A proposed mechanism for the Bohuslän herring periods

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During the last 500 years large numbers of herring have occasionally appeared in winter along the Swedish Skagerrak coast. These “Bohuslän” herring periods, sometimes lasting for several decades, were probably caused by a temporary shift of the over-wintering grounds of North Sea herring. In normal years North Sea herring over-winter in the adjacent waters of the northeastern North Sea. As yet there is no commonly accepted explanation for the occasional shifts of the over-wintering grounds towards the Skagerrak.

The environmental cause of the Bohuslän herring periods was investigated by looking at the most recent episode of herring invasions in the Skagerrak. In the winters of 1962–1965 large numbers of North Sea herring again entered the Skagerrak and these invasions showed many features of the old Bohuslän herring periods. The only anomalous environmental parameter at this time was a high frequency of easterly winds in the autumns of 1962 and 1963. It is assumed that these easterly winds forced surface water out of the Skagerrak and thereby strengthened the subsurface Norwegian Trench Current that flows into the Skagerrak. This current could easily transport herring from the normal over-wintering area near Egersund Bank towards the Skagerrak. It is shown that former Bohuslän or Skagerrak herring periods started in years when the North Atlantic Oscillation was in a negative phase and when easterly winds must have dominated in autumn too.

Bohuslän herring periods were more persistent than the periods of easterly winds. The persistence of the herring migrations is explained by “site-fidelity” of the older herring. Once a new migration has been adopted by the population it is repeated in subsequent years even when the original environmental cause has disappeared. An existing migration pattern can be changed only by a new, strong year class, that has not yet developed an attachment to the traditional over-wintering area. It is shown that the two most recent episodes of Skagerrak invasions were indeed initiated by strong recruiting year classes.

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Key words: herring, North Sea, Skagerrak, Bohuslän periods, North Atlantic Oscillation.

Received 16 February 1998; accepted 11 September 1998.

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Introduction

The episodic appearance of large numbers of herring along the Swedish Skagerrak coast is one of the best known and, at the same time, least understood examples of long-term natural variation in pelagic fish stocks in western Europe. These Bohuslän herring periods, called after the Swedish coastal region north of Göteborg (Fig. 1), gave rise to a great fishery and economic prosperity in the region. The herring arrived each year in autumn and stayed near the Swedish coast throughout the winter. However after a few decades the herring would no longer appear in autumn and the fishery would collapse. Historic records show that Bohuslän herring periods have occurred with a regularity of about once in a century, at least during the last 500 years. Many authors have described the Bohuslän periods (e.g. Pettersson, 1911, 1926; Svansson, 1965; Ackefors, 1970; Höglund, 1978; Cushing, 1982; Lindquist, 1983; Alheit and Hagen, 1996, 1997), but there is still no commonly accepted theory for the environmental or biological mechanism of the phenomenon.

The most recent Bohuslän period lasted from 1877 to 1906. In addition to the real Bohuslän periods there have been times when large quantities of adult herring occurred in the open Skagerrak during winter, but did
not approach the Swedish coast. Höglund (1978) called this the “Open Skagerrak periods”. Three such periods have been recorded in the 20th century: 1907–1920 (immediately following the last Bohuslän period), 1943–1954, and 1963–1965. Open Skagerrak periods presumably also occurred in earlier centuries, but they were not documented since the herring were only exploited when they came into the coastal area.

The concentrations of herring that appeared in winter in the Skagerrak obviously arrived from the North Sea (Pettersson, 1911). However for many years it was not clear whether the Bohuslän herring were North Sea autumn spawners, or whether they belonged to the more northern population of Norwegian spring spawners. Devold (1963) thought that Bohuslän herring were Norwegian spring spawners that shifted their spawning grounds back and forth between the Norwegian west coast and the Bohuslän coast. However Höglund (1972) demonstrated that the herring of the Bohuslän period in the eighteenth century belonged to a race of autumn-spawning herring which could only have been North Sea herring. The same conclusion was drawn by Jensen (1963) with respect to the herring of the last Bohuslän period.

The conclusion that Bohuslän herring must have been over-wintering North Sea herring can also be drawn from an inspection of the normal over-wintering grounds of North Sea herring in relation to the Skagerrak (Fig. 2). These over-wintering grounds are situated in the northeastern North Sea, along the western edge of the Norwegian Trench. This is precisely the position where a subsurface flow of Atlantic water into the North Sea exists, the Norwegian Trench Current (NTC). This current follows the outer edge of the Norwegian Trench all the way to the Skagerrak (Fig. 3). The over-wintering North Sea herring can be easily transported into the Skagerrak if they let themselves drift with the NTC. This is presumably what happened during Bohuslän and Open Skagerrak herring periods.

The question of what caused the North Sea herring to move into the Skagerrak received much attention during the last Bohuslän period and afterwards. A review of the scientific theories that prevailed in those days is presented by Svansson (1965), Höglund (1972), and Cushing (1982). The Swedish hydrographers Pettersson and Ekman (1891) thought that the invasions of herring were somehow related to the transport of water from the

![Figure 1. The Skagerrak and other localities mentioned in the text.](image)
Norwegian Trench into the Skagerrak. They assumed that the sub-surface inflow of saline, Atlantic water into the Skagerrak was a “reaction current” to the outflow of brackish Baltic water. Variations in the inflow of Atlantic water were thus assumed to be caused by variations in Baltic outflow. In later years Pettersson changed his mind and assumed that the variations in Atlantic inflow originated from the Atlantic Ocean. They would be the result of internal waves that propagated via the Norwegian Trench into the Skagerrak (Pettersson, 1926). These internal waves in the ocean would be generated by gravitational forces exerted by the moon and the sun. An extra-terrestrial cause of the Bohuslän periods had earlier been suggested by Ljungman (1880), who thought that the herring periods were caused by cyclic changes in the hydrography of the area related to the sunspot cycle. Neither the sunspot theory nor the internal wave hypothesis were generally accepted as adequate explanations of the Bohuslän herring periods (Jenkins, 1927).

Later generations of scientists also examined the phenomenon. Storrow (1947), for example, noticed that Bohuslän herring periods coincided with episodes of dry weather over Great Britain and increased duration of coastal ice cover at Iceland; an observation that was confirmed by Beverton and Lee (1965). Many scientists also drew attention to the apparent alteration of Bohuslän periods with the fishery for spring-spawning herring along the west coast of Norway (e.g. Pettersson, 1911; Storrow, 1947; Devold, 1963; Cushing, 1982). Recently, Alheit and Hagen (1996, 1997) showed that Bohuslän periods coincided with the expansion of other herring fisheries that exploited herring at the southern limit of its range and a decline of fisheries that exploited pilchard at the northern limit of its range. Both effects were presumably due to the low winter temperatures that prevailed during Bohuslän
periods. The authors also showed a relationship between Bohuslän periods and negative phases of the North Atlantic Oscillation.

The association of Bohuslän periods with climatic events or changes in other fisheries, however, does not explain the mechanism behind these periods. Since the time of Pettersson, in fact, few scientists have attempted to provide a causal explanation for the episodic herring invasions. Devold’s theory (1963) that Bohuslän periods were caused by a shift of spawning area of Norwegian spring spawners was disproved by Höglund (1972) who showed that Bohuslän herring had been autumn-spawning herring. The only new suggestion was presented by Jensen (1963), who showed that a sharp decline in Bohuslän catches in 1896 coincided with a drop in the north/south air pressure gradient – and thus to a decrease in easterly winds – over the entrance of the Skagerrak in summer and autumn. He assumed that the strong easterly winds in summer and autumn during earlier years had strengthened the outgoing Baltic Current, and thereby also the ingoing current from the North Sea, thus carrying more North Sea fish into the Skagerrak. This interesting theory, however, has received little attention to date.

The purpose of the present paper is to investigate the causal mechanism of Bohuslän periods using information collected during the most recent “Open Skagerrak” period. In the winters of 1962–1965 large numbers of spent North Sea herring migrated into the Skagerrak, giving rise to a spectacular but short-lived expansion of the catches in the area. A brief description of this fishery will show that it contained many characteristics of the earlier Bohuslän herring fisheries. It is assumed, therefore, that the event was triggered by a similar environmental stimulus to that which caused the earlier Bohuslän periods.

The next step is to look at the environmental variables during the 1962–1965 period to see which of them deviated from the normal pattern. Three alternative hypotheses for the cause of a Skagerrak herring period will be tested: (1) the invasions were an avoidance to cold water on the traditional over-wintering grounds in the North Sea; (2) the invasions were an avoidance to a new water type that contained more boreal plankton;
and (3) the invasions were caused by an acceleration of the Norwegian Trench Current, resulting from a change in wind conditions over the entrance of the Skagerrak.

The first and second hypotheses are based on the correlation between Bohuslän periods and episodes of cold winters and boreal influence over northwestern Europe. The third hypothesis is based on the observations by Jensen (1963) of a relationship between Bohuslän herring catches and easterly winds.

The 1962–1965 Skagerrak invasions as the initial stage of a Bohuslän herring period

The most recent invasions by North Sea herring of the Skagerrak occurred during the winters of 1963/1964 and 1964/1965 and to a lesser extent in the winter of 1962/1963. As the invasions coincided with the introduction of mechanized purse seining in the North Sea and Skagerrak many scientists attributed the increased catches in the Skagerrak to the changes in fishing method, rather than to changes in the herring stock itself (ICES, 1971; Burd, 1978). A few scientists, however, realized that the large catches in the Skagerrak might be also a result of a new migration of the herring and that the new herring bore resemblance to the earlier Bohuslän herring periods (Zijlstra, 1965; Höglund, 1978).

A close look at the development of the fishery in the Skagerrak shows clearly that the expansion of catches in this area was caused not only by the introduction of purse seining, but also by a change in behaviour of the herring. In the autumn of 1962, 1 year before the Norwegian purse seiners started operating in the northeastern North Sea, new herring concentrations appeared near Egersund Bank and in the entrance of the Skagerrak (Höglund, 1965). These herring belonged to the exceptionally strong 1960 year class. Some of the herring moved into the Skagerrak but most of them stayed in the Egersund area throughout the winter of 1962/1963 (Schubert, 1965).

In the following autumn (1963) large concentrations of the 1960 year class again appeared in the Egersund area. This time the Norwegian purse seiners had discovered the herring and they started an intensive fishery in the area. Towards the end of the year the herring concentrations moved into the Skagerrak followed by the Norwegian purse seine fleet (Haraldsvik, 1968). From November to February the main fishery took place along the western and southern slopes of the Norwegian Channel from Egersund to Hantsholm (Höglund, 1966).

The migration into the Skagerrak was repeated one more time in the autumn and winter of 1964/1965. Again the herring schools consisted mainly of spent herring of the 1960 year class but there were also herring of other age groups present (Höglund, 1966, 1967; Haraldsvik, 1968). The news about herring concentrations in the Skagerrak had spread far, and during this winter the entire herring fleet from the North Sea concentrated on them. As in the previous year the fishery lasted until the end of February when the adult herring left the Skagerrak.

In the autumn of 1965 adult North Sea herring still concentrated near the entrance of the Skagerrak but they did not move further east as they had done the previous years (Haraldsvik, 1967; Höglund, 1967). After 1965, adult North Sea herring disappeared altogether from the entrance of the Skagerrak (Haraldsvik, 1968; Van de Kamp, pers. comm.).

The above reports on the fishery in 1962–1965 show good agreement with the accounts of the fishery during Bohuslän periods (Höglund, 1972, 1978). In both cases the herring appeared in the Skagerrak in November and stayed until February/March. Also the distribution of the herring was similar; in the winter of 1964/1965 the herring approached the Bohuslän coast (Schubert, 1966; Haraldsvik, 1968), although they did not actually move into the inshore waters (Fig. 4). The main differences between the 1962–1965 Skagerrak invasions and the former Bohuslän periods seem to have been a matter of intensity and duration of the event. It is concluded, therefore, that the 1963–1965 Skagerrak invasions were most likely triggered by the same environmental stimulus that caused the earlier Bohuslän periods.

It is interesting to note that not all of the herring in the eastern North Sea moved into the Skagerrak during the winters of 1963/1964 and 1964/1965. Catch distributions for the Dutch trawl fishery in the northeastern North Sea (Fig. 5) show that some of the herring must have retained their normal over-wintering position along the western edge of the Norwegian Trench.

Materials and methods

Environmental data for the northeastern North Sea for the years 1962–1964 have been compared to the long-term mean in order to see whether anomalous conditions existed at the time of the Skagerrak invasions. The parameters considered are water temperature, boreal plankton content, and wind, respectively. If the herring invasions were induced by an environmental parameter, it must have worked in the area from where the herring started their migration and at the time when the migrations started. The search for an anomalous environmental condition can thus be narrowed to the north-eastern North Sea, and to the period October/November.

Temperature data for the northeastern North Sea between 57°–61°N and 2°–4°E were provided by the ICES Hydrographic Service. Mean values for bottom and
surface temperature within this area were calculated for October and November for all years between 1955 and 1996.

The possible occurrence of a different type of water, characterized by boreal plankton species, was investigated by looking at data from the Continuous Plankton Recorder (CPR) survey. The boreal plankton species selected were *Calanus hyperboreus*, *Euchaeta norvegica*, and *Metridia longa*. These copepods are common in the Norwegian Sea and East Iceland Current but occasionally occur in the North Sea where they indicate a boreal influence (Edinburgh Oceanographic Laboratory, 1973).

Monthly data on the occurrence of these species in the years 1948–1996 were kindly provided by the Sir Alister Hardy Foundation for Ocean Science. As the CPR sampling intensity in the northeastern North Sea was low after 1985, samples had to be combined for a wide area (56–60°N and 2–8°E) in order to obtain sufficient values for the calculation of monthly averages.

The third environmental variable considered was the wind in the entrance of the Skagerrak. This variable was used as a substitute for information on water currents. There are no long-term current measurements in the entrance of the Skagerrak, mainly because the intensive trawling along the slopes of the Norwegian Trench prohibits the prolonged use of moored current meters. In the absence of direct measurements, changes in water flow can only be estimated indirectly on the basis of wind speed and direction. The main problem in this approach, however, is that the water currents near the entrance of the Skagerrak are complex, and that even sophisticated hydrodynamic models do not accurately simulate the fluxes through the upper 100 m at the entrance of the Skagerrak (Svendsen et al., 1996).

The main hydrodynamic model for this area, the NORWECOM model, predicts that the inflow of water from the Norwegian Trench into the Skagerrak reaches maximum values for wind directions from the southeast (Svendsen, pers. comm.). Even without using a hydrodynamic model it seems reasonable to assume that easterly winds will force surface water out of the Skagerrak, and thereby strengthen the subsurface counter current that flows into the Skagerrak from the Norwegian Trench (Jensen, 1963).

The Norwegian Meteorological Institute kindly provided wind data for the Oksoy Fyr lighthouse (position: 58°04’N, 8°03’E) near Kristiansand. This position is representative for the wind conditions over the entrance of the Skagerrak. The data consisted of monthly frequency distributions of mean wind speed, measured over
6-h intervals, and grouped by 30° sectors. For each autumn (September to November) in the period 1960–1965, the wind stress from various directions was estimated by summing the squared wind speeds per 6 h interval in each of the 30° sectors, and then dividing the sums by the total number of intervals. In the same way, the long-term average for September to November was calculated for the years 1957–1975.

It would also have been interesting to compare wind and Skagerrak herring invasions for the earlier Open Skagerrak periods and Bohuslän periods. Unfortunately no detailed wind measurements over the entrance of the Skagerrak were available for the years prior to 1951. As a substitute for local wind data in earlier years, the North Atlantic Oscillation (NAO) index has been used. The NAO index is the difference between the normalized surface-pressure anomaly for the Azores and that for Iceland (Lamb and Peppler, 1987). This index is available by month and by season for all years since 1884 (Hurrell, 1997). A positive NAO-index corresponds to an atmospheric low over Iceland resulting in a strong westerly circulation over the North Atlantic. A negative index corresponds to the opposite situation, with increased easterlies over northwestern Europe (Alheit and Hagen, 1997; Fromentin and Planque, 1996). One may assume, therefore, that in general easterly winds will have prevailed over the Skagerrak during months with a negative NAO-index.

Results

Water temperatures for October and November in the area where the herring assemble in autumn are presented in Figure 6. Surface temperatures were relatively low in October and November 1962, and also in October 1963.
However in the entire series from 1955 to 1996, the years of the Skagerrak invasions (1963 and 1964), nor the year leading up to them (1962), stand out as exceptional. Bottom temperatures show more of a depression in the mid-1960s but also in this case the values for 1963–1964 do not stand out as exceptional. Besides the low bottom temperatures do not coincide exactly with the herring invasions. The first aggregations of herring near the entrance of the Skagerrak appeared in 1962 when bottom temperatures were about normal. On the other hand the herring invasions had stopped earlier than 1966 when the November bottom temperatures reached a minimum.

The annual occurrence of three boreal copepods in the northeastern North Sea during the period 1950–1996 is presented in Figure 7. During the years of the Skagerrak herring invasions (1962–1964), only one boreal copepod, *Euchaeta norvegica*, was present in some numbers in the northeastern North Sea. The abundance of this species in 1962–1964, however, was no means abnormally high. The two other boreal copepods considered, *Calanus hyperboreus* and *Metridia longa*, were completely absent from the northeastern North Sea during these years. We may conclude, therefore, that the plankton composition in the northeastern North Sea does not show evidence of an increased presence of boreal water during the years of the most recent Skagerrak herring invasions.

Information on wind strength and direction over the entrance of the Skagerrak is presented in Figure 8. For each autumn in the period 1960–1964, the wind stress is shown from each direction, and a comparison is made with the long-term mean. It is seen that the year 1960 was very exceptional, with a strong predominance of (north) easterly winds. Also the three subsequent years (1961–1963) showed an abnormally high incidence of easterly winds during autumn. During the last year in the series, 1964, the opposite situation existed with less than average easterly winds. Hence the Skagerrak herring invasions started in years when easterly winds in autumn were above average (1962 and 1963). However during the last year of the herring invasions (1964) the easterly winds in autumn were below average.

The North Atlantic Oscillation index, shown in Figure 9, provides indirect information on wind conditions during earlier years. Two series of the NAO-index are presented, one referring to the winter period from December to March, and one referring to the autumn months. Also shown are the periods of Bohuslän and Open Skagerrak herring fisheries. It is seen that some correspondence exists between the NAO-index and the time of the Skagerrak herring fisheries. This correspondence is better for the autumn NAO-index than for the winter index. It is particularly the start of the Bohuslän or Skagerrak periods that coincides with a minimum of the autumn NAO-index. Once a herring fishery in the Skagerrak had started it continued for several years regardless of the development of the NAO-index. The data suggest some proportionality between the size of the negative NAO-anomaly in autumn and the duration of the subsequent herring period in the Skagerrak.

![Figure 6. (a) Mean surface and (b) mean bottom temperature in October (broken line) and November (solid line) for the area 57°00N–61°00N, and 02°00E–04°00E.](image-url)
Assuming that a negative NAO-index corresponds to easterly winds in the Skagerrak region the results suggest that all Skagerrak herring periods started in years with strong easterly winds in autumn. The continuation of the fishery in subsequent years, however, did not depend on a continuation of the easterly winds.

Discussion

The environmental data collected during the last episode of Skagerrak herring invasions (1962–1965) do not show a substantial change in water temperature or plankton composition in the northeastern North Sea. There is no reason to assume, therefore, that the Skagerrak invasions were a response to deteriorating hydrographic conditions in the traditional over-wintering area of the herring. The only anomalous environmental condition at the start of the invasions was the wind. In the first 2 years of the invasions (1962 and 1963), abnormally strong easterly winds blew over the entrance of Skagerrak during autumn. Data on the North Atlantic Oscillation suggest that the start of previous Skagerrak herring periods also coincided with strong easterly winds over the northeastern North Sea and Skagerrak during autumn.

It is likely that the easterly winds will have forced surface water out of the Skagerrak and thereby induced a subsurface, compensation current into the Skagerrak. Most likely, this compensation current occurred in the form of an enhanced Norwegian Trench Current (NTC) in the entrance of the Skagerrak. Under normal conditions, there already exists a subsurface inflow by the NTC into the Skagerrak (Svendsen et al., 1996), and it is likely that this current will increase at the time when surface water is forced out of the Skagerrak. Unfortunately it is not possible to verify this assumption with existing current measurements. So far no current measurements have been conducted in the entrance of the Skagerrak under the anomalous conditions of persistent easterly winds in autumn. It is known, however, that strong winds in general can displace the surface waters of the Skagerrak, and thereby induce counter currents in deeper layers. Observations during the SKAGEX program in 1989–1990 showed upwelling along the Norwegian coast in response to the removal of surface water by strong northwesterly winds (Danielssen et al., 1991).

An enhanced NTC would be the perfect vehicle to transport herring along the western slope of the Norwegian Trench from the Egersund Bank area into the Skagerrak. Under normal conditions the velocity of

Figure 7. Annual abundance of three boreal copepods in the area 56–60°N and 2–8°E, 1948–1996.
the NTC in the region of Egersund Bank is about 10 cm s$^{-1}$. Due to the steepening of the topography northwest of Hantsholm, the velocity here increases to 20–40 cm s$^{-1}$, and it stays relatively high all the way to Skagen (Svendsen, pers. comm.). Even these normal currents are more than sufficient to carry herring from the Egersund Bank into the inner Skagerrak within one month. The herring concentrations in the Egersund Bank area, therefore, have to swim constantly against the residual current in order to retain their position. It is easy to envisage how an increased NTC could displace the herring along the western slope of the Trench in the direction of the Skagerrak. Once the herring reach the area off Hantsholm where the current accelerates they may pass a point of no return and be swept far into the Skagerrak.

The assumption that Bohuslän herring entered the Skagerrak by a subsurface compensation current is not a new idea. Pettersson and Ekman (1891) assumed that the Atlantic water flowing into the Skagerrak was a compensation current for the outflowing Baltic water and they already thought that the Bohuslän herring entered the Skagerrak with this compensation current. The problem with their theory was that the Baltic outflow was not correlated with the Bohuslän herring periods, so the invasion of herring into the Skagerrak could not be explained by variations in the compensation current. This was probably the reason why Pettersson later abandoned the idea that the Atlantic inflow into the Skagerrak was a compensation current of the Baltic outflow (Pettersson 1926).

Jensen (1963) suggested that Bohuslän herring invasions were due to a local compensation current in the entrance of the Skagerrak resulting from easterly winds in the region. His idea, however, did not gain popularity presumably because local wind conditions were not as persistent as the Bohuslän herring fishery. Most scientists felt that the cause of the Bohuslän periods should be something that showed the same persistence over time as the herring invasions. Therefore, attention was focused on climatic variations as a possible cause of the Bohuslän periods (Cushing, 1982; Alheit and Hagen, 1996, 1997). The results presented in this paper, however, largely support the theory presented by Jensen (1963). The herring invasions in the Skagerrak that occurred just after the publication of this paper, again coincided with strong easterly winds in autumn. This is strong evidence that the easterly wind indeed triggered the Skagerrak herring invasions presumably by accelerating the subsurface compensation current into the Skagerrak.

Still the problem remains that the herring invasions in the Skagerrak showed a greater persistence over time than the easterly winds. The easterly winds dropped below average in the autumn of 1964, for example, and yet the herring returned again to the Skagerrak. A decline of easterly winds must also have happened some years after the start of the last Bohuslän period when the NAO-index returned to normal values around 1885. The decline in easterly winds at that time apparently did not affect the migration of herring into the Skagerrak either.

Figure 8. Average squared wind speed (m$^2$ s$^{-1}$) per 6 h interval from different wind directions for the period September to November at Oksoy Fyr lighthouse, pos. 58°04’N, 08°03’E. Annual values for 1960–1964 compared to long-term mean for 1957–1975 (broken line).
To explain the persistence of the herring migrations into the Skagerrak we have to assume a certain conservatism in the behaviour of the herring. This is not an unrealistic assumption; herring are known to develop an attachment to specific areas. This attachment may concern the spawning area (Corten, 1993; McQuinn, 1997), but also the feeding area (Devold, 1968; Jakobsson, 1969) or over-wintering area (Dommasnes et al., 1994). The attachment is normally developed during the first year of the adult life when the recruiting herring either follow the older herring or, alternatively, chose a spawning, feeding, or over-wintering area by themselves.

In the context of the present paper it is interesting to note the extreme conservatism in the choice of over-wintering area by Norwegian spring-spawning herring. Dommasnes et al. (1994) described how the entire stock of these herring started to over-winter in 1987 in the Ofotfjord and Tyskfjord in northern Norway. Once the population had stayed in this area for one winter it returned there each subsequent year, despite a gradual decrease in oxygen content of the water. This behaviour of the herring can be explained by an intrinsic behaviour pattern that leads a population to stick to an established migration pattern irrespective of the environmental conditions. Presumably the episodic over-wintering of North Sea herring in the Skagerrak is comparable to the over-wintering of Norwegian spring spawners in the Ofotfjord and Tyskfjord. Once the North Sea herring had spent a winter in the Skagerrak they returned there in the following winters simply because of "conservatism".

In a situation where the behaviour of older herring is governed by existing traditions, a change of migration pattern can only be initiated by a new year class that has not yet developed a specific site attachment. If because of a temporarily changed environment the recruiting year class over-winters in a new area, it develops an attachment to this new area and returns there in subsequent years. If the strength of the year class is such that it dominates the rest of the population, it may lead subsequent year classes to the newly established over-wintering area and a new tradition is born.

According to this theory Skagerrak herring periods must have been started by new, strong year classes of North Sea herring. For the 1962–1965 invasions this certainly was the case. In all the years of the herring invasions the catches in the Skagerrak consisted mainly of the strong 1960 year class. These fish accumulated near the entrance of the Skagerrak as 2-year-olds in 1962 and migrated into the Skagerrak in 1963 during the first winter of their adult life. At that time, the year class constituted 71% in numbers of the adult population of North Sea herring (ICES, 1977).
Also, the 1943–1954 Open Skagerrak period started at the time when a strong year class recruited to the North Sea population. Andersson (1947, 1948) reported that the invasions were started by herring of the 1939 year class. This must have been a strong year class in the North Sea as it dominated catches on the Fladen Grounds in 1945 and 1946. North Sea herring did not mature until their fourth year of life in the years prior to 1952 (Burd and Cushing, 1962), so the year in which the 1939 year class entered the Skagerrak (1943) was the first winter of their adult life.

The proposed mechanism for the start of a Skagerrak herring period explains why not all the herring immediately participate in the new migration. The observations on the Dutch trawl fishery in the northeastern North Sea in 1962–1965 showed that part of the population did not engage in the new migration but stayed with the traditional over-wintering sites along the western Trench slope. Presumably this was the older fraction of the population that had already developed an attachment to the Trench slope, and that returned to this site even when the current towards the Skagerrak increased.

The distribution of the recruiting year class is also a factor that increases the chance of passive drift into the Skagerrak. Young herring in the North Sea are distributed generally to the south of the older herring, so the recruiting year class will be found relatively close to the entrance of the Skagerrak. Even if there is no difference in behaviour between young and old herring, the recruiting year class still has a greater chance of being transported into the Skagerrak during a period of increased NTC.

So far, only the start of a Skagerrak herring period has been considered, and not the end of it. Unfortunately the 1960s did not provide an opportunity to study the termination of a Skagerrak herring period under natural conditions. The concentrated fishing effort by the international fleet in the winters of 1963/1964 and 1964/1965 must have exterminated most of the over-wintering population in Skagerrak. Höglund (1978) thought that this was the main reason for the disappearance of the herring from the Skagerrak and he assumed that under normal conditions the herring would have returned for many more years.

Under normal conditions the end of a Skagerrak period, like its beginning, is presumably the result of a change in tradition brought about by a strong recruiting year class. If the hydrographic conditions during the first winter of this new year class are such that no passive drift into the Skagerrak occurs the fish will stay in the Trench area throughout the winter and thereby re-establish the old tradition of over-wintering in this area. This was probably also what happened at the end of the 1960s Skagerrak period. In the autumn of 1965, the size of the 1960 year class had been reduced to only 16% of the total adult stock (ICES, 1977). The recruiting year class 1963 was more than three times as numerous as the surviving fraction of year class 1960 and was thereby in a position to make its own choice regarding its over-wintering area.

From the above considerations it appears that the start of a Skagerrak herring period may require the simultaneous occurrence of strong easterly winds and a strong recruiting year class of North Sea herring. This coincidence is a matter of chance but it is most likely to occur during periods when the NAO is in a negative phase. Such negative phases of the NAO are also characterized by cold winters over western Europe and widespread ecological changes in Europe and North America. There is no causal relationship, however, between the cold winters and the Bohuslän periods; the correlation is merely caused by the common dependence on easterly winds during autumn and winter.

A similar explanation can be given for the negative correlation between Bohuslän herring periods and the fishery for spring-spawning herring along the west coast of Norway. Krovnin and Rodionov (1992) showed that good year classes of Norwegian spring-spawners as a rule appeared in years when a deep Icelandic low, coupled with a strong Azores high, increased the advection of Atlantic waters by the Norwegian Current. This increased current was favourable for the transport the larvae from the hatching grounds along the Norwegian west coast to the nursery areas in the northern Norwegian Sea and Barents Sea. The positive effect of southwesterly winds on the transport of the larvae was also demonstrated by Svendsen et al. (1995a). The atmospheric conditions described by Krovnin and Rodionov correspond to a positive phase of the NAO. Hence, a positive phase of the NAO leads to an increase in recruitment and stock size of Norwegian spring spawners and a negative phase will have the opposite effect. At the same time, a negative phase of the NAO is one of the conditions for the start of a Bohuslän herring period. The alternation of Norwegian and Bohuslän fisheries is thus caused by different responses of two herring stocks to the NAO. The Norwegian spring spawners respond to the NAO by changes in population size whereas the North Sea herring merely shift their over-wintering area.

Conclusions

The start of Bohuslän herring periods is probably induced by an environmental factor. This factor is not a large-scale climatic change but a variation in currents in the entrance of the Skagerrak as a result of easterly winds. A subsurface, “compensation” current, induced by the easterly winds, could easily carry herring from their normal over-wintering areas in the North Sea towards the Skagerrak.
The persistence of the herring invasions in the Skagerrak, however, cannot be explained by this environmental factor. The invasions into the Skagerrak continued after the period of easterly winds had ended. In this case the biology of the fish plays a role; in particular the tendency of adult fish to stick to the established over-wintering grounds. This "site-fidelity" of the adult fish makes the population resistant against rapid changes in migration pattern.

A change in the established migration pattern can only be initiated by a new, strong year class that has not yet developed an attachment to the existing over-wintering area. If this new year class outnumbers the older fish in the population it may "choose" a different over-wintering area for some environmental reason, and thereby start a new tradition.

The start of a new Skagerrak period does not happen easily. It requires the rare combination of a strong recruiting year class and a period of strong easterly winds in autumn. Such a combination is likely to occur only during periods when the NAO is in a negative phase.

Acknowledgements

My interest in Bohuslän herring was revived by Artur Svansson who drew my attention to the papers by Otto Pettersson and who also provided translations for me. Harry Dooley supplied the temperature data from the ICES files, and Chris Reid allowed me to use material from the CPR data base at SAHFOS. Many colleagues provided valuable comments on the manuscript, in particular Einar Svendsen, Bill Turrell, Harry Dooley, Wim Wolff, and Winfried Gieskes.

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