

Fisheries Research 50 (2001) 189-204



www.elsevier.com/locate/fishres

Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance

Ad Corten

Netherlands Institute for Fisheries Research RIVO-DLO, PO Box 68, 1970 AB IJmuiden, Netherlands

Abstract

Catch distributions and results of acoustic surveys indicate that North Sea herring had an unusually northern distribution during the summers of 1988–1990. Some of the herring may even have temporarily left the North Sea, and migrated to the Faroe plateau. The anomalous distribution of the herring in 1988–1990 appears to be related to a short-term climatic variation. The years were characterized by high water temperatures during the preceding winter, and by a low abundance of *Calanus finmarchicus*, the principal food of the herring. The low abundance of *C. finmarchicus* was probably related to the high water temperatures. Both the high temperature and the scarcity of food could explain the northern distribution of the herring.

Apart from the 1988–1990 anomaly, a long-term northward shift of catches occurred from 1960 to 1990. This northward trend in catches coincided with a gradual increase in winter temperature, and a sustained decrease of *C. finmarchicus*. The long-term shift in herring catches, therefore, could signify a gradual change in distribution of the stock, brought about by the same factors that caused the 1988–1990 anomaly. If the recent climatic trend towards higher winter temperatures continues, the anomalous distribution of herring in 1988–1990 could become the normal pattern in future years. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Herring distribution; Temperature; Climatic variation; Calanus

1. Introduction

The catch distribution of North Sea herring, based on data reported to ICES, has shown pronounced shifts in recent decades. Some of these shifts were related to changes in the exploitation of the stock, but others were apparently caused by natural changes in stock composition and/or distribution.

A remarkable northward shift of the summer fishery occurred in the years following the period of closed fishing from 1977 to 1983. In earlier years, the fishery always took place mainly in the western and northwestern North Sea. Fig. 1 shows the typical distribution of summer catches in the period 1955–1960; a distribution which remained largely the same throughout the 1960s and 1970s. In the 1980s, however, the

catches originated from the northern and northeastern North Sea (Corten and van de Kamp, 1992). The shift in catch distribution seemed to be a gradual process with catches reaching their most northeastern distribution during the last 3 years of the observations (1988–1990). Corten and van de Kamp (1992) assumed that the shift in the fishery was caused by a change in the distribution of the stock, but they could not identify the causes of such a change.

The present study investigates whether the anomalous catch distribution of the late 1980s persisted in subsequent years. Catch distributions for 1985–1995 were compared with results of acoustic surveys to see whether the pattern of the catch distributions was confirmed by fishery-independent data. This will answer the question whether the anomalous catch

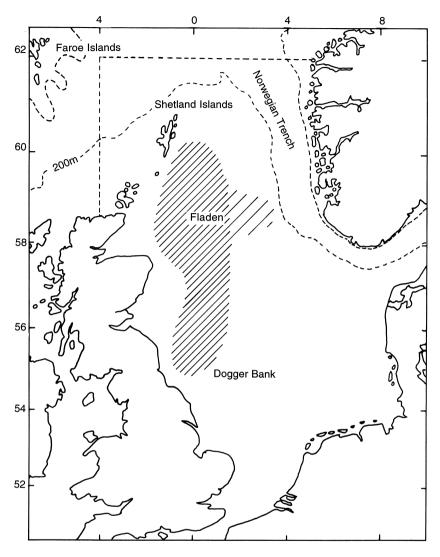


Fig. 1. Traditional fishing areas for North Sea herring in June and July. Based on international catch data for 1955-1960.

distributions in 1988–1990 indicated a real change in stock distribution, or whether they were due to a change in exploitation. Finally, shifts in catches and stock distribution are compared with environmental data in order to identify the causes of any change in stock distribution.

Earlier work has shown that the summer distribution of herring is affected mainly by temperature (Jakobsson, 1969; Maravelias and Reid, 1997) and by food, in particular, *Calanus finmarchicus* (Østvedt, 1965; Bainbridge et al., 1978; Maravelias and Reid,

1997). *C. finmarchicus* is the main food of herring in the North Sea and in the adjacent waters of the Norwegian Sea and northeast Atlantic (Bainbridge et al., 1978; Dalpadado et al., 1996).

The northern distribution of herring catches in the late 1980s was a persistent pattern that must have been caused by environmental changes acting over a wide area and lasting for several years. If temperature was the responsible factor, we are looking for a sustained change in temperature, probably in an upward direction. Herring is a northern species, for which the North

Sea is close to the southern limit of its distribution area. A northward shift in distribution could be a response of the fish to an increase in temperature.

Alternatively, the northward shift of the herring could be a reaction to changes in food abundance. The changes in herring distribution described in this paper occurred in June–July, i.e. at the end of the feeding season. A northern distribution of herring at this time of the year indicates that the fish have been feeding to the north of their normal feeding area. This might be related to a reduced abundance of food on the normal feeding grounds, or to an increased abundance on more northern grounds.

To provide some background information on North Sea herring, the annual migrations of the adult stock are depicted in Fig. 2. The North Sea stock consists of three populations, each characterized by a specific spawning area and season. Based on the position of the spawning areas, these populations are called the northern, central and southern North Sea herring. All populations share a common feeding ground in the central and northern North Sea, although the southern population does not migrate as far north as the other two. Herring of the central and northern populations spawn in August-September in the western North Sea. After spawning the herring move eastward, to overwinter in the region of the Norwegian Trench. In spring, the fish migrate north along the Norwegian Trench, and then west towards the waters around Shetland. Feeding starts in April-May in the northeastern sector, and continues in June-July in the northwestern sector. Herring of the southern population spawn in December-January in the eastern English Channel, and then overwinter in the southern North Sea. In spring, the fish move directly to the feeding grounds in the central and northern North Sea.

2. Data

2.1. Catch distribution

Data on the distribution of international catches after the reopening of the herring fishery were obtained from reports of the ICES Herring Assessment Working Group (Anon., 1986 and subsequent reports). During the first 2 years after the reopening of the

herring fishery (1983–1984), no detailed information on catch distribution was reported to ICES. Starting from 1985, the ICES Herring Assessment Working Group presented monthly charts of catches by statistical rectangle (30' latitude by 1° longitude). The data for these charts were provided directly by working group members, and they were corrected for any known misreporting of catches by fishermen. For this reason, the working group data in some years deviate from the official catch statistics reported to ICES by national statistical offices.

For the present study, catches by rectangle were grouped into the following larger sectors of the North Sea (see Fig. 3):

Shetland	60–62°N	West of 2°E
Viking	60–62°N	East of 2°E
Fladen	$58-60^{\circ}N$	West of 2°E
Utsira	$58-60^{\circ}N$	East of 2°E
Forties	56–58°N	West of 2°E
Fisher	56–58°N	East of 2°E

The analysis of catch data was restricted to the waters north of 56°N. Catches further south contain a substantial element of juvenile herring, which confuses the picture of adult herring distribution.

2.2. Acoustic surveys

Data on the distribution of the total herring stock during the month of July were available from the ICES coordinated acoustic surveys in the North Sea. These annual surveys were started in 1983, but complete coverage of the northern North Sea was not obtained until 1984. Therefore, only results from 1984 onwards can be used to study the distribution of the herring stock.

Preliminary results of the surveys were presented in annual reports to the ICES Statutory Meetings (Simmonds et al., 1985 and subsequent reports). Due to differences in reporting and analysis between years, the data reported in the annual reports are not directly comparable for all years of the survey. For the present study, a revised data set was used in which data for all years of the survey had been processed in a uniform way. This data set was kindly provided by J. Simmonds and M. Bailey of the Marine Laboratory in Aberdeen. The data included numbers per rectangle of

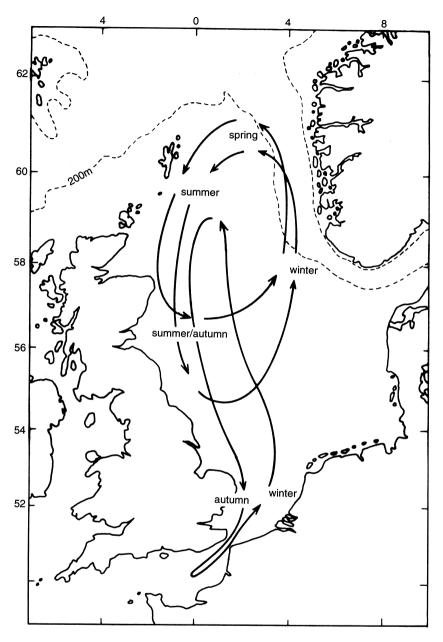


Fig. 2. Annual migrations of adult North Sea herring. Adapted from Anon. (1965), and from Cushing and Bridger (1966).

mature autumn spawning herring for all surveys from 1984 to 1996.

Despite the uniform processing of data, the survey results prior to 1990 may contain a relatively large amount of random error. New countries joining the survey needed some time to gain experience in identifying echo traces, and in classifying herring as spring or autumn spawners. This problem may have occurred for instance during the 1988 survey in the northeastern North Sea, when one country classified all herring of 4 years and older as spring spawners, whereas other countries classified the same herring as autumn spaw-

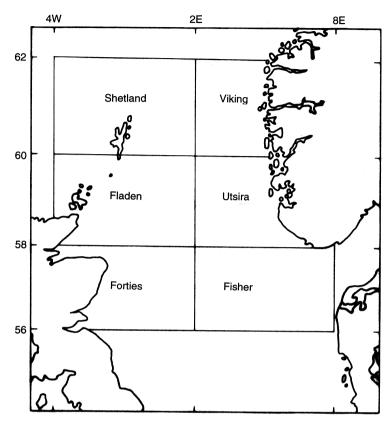


Fig. 3. North Sea sectors used for analysis of catch data and acoustic surveys.

ners. From 1990 onwards, participation in the surveys has stabilized, and results are considered to be more consistent.

2.3. Water temperature

Variations in water temperature in the northern North Sea during spring largely result from differences in winter cooling from one year to another. Therefore, the water temperature at the end of the winter may be considered a suitable index for the temperature regime during the early phase of the spring migration of the herring.

The most consistent series of water temperature data available for the northern North Sea was a series of bottom temperatures for the month of February, collected during the International Bottom Trawl Surveys. Although these data do not refer precisely to the time when the herring start their migration (March/

April), it is assumed that bottom temperatures do not change drastically between February and March. Data for the surveys in 1970–1991 were derived from a report published by ICES (Dooley, 1992), and for the surveys in 1992–1996 from annual reports on the IBTS (Anon., 1992 and subsequent reports).

The bottom temperature at 60° N, 2° E was chosen as an index for the temperature in the northeastern North Sea. This is a standard ICES hydrographic position for which a complete temperature series is available from 1970 onwards. The position is about 40 nm west of the Trench slope, and it is considered to be representative of the area from where the herring start their feeding migration at the end of the winter.

A longer time series of overall winter conditions in the North Sea can be derived from deep water temperatures in the Skagerrak. The Skagerrak acts as a sink for cold bottom water from the North Sea, and the temperature in the deeper part of the Skagerrak reflects

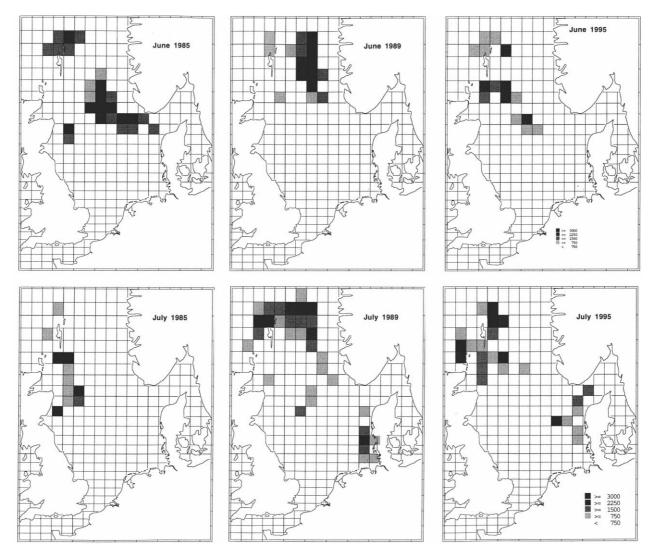


Fig. 4. Examples of variation in catch distribution between years.

the mean winter temperatures on the North Sea plateau during the previous few years (H. Dooley, pers. comm.). A series of deep Skagerrak temperatures for the period 1947–1996 was kindly provided by the ICES Hydrographic Service.

2.4. Food

The main food of herring in spring consists of the copepod *C. finmarchicus* (Dalpadado et al., 1996; Bainbridge et al., 1978). This species overwinters in deep water along the shelf edge, and invades the North Sea in early spring (Backhaus et al., 1994). The fastest migration route is through the Norwegian Trench into the northeastern North Sea. Another, slower transport takes place into the northwestern North Sea by means of the Fair Isle Current and the East Shetland Atlantic Inflow. The fast transport of *C. finmarchicus* into the northeastern North Sea is considered as the cause of the early spring bloom in this area (Backhaus et al., 1994).

Data on the abundance of *C. finmarchicus* used in this study originated from the Continuous Plankton Recorder Survey in the North Sea and eastern North Atlantic (Warner and Hays, 1994). A data series for the period 1962–1992, consisting of annual averages of the numbers per CPR sample, was kindly provided by Benjamin Planque. The series has been published earlier by Planque and Fromentin (1996). These authors showed that the annual abundance of *C. finmarchicus* is closely related to its peak abundance in April–June. Therefore, the series of annual abundance indices may be used as an approximation of food abundance during the main feeding season of the herring.

3. Results

3.1. Catch distribution

Both in June and July, the distribution of catches varied considerably between years. To illustrate this variability, the distribution of catches by rectangle in these months for the years 1985, 1989, and 1995 is compared in Fig. 4. These years are examples of three different types of distribution: a southeastern distribution in 1985, a northeastern distribution in 1989, and a

western distribution in 1995. For the year 1985, only the data for June should be considered. In July, the Norwegian fishery was closed because the Norwegian quota had been taken. Consequently, no catches were taken in the eastern sector during July. However, in 1989 and 1995, the catch distribution did not change much between June and July. Considering the southeasterly distribution of catches in June 1985, one may assume that also in July of that year the herring were probably still present in the easterly sector.

The development of catches by sector over the period 1985–1995 is presented in Fig. 5. The data show a temporary northward shift of catches in 1989–1990 with increased catches at Viking in June and July, and at Shetland in July. At the same time, there is a dip in catches in the more southern sectors of Fladen, Forties and Fisher (the last two mainly in June). The June catches at Shetland do not conform with the general northward shift in 1989–1990, but we shall return to this topic later.

The data in Fig. 5 also indicate a long-term reduction of catches in the eastern sectors Utsira and Fisher in June. This coincides with a gradual increase in the Fladen sector over the whole period, especially in June.

The general trends in catch distribution can be illustrated by combining data for different months and sectors. Fig. 6 shows that the combined catches for the two northern sectors increased from 1985 to 1989, and declined after 1989. This trend was not the effect of changes in absolute stock size during this period, since the relative distribution of catches shows the same trend.

The combined catches for the eastern sectors in June and July gradually decreased over the years, both in absolute quantities and as a percentage of the total North Sea catch. This trend is even more pronounced if the data for June are considered in isolation (Fig. 6).

3.2. Acoustic surveys

For the analysis of acoustic data, the same sectors were used as for the catch data. Time series of acoustic estimates by sector for the mature component of the stock are presented in Fig. 7. In the Shetland sector, acoustic abundance was high in the years 1988–1991, and also in 1996. The Shetland maximum in 1989–

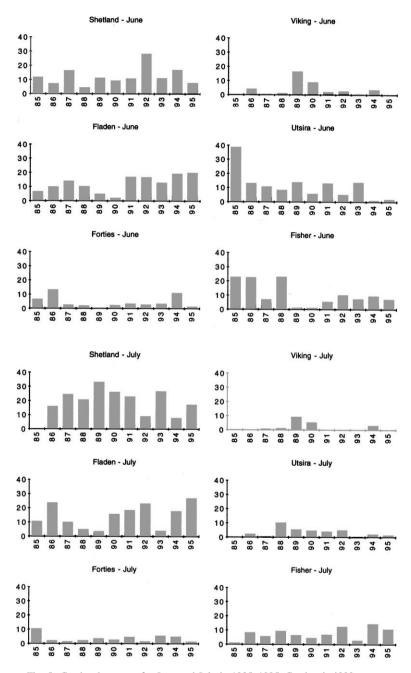


Fig. 5. Catches by sector for June and July in 1985-1995. Catches in '000 tonnes.

1990 coincided roughly with peaks in the sectors Viking and Utsira.

In the Fladen sector, a gradual increase in abundance is noticed during the whole period 1984–1996. In the other western sectors (Shetland and Forties),

there is no clear trend over this period. The eastern sectors all show a culmination of acoustic abundance around 1990–1992, followed by a decline.

When the two northern sectors are combined (Fig. 8) the years 1988–1990 again have a high abundance in

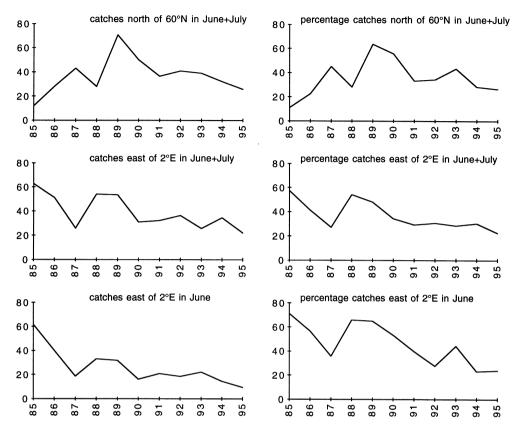


Fig. 6. Catches in northern and eastern North Sea. Left-hand side graphs in 1000 tonnes, right-hand side graph in percentage of total North Sea catch.

the north. This is not the effect of an overall increase in stock size in these years; also the proportion of the total stock found in the northern areas was high in these years. The acoustic data thus indicate a northward shift of adult herring distribution in 1988–1990.

Acoustic estimates for the eastern half of the North Sea were high in 1988–1992, and then dropped to a low level. For the western half, acoustic estimates showed an increasing trend when expressed in absolute numbers. Expressed as a proportion of the total estimate for the North Sea, the abundance in the western half declined from 1984 to 1991, and then increased again in later years.

3.3. Relationship between northern distribution and water temperature

Bottom temperatures for position 60°N, 2°E in February are plotted in Fig. 9 for the years 1970–

1996. It is seen that the temperatures reached their maximum values in the years 1989–1990, but stayed high also in 1991–1993.

Both the combined catches in June and July in the northern area, and the acoustic estimates in July for the northern area, are significantly correlated with February temperatures (Fig. 10, Table 1). The correlations remain significant also when catches or acoustic estimates in the northern area are expressed as a proportion of the values for the total North Sea. This indicates that the correlation is not due to a chance coincidence between high temperatures and a temporary increase in total stock size.

The temperature series for 1970–1996 indicates a long-term increase in winter temperature in the North Sea. To investigate whether this trend already occurred in earlier years, the longer time series of deep water temperatures (>500 m) in Skagerrak was considered (Fig. 11). The data show that temperatures

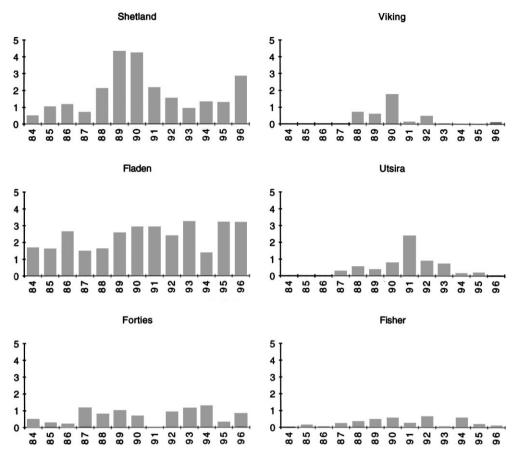


Fig. 7. Acoustic estimates (billions of fish) by sector.

in the deep parts of Skagerrak have risen consistently over the last 50 years, which means that winter temperatures on the North Sea plateau must also have increased over this period. If winter tempera-

ture has an effect on the distribution of the herring, the long-term increase during the last 50 years could have caused a gradual northward shift of the population.

Table 1 Correlation between northern distribution of the herring and two environmental variables

Explanatory variable	Index northern distribution herring	r	p
Bottom temperature at 60°N, 2°E in February	Catches north of 60°N in tonnes	0.604	0.05
	Catches north of 60°N as percentage of total North Sea catch	0.612	0.05
	Acoustic estimate north of 60°N in numbers of fish	0.804	0.01
	Acoustic estimate north of 60°N as percentage of total North Sea estimate	0.646	0.05
log annual abundance, C. finmarchicus	Catches north of 60°N in tonnes	-0.777	0.05
	Catches north of 60°N as proportion of total North Sea catch	-0.768	0.05
	Acoustic estimate north of 60°N in numbers of fish	-0.669	0.05
	Acoustic estimate north of 60°N as proportion of total North Sea estimate	-0.529	Not significant

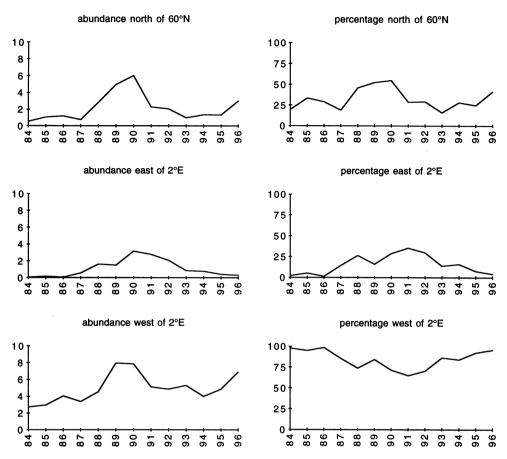


Fig. 8. Acoustic estimates in northern, eastern and western North Sea. Left-hand side graphs in billions of fish, right-hand side graphs in percentage of total North Sea.

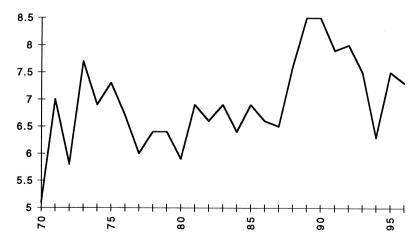


Fig. 9. Bottom temperature at position 60°N, 2°E. Data from ICES Hydrographic Service.

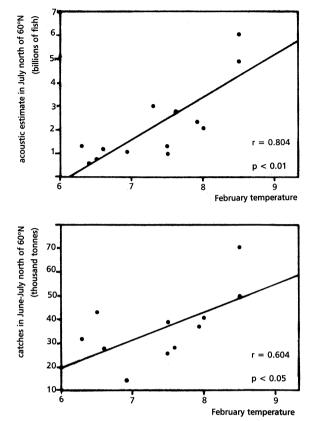


Fig. 10. Correlation between bottom temperature in February and indices of northern distribution of herring during subsequent summer

3.4. Relationship between northern distribution and food

A time series of average annual abundance of *C. finmarchicus* for the years 1962–1992 is shown in Fig. 12. The data refer to the North Sea and adjacent part of the North Atlantic as defined in Planque and Fromentin (1996). *C. finmarchicus* shows a declining trend over the years with minimum values in the years 1989–1992. The data series for *C. finmarchicus* overlaps with the time series for herring distribution only for a short period (1984–1992 for acoustic surveys, and 1985–1992 for catch distributions). Despite the limited number of data pairs, there is a significant negative correlation between *C. finmarchicus* and both indices of northern distribution of the herring (Table 1, Fig. 13).

3.5. East/west shifts in distribution

In addition to the north–south shifts in herring distribution, the data presented in this report indicate shifts in east/west direction. These shifts are apparent both in the catch distribution and in the results of acoustic surveys. Although the east/west shifts are probably also caused by environmental factors, their study requires more detailed environmental data than were available for the present paper.

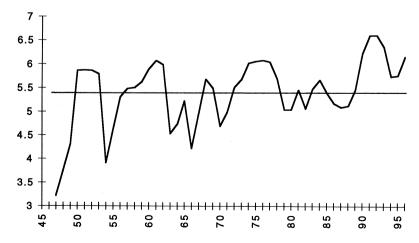


Fig. 11. Annual average temperature in Skagerrak below 500 m. Data from ICES Hydrographic Service.

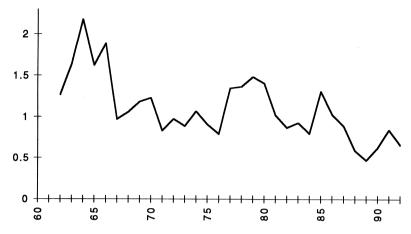


Fig. 12. Annual average abundance *C. finmarchicus* in North Sea and adjacent part of North Atlantic, expresssed in numbers of individuals per CPR sample. Data provided by B. Planque.

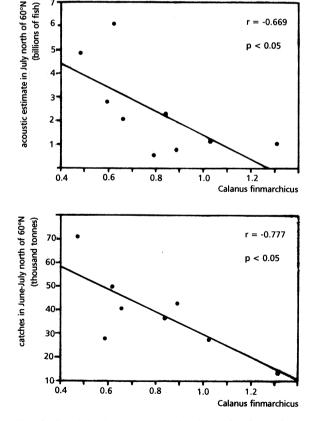


Fig. 13. Correlation between annual abundance of *C. finmarchicus* and indices of northern distribution of herring during summer.

4. Discussion

4.1. Changes in stock distribution

Acoustic survey data showed a very northern distribution of the herring stock in the years 1988–1990. Therefore, the northward shift in catches during these years, reported earlier by Corten and van de Kamp (1992) was indeed caused by a shift in distribution of the stock, and not by a change in exploitation.

There is a discrepancy between catch data and acoustic estimates for the year 1988. Catch data for this year do not show high values for the northern areas, whereas the acoustic data indicate a very northern distribution. A possible explanation for this discrepancy is that a large part of the herring stock had migrated far north in June, and was out of reach of the fleet. In the first half of June, the Dutch fleet could not find herring on the normal fishing grounds in the northwestern North Sea. It was only in the second half of the month that the fleet located some herring in waters to the north of Shetland (personal observation). One month later the acoustic survey still found the main part of the herring stock close to the northern edge of the North Sea.

There are indeed indications that North Sea herring extended their spring migration beyond the shelf edge and out of the North Sea in 1988–1990. Jacobsen

(1990) recorded herring with North Sea characteristics in Faroese waters during an acoustic survey in June 1990. Similar herring had been taken during exploratory fishing trips southeast of the Faroes in June 1988 and 1989. The herring arrived in Faroese waters in May, and they left the area in July in an easterly direction. The occurrence of these herring in Faroese waters was an unusual phenomenon, which means that they must have come from somewhere else, presumably the North Sea or the waters west of Scotland. The presence of North Sea-type herring in Faroese waters in 1988, therefore, is strong evidence that the North Sea stock had a very northern distribution also in 1988.

The northward shift in distribution of North Sea herring catches in the 1980s, reported by Corten and van de Kamp (1992), was partly reversed after 1990. This did not mean, however, that the distribution of catches returned completely to the normal pattern of earlier years. Catches in the first half of the 1990s still originated from relatively northern positions in comparison to the years before 1960. In the early 1990s, between 25 and 40% of all herring catches originated from waters north of 60°N (Fig. 6), whereas this area made an insignificant contribution to the total North Sea catch in the years prior to 1960 (Fig. 1). This suggests that, apart from the extremely northern distribution of the stock in 1988-1990, there has been a more gradual northward shift of the stock during the entire period 1960-1990.

The very northern distribution of the herring in 1988–1990 coincided with a high level of adult stock size, and a high mean age of the population. The adult stock size reached a peak of 1.26 million tonnes in 1989, and the percentage of fish older than 3 years reached a level of 44% (Anon., 1998). However, Corten and van de Kamp (1992) showed that neither of these two factors was probably responsible for the northern distribution. During an earlier episode of high stock size in 1955–1960, the adult stock was 1.4 million tonnes on average, and the fish older than 3 years made up 52% of the population. Yet there were no indications of a northern distribution of the stock in these years, as is shown in Fig. 1.

4.2. Environmental causes

The northern distribution of herring in 1988–1990 coincided with high winter/spring temperatures, and

low abundances of *C. finmarchicus*. Each of these two parameters could be the cause of the northern distribution of the herring.

An increase in water temperature is likely to result in a northward displacement of the herring. Herring is a northern species, for which the North Sea is a southern part of its distribution area. The fish requires a specific temperature regime during the year to control its physiological processes. One of these processes is gonad development. Too high a water temperature may accelerate gonad development and result in maturation before the normal spawning time. Although gonad development in most fish is primarily regulated by day length, water temperature often affects the degree of photostimulation (Lam, 1983). For herring, it has been observed that low temperatures will slow down gonad development (Dragesund, 1960; Jakobsson, 1969). Pre-spawning herring in the North Sea often assemble in pockets of cold bottom water, apparently in order to slow down gonad development, and to postpone spawning until the right time (Postuma, pers. comm.). If gonad development is to proceed at the same rate from year to year, the fish has to follow the same temperature regime. A high water temperature at the start of the season may stimulate the herring to migrate towards more northern (and cooler) waters, in order maintain a normal body temperature during the feeding period.

A low abundance of *C. finmarchichus* means a shortage of food for the herring. The distribution of *C. finmarchicus* is restricted to the northern half of the North Sea with the highest concentrations occurring in spring along the Norwegian coast and along the northern edge of the North Sea (Planque and Fromentin, 1996). High numbers of *C. finmarchicus* are also found beyond the northern border of the North Sea in the Norwegian Sea and towards Iceland and the Faroes.

In years of low abundance, the distribution of *C. finmarchicus* contracts towards the northern part of its distribution area. Data reported by Planque and Fromentin (1996) indicate an overall low abundance of *C. finmarchicus* in the North Sea and adjacent northeast Atlantic in the years 1987–1992. This means that the distribution of the species in these years must have been restricted to more northern waters. The herring will have encountered a scarcity of food on their normal feeding areas, and this food shortage may

have stimulated them to extend their feeding migration northward into areas where *C. finmarchicus* was still abundant.

On the basis of the results reported in this paper, it is not possible to decide which of the two factors, temperature or food, was responsible for the northward displacement of herring in 1988-1990. For the present study period (1984-1996), each of the two factors can give a satisfactory explanation of the northward shift in herring distribution. Even the long-term northward shift of herring catches since 1960 can be explained by either of the two factors. Winter temperatures in the North Sea show an increasing trend since 1947, and C. finmarchicus shows a declining trend at least since 1962. To decide which of the two factors is actually responsible for the northward shift of herring requires an analysis on a more detailed temporal and spatial scale than was used in the present paper.

The reason why the effects of temperature and food are difficult to separate, is the fact that both parameters are correlated with each other. Fromentin and Planque (1996) have demonstrated that the annual abundance of *C. finmarchicus* in the North Sea and adjacent waters is inversely correlated with winter temperature. One of the explanations for this is that *C. finmarchicus* is a cold water species, for which the North Sea is the southern limit of its distribution range. An increase in temperature will have a negative effect on the species' survival and reproduction in the North Sea.

5. Conclusions

The extremely northern distribution of herring catches in the North Sea in the summers of 1988–1990 signified a real northward shift in distribution of the stock in comparison to other years in the period 1984–1996. A comparison of recent catch distributions with data for the period prior to 1960 suggests that, in addition to the pronounced anomaly for the years 1988–1990, there has been a more sustained northward shift of the summer distribution of the herring during the period 1960–1990.

The northward shift of the herring could be explained either by an increase in winter temperature, or by a reduced abundance and northward contraction

of *C. finmarchicus*, the main food for the herring. Short-term fluctuations in both parameters could explain the herring anomaly of 1988–1990, whereas their long-term trends could explain the sustained northward shift of herring since 1960.

If current trends in temperature and/or Calanus continue in the near future, the anomalous distribution of North Sea herring during 1988–1990 could become the normal pattern in future years. This would have consequences for zonal attachment and related management aspects of the North Sea herring stock.

Acknowledgements

I would like to thank Martin Bailey and John Simmonds for letting me use their revised acoustic data, Harry Dooley for supplying me with data from the ICES hydrographic data base, and Benjamin Planque for providing me with the data series on *Calanus finmarchicus*. Valuable comments on the manuscript were provided by Wim Wolff, Winfried Gieskes, Reidar Toresen, en Gert van de Kamp. The study was part of the EU-sponsored SEFOS project.

References

Anon., 1965. Report of the Assessment Group on herring and herring fisheries in the north-eastern Atlantic. ICES, Doc. CM 1965, Herring Committee No. 1.

Anon., 1986. Report of the Herring Assessment Working Group for the area south of 62°N. ICES, Doc. CM 1986/Assess:19.

Anon., 1992. Report of the International Bottom Trawl Survey in the North Sea, Skagerrak and Kattegat in 1992: Quarter 1. ICES, Doc. CM 1992/H:20.

Anon., 1998. Report of the Herring Assessment Working Group for the area south of $62^{\circ}N$. ICES, Doc. CM 1998/ACFM:14.

Backhaus, J.O., Harms, I.H., Krause, M., Heath, M.R., 1994. An hypothesis concerning the space–time succession of *Calanus finmarchicus* in the northern North Sea. ICES J. Mar. Sci. 51, 169–180.

Bainbridge, V., Forsyth, D.C.T., Canning, D.W., 1978. The plankton in the northwestern North Sea, 1948 to 1974. Rapp. P.-v. Réun. Cons. Int. Explor. Mer. 172, 397–404.

Corten, A., van de Kamp, G., 1992. Natural changes in pelagic fish stocks of the North Sea in the 1980s. ICES Mar. Sci. Symp. 195, 402–417.

Cushing, D.H., Bridger, J.P., 1966. The stock of herring in the North Sea, and changes due to fishing. Fish. Invest. London, Ser. 2 25 (1), 1–123.

- Dalpadado, P., Melle, W., Ellertsen, B., Dommasnes, A., 1996. Food and feeding conditions of herring *Clupea harengus* in the Norwegian Sea. ICES, Doc. CM 1996/L:20.
- Dooley, H.D., 1992. Distribution of temperature and salinity, North Sea, IYFS (February) 1970–1991. ICES Copenhagen.
- Dragesund, O., 1960. Observationer over sildas gyting i Fangenskap. Fauna 4, 137–143.
- Fromentin, J.M., Planque, B., 1996. Calanus and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Mar. Ecol. Prog. Ser. 134, 111–118.
- Jacobsen, J.A., 1990. A survey of herring south of the Faroes in June 1990. ICES, Doc. CM 1990/H:34.
- Jakobsson, J., 1969. On herring migrations in relation to changes in sea temperature. Jökull, Vol. 19. Marine Research Institute, Reykjavik, pp. 134–145.
- Lam, T.J., 1983. Environmental influences on gonadal activity in fish. In: Hoar, W.S., Randall, D.J., Donaldson, E.M. (Eds.), Fish

- Physiology, Vol. 9, Part B. Academic Press, London, pp. 65–101. Maravelias, C.D., Reid, D.G., 1997. Identifying the effects of oceanographic features and zooplankton on prespawning herring abundance using generalized additive models. Mar. Ecol. Prog. Ser. 147, 1–9.
- Østvedt, O.J., 1965. The migration of Norwegian herring to Icelandic waters and the environmental conditions in May– June, 1961–1964. Fisk. Dir. Skr. Ser. Havunders. 13 (8), 29–47.
- Planque, B., Fromentin, J.M., 1996. Calanus and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. Mar. Ecol. Prog. Ser. 134, 101–109.
- Simmonds, E.J., Bailey, R.S., Aglen, A., Johannessen, A., Lahn-Johannessen, J., Smedstad, O., van de Kamp, G., 1985. Report on the 1984 herring acoustic survey in the northern North Sea. ICES, Doc. CM 1985/H:34.
- Warner, A.J., Hays, G.C., 1994. Sampling by the Continuous Plankton Recorder survey. Prog. Oceanogr. 34, 237–256.