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LEARNING PROCESSES IN HERRING MIGRATIONS

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Abstract

Herring migrations seem to be controlled not only by genetic factors and hydrography, but also by learning processes. The choice of spawning grounds is clearly an example of a tradition that is passed on by one generation of herring to the next. Similar "traditional" behaviour patterns may affect the choice of feeding and overwintering grounds. The conservatism in herring behaviour could mask the effect of hydrographic changes on herring distribution.

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INTRODUCTION

In studying the relationship between fish distribution and hydrographic conditions, one often assumes that the fish - with an "open mind", - selects the area where environmental conditions are most suitable at a particular moment. If this were the case, there would be a straightforward relationship between fish distribution and hydrographic conditions. Once this relationship had been properly defined, it would be possible to predict the distribution of the fish entirely on the basis of hydrography.

There are two elements in the behaviour of fish that may complicate the simple relationship between distribution and environmental conditions. The first element is tradition; the tendency to stick to routines that have proved successful in the past. The second element is random variation in behaviour; the (necessary) complement of tradition and conservatism. This paper will concentrate on the first element: traditional behaviour in respect to distribution and migration. The phenomenon will be illustrated in North Sea herring and Norwegian spring spawning herring; two stocks in which migrations have been studied extensively.

SELECTION OF SPAWNING GROUNDS

Herring are well known for their tendency to return to the spawning ground where they have spawned the first time of their life. This fact has been established for instance by tagging experiments on Canadian herring (Hourston 1982), and by the study of meristic characters in North Sea herring (Zijlstra 1958). Many authors have discussed the question whether the place of first spawning is also the place where the herring actually was born. In a wide geographical context, this probably is the case. For example, fecundity data show that herring born in the southern North Sea and English Channel probably constitute a population that is genetically distinct from the ones in the central and northern North Sea (Zijlstra 1973).

Looking at the spawning grounds on a finer geographical scale, it is seen that separate spawning sites can be defined within each larger spawning area. As an example, Figure 1a shows the individual spawning sites that existed in the southern and central North Sea and English Channel in the years 1955-1975 (from Postuma et al. 1975). It seems unlikely that the herring spawning at each of these sites constituted genetically separated subpopulations, in which all recruiting herring returned exactly to their own place of birth. Immediately after hatching, the larvae are swept away from the spawning ground by the tidal current, and they won't have time to memorize the exact location of their place of birth.

Yet, the subpopulations of each spawning site tended to maintain their integrity over the years, as was shown by the consistency of meristic characters (Zijlstra 1958). When several of these subpopulations were destroyed by overfishing in the 1960s, they did not re-appear after the rebuilding of the total North Sea stock in the 1980s. This is shown by a comparison between the spawning sites in the period 1955-1975 (Figure 1a) and the spawning sites in the period 1976-1992 (Figure 1b). Despite a recovery of the total North Sea stock from 75000 tons in 1975 to 1.4 million tons in 1992, the actual number of individual spawning sites hardly increased during this period. Many of the former spawning sites that were fished out in the 1960s were not re-occupied since.

The most likely explanation for the reluctance of herring to re-colonize former spawning sites is a traditional element in its behaviour. Presumably, a recruit herring has a only rough idea in what area and season it is going to spawn. At spawning time, it joins a school of older herring that are heading for a particular spawning site. Once the recruiting herring has also spawned at this site, the geographic position is locked in its brain. In subsequent years, it will have a strong tendency to return to this place of first spawning.

The herring has become a member of a particular subpopulation; not by genetic determinism, but by learning the tradition of a "social group".

By this mechanism, recruiting herring will only spawn at sites that are visited by older herring. If the adult herring of a certain subpopulation are all removed by fishing, no recruit herring will find their way to that particular spawning site any more.

Of course there must be exceptions to this rule. If the herring were overly traditional, they would become vulnerable to natural changes in their habitat. There are indications that recruit herring can venture into unknown territory, and re-colonize spawning grounds that were abandoned long ago by former generations. The re-colonization of the Aberdeen Bank spawning ground in 1983, after an absence of spawning in this area for 15 years, is an example of this (Corten, 1990). This event occurred when a large year class recruited, and the population of older fish was relatively small. Under such conditions, the older fish are outnumbered by recruits, and the younger generation may sometimes make its own choice. Another example of the re-occupation of a former spawning ground was shown by the Norwegian spring spawning herring. A small component of this stock has spawned off Karmøy in southern Norway since 1989 (Bergstad et al. 1991). This spawning took place on traditional spawning grounds that had been abandoned 30 years before.

Such events, however, are an exception. In general, once a spawning site has been abandoned by the population, it is not easily re-occupied by later generations.

TRADITIONAL ELEMENTS IN FEEDING MIGRATIONS

If herring are able to learn how to find a suitable spawning place, they probably can learn other migration routes too. The spawning migration is only one of the activities that herring are engaged in during their yearly cycle. Other activities are feeding migrations, and overwintering. Possibly, both of these activities are also influenced by tradition and learning.

During their feeding migration, herring do not seem to be distributed randomly over the whole area where food may be encountered. Instead, they seem to follow certain routes that are consistent from one year to another. This was shown for instance during a herring tagging experiment in the North Sea in 1983-85. (Morrison and MacDonald, 1986). In July 1983, a total of 48 000 herring were tagged with microwire tags in the Shetland area. Recovery of the tags required the use of special equipment; hence a purse seiner was chartered in 1984 and 1985 to catch herring in the Shetland area and screen the catches for tagged fish. Both in 1984 and 1985, the recovery rate differed markedly between June and July: very few tagged fish were found in June, and the bulk of the recoveries came from catches in July. The size composition of the herring did not differ markedly between the two months, and performance of the detector was supposedly constant. The conclusion was that different groups of herring occurred in the Shetland area in June and July, and that each group maintained its integrity from one year to another. The group that had been tagged in July 1983 only showed up in July in subsequent years. The herring that occurred each year in June apparently belonged to a different section of the population. The complicated stock structure of herring on the feeding grounds near Shetland was one of the most surprising findings of the microwire tagging experiment; a result that largely invalidated the experiment for stock assessment purposes.

In the feeding season, just like during spawning, the total herring stock seems to split into different subpopulations, each of which has its unique migration pattern, which is maintained from one year to another. As in the spawning migrations, it is unlikely that these feeding migrations are genetically determined. Presumably, the recruiting herring just by chance joins one of the existing "feeding populations", and then in subsequent years sticks to the pattern that it has "learned" during this first migration.

In the choice of feeding grounds, herring may alter existing traditions if it finds out that a particular area has become less suitable as feeding ground. Corten and Van de Kamp (1992) described long-term changes in feeding migrations of North Sea herring over the period 1950 - 1990. In the 1980s, the feeding grounds of herring during June/July had changed from the western North Sea to the northeastern North Sea. The herring extended their migrations further north than usual, and changed their vertical distribution from the bottom layers to the surface layer.

Another, possibly related, change in herring migration was the summer migration of Baltic herring through Kattegat and Skagerrak into the North Sea. This migration was documented starting from 1986 (Anon. 1991), and there are no reports of such large scale migrations in earlier periods.

Both the change in feeding migrations of North Sea herring and Baltic herring most likely had an environmental cause. These causes have not yet been properly identified. It is possible, however, that the changes in herring migration were more consistent than the hydrographic changes that triggered it. The herring may have shown a delayed response, taking some years to alter its migration pattern after food supply in the traditional feeding area declined. Once a new tradition had become established, this may have been continued for a while after hydrographic conditions had returned to the original state.

Looking at more northern waters, the Norwegian spring spawning herring for many decades showed a steady pattern in its feeding migration. After spawning off southern Norway the herring would migrate in an anti-clockwise direction from the Norwegian coast to the polar front between Jan Mayen and Iceland, then southwest to Iceland, and finally back to southern Norway (Dragesund et al., 1980). After the collapse of the stock in the late 1960s (and the change in hydrographic conditions off Iceland), the herring no longer undertook these extended migrations, but remained in the vicinity of the Norwegian coast throughout the year. Only recently, after the recruitment of the strong 1983 year class in 1986, has there been a new attempt to exploit the oceanic feeding grounds (Holst and Iversen 1992, Røttingen, 1992). In recent summers, feeding herring were found scattered over the Norwegian Sea east of 5° W, an area that is to the northeast of the traditional feeding grounds. Whether this new area has better food conditions than the old one is unknown (Røttingen 1992). The herring may simply not yet have rediscovered the old feeding grounds, because the experience of the old generations has been lost. Røttingen (1992) has already suggested that the presence of older, "experienced" herring may be necessary to guide new generations to the traditional feeding grounds.

OVERWINTERING MIGRATIONS

The choice of overwintering grounds is probably also determined to some extent by tradition. In the 1960s, the majority of North Sea herring used to overwinter in Norwegian waters. This is where the heavy exploitation by Norwegian purse seiners took place in 1963 and 1964 (Egersund area). After the depletion of the overwintering stock in this area, apparently no "fresh" herring moved in from other parts of the North Sea. The remaining fractions of the North Sea stock that overwintered in the Shetland area, did not spread out into the Norwegian zone. When a joint Norwegian/EC Study Group in 1979 had to describe the current distribution pattern of the herring, it was concluded that herring were virtually absent from the Norwegian zone throughout the year (Anon. 1979). Only after the recruitment of the first strong North Sea year class in 1984 did this type of herring show up again in the Norwegian zone.

It seems that herring can become attached to a certain overwintering ground in the same way as it becomes attached to a spawning or a feeding ground. By selectively fishing on a certain overwintering ground, the subpopulation in that area may be exterminated in the same way as a spawning subpopulation.

A fine example of traditional overwintering behaviour is provided by the Norwegian spring spawning herring. In recent years, the entire stock has spent the winter in the Ofotfjord and Tysfjord in northern Norway (Dommasnes et al. 1992). The high abundance of herring during winter in the Ofotfjord has led to a permanent reduction in oxygen concentration in this area. The choice of this overwintering site clearly depends on a (recently established) tradition, and not on optimum hydrographic conditions. It will be interesting to see at what point the deteriorating of hydrographic (oxygen) conditions will outweigh the strength of tradition, and the herring population will decide to choose a new overwintering ground.

DISCUSSION

Many types of animals show a tendency to return to specific places that they have got acquainted with during an earlier stage of their life. The phenomenon is well documented for instance in birds; here the terms "site attachment" and "site fidelity" have been used in this respect (Ketterson and Nolan, 1990). While the animal at the time of birth may have an instinctive preference for migrating in a certain direction, the attachment to a specific site clearly depends on learning processes.

There is some evidence that learning also plays a role in the behaviour of fish populations. In herring, there are indications that certain sections of the population return each year to the same sites for spawning, feeding, and overwintering. Possibly these habits are copied by recruit herring from older ones. If a well-proven behaviour pattern is copied by a young generation from the older ones, it becomes a tradition. Such a tradition has survival value; copying an efficient migration pattern from an older generation will save energy and hence increase the chances for survival and reproduction.

Of course, traditional behaviour should not be exaggerated. The best chances for survival of a population are provided by a mix of tradition and adventure. If for some reason an existing behaviour pattern does no longer produce the required results, the population should not stick to the old routine, but explore new avenues. This is the only way it can adjust to environmental changes, or to new threats from outside.

The existence of traditional elements in the behaviour of herring is a complicating factor in the study of the relation between herring and its environment. Scientists studying this relationship should be aware of the fact that herring may show a delayed response to hydrographic changes, due to a certain conservatism in its behaviour.

The conservative behaviour is also relevant to fisheries management. A large herring stock may be composed of several subpopulations, each of which has its own traditional migration patterns. By a concentration of fishing effort on certain subpopulations, these elements may become extinct before the total stock shows signs of overfishing. The introduction of small management units for the herring fishery along the west coast of Canada in the early 1970s was already based on this knowledge (Hourston 1982).

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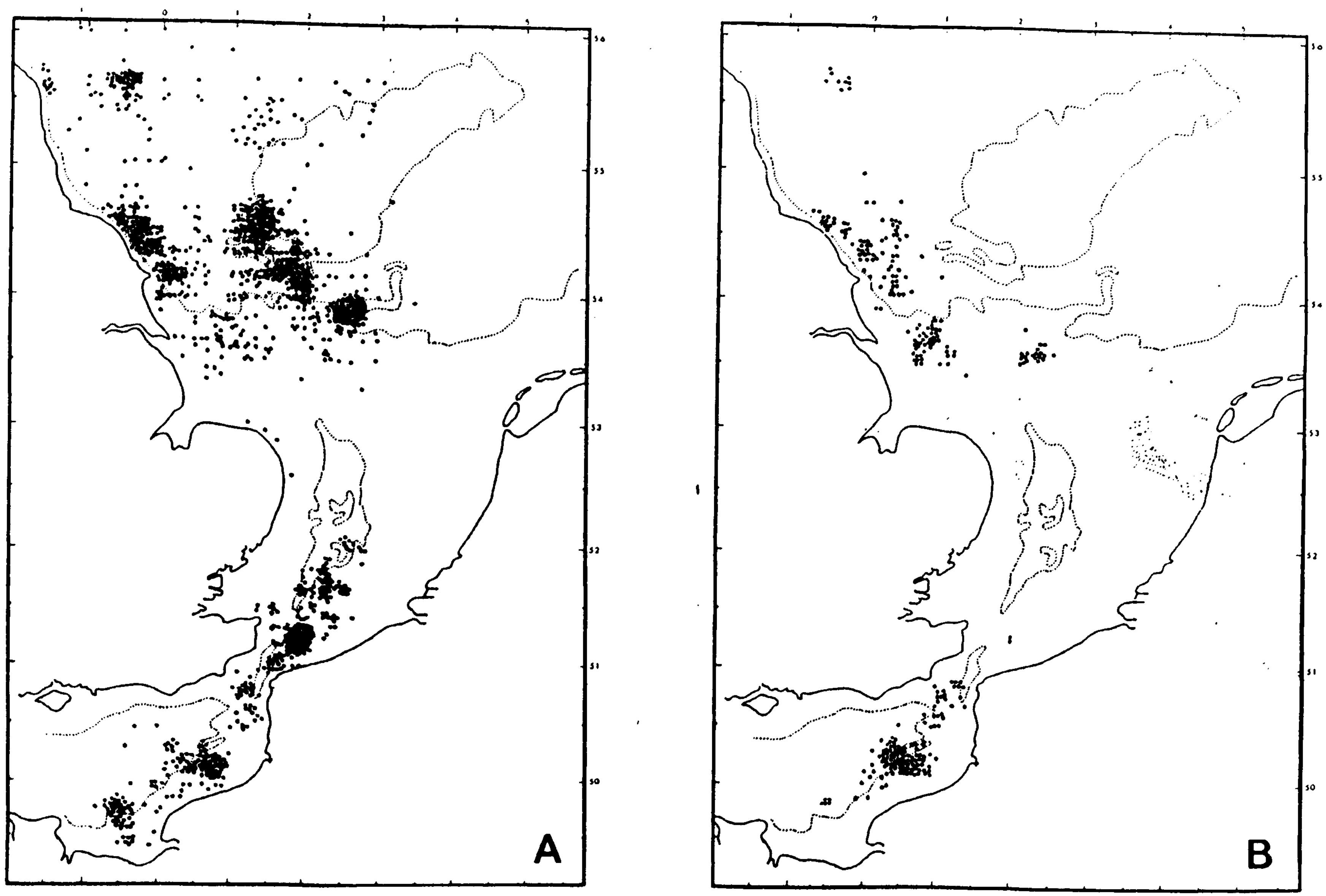

Figure 1. Position of individual spawning localities in the central and southern North Sea as indicated by catches of spawning herring. Each dot represents one sample of spawning herring. Data summarised for the period 1955-1975 (Figure A) and 1976-1992 (Figure B).