. Another explanation is that the population size could have become so large that the strategy of hibernating in dense concentrations in the traditional two small fjords may become less successful. A marked decrease in oxygen contents in the fjords with hibernating herring has been observed (Dommasnes *et al.* 1993, Røttingen *et al.* 1994). According to that view, if the population continues to increase we may expect in the future a

sudden shift to the old hibernating areas in the East Icelandic Current and in the polar front further north.

The choice of overwintering area should be expected to be an adaptive response to predation, energy costs, gonad development and other factors. Since herring do not feed during the winter, the effects of cold temperature in reducing metabolic costs are likely to be significant. The lowest temperature is found where the herring hibernate in the Norwegian Sea (Dommasnes *et al.* 1994, Røttingen *et al.* 1994). The Atlantic water masses in fjords are warmer and Atlantic water outside the shelf still warmer. On the shelf there are additional disadvantages as high predation pressure and strong currents and herring has never been observed to hibernate in this area. The wintering area may thus be determined by a choice between discrete alternatives.

In spite of the flexibility in different life stages there are also strategies of minimizing risk. Norwegian spring spawning herring usually spawn the first time at an age of three or four years (Blaxter 1985, Hamre 1988). They may attain an age of up to 20 years old and could thus have up to about 15 spawning opportunities. Herring is typical of species exhibiting great variations in reproductive success. Strong year classes occur on a time horizon of 10-20 years (Cushing 1981). Fitness of individual herring could thus depend more on the number of spawnings than the number of eggs each year. This should lead the herring to adopt a low-risk strategy, with survival to next spawning as the most important factor.

A way to adopt such a strategy in an unpredictable environment is to be conservative until it is necessary to change strategy. Laboratory experiments have shown that when fish can choose between two patches with the same mean food level but with different variance, they prefer the patch with lowest variation when satiated but the risky patch when hungry (Young *et al.* 1990). As long as conditions are favourable, herring should thus stay in an area, but at a certain stage it may become necessary to take risks. Such reasoning could explain both the feeding and spawning migrations (see also Corten 1993). A theoretical model on pelagic fish also supports a low-risk strategy (Salvanes and Giske 1995). According to this model, pelagic fish should be unselective feeders, since the benefit of ascending to a habitat with improved visibility permitting selective feeding is less than the cost of increased predation in that habitat.

Adoption of low-risk strategies by herring is supported by several observations. Herring seem to feed close to the coast until the increasing population size and resulting increase in competition for food, releases westwards migration. That herring still overwinter in crowded fjords even when the population size is much larger than when herring hibernated in the

Norwegian Sea before the collapse also indicates a conservative strategy. The threshold initiating strategy change in herring seems to be high. This could reflect threshold levels in individual fish, but collective decisions taken by schools may increase the threshold further. In addition, neighbouring schools could influence each other. It may have high costs to be the first school wintering in the Norwegian Sea if the rest of the stock returns to the coast. The risk of predation can be high without the dilution effect caused by neighbouring schools.

Since strategies are clearly going to be subject to compromise, herring may be thought of as adopting a preferred-conservative strategy. A preferred-conservative strategy is concurrent with observation that herring populations display persistent repeatable features during their life history while retaining the ability to be extremely flexible under highly variable circumstances. Herring may be forced to move from preferred locations when for instance food or predator pressure becomes limited beyond some threshold. Under such conditions the herring have to leave the low-risk situation and try their luck in the dynamic environment.

## STATUS AND CURRENT BOTTLENECKS

For Norwegian spring spawning herring the environment in the Norwegian Sea is to a certain degree unknown, a *Mare Incognitum*. Yet herring seem to be able to utilise the knowledge that major features of the zooplankton production are predictable in time and space. Although there may be an optimal environment at any moment, many localities exist where herring can survive and grow and the problem for the herring becomes one of choosing acceptable solutions. Which place is the best can also be influenced by what the rest of the population does. The mere fact that herring persists demonstrates it has the ability to adjust its behaviour to a changing environment by shifts in feeding, spawning and overwintering migrations.

Adoption of a low-risk strategy by the herring together with the observations on flexible migration patterns creates some kind of paradox. The idea of the herring as having a preferred-conservative strategy is appealing to explain this paradox. Apart from some local populations, Norwegian spring spawning herring cannot be divided into genetically different units (Smith and Jamieson 1986) and thus seems to have a flexible migratory reaction norm that is expressed in different ways under different conditions.

A bottleneck for an improved understanding of the spatial dynamics of herring is near-field studies with detailed recordings of search patterns of schools by use of high resolution sonar, differential global positioning system (GPS) and continuous recordings of zooplankton distribution. Studies on the mesoscale distribution of zooplankton lag behind those of fish

schools, and acoustic or optical methods are required to get satisfactory resolution in time and space. More quantitative knowledge about the predator pressure and abundance of competitors is also needed. Continuous current measurements in deep water (ADCP Doppler) could give better estimates of swimming speed. Data storage tags on individual herring and satellite pictures of temperature and chlorophyll could also give valuable information.

With increasing knowledge it will be possible to test more specific hypotheses on orientation mechanisms by collecting selected field data on distribution and swimming direction. Temperature preferences, reaction to temperature gradients and bioenergetic studies on the energy costs of swimming can be investigated in the laboratory.

Low population size during the rebuilding of the stock seems to have restricted the seasonal feeding migration to Norwegian waters. In connection with an increasing population size during the last few years the distribution has extended towards the west into international waters. This season (1996) is the first when the stock has reached a similar population size as before the collapse in the late 1960s. It is thus tempting to speculate, that herring will now resume its original migration pattern with overwintering grounds northeast of Iceland. This shift would have large consequences not only ecologically but also economically for the coastal and oceanic fishing fleets of the fishery nations involved. The distribution of herring in the economic zones could change dramatically in the next few years, and influence the determination of fishing quotas.

In this situation it would be very useful for fisheries management to have some kind of predictive tool like a dynamic model of the herring migration. Devising such a tool is a difficult task and is hindered by bottlenecks in our understanding of the dynamics of the herring population in the Norwegian Sea. A dynamic modelling approach based on the costs and benefits of migration may be worth while. At a critical distance between the feeding area in late summer and the previous wintering area, the herring may change wintering area. The difficulties to accurately estimate such threshold values must, however, be appreciated. One question is how much of the physical and biological environment in the Norwegian Sea is deterministic and how much is stochastic. Predation and feeding may include strong stochastic elements that should be included as a part of dynamic models. Increasing knowledge about proximate orientation mechanisms and about the role of decisions of individual fish within the dynamics of large schools should also influence models.

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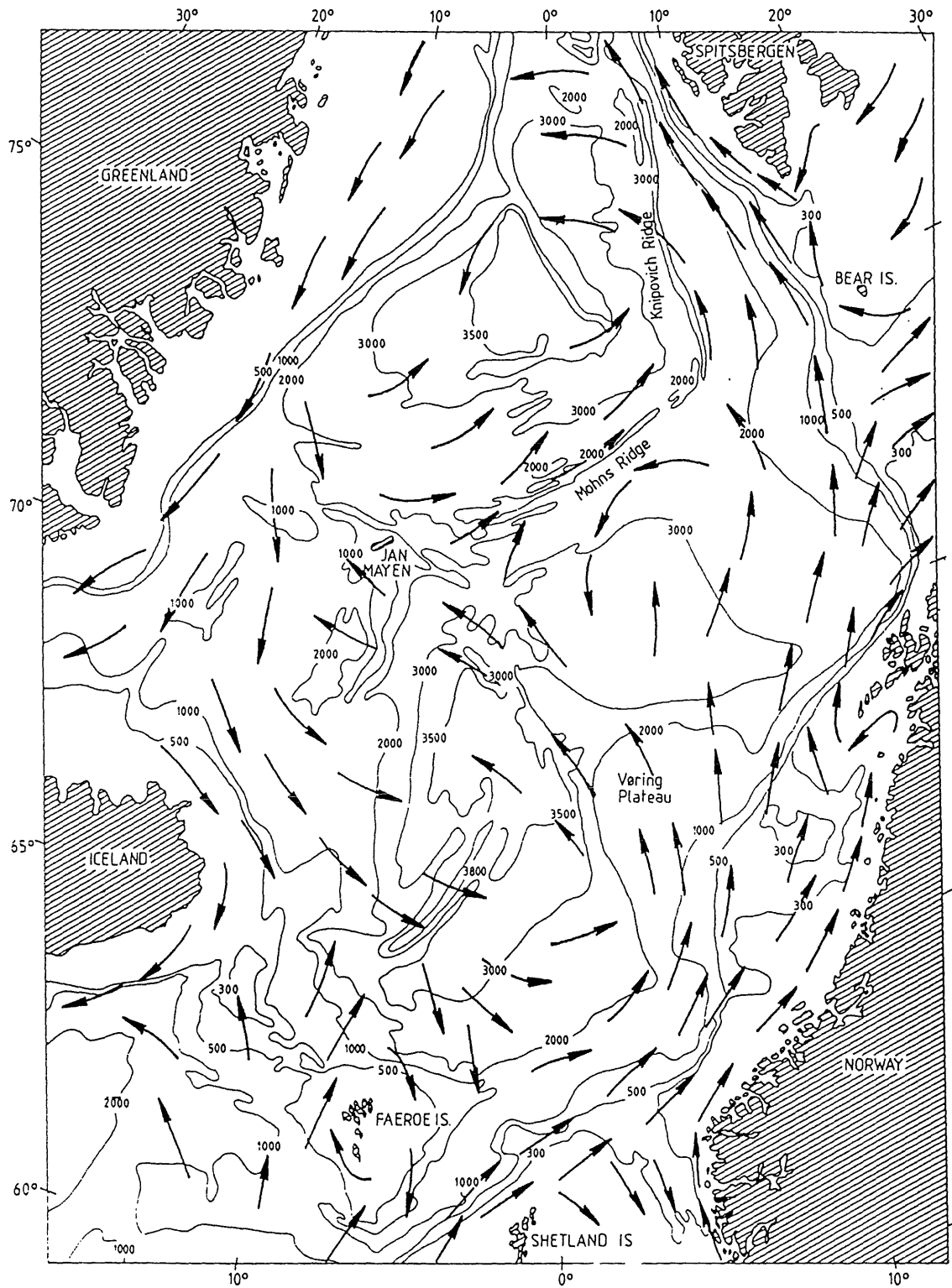
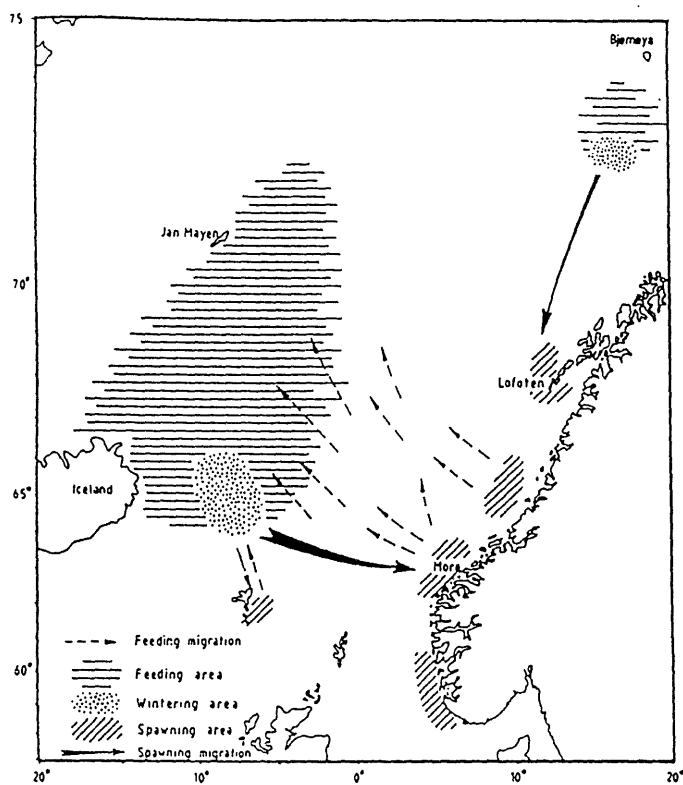


Figure 1. Bathymetry and surface currents of the Norwegian Sea (after Blindheim 1989). Depth in metres.

a)



b)

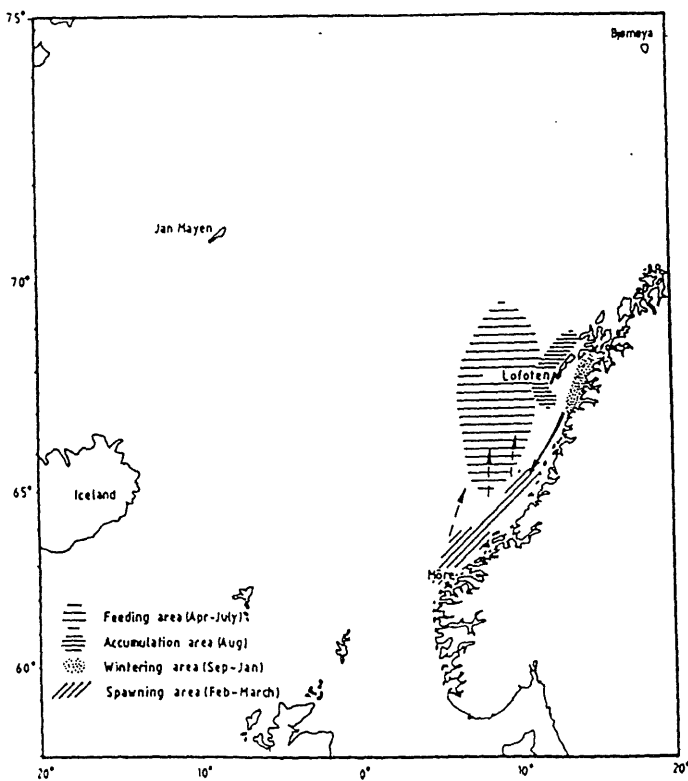


Figure 2. Distribution and migrations of Norwegian spring spawning herring before 1970 (a) and in the period 1986 - 1988 (b). (After Røttingen 1990).

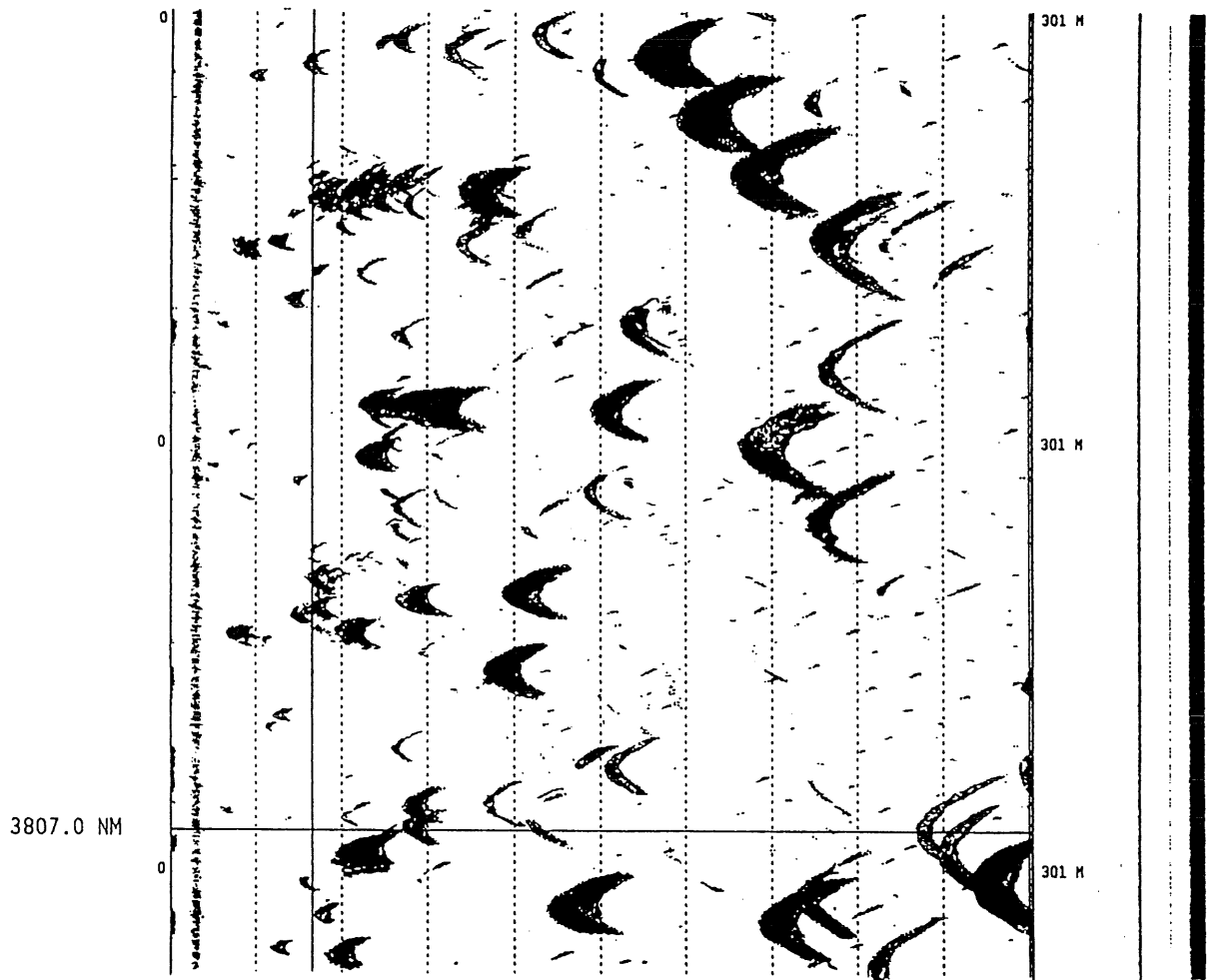


Figure 3. Recordings of herring schools by the SIMRAD SA950 sonar in the Norwegian Sea. The sonar is tilted  $-5^\circ$  and directed  $90^\circ$  port. The dotted horizontal lines are spaced 30 m apart, and the figure shows a recording along a transect of about 1 nautical mile.

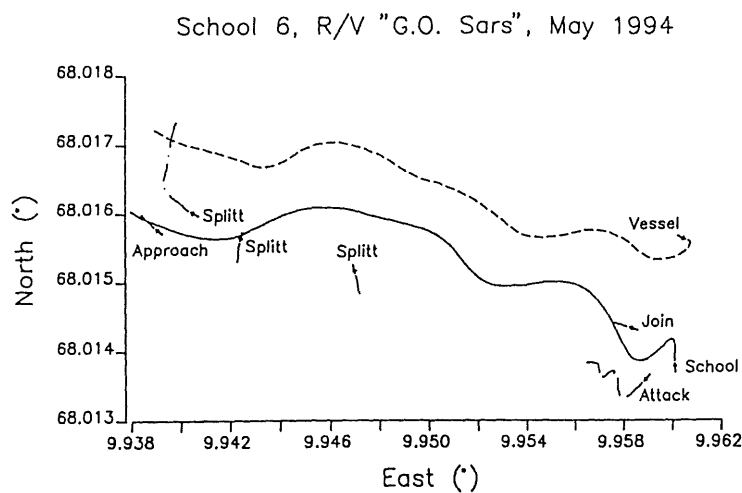


Figure 4. Swimming path of a herring school followed for one hour in the Norwegian Sea.

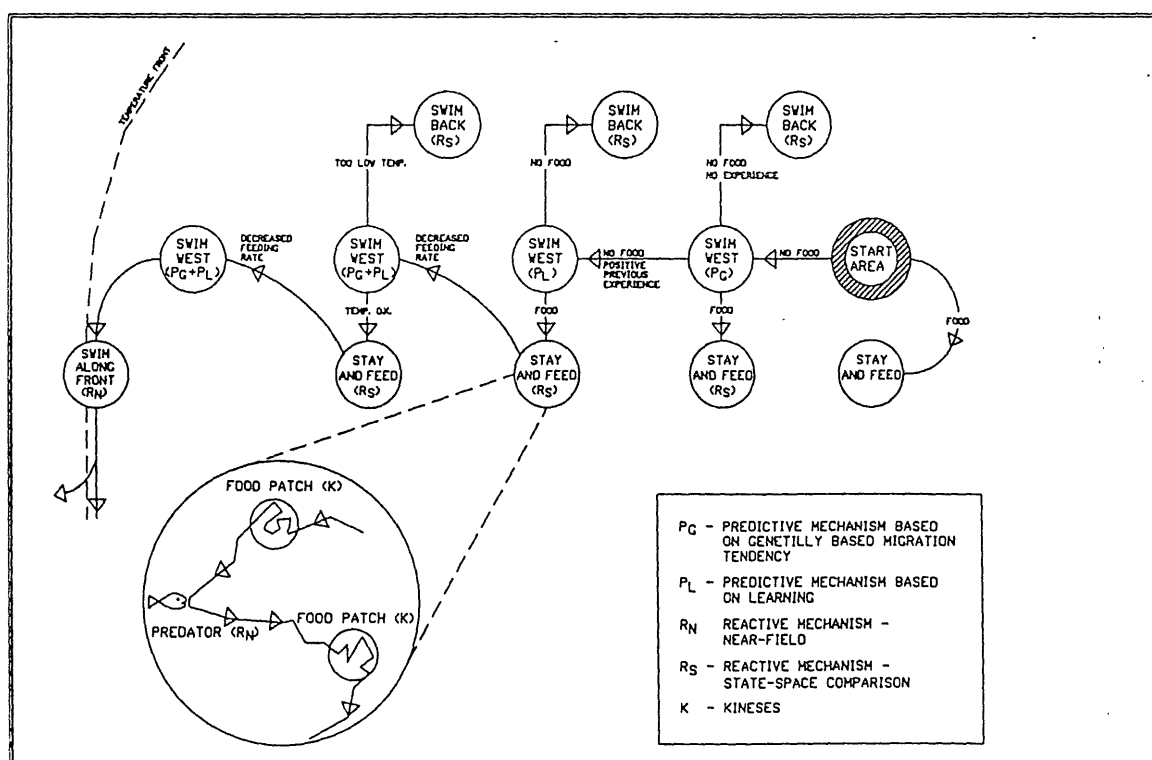


Figure 5. Proposed mechanisms for the control of migration and distribution of Norwegian spring spawning herring.

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