Herring and Climate

Changes in the distribution of North Sea herring due to climate fluctuations

Cover: Herring trawlers on Aberdeen Bank
photograph Ad Corten

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Herring and Climate

Changes in the distribution of North Sea herring due to climate fluctuations

Proefschrift

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aan Jolan

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Voorwoord

Het schrijven van een proefschrift is bedoeld als sluitstuk van een universitaire opleiding. Door zich diepgaand in een bepaald wetenschappelijk vraagstuk te verdiepen, verkrijgt de promovendus vaardigheid in wetenschappelijk onderzoek en demonstreert deze vaardigheid in een proeve van bekwaamheid: het proefschrift. In mijn geval heeft deze afronding van de universitaire opleiding wat meer tijd gekost dan normaal. Sinds het begin van mijn studie (1961) en de afronding van mijn proefschrift (2001) zijn precies 40 jaar verlopen. Vóórdat de lezer nu tot de conclusie komt dat ik een typisch geval ben van de "eeuwige student", haast ik mij te vertellen dat ik al in 1967 mijn doctoraalexamen heb afgelegd. Mijn drang om te promoveren was op dat moment echter niet groot. Na vele jaren in de schoolbanken wilde ik eindelijk wel eens de echte maatschappij in. Zo zocht ik – net als vele andere studenten van mijn generatie – meteen na mijn doctoraalexamen een baan buiten de universiteit en van promoveren was waarschijnlijk nooit meer iets gekomen wanneer mijn loopbaan vele jaren later niet een onverwachte wending had genomen.

Ik koos bewust voor een baan als visserijbioloog. Dat had twee redenen: ik was al heel jong gefascineerd geraakt door vissen en hun leefmilieu en tegelijk had ik een sterke drang om werk te doen dat praktisch nut opleverde. De keuze van visserijonderzoek lag daarom voor de hand: in dit werk kon ik mijn passie voor vissen uitleven en tegelijk ook nog iets nuttigs doen voor de visserij. Na eerst enkele jaren als visserijbioloog in Afrika gewerkt te hebben, kwam ik in 1971 terecht bij het Rijksinstituut voor Visserij Onderzoek (RIVO) in IJmuiden, waar ik de leiding kreeg van het onderzoek aan haring.

Juist in die periode bevond de haringstand op de Noordzee zich in een crisissituatie. Door ernstige overbevissing was het bestand dermate gereduceerd dat sommige onderzoekers vreesden voor het voortbestaan ervan. Het was mijn taak om, samen met buitenlandse collega's, harde gegevens te verzamelen waarmee we visserijbeheerders konden overtuigen van ernst van de situatie en adviezen konden geven over de te nemen maatregelen. Ik vond het heerlijk werk; dit was mijn ideaal van visserijonderzoek. Het besef dat het lot van de Noordzeeharing mede in onze handen lag, schiep een sfeer van enthousiasme en kameraadschap onder de haringbiologen van alle landen rond de Noordzee. Op grond van onze onderzoeksresultaten konden wij beleidsmakers uiteindelijk ertoe bewegen de haringvisserij op de Noordzee gedurende 6 jaar te sluiten en op die manier de haringstand op het nippertje te redden.

Het beleidsadviserend werk eiste in die jaren mijn volledige aandacht en mijn interesse in fundamenteel wetenschappelijk onderzoek was gering. Net als de meeste van mijn collega's ging ik ervan uit dat we eigenlijk al over voldoende kennis van de biologie en ecologie van de haring beschikten en dat onze taak vooral bestond uit het toepassen van bestaande kennis om de haringvisserij te reguleren.

Mijn drang om bij te dragen aan een optimaal beheer van de haringstand bracht mij soms in conflict met beleidsmakers. Door mijn nauwe betrokkenheid bij het herstel van de haringstand in de 70- en 80-er jaren voelde ik een persoonlijke verantwoordelijkheid voor het beheer van deze visstand. Ik kon mij ergeren aan het feit dat biologische adviezen niet werden overgenomen door beleidsmakers, of erger nog, dat biologen vanaf 1992 helemaal geen concrete adviezen meer mochten geven. In 1993 presenteerde de Nederlandse overheid een nieuw visserijbeleid, waarin aangekondigd werd dat ons land niet langer zou streven naar stabilisatie van vangsten en het instandhouden van een buffervoorraad vis in zee. Het feit dat ik als ambtenaar openlijk mijn bezorgdheid over de consequenties van dit nieuwe beleid uitsprak, werd mij niet in dank afgenomen; noch door het Ministerie van LNV, noch door de leiding van het RIVO. Vanaf dat moment nam mijn carrière een duikvlucht en binnen 3 jaar was ik volledig uitgerangeerd op het RIVO. Ik werd geschorst wegens "verstoorde werkrelaties" en er restte mij niets anders dan thuis te wachten op mijn ontslag.

Het was in deze periode dat mijn vrouw mij aanspoorde om mijn tijd en energie voor iets constructievers te gebruiken dan de strijd tegen ambtelijke molens. Op haar aanraden besloot ik van de nood een deugd te maken en de onverwachts beschikbaar gekomen tijd te gebruiken voor het schrijven van een proefschrift. Het onderwerp daarvoor had ik al lange tijd in mijn hoofd: natuurlijke veranderingen in Noordzeeharing. Tijdens mijn werk als haringbioloog was het mij opgevallen dat de haring zich niet altijd gedroeg op de manier die ik verwachtte. Soms leek het alsof de visstand niet alleen beïnvloed werd door de visserij maar ook door natuurlijke veranderingen in zee. Ik had deze theorie al enkele malen geponeerd in wetenschappelijke artikelen, zonder dat ik echter in staat was geweest bewijsmateriaal ervoor aan te dragen. Mijn gedwongen werkloosheid vormde nu een mooie gelegenheid om dit onderwerp verder uit te diepen. Door het werk in de vorm van een promotie-onderzoek te gieten, verwierf ik enerzijds de steun van professionele begeleiders van de Rijksuniversiteit Groningen, en anderzijds legde ik mijzelf de verplichting op om het onderzoek ook daadwerkelijk af te maken.

Het besluit om een proefschrift te gaan bewerken, bleek een gelukkige keuze te zijn. Niet alleen vormde het onderzoek een welkome afleiding in de periode dat mijn betrekking bij het RIVO aan een zijden draadje hing, maar gaandeweg werd ik ook steeds enthousiaster voor het onderwerp dat ik gekozen had. Eindelijk had ik de tijd om bestaande gegevens uit te pluizen en oude literatuur over natuurlijke veranderingen in zee grondig te bestuderen. In het verre verleden hadden vele onderzoekers zich al intensief met dit onderwerp bezig gehouden en het gaf mij een sterk gevoel van verbondenheid met deze voorbije generatie om de draad van hun werk weer op te pakken. Daarnaast, en dat geldt natuurlijk voor ieder soort van onderzoek, is het bedrijven van wetenschap een soort puzzelen op hoog niveau en het vinden van kleine stukjes van deze puzzel levert een enorme voldoening.

Door een onverwacht positieve uitkomst van de juridische procedures tegen mijn schorsing mocht ik na een jaar weer terugkeren op het RIVO, zij het in een nieuwe functie waarbij ik belast werd met beleidsongevoelig onderzoek aan zoetwatervis. Vanaf dat moment moest ik het werk aan mijn proefschrift voortzetten in mijn vrije tijd, waardoor het tempo natuurlijk sterk werd vertraagd. In 1998 nodigde de Nederlandse Redersvereniging mij uit om namens het RIVO onderzoek te gaan verrichten in Mauritanië (West Afrika) waar zich een belangrijke nieuwe Nederlandse visserij ontwikkelde. Deze taak vormde een mooie uitdaging, maar tegelijkertijd dreigde de afronding van mijn proefschrift erdoor in de knel te komen. Op iedere reis naar Afrika ging daarom mijn laptop met proefschrift mee en sommige hoofdstukken zijn voor een deel geschreven in mijn vrije uren in Mauritanië, hetzij aan boord van trawlers, hetzij in het Oasian hotel in Nouadhibou. Het was een merkwaardige sensatie om artikelen over Noordzeeharing te schrijven aan de rand van de Sahara, maar het was opvallend hoe goed ik me daar kon concentreren. Vanuit Afrika zie je veel zaken in Europa in een beter perspectief en dat geldt ook voor onderwerpen op wetenschappelijk terrein.

Een voorwoord is de plaats om iedereen te bedanken die een bijdrage heeft geleverd aan de totstandkoming van dit proefschrift. Door de ongewone omstandigheden waaronder ik aan dit werk begon, heb ik vaak een extra beroep moeten doen op anderen. Ik ben daarbij zelden teleurgesteld; in tijden van tegenspoed leert men inderdaad zijn vrienden kennen. De steun die ik van veel RIVO-collega's gekregen heb, met name op het moment dat mijn positie op het instituut als uitzichtloos beschouwd werd, heb ik als zeer hartverwarmend ervaren. Ik denk daarbij aan Gert van de Kamp, mijn rechterhand gedurende 25 jaar, en degene aan wie ik veel van mijn ideeën over natuurlijke veranderingen bij haring te danken heb. Aan Suze en Cecile, die mij enorm geholpen hebben met het opsporen van literatuur. Aan Bas de Groot, die mij altijd opvrolijkte met zijn grollen en zijn relativerende kijk op het ambtelijk gezag. Aan Eric Visser, bij wie ik terechtkon met computerproblemen, en aan Erwin Winter die mijn interesse deelde in het gedrag van vissen. Verder waren er de assistenten van mijn oude pelagische afdeling, Simon Rijs, Martien Warmerdam en

Jan Beintema, die mij ook tijdens mijn schorsing het gevoel gaven dat ik nog altijd thuishoorde op het RIVO. Al deze collega's en nog vele andere zorgden ervoor dat ik ook tijdens mijn schorsing geen drempel voelde om naar het RIVO te gaan om daar de benodigde gegevens en literatuur op te sporen. De man van wie het vak van "haringbioloog" geleerd heb, Klaas Postuma, was al geruime tijd gepensioneerd maar hij volgde nog altijd belangstellend mijn belevenissen in het onderzoek. Dat zelfde gold voor mijn oud-collega Kees Kuiter, die afzwaaide vlak voordat ik aan mijn proefschrift begon, maar die de 24 jaren daarvoor mijn vaste vraagbaak had gevormd op haringgebied.

Ook buiten het RIVO hebben veel mensen een bijdrage geleverd aan mijn proefschrift. Ik moet daarbij natuurlijk in de eerste plaats de mensen noemen van de RUG: mijn co-promotor Winfried Gieskes, die mij regelmatig tot wanhoop dreef met zijn drang naar perfectie, en mijn promotor Wim Wolff die mij daarna geruststelde met de opmerking dat mijn teksten helemaal niet zo slecht waren voor een beginner. Beiden hebben een eindeloos geduld getoond in het lezen en corrigeren van mijn stukken. Een belangrijk deel van mijn gegevens heb ik verzameld op het laboratorium van de Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in Plymouth. Ik denk met plezier terug aan de Christmas parties op dat instituut en natuurlijk ook aan de steun die ik kreeg van Chris Reid en zijn collega's. Mijn verblijf in Plymouth werd mogelijk gemaakt door een subsidie van de Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO).

Veel buitenlandse collega's leverden nuttig commentaar op mijn teksten. Op hydrografisch gebied gebeurde dit door Bill Turrell, Einar Svendsen, Morten Skogen, Arthur Svansson, Diane Portis en Harry Dooley, en op biologisch gebied door mijn oud-collega's van de ICES haringwerkgroep Martin Walsh, Reidar Toresen en Rob Stephenson. Omdat mijn proefschrift veel raakvlakken had met hydrografie en oceanografie moest ik regelmatig te rade bij deskundigen op dit vakgebied. Ik wil hier Sybren Drijfhout, Meinte Blaas, Ernst van der Avoird, Hendrik van Aken en Arie Kattenberg bedanken voor hun raadgevingen op hydrografisch en meteorologisch gebied.

Diverse haringschippers hebben mij in de loop der jaren ideeën aangedragen over het gedrag van de haring. Van deze mensen, met wie ik vaak weken op zee heb doorgebracht, wil ik hier Klaas van de Plas, Piet Haasnoot en Aad Jonker noemen. Behalve met de vissers op zee heb ik ook een plezierig contact gehad met de pelagische sector aan de wal. Van 1998 tot 2000 was het mij niet toegestaan mijn werkzaamheden voor het Mauritanië-project te verrichten op het RIVO, maar gelukkig bood de Redersvereniging mij als "wetenschappelijk asielzoeker" onderdak op het kantoor van The Group. In dit ballingsoord hebben Ellen, Rosita en Hans meegeleefd met mijn werk, en mij een aangename werkplek bezorgd. Ik ben André Köbben erkentelijk voor de belangstelling die hij getoond heeft, zowel uit wetenschappelijk als uit menselijk oogpunt, voor mijn conflict op het RIVO. Hij liet mij zien dat "klokkenluiders" steevast tegen dergelijke problemen aanlopen en dat gaf mij de geruststelling dat mijn problemen niet in eerste instantie veroorzaakt werden door een karakterafwijking bij mijzelf.

In de laatste, maar zeker niet de minste plaats wil ik mijn vrouw en kinderen bedanken: Jolan, Ben en Etelka. Hun wetenschappelijke bijdrage was misschien niet zo groot, maar hun morele steun was des te belangrijker. Dit geldt in het bijzonder voor Jolan, die ondanks haar scepsis ten aanzien van academische geleerdheid mij stimuleerde om met het proefschrift te beginnen en die nooit klaagde toen het steeds meer tijd bleek te gaan kosten. Het heeft haar vele eenzame avonden en weekenden gekost, en het is om deze reden dat dit proefschrift aan haar is opgedragen.

Chapter 1

Introduction

1.1. Natural variability in North Sea herring: a forgotten subject

The stock of North Sea herring (*Clupea harengus* L.), like all other exploited fish populations, is subject to both fishery-induced changes and to changes caused by variations in the environment. During periods when fishing pressure is low, natural variations tend to dominate the developments in the stock. This used to be the normal situation during the early history of the North Sea herring fishery. More than most other fish species, herring had a reputation of unpredictable change. Parrish (1963) described this unpredictability and its consequences for the fishing industry in his chairman's summary of the 1960 ICES Herring Symposium as follows:

"A feature of these (herring) fisheries, and indeed of the herring fisheries in other parts of the world, has been the large and often sudden short- and long-term fluctuations and trends in their productivity, bringing periods of great prosperity, and ones of equally striking hardship to the fishing communities and industries engaged in them. In some cases, these fluctuations have been short-lived and sporadic, as in almost all marine fisheries, but in others they have been sufficiently large and sustained as to lead to the complete collapse of traditional fisheries."

Before World War II, natural variability was the main subject of scientists working on North Sea herring. This situation, however, changed drastically in the first decades after World War II. With the advent of modern fishing methods, the effects of fishing started to outweigh the natural changes in the stock. In the period 1950 – 1977, the unrestricted fishery reduced the stock to only 70,000 tonnes, which was less than 2% of its level just after World War II (Anon. 1995). Under these circumstances, it was understandable that scientists turned their attention away from natural variation and instead focused on the effects of fishing. All research was directed at quantifying the effects of the fishery, and at recommending regulatory measures that would halt the overexploitation of the stock. During nearly 4 decades (1960 – 2000), very little attention was given to the subject of natural variability. This extreme focus on fishery-induced effects led to a situation where the existence of natural variations in the herring stock was almost forgotten.

The present study is an attempt to restore the balance. Due to stringent conservation measures since 1977, the North Sea stock had recovered to a level of 900,000 tonnes in 1999 (ICES 2000). This successful recovery was the result of a management policy agreed between Norway and the European Union. Under this agreement, managers attempt to stabilise fishing mortality at a level of 20% per year. This management policy is expected to increase the stock above a target level of 1.3 million tonnes by the end of 2001. Now that fishing pressure has been reduced, the natural variability of the stock will become visible again in the years ahead. Even when fishing mortality is kept constant, the stock will continue to change in response to hydrographic variations. The natural changes that used to affect the herring stock in the years before World War II will therefore reappear, and interfere with management measures. Given this outlook, it is important to resume the study of natural variability in the herring stock. Without a better understanding of this variability and its hydrographic causes, fisheries scientists will not be able to separate fishery effects from natural changes, and to predict the response of the stock to management measures.

1.2. Long-term variations in herring linked to climate?

It is a common assumption that long-term changes in herring, and in fact in many other fish species, are somehow related to climate variations (Pettersson 1926, Beverton and Lee 1965, Cushing 1982, Southward et al. 1988, Aebisher et al. 1990, Kawasaki et al. 1991, Glantz 1992, Beamish 1995, Alheit and Hagen 1997). There are of course other possible explanations for the observed changes in the fish stocks (e.g. autonomous changes in behaviour or population dynamics), but the climate hypothesis is both the most simple and the most attractive one. Simple, because it assumes that the fish respond to changes in their environment, and that this response is to some extent proportional to the environmental change. Attractive, because it is a hypothesis that can be tested, and that also holds the promise of a better understanding of the variations in the fish stocks, once the relationship with the environment has been quantified.

Climate variations can be defined as multi-annual changes in average weather conditions (Korevaar 1990, Jones 1990, Glantz 1992, KNMI 2000). The line between weather variations and climate variation is not sharply defined, but we can arbitrarily define climate variations as changes in mean weather conditions that last for more than 5 years.

Variations in climate may occur at very different time scales. At the far end of the range, we find the alternation between Glacial and Inter-Glacial Periods, which occur at a time scale of about 100,000 years. Within the current Inter Glacial, which started about 8000 BC, there have been several cold and warm episodes that alternated on a time scale of centuries. The most recent cold period, the so-called Little Ice Age, lasted from about 1550 to 1850 (Glantz 1992). Superimposed on these secular changes, we find shorter variations in the order of decades. A well-known example in our region is the North Atlantic Oscillation (NAO). The NAO, which will be further discussed in section 1.4.3, consists of a long-term variation in the mean atmospheric pressure distribution over the North Atlantic in winter (Fig.1.1). It causes an alternation between periods of several years in which the winters in Western Europe are generally mild, and periods in which winters tend to be colder. The NAO does not have a rigid periodicity, but oscillations occur on a time scale of about 10 years (KNMI 2000). The NAO bears some resemblance to the El Niño Southern Oscillation (ENSO) in the Pacific. This is a shorter, more pronounced climate variation, which occurs on a time scale of 3-7 years (Jones 1990, Miller and Fluharty 1992, KNMI 2000).

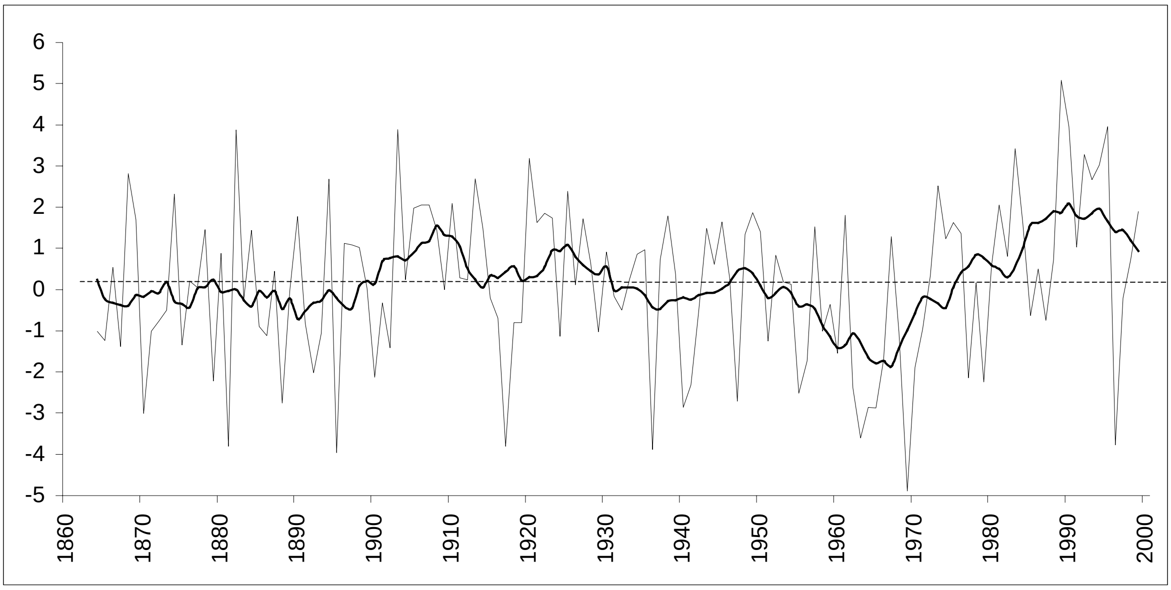

Figure 1.1. North Atlantic Oscillation (NAO) index based on the difference of normalised sea level pressures between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland in Dec-Mar. Heavy line represents 11-year running average. Data from Hurrell (2000a).

Long-term variations in air temperature and circulation will eventually be translated into changes in the sea. The relationship between atmospheric change and hydrography may sometimes be very direct, and sometimes more complicated. An example of a direct relationship is the effect on water temperature in the North Sea during winter. When the NAO is in a positive phase, the increased westerly circulation will result in an increase of average air temperature during winter (KNMI 2000). This relatively high air temperature will reduce the winter cooling of the surface water. The increased cloud cover that accompanies this type of weather will further prevent heat loss through radiation (Svendsen and Magnusson, 1992). In addition to this direct effect, the NAO may influence the North Sea indirectly through changes in the circulation of the North Atlantic. These changes may start in remote parts of the North Atlantic (Gulf of Mexico, Labrador Sea) and influence the North Sea system with a time lag of several years. We shall return to this subject in section 1.4.3.

Since climate variations occur on the same time scales at which we observe long-term changes in herring stocks, it is tempting to assume that the changes in herring are somehow related to these climate variations. However, so far it has been very difficult to link observed changes in herring to specific climate variations. This problem exists not only in herring, but also in other fish species such as cod (Daan et al. 1994). There are at least three reasons why changes in herring and other fish species are difficult to relate to environmental change:

(a) It is difficult to isolate natural changes in fish stocks from man-induced effects. In a situation of moderate or heavy exploitation, the changes in adult stock size caused by the fishery may affect recruitment, growth of the fish and distribution of the stock. This tends to mask changes that are caused by climate variation.

(b) Hydrographic variation in one area can be the combined effect of several independent processes, some of which are of climatic origin, and others which result from other causes. Gray and Christie (1983) found cyclic variations of 7, 11, and 18 year in the water temperature of the North Atlantic. These cycles were attributed to fluctuations in the rotating pole of the earth (7 years), the sunspot cycle (11 years), and the long-term lunar tide (18 year). The effects of these tidal and extra-terrestrial variations will interfere with the effect of climate variations. This makes it difficult to relate an observed hydrographic variation to one particular climatic factor.

(c) There is surprisingly little actual information on long-term hydrographic variation in the North Sea. We have only sporadic measurements of the in- and outgoing currents across the borders of the North Sea. The best estimates of the in- and outflow along the northern border differ by a factor 3 (Blaas 1997). Most of our ideas about long-term variability in water circulation are based on computer models in which water circulation is modelled on the basis of local wind stress (Backhaus and Maier-Reimer 1983, Bartsch 1993, Skogen et al. 1995). These models can not simulate variations that are due to oceanic effects originating outside the boundaries of the model area.

The last point is especially relevant for the present study. If hydrodynamic models do not show changes that correspond to observed variations in herring distribution, this is no proof that the variations in the herring have no hydrographic cause. For example, hydrodynamic models do not show a reduction of Atlantic inflow into the north-western North Sea in the 1970s that could explain the sustained reduction in transport of herring larvae across the North Sea during this decade (Corten 1986, Skogen 2000). Yet, the development of a large sprat stock in the north-western North Sea at that time also pointed to a reduction of the Atlantic influence in the area (Corten 1990).

Long-term changes in herring could be symptoms of variations in currents or other hydrographic parameters that have not yet been detected by hydrographic monitoring programmes. In some cases, herring may be quicker to detect changes in the sea than hydrographers. The observed changes in herring distribution, therefore, could be used to formulate new hypotheses about the existence of hydrographic changes that went unnoticed until now. Such hypotheses could be tested either by collecting more detailed hydrographic data, or by investigating parallel changes in other parts of the ecosystem.

1.3. Earlier investigations into long-term variations in herring

The phenomenon of natural variation in herring stocks has occupied fisheries biologists in Western Europe already from the earliest days of fisheries research. The interest in the subject was understandable; the herring fishery was by far the most important of all commercial fisheries (Mitchell 1864), and sudden changes in abundance of the herring could seriously influence local economies. When herring stocks declined, scientists were asked to explain the phenomenon and to predict how long the decline would last.

The literature on herring is extensive. Already in 1918, a British scientist noticed that “ There are in existence books, pamphlets, reports, Acts of Parliament having reference to the herring, sufficient in number to stock a good-sized library” (Samuel 1918). A large part of the literature from the pre-World War II period deals wit natural variations in the herring stocks and their effects on the fisheries. It is not my intention to present a comprehensive review of this earlier work. In the following paragraphs, I shall merely present some examples of the most relevant or interesting historic theories and case studies.

1.3.1. Bohuslän herring

Perhaps the best-known and most intriguing natural variation in a herring fishery in Western Europe has been the alternation between periods of high and low abundance in the Skagerrak along the coast of the Swedish province Bohuslän (the area north of Götenborg). During the so-called Bohuslän herring periods, large quantities of herring appeared in winter along the coast, giving rise to an important fishery. After the fishery had gone on for some decades, the herring would suddenly stop appearing, and the fishery would collapse. Bohuslän herring periods occurred with a frequency of about once in a century, and nine such periods are known from the last 1000 years (Alheit and Hagen 1997).

Once a herring period had started, the Swedes knew from experience that the fishery would probably not last indefinitely, but they had no idea what caused the herring to disappear from their shores. During the “great” Bohuslän fishery of the 18th century (1747-1809), the Swedish government started to take conservation measures aimed at preventing a collapse of the fishery. At that time, most of the catches were used to extract fish oil, and the waste products of the oil factories were dumped back into the sea. Many people were concerned that the pollution caused by this practice would scare the herring away, and by royal decree of 1786, the dumping of herring carcasses in the sea was prohibited (Höglund 1972). However, this measure did not prevent the eventual collapse of the fishery in 1809. In an attempt to find a scapegoat for the decline of the fishery, the Swedes claimed that the herring had been scared away “by the firing (of canons) of British and other ships of war attending convoys” (Mitchell 1864).

The next Bohuslän period occurred from 1877 - 1906. By this time, Swedish scientists had discovered strong fluctuations in salinity and temperature profiles in the Skagerrak, due to the occurrence of internal waves (Pettersson and Ekman 1891). They used this new discovery as the explanation for the changes in herring abundance in the area. Petterson (1911) assumed that the internal waves would transport the herring from the North Sea into the Skagerrak. In order to explain the periodicity of the herring periods, he postulated that the internal waves also had a long-term periodicity, governed by the position of the sun, moon and planets, and that the herring periods, therefore, could be predicted on the basis of astronomical calculations (Pettersson 1926). The idea that the movements of the herring were affected by celestial bodies was not entirely new. Already in 1880, the Swedish herring scientist Ljungman had suggested that the Bohuslän herring periods were related to the 111-year sunspot cycle (Ljungman 1880).

Pettersson’s theory about internal waves and extra-terrestrial influences on the herring stock did not stand the test of time. One reason was that historical Bohuslän periods did not occur with the rigid periodicity of 111 years that was assumed by his theory (Höglund 1978). Another criticism was that internal waves are merely vertical oscillations of the water, and therefore can not transport herring from one area to another. The mystery of the Bohuslän herring periods had to wait for another explanation.

Some decades later, scientists noticed that Bohuslän herring periods tended to coincide with episodes of cold weather over Western Europe (Storrow 1947, Beverton and Lee, 1965). It appeared that the Bohuslän herring periods in the Skagerrak also alternated with periods of herring abundance along the Norwegian west coast. The Norwegian scientist Devold (1963) drew the seemingly obvious conclusion that the fishery in both regions was based on the same herring stock; a stock that shifted its spawning ground back and forth between the Swedish Skagerrak coast and the Norwegian Atlantic coast. His theory became the subject of a heated discussion with the Swedish scientist Höglund, who argued that the Bohuslän herring had been North Sea herring and not Norwegian spring spawners. Höglund (1972) proved his theory in a convincing way by excavating herring remains of the Bohuslän fishery in the 18th century, and showing that these herring had the characteristics of North Sea herring. The fact that herring remains from the 18th century could still be recovered, was due to the ban of 1786 on dumping of herring carcasses from the oil factories into the sea. This law had forced fish processors to store the carcasses in specially constructed pits. Under the anoxic conditions in these pits, the herring bones had been conserved for two centuries.

The observation that Bohuslän herring periods coincided with cold winters over Western Europe was further investigated by Alheit and Hagen (1997). They found that Bohuslän periods during the last centuries had occurred during cold periods in which European herring populations at the southern fringe of their distribution area had expanded, and the fisheries for sardine, a more southern species, had declined. The authors found that the Bohuslän herring periods coincided with negative phases of the North Atlantic Oscillation, which suggested a climatic cause of the herring periods. They could not explain, however, how a negative phase of the NAO would encourage North Sea herring to migrate into the Skagerrak. By the end of the 20th century, the Bohuslän herring periods remained as great an enigma as they had been at the beginning of the century.

The search for the cause of Bohuslän herring periods has been described here in some detail, as it is representative for the problems encountered in other studies on natural variability in herring stocks. A lack of knowledge about the actual movements of the herring, a lack of knowledge about the variations in the environment, and a complicated relationship between the two variables, all prevented scientists to find a satisfactory explanation of the observed changes. In the next paragraphs, we shall consider some of the observed natural variations of herring in the North Sea itself and in the English Channel.

1.3.2. Changes in the North Sea

In the North Sea, the herring fishery did not show the extreme variations that were seen in the Skagerrak. Still, a number of long-term changes, some of which severely affected the economy of local fishing communities, were recorded also in this area.

The traditional driftnet fishery continued to be the most important herring fishery in the North Sea until about 1955. This fishery was conducted mainly in the second half of the year in the western half of the North Sea. The main long-term change in this fishery consisted of a shift from Shetland/Orkney to the Buchan area (off Peterhead and Aberdeen) from 1947 to 1954, and a reversal of this shift in the 1960s (Glover 1957, Bainbridge and Forsyth 1972). By combining detailed catch statistics with the results of an extensive plankton sampling programme, Bainbridge et al (1978) showed that the latitudinal shifts in the position of the herring fishery coincided with changes in the composition of the plankton on the fishing grounds. Broadly speaking, the southward shift of herring catches coincided with an increased plankton abundance on the southern fishing grounds, and vice versa. The changes in plankton distribution appeared to be related to variations in the inflow of Atlantic water into the north-western North Sea.

Many years earlier, Storrow (1932) had already drawn attention to the possible effect of variations in the Atlantic inflow into the north-western North Sea. He assumed that this influence extended far south into the central North Sea, and thereby affected also the herring fishery off the Northumberland coast.

A conspicuous natural change in North Sea herring was the sudden increase in growth rate of juvenile herring around 1950. This increased growth rate resulted in a reduction of the age of first maturation from 4-5 years to 3 years (Burd and Cushing 1962). The increased growth coincided with an increased abundance of *Calanus* in the distribution area of the juvenile herring, and was therefore probably a direct consequence of better feeding conditions (Burd 1963).

Natural changes also played a role in the decline of the spawning population in the southern North Sea and English Channel. Following the introduction of bottom trawling on the spawning grounds in the southern North Sea shortly after World War

II, there had been a marked reduction in the catches on these grounds. Most scientists attributed the reduction in catches to overexploitation (Aasen and Jones 1957), but Kreft (1963) drew attention to the widespread occurrence of environmental changes and their possible effects on the herring stocks. He put forward an "environmental hypothesis" that explained the reduction of the southern population by a natural shift of recruits to the more northern populations. In hindsight, it is clear that overfishing was the main cause of the depletion of the southern spawning population, but the effects of fishing were indeed aggravated by a natural decline in the recruitment to this population (Burd 1978).

The introduction of new fishing gears such as bottom trawl, pelagic trawl and purse seine, allowed fishermen from about 1960 onwards to exploit North Sea herring outside the traditional fishing areas. The changes in the fishery caused by the rapid introduction of new technology tended to mask changes that were caused by natural variations in the stock (Parrish 1963). A good example was the development of the winter fishery in the Skagerrak in 1963-65. In these years, the new Norwegian purse seine fleet discovered large quantities of herring in the Skagerrak during the winter, and it took large catches from this area during two consecutive winters. There was remarkably little interest from the scientific community in the biological background of the new fishery. Most scientists apparently assumed that the high catches were due to the introduction of a new fishing method (purse seining) that allowed fishermen to exploit herring concentrations that hitherto had been unavailable. Only few scientists considered the possibility that the high catches in the Skagerrak were the result of a new migration of herring into this area; a migration that bore resemblance to the earlier ones during Bohuslän periods (Zijlstra 1964a).

In the years after 1960, scientific interest in natural variability of the herring stocks waned. This was due to the increasing impact of fishing on the stocks; an impact that completely overshadowed the natural variability. The new fishing gears that had been introduced in the fishery, in combination with echo sounders and sonar, could be used to catch the herring any time of the year in any part of the North Sea. In the absence of adequate conservation measures, the herring stock declined rapidly. Under these conditions, it was not surprising that scientific interest shifted from natural variations to man-induced effects. During the 1960s and 1970s, all herring research was focused at quantifying the relationship between fishing effort and fishing mortality, and on advising conservation measures that would curb the disastrous effects of the fishery.

It was only in the 1980s that the attention for natural variations slowly revived. A major boost for this revival was the publication of Cushing's (1982) book "Climate and fisheries". Scientists (re-)discovered that herring stocks (and other fish stocks) did not behave according to the predictions based on their models. A good example was the slow recovery of the North Sea herring stock after the closure of the fishery in 1977. This closure was introduced after scientists had detected a severe reduction of recruitment to the stock. The North Sea stock at that time consisted of three populations, the southern, central and northern one, which were rather different in size. As the recruitment failure was attributed to a shortage of spawning fish, it was expected that recovery would start in those populations that still contained the largest number of adult individuals, i.e. the central and northern populations. Contrary to these expectations, recruitment to the central and northern populations continued to be low until 1980. On the other hand, the spawning population in the English Channel, which was by far the smallest at the time of the closure, already produced a strong year-class in 1978. In an analysis of the recruitment to individual populations during the 1970s, Corten (1986) found that something unusual had happened to the larvae from the central and northern populations during the years of the recruitment failure. Instead of drifting across the North Sea to the normal nursery areas in the German Bight and Skagerrak (Fig. 1.3), the larvae were observed to remain near their hatching areas in the western North Sea. Corten assumed that the stagnation of the transport of the larvae was due to a change in the residual circulation of the North Sea. Whether this explanation was correct or not, the data on larval distribution clearly suggested that the recruitment failure of the central and northern populations in the 1970s had been caused not only by a shortage of spawning fish, but also by an adverse environmental factor that reduced the number of larvae actually reaching the nursery areas.

During the years when herring larvae failed to reach the eastern North Sea, the sprat stock in the western North Sea showed a spectacular expansion. Although some scientists originally assumed that this expansion was due to a reduced competition from the herring, the final conclusion was that the expansion of the sprat was due to “unknown climatic factors” (Bakken and Bailey, 1990). Since sprat is a more neritic species than herring, the expansion of this species in the northwestern North Sea could possibly be due to a reduction of Atlantic influence in this area (Corten 1990). The Sprat Biology Workshop in 1986 considered the evidence for this theory but concluded that “A possible relationship between changes in the hydrographic regime and sprat abundance needs to be thoroughly analysed before conclusions can be drawn” (Bakken and Bailey 1990). After 1979 the transport of herring larvae across the North Sea returned to normal, and the sprat stock in the western North Sea declined. These events suggested that the current system in the northwestern North Sea had returned to normal. In 1983, a sudden revival of herring spawning was detected on the old spawning grounds off Aberdeen. These spawning grounds had been deserted 17 years before, and since then spawning in the northern North Sea had been restricted to the Shetland/Orkney area. The return of spawning herring to Aberdeen Bank in 1983 seemed to confirm the theory that the circulation pattern in the north-western North Sea had returned to the normal pattern of the years prior to 1970 (Corten 1990).

So, despite the confounding effects of overfishing, natural changes in the herring stock could be still be detected in the 1970s and 1980s. These natural changes were not restricted to herring. Aebischer et al. (1990) showed that in the north-western North Sea parallel changes occurred at four trophic levels: phyto- and zooplankton, fish and birds. Near the Shetland Islands, the sandeel population increased in the 1970s and decreased in the 1980s. These variations in stock size could not be entirely explained by the effects of the fishery (Bailey 1989). The high abundance of young sandeel in the inshore waters around Shetland in the mid-late 1970s could have been the result of a cessation of the Atlantic inflow east of Shetland (Turrell 1992a). The changes in sandeel stock strongly affected some local bird populations, in particular the arctic terns (Bailey et al. 1991).

Evidence for long-term natural variation was also detected in the bivalve *Artica islandica* on the Fladen Grounds (an area in the north-western North Sea). Annual growth increments in the shells, measured over more than 100 years, showed a long-term variation with a period of about 33 years (Witbaard et al. 1997). It was assumed that the long-term variations in growth of this mollusc were related to changes in the circulation system in the area, and to inter-annual changes in the influx of water into the North Sea (Witbaard 1996).

After the re-opening of the herring fishery in the North Sea in 1983, the herring appeared to have changed its distribution during summer. Whereas in the years before the closure most catches in June were taken in the western North Sea, the fishery now took place in the north-eastern part of the North Sea. This north-eastern distribution of herring catches coincided with an increased immigration of western mackerel into the north-eastern North Sea (Corten and Van de Kamp 1992). The fact that both species simultaneously shifted their distribution to the north-eastern North Sea suggested a common hydrographic cause. Earlier, Walsh and Martin (1986) had already speculated that the northward displacement of mackerel overwintering and feeding grounds was related to an increased strength of the North Atlantic Drift. Considering the fact that the new concentrations of herring and mackerel in the northern North Sea were found in the region of the shelf edge, Corten and Van de Kamp (1992) assumed that the changes in these stocks were related to variations in transport of oceanic water along the shelf edge.

1.3.3. Changes in the English Channel

In the western English Channel, the traditional herring fishery near Plymouth sharply declined in the 1930s. At the same time, spawning of pilchard, a more southern clupeoid species, increased in the area (Southward et al. 1988). A number of studies showed that the replacement of herring by pilchards was accompanied by other changes in the ecosystem; in particular a replacement of oceanic plankton and demersal fish species by neritic ones (Southward 1963, Cushing 1995). The ecological changes were accompanied by a decline in the phosphate content of the water in winter. In the late 1950s, the changes in plankton, demersal fish and winter phosphate were reversed, but the herring did not return to Plymouth. The long-term ecological changes in the English Channel have been named the "Russell Cycle", after F.S. Russell who first reported these changes (e.g. Russell 1935, Russell 1973).

1.4. The possible influence of the North Atlantic

We have seen that speculations about the influence of the North Atlantic are a recurring theme in the quest for the causes of long-term variability of North Sea herring. It is easy to understand why the "Atlantic influence" hypothesis has been so popular in the past:

(a) The North Sea has a large border with the North Atlantic, and an extensive exchange of water masses occurs across this border.

(b) Ocean currents are assumed to change relatively slowly, due to their large momentum. They will exhibit more inertia than the relatively small currents in the North Sea. If we look for long-term hydrographic variations to explain sustained changes in herring stocks, the ocean is a more likely place to find them then the small and shallow North Sea.

(c) Observations on plankton in the northwestern North Sea have already provided some evidence for the existence of variations of the Atlantic inflow into this area (Bainbridge and Forsyth 1972).

Since the Atlantic inflow theory will also be one of the main hypotheses in the present study, it is useful to consider briefly our current knowledge about the effects of the North Atlantic on the North Sea. This will be done by first describing the accepted model of water exchange between North Sea and North Atlantic, and the various ways in which these exchanges might affect the herring. Secondly, the methods are described by which the Atlantic inflow into the North Sea can be monitored, and variations of the inflow detected. Finally, a number of ways is considered in which climate variations over the North Atlantic might directly or indirectly affect the inflow of Atlantic water into the North Sea.

1.4.1. Main Atlantic inflows into the North Sea

Figure 1.2 presents a simplified picture of the average water exchange between the North Sea and the North Atlantic (based on Otto et al. 1990, Turrell 1992b, Turrell et al. 1996, Svendsen, Aglen et al. 1995). It should be stressed that this scheme corresponds to the long-term average situation. The actual flows at a particular moment will depend very much on the prevailing wind conditions (Riepma 1980, Pingree and Griffiths 1980). The residual currents in the North Sea (except for the in- and outflows through the Norwegian Trench) respond to local wind conditions within about 2 days (Riepma 1980).

The main inflow of Atlantic water across the northern border consists of a sub-surface current that enters the north-eastern North Sea along the western slope of the Norwegian Trench. This “Norwegian Trench Current” (NTC) is in fact a branch of the Shelf Edge Current that flows along the entire West-European shelf. When it enters the North Sea (following the shelf edge into the Norwegian Trench), it sinks beneath the lighter, less saline surface water of the northern North Sea. During its southward passage into the Norwegian Trench, the Atlantic water of the NTC mixes with the outgoing Norwegian Coastal Current, and most water of the NTC is thereby diverted out of the North Sea again. Only a small proportion of the original volume of the NTC flows all the way south towards the Skagerrak. The NTC is responsible for the major input of nutrients into the eastern North Sea and Skagerrak. It is also assumed to transport *Calanus finmarchicus*, the main food organism of the herring, back into the North Sea after these copepods have spent the winter in the deeper waters along the shelf edge (Backhaus et al. 1994).

The inflow along the north-western border of the North Sea consists of two currents that extend to the surface. One is the Fair Isle Current that enters the North Sea between the Orkney and Shetland Islands, and the other is the East Shetland Atlantic Inflow that enters the North Sea to the east of Shetland. The Fair Isle Current (FIC) is the most consistent and best documented of the two (Dooley 1981, 1983). It flows south until the latitude of Aberdeen, where most of its waters are turned east towards the Skagerrak. A small proportion of the current continues south along the English

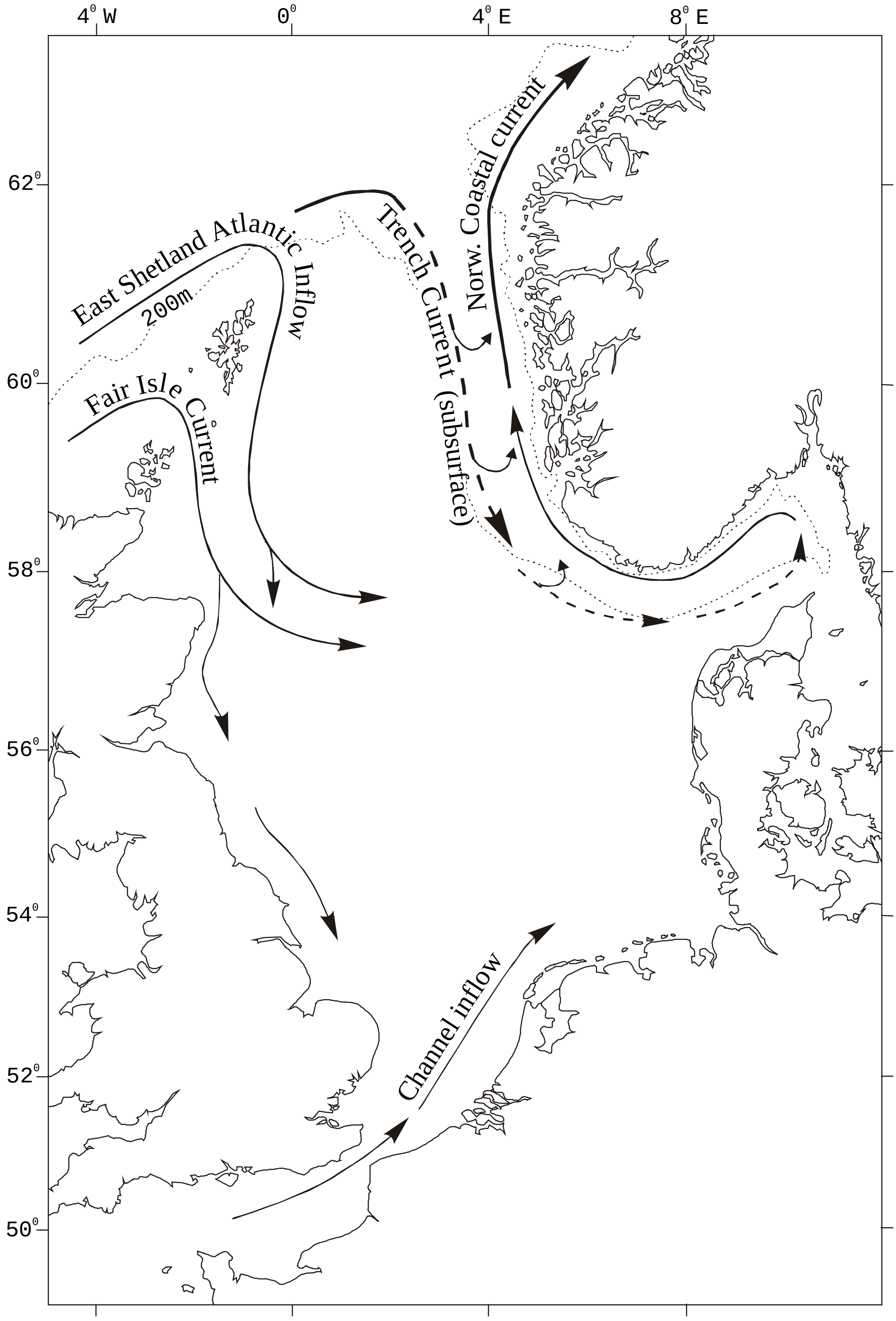

Figure 1.2. Schematic presentation of water exchange between North Sea, North Atlantic and English Channel

coast and reaches the area off Northumberland. The FIC provides an important input of nutrients to the north-western and western North Sea throughout the year, and thereby presumably affects the food abundance and distribution of the herring. In addition, it affects the hydrographic conditions on the spawning grounds in the northwestern North Sea, and presumably also the initial transport of herring larvae that are born on these grounds (Fig. 1.3).

The East Shetland Atlantic Inflow (ESAI) seems to be a more variable inflow of Atlantic water into the North Sea (Turrell 1992a, b). Although the inflow to the east of Shetland used to be considered as one of the main inputs of Atlantic waters into the North Sea, an extensive series of measurements in 1976 failed to show the existence of a significant inflow in this area (Riepma 1980). In hindsight, the year 1976 (and more generally the mid-1970s) appear to have been an anomalous period, due to the occurrence of the Great Salinity Anomaly (Dooley et al. 1984, Belkin et al. 1998) and the absence of an inflow east of Shetland in that year may not represent the normal situation. During extensive current measurements between September 1987 and February 1988, the existence of the ESAI was clearly demonstrated (Turrell et al. 1992). The volume of this inflow was estimated at about twice the volume of the Fair Isle Current. If this represents the average situation, the ESAI may have a profound effect on the circulation and ecology of the northern North Sea (Turrell et al. 1992).

Contrary to the northern North Sea, the southern North Sea receives only a limited input of Atlantic (or actually Celtic Sea) water. This is due to the restrictions posed by the narrow passage through the Strait of Dover. The inflow of Atlantic water into this area is strongly dependent upon the wind conditions over the English Channel and southern North Sea (Pingree and Griffiths 1980, Salomon and Bretton 1993). It has been shown that variations of Atlantic inflow, caused by sustained changes in wind force and direction during winter, can lead to variations in the abundance of southern fish species in the North Sea (Corten and van de Kamp, 1996). Variations in Atlantic inflow trough the Strait of Dover will affect the transport of herring larvae from the hatching grounds in the eastern Channel to the nursery grounds in the southern North Sea (Fig. 1.3). The Atlantic inflow is also a major source of nutrients for the southern North Sea, and thereby will affect plankton production and feeding conditions for juvenile herring in this area.

1.4.2. Estimating the volume of the inflows

The main problem in testing the hypothesis of multi-annual changes in the Atlantic inflow is that there are virtually no long-term series of actual current measurements in the areas where the in- and outflows occur (Otto et al. 1990, Svendsen and Magnusson 1992). This lack of direct measurements is due mainly to the intensive fishing effort in these areas, which prohibits the use of moored current meters during any length of time.

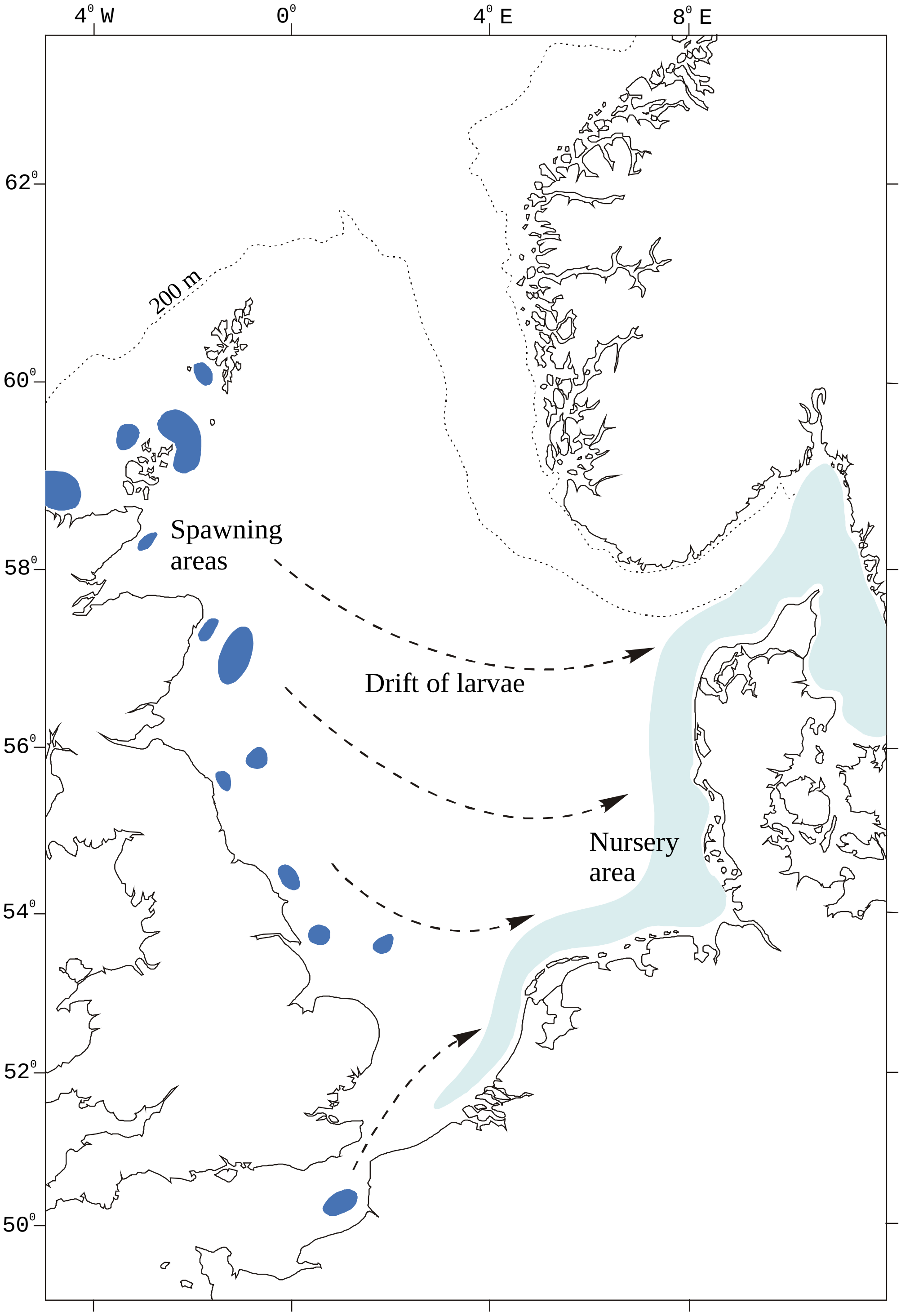

Figure 1.3. Herring spawning grounds in the western North Sea, nursery areas in the eastern North Sea and Skagerrak, and drift routes of larvae.

In the absence of direct measurements, some authors have attempted to estimate the inflows indirectly by using parameters that are somehow related to these inflows, such as wind and salinity. These exercises, however, yield variable results. A review of recent estimates of Atlantic inflow along the northern border of the North Sea (Blaas 1997) showed that these estimates ranged from 0.6 Sv to 1.8 Sv (1 Sverdrup = 1 million cubic meters per second). This illustrates the large uncertainty in this type of estimates.

The most common approach is to construct hydrodynamic models that simulate currents on the basis of tides, wind stress over the North Sea and adjacent areas, and freshwater input from rivers (Maier-Reimer 1979, Backhaus and Maier-Reimer 1983, Davies 1983, Bartsch et al. 1989, Furness 1992, Bartsch 1993 , Skogen et al. 1995). These models can fairly well simulate the general circulation of the North Sea, and the wind driven in- and outflows across the borders in the north and in the south. Models that include the entire shelf area of western Europe and mean density gradients in the ocean can even simulate the sub-surface Norwegian Trench Current into the North Sea (Svendsen, Fossum et al. 1995, Svendsen et al. 1996). However, none of the models produced so far shows a sustained reduction of Atlantic inflow into the north-western North Sea during the 1970s that might explain the reduced drift of herring larvae and the expansion of the sprat stock in this period, nor a sustained increase of Atlantic inflow after 1980 that could explain the reversal of the changes (e.g. Skogen 2000). There are two possible explanation for this lack of agreement between hydrodynamic models and observed ecological changes: the ecological changes are not due to variations in Atlantic inflow, or the models do not accurately simulate the variations in Atlantic inflow.

There is some evidence for the latter theory. Turrell et al. (1992) found that the East Shetland Atlantic Inflow was predominantly not wind-driven. Local winds did moderate the current to some extent, but the current seemed to be driven mainly by density differences between North Sea and the North Atlantic. Huthnance (1995) also states that density gradients determine much of the cross-slope water exchange (and thus the inflow of Atlantic water into the North Sea). Variations in the density-driven inflows into the North Sea will be caused both by variations in the density structure of North Sea water, and by variations in the density of Atlantic water along the shelf edge (Turrell 1992b, Huthnance 1995, Turrell et al 1996). The latter will be caused by a variety of processes in the North Atlantic, including atmosphere/ocean interactions in other parts of the ocean and at other moments in time. The existence of such mechanisms implies that present hydrodynamic models of the North Sea, which do not include actual density gradients nor sea level variations at the oceanic boundaries, will be inadequate to simulate variations of Atlantic inflow with a reasonable degree of accuracy (Svendsen and Magnusson 1992).

A second method to estimate the Atlantic inflow into the northern North Sea indirectly, is to use salinity as an index of Atlantic inflow. Atlantic water normally has a salinity of more than 35.3 ‰, whereas the salinity of North Sea water is less than 35.0 ‰. An increased inflow of Atlantic water would thus be reflected by a higher salinity in the northern North Sea and vice versa. Martin et al. (1984) used salinity data as evidence for a reduced Atlantic inflow in the years 1977-1979. Many years before, Bainbridge and Forsyth (1972) already used salinity data to support their theory of a reduced Atlantic inflow in the 1960s.

However, the use of salinity as a quantitative index of Atlantic inflow is problematic. The water that enters the North Sea by the Fair Isle Current (Fig. 1.2) does not consist of pure Atlantic water, but of a mixture of Atlantic water and Scottish coastal water (Dooley 1981). The salinity of this inflow will vary, depending on the composition of the mixture. A second problem is that the salinity of the Atlantic water itself is not constant. It may vary by at least 0.15 ‰, depending on its origin (Turrell et al. 1993). During the Great Salinity Anomaly of the 1970s, the salinity of the Atlantic water adjacent to the northern North Sea dropped to only 35.2 ‰ (Dickson et al. 1988). During the early 1990s, in contrast, the salinity of Atlantic water entering the North Sea increased to 35.5 ‰ (Heath et al. 1991, Becker et al. 1992), due to the southern origin of this Atlantic water. These variations in the salinity of the inflowing water present a problem in quantifying the Atlantic inflow on the basis of salinity values in the northern North Sea (Dooley 1974). As Turrell (1992a) puts it, “ The absence of high salinity water in the northern North Sea may not be directly associated with a reduced Atlantic inflow”. Finally, the salinity of water in the border areas of the North Sea will also be affected by local precipitation and evaporation. This is an additional complication in estimating the volume of Atlantic inflow on the basis of North Sea salinity.

The third indirect method to investigate long-term variations of the Atlantic inflow is to use plankton indicator species. If the inflow of Atlantic water into the North Sea changes, also the plankton community in the northern North Sea will change. Atlantic water contains a number of typical Atlantic plankton species that can not survive the winter in the North Sea. Each summer these species have to re-invade the North Sea, using the Atlantic inflow for their transportation. Their abundance in the North Sea in summer, therefore, will be partly a function of the volume of Atlantic water that has entered the North Sea, and partly of the concentration of the plankton organisms in the inflowing Atlantic water.

The use of plankton species as indicators of different water masses is already an old idea (Hardy 1924, Savage 1931, Storrow 1932, Russell 1935). The main problem of the method is that plankton is distributed very patchy, both in time and in space. A few isolated samples, therefore, are insufficient to draw conclusions about long-term changes in water composition in a particular area. To overcome the problem of patchiness in space, the great pioneer of plankton research in the United Kingdom, Sir Alister Hardy, developed an instrument that was designed to monitor plankton continuously over large stretches of sea. This instrument, the Continuous Plankton Recorder (CPR), has been used since the end of world War II for a systematic sampling programme in the North Sea and the North Atlantic (Warner and Hays, 1994). The CPR programme has produced a wealth of plankton data that can now be used to study trends in Atlantic plankton species in the North Sea and the adjacent part of the North Atlantic.

Until now, little use has been made of CPR material in the study of variations of Atlantic inflow into the North Sea. There is only one paper on the subject, in which one diatom species, *Thalassiothrix longissima*, was used as indicator for Atlantic water (Reid et al. 1992). Using only one species, however, makes it difficult to separate the variability caused by changes in Atlantic inflow from variations caused by the population dynamics of the species itself. A more convincing proof of variations in Atlantic inflow requires that the same pattern of long-term variation can be demonstrated in a number of different plankton species that all depend on the Atlantic inflow for their transportation into the North Sea.

1.4.3. Climate variations that may affect the Atlantic inflow into the North Sea

In section 1.2 it was pointed out that the climate in the North Sea region is subject to a number of climate variations, ranging in time scale from a few years to several thousands of years. For the purpose of the present study, I was interested in climate variations on a time scale of approximately 5-50 years. Effects of such climate variations on North Sea herring might be detectable during the period for which we have sufficiently detailed catch statistics and survey data.

The main climate variation on this time scale in our region is the North Atlantic Oscillation (NAO). The NAO consists of an alternation between periods in which the north/south air pressure gradient over the North Atlantic during winter is generally strong, and periods in which this gradient tends to be weak (Rogers 1984, Lamb and Peppler, 1987, Hurrell 1995, Dickson et al. 1996). The NAO is described by the NAO-index, which is commonly defined as the difference between the normalised mean winter (December – February) surface pressure anomaly for the Azores and that for Iceland (Rogers 1984). During a positive phase of the NAO when the pressure gradient is generally strong, most winters in Western Europe are characterised by a strong westerly circulation and relatively high temperatures. In a negative phase when the pressure gradient tends to be lower, the westerly circulation over Europe is weaker on average, and it is more often replaced by a north-easterly circulation that results in cold winters. It should be stressed that the NAO refers to the long-term pattern of pressure distribution over the North Atlantic (the average over at least 5 years). Superimposed on this long-term pattern is a strong year-to-year variability (Fig. 1.1). The NAO does not have a fixed oscillation time; its index shows irregular changes from positive to negative phases at intervals in the order of 10 years.

The direct effects of the NAO on the North Sea are changes in wind-driven circulation and water temperature. During a positive phase of the NAO, the increased westerly winds during winter will stimulate the anti-clockwise circulation of the North Sea (Pingree and Griffiths 1990), and thereby the inflow of Atlantic water by the Fair Isle Current (Turrell 1992a), the Norwegian Trench Current (Reid et al. 2000) and the inflow through the Strait of Dover (Salomon and Bretton 1993). The transport of relative warm air from the North Atlantic to the North Sea area will result in a reduced cooling of surface waters during winter (section 1.2).

In addition to these direct effects, the NAO may affect the North Sea in a number of indirect ways. One possible effect is through a change in strength of the Shelf Edge Current (SEC); a narrow (30-50 km) current that flows north along the continental slope of western Europe. The SEC is the main supplier of Atlantic water to the northern North Sea. A branch of this current enters the North Sea along the western edge of the Norwegian Trench, and this flow constitutes the largest input of Atlantic water into the North Sea (section 1.4.1). Water of the SEC also mixes with shelf waters west of Scotland, and then enters the North Sea by the Fair Isle Current and the East of Shetland Atlantic Inflow (Dooley 1981, Turrell et al. 1992). Changes in the strength and composition of the SEC may thus affect the inflow of Atlantic water into the North Sea. Although the SEC seems to be driven primarily by meridional density gradients and tidal forces, local wind forcing may also affect the current (Blaas 2000, pers. comm.). Since local winds will be influenced by the NAO, the NAO will affect the SEC and thereby ultimately the Atlantic inflow into the North Sea. Maybe the SEC is influenced not only by winds in the shelf area, but also over wider parts of the North Atlantic. Backhaus et al. (1994) assume that the SEC is influenced by the wind-driven transport across the eastern North Atlantic, with an increased eastward transport resulting in an increased strength of the SEC. This effect of the NAO on the SEC could be even greater than the effect through local wind forcing.

The effect of the westerly winds on the Shelf Edge Current, and thereby on the inflow of Atlantic water into the North Sea, may be simulated by hydrodynamic models (Svendsen et al. 1996, Skogen 2000). There are other effects of the NAO on the North Atlantic circulation, however, that are not yet amenable to mathematical simulation. These effects may occur through atmosphere/ocean interactions in other parts of the North Atlantic, particularly the western half. Some authors assume a connection between the Gulf Stream and the North Atlantic Current (Dooley et al.

1984). If this connection exists, changes in the position and strength of the Gulf Stream might influence the circulation in the eastern part of the North Atlantic. This could affect the density of oceanic water along the shelf edge, and thereby the density-driven inflow into the North Sea.

An example of a possible effect of the NAO on the Gulf Stream is the correlation between the NAO-index and the position of the north wall of the Gulf Stream (Taylor 1996, Taylor and Stephens 1998, Taylor et al. 1998). This correlation is greatest for a time lag of 2 years between NAO and Gulf Stream position. The NAO may affect not only the position of the Gulf Stream, but also its strength. According to Worthington (1977), the strength of the Gulf Stream probably depends partly on the formation of 18°C water in the Sargasso Sea. The formation of this 18°C water is related to the severity of winters in the western Atlantic (Dooley et al. 1984), and thereby also to the NAO (Dickson et al. 1996).

The changes in the formation of 18°C water, and thereby on Gulf Stream transport, are an example of the possible influence of the NAO on the thermohaline circulation (THC) of the North Atlantic. Other effects of the NAO on the THC may occur in the northern regions of the North Atlantic through changes in the formation of intermediate and deep water in the Labrador Sea and in the Greenland/Iceland Sea (Dooley et al. 1984, Greatbatch et al. 1991, Deser and Blackmon 1993, Taylor 1996). The convection of cold water in the Greenland/Iceland Sea is assumed to be one of the driving forces behind the North Atlantic Current. This convection seems to be linked with the NAO: the convection is strongest during a negative phase, and weak or absent during a positive phase (Dickson et al. 1996). Therefore, by affecting the convection of cold water in the Greenland/Iceland area, the NAO may influence the circulation in the rest of the eastern North Atlantic, and thereby ultimately the inflow of Atlantic water into the North Sea.

A last example of the possible effects of the NAO on the Atlantic inflow into the North Sea concerns the formation of large salinity anomalies in the North Atlantic. These anomalies consist of large bodies of cold, low salinity water that are formed under special conditions in the area north of Iceland (Dickson et al. 1988, Belkin et al. 1998). The anomalies slowly circulate around the North Atlantic on a time scale of decades, causing pronounced effects in the regions where they pass. The “Great Salinity Anomaly”, that passed the North Sea in 1977-78, was originally formed in the waters north of Iceland during the NAO minimum of the early 1960s (Dickson et al. 1988). The passage of this anomaly in the vicinity of the North Sea in 1977-78 caused a drop of salinity in the North Sea (Martin et al. 1984), and presumably also reduced the density-driven inflow of Atlantic water (Turrell et al. 1996). This is an example of how the NAO could possibly affect the Atlantic inflow into the North Sea with a time lag of more than 15 years.

The above examples of potential effects of the NAO on water circulation in the North Atlantic illustrate that the relation between NAO (and other climate variations) and Atlantic inflow into the North Sea may be extremely complex. Variations of the Atlantic inflow into the North Sea may be related to weather conditions in different parts of the ocean, at an earlier time. Such “unexpected” variations in Atlantic inflow may drive ecological changes in the North Sea. It is important to keep this possibility in mind when trying to explain long-term ecological variations.

1.5. Delimitation of subject and formulation of working hypotheses

1.5.1. Delimitation of subject

The subject of natural variation in herring is very broad, and it is tempting to extend the study to all life stages of the herring and to all populations of the North Atlantic. However, this will restrict the depth to which each variation can be studied. Natural variations during different life stages and in different stocks may be caused by a variety of climatic factors. If the objective is to find relationships between long-term variations in herring and environment, it is better to concentrate on a particular area and particular change, rather than trying to encompass the entire field of natural variation in all herring stocks of the North Atlantic. For this reason, it has been decided to focus the study on a limited area, and on a limited number of natural variations.

Geographically, the present study will be limited to the North Sea and the adjacent waters of the Skagerrak. The North Sea is an obvious choice, since this has been the traditional fishing area for the Dutch fleet, and the area for which a large amount of data is available at the Dutch Fisheries Research Institute (RIVO-DLO). The North Sea is also a natural unit for herring, since the stock in this area does not show much exchange with stocks in adjacent areas. The only exception is the Skagerrak, which is an important nursery area for North Sea herring, and sometimes also an overwintering area.

The second restriction is that the study will consider mainly changes during the adult life stage of the herring, in particular changes in migration and distribution. It is in the adult life stage that natural variability is most easily detected. Fishermen follow the adult herring from year to year, and changes in migration pattern are easily detected from catch statistics. One should realise, however, that changes in the migrations of the adult fish are only one aspect of natural variability in the herring stocks. Other, sometimes even more important changes occur during the egg, larval and juvenile stage. Only one example of changes during the early life stage of the herring will be considered, viz. the changes in transport of herring larvae across the North Sea during the 1970s.

The third restriction is that natural variations will be considered only during the period since the end of World War II (1945). It is for this recent period that reliable catch statistics are available, together with a reasonable amount of environmental data. Of course natural variations will have been equally important in the years before World War II, but due to the absence of international sampling programmes, the information on changes during these years is very limited.

The last restriction is that the study will be limited to medium-term natural variations, i.e. variations on a time scale of 5-50 years. Shorter variations are considered to fall within the normal pattern of inter-annual variability. The long-term variations on a time scale of more than 50 years are not included either, since they can not be studied on the basis of 50 years of data.

The objective of the present study is thus to identify climatic factors that caused long-term changes in North Sea herring during the 2nd part of the 20th century, particularly in the distribution of the adult stock component.

1.5.2. Hypotheses

I assume that long-term changes in the distribution of North Sea herring are caused by equally long-term environmental variations. Such long-term environmental variations, also called climate variations, may consist of changes either in atmospheric circulation or in ocean circulation.

The main long-term variation in atmospheric circulation in Western Europe is the North Atlantic Oscillation. Considering the many ways in which the NAO directly affects North Sea hydrography (water circulation, temperature, plankton production), I hypothesise that this phenomenon will be responsible for at least some of the observed changes in herring distribution.

In addition to variations in atmospheric climate, I hypothesise that variations in ocean climate will be responsible for some of the changes in North Sea herring. Long-term changes in ocean currents will affect the hydrography and plankton in those parts of the North Sea that border the North Atlantic, and thereby the herring in these areas.

Because the fluctuations in ocean climate may stem from other causes than the NAO, or are caused by NAO-related atmosphere/ocean interactions in other parts of the North Atlantic, it is unlikely that oceanic changes along the border of the North Sea will be synchronised with the NAO. Therefore, changes in herring distribution that are caused by oceanic effects will not necessarily be synchronised with the NAO.

1.6. Outline of the thesis

The theory that some of the changes in herring and other fish species in the north-western North Sea are caused by long-term variations of the Atlantic inflow into this area, hinges on the assumption that these variations of Atlantic inflow indeed exist. The first step in testing the theory, therefore, is to find independent evidence for the existence of these presumed variations of Atlantic inflow. This problem is addressed in **chapter 2** by an analysis of CPR plankton data for the north-western North Sea. Long-term variations of Atlantic plankton species in the North Sea and in the adjacent waters of the North Atlantic are investigated, to see whether plankton data provide support for the hypothesis that the Atlantic inflow was reduced during the 1970s, and that it increased again in the early 1980s.

The mechanism by which variations in Atlantic inflow affect the herring is considered in more detail in **chapter 3**. In this chapter, the disappearance of spawning herring from Aberdeen Bank in the late 1960s, and the re-appearance of a spawning population in 1983 is analysed. The first question addressed is whether the re-appearance of larvae in 1983 was due to resurgence of a rudimentary population that had always survived in the area, or whether herring from elsewhere had colonised the old spawning ground. If the spawning herring came from elsewhere, why did they suddenly choose the Aberdeen Bank as their spawning area, and how could an increased Atlantic inflow affect their choice?

The changes in herring distribution in the eastern North Sea are analysed in the next three chapters. The most conspicuous natural change of herring in this area was the episodic immigration into the Skagerrak during the historic Bohuslän periods. This phenomenon, and its relationship with the NAO, is considered in **chapter 4**. This chapter focuses on the invasions of North Sea herring into Skagerrak during the winters of 1963/64 and 1964/65 and compares these to the earlier Bohuslän periods. Could the invasions in 1963/64 and 1964/65 be considered as the initial stage of a Bohuslän period, and if so, what was the environmental factor that triggered them? A number of candidate-factors is considered, including temperature, boreal plankton (as indicators of the origin of the water), and wind-induced currents. A theory is formulated that explains the Bohuslän herring periods on the basis of environmentally induced changes in combination with conservative behaviour of the herring.

The next two chapters deal with changes of herring feeding migrations in the north-eastern North Sea. In **chapter 5** the northern distribution of herring in the years 1988-1990 is analysed. In an earlier study, Corten and van de Kamp (1992), had found that the distribution of herring catches in the years after the re-opening of the fishery in 1983 had shifted to the north-eastern North Sea. This shift in distribution of catches was most pronounced in the month of June. The analysis in chapter 5 shows that the north-eastern shift of catches was actually the combined effect of two separate processes; one that shifted catches to the north, and another that shifted catches to the east. The northward shift of catches coincided with a period of mild winters. This leads to the hypothesis that the northward shift was an effect, either directly or indirectly, of high water temperatures at the start of the feeding season.

The eastward distribution of catches in the 1980s is explored in **chapter 6**. Here I hypothesise that the eastward distribution of catches was due to a delayed migration of the herring from the eastern to the western North Sea; a delay that was due to favourable feeding conditions in the eastern North Sea. This hypothesis is tested by considering data from the Continuous Plankton Recorder Programme on food abundance in the eastern North Sea.

A recurrent conclusion in several of the chapters (3,4, and 6) is that the migrations of adult herring contain an element of conservatism. The herring apparently tend to adhere to an existing migration pattern, even if the environment changes. This element in the behaviour of the herring complicates the study of the relationship between herring and its environment. The role of conservatism and tradition in different types of herring migration is further explored in **chapter 7**.

Chapter 8 summarises the natural changes that have been observed in North Sea herring, and the environmental factors that were supposed to drive them. It also addresses the question whether the various environmental causes could in the end all be related to the same climate variation.

Chapter 2

Evidence from plankton for multi-annual variations of Atlantic inflow in the northwestern North Sea

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Abstract

Long-term variations in Atlantic plankton species in the North Sea were investigated in order to find support for the hypothesis of a reduced inflow of Atlantic water into the North Sea during the 1960s and 1970s. The material was derived from samples of the Continuous Plankton Recorder Survey during 1948-1996. Fourteen Atlantic plankton species were selected as potential indicators of Atlantic inflow in the North Sea. Principal Component Analysis allowed the classification of these species into a number of sub-groups, each of which showed a different variation over time. One of these groups, consisting of *Candacia armata*, *Metridia lucens*, and *Tomopteris* spp., showed temporal variations that were apparently related to changes in Atlantic inflow. This group was at a low level in the North Sea from 1965 to 1982, and it increased in subsequent years. These variations correspond in time and direction with observed changes in pelagic fish stocks in the area.

2.1. Introduction

Developments in pelagic fish stocks in the northwestern North Sea during the last four decades have suggested a sustained reduction of Atlantic inflow into this area in the 1960s and 1970s, and an increased inflow after 1980 (Corten, 1986, 1990). The indications of a reduction of the inflow in the 1960s and 1970s were the following:

(a) A northward shift of herring fishing grounds and spawning areas in the northwestern North Sea after 1965.
(b) An apparent stagnation of the transport of herring larvae from their hatching grounds in the western North Sea to the nursery areas in the eastern North Sea in 1972-1979, leading to a serious recruitment failure of the herring.
(c) The expansion of sprat, a neritic species, in the western North Sea in the late 1960s and 1970s.
(d) The disappearance of mackerel, an Atlantic species, from the northern North Sea in the 1960s and 1970s.

After 1980 the changes in pelagic fish stocks were reversed. Herring larvae reached the eastern North Sea again, and the recruitment of this species recovered. The sprat stock in the western North Sea declined, and the mackerel entered the North Sea again during summer, and in later years even stayed there during part of the winter (Corten and Van de Kamp, 1992). The important herring spawning grounds on Aberdeen Bank, which had been abandoned by the herring in the late 1960s, were re-colonised again from 1983 onwards. Finally the horse mackerel, another Atlantic species, started to overwinter in the North Sea in the 1980s (Reid et al., 1999). All these events suggested that the Atlantic inflow into the North Sea had increased again after 1980.

The possibility, or even likelihood, that ecological changes in the North Sea are related to variations in Atlantic inflow has been mentioned by several authors in the past (e.g. Storrow, 1932; Fraser, 1952; Turrell et al., 1996; Witbaard, 1996; Witbaard et al., 1997). Ecological changes, presumably related to long-term variations in Atlantic influence, have also been reported for the nearby English Channel, another area along the periphery of the northeast Atlantic (Southward, 1963, 1980; Cushing, 1980; Southward et. al., 1988).

Along the northern border of the North Sea, important inflows of Atlantic water occur (Fig. 2.1). Especially the two inflows on the northwestern side, the Fair Isle Current and the East Shetland Atlantic Inflow, are considered to provide essential inputs of nutrients to the northern and central North Sea (Dooley, 1981; Turrell, 1992a,b, Turrell et al., 1992). A change in these currents, particularly if sustained for a number of years, would significantly affect food production for pelagic fish. In addition, pelagic fish might respond directly to a change in currents because of their preference for specific types of water.

It is difficult, however, to find direct evidence for variations of the Atlantic inflow from hydrographic data. There are no long-term series of current measurements at the positions of the major inflows, since intensive trawling in these areas prohibits the use of moored current meters. Salinity and temperature data for the North Sea do not give clear indications about changes of Atlantic inflow, since these parameters also vary in the inflowing water itself.

An indirect method to study variations of Atlantic inflow is to look at the plankton composition in the North Sea. The inflowing Atlantic water is characterised by a number of plankton species that are not indigenous to the North Sea. Even after the Atlantic water has been mixed with North Sea water, its presence can be detected from the occurrence of these Atlantic "indicator species". Earlier plankton workers have often estimated the amount of Atlantic influence in the northern and central North Sea on the basis of such plankton indicator species (Storrow, 1932; Fraser, 1952; Glover, 1955, 1957; Rae, 1956; Williamson, 1963; Glover and Robinson, 1965; Bainbridge and Forsyth, 1972; Bainbridge et al., 1978).

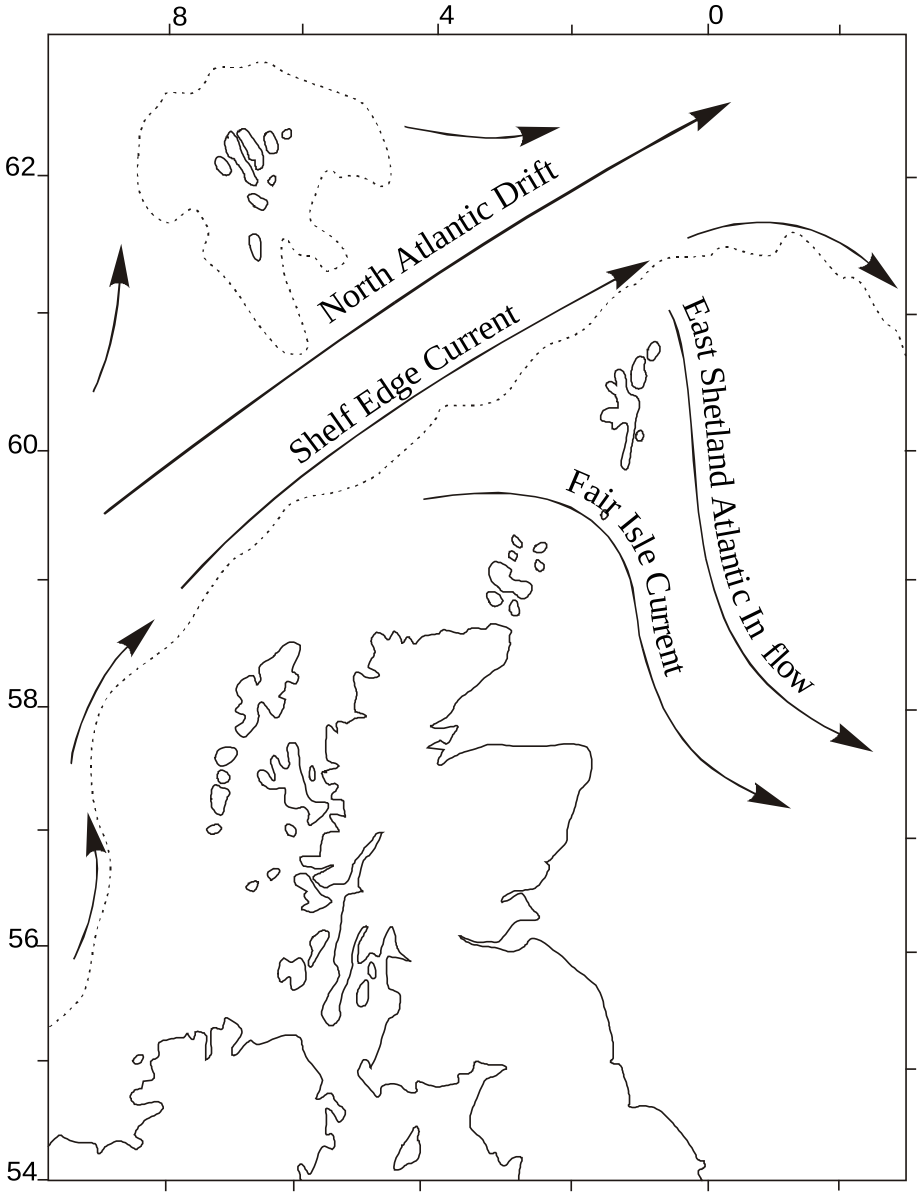

Figure 2.1. Inflow of Atlantic water to the northwestern North Sea. After Svendsen et al. (1995).

In the present study, the hypothesis of a reduced Atlantic inflow in the 1960s and 1970s is investigated by considering the presence of Atlantic indicator species in the North Sea during the years 1948-1996. Variations in Atlantic plankton in the North Sea are considered to reflect variations of Atlantic inflow, provided two conditions are met: (a) the variations in Atlantic species in the North Sea should be independent of variations of the same species in the area where the inflowing water originates from, and (b) the variations of Atlantic species in the North Sea should be independent of variations of indigenous species in the same area.

2.2. Material and methods

Time series of the abundance of various plankton species in the North Sea and to the west of the British Isles were obtained from the Continuous Plankton Recorder (CPR) data base at the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in Plymouth. CPR samples are collected by ships of opportunity (mainly merchant vessels) on standard shipping lines across the North Sea and North Atlantic. The sampler is towed at a depth of approximately 10 m, and the water is filtered over a silk gauze with a mesh size of 270 µm. After the tow, the gauze is cut into sections that represent about 10 miles distance, and a filtered volume of approximately 3 m^3. A full description of the methods used in collecting and analysing the CPR samples is given by Warner and Hays (1994). For the present study, data were extracted for the entire period for which data were available in standard format, viz. the years 1948-1996.

The study focused on plankton species that arrive in the North Sea with the inflowing Atlantic water. In practice, these species show many gradations in "Atlantic character" . The most extreme Atlantic species are only found at the fringes of the North Sea. These species have a low tolerance for North Sea water, and they stop reproducing and perish when they are transported farther into the North Sea. At the other side of the range we find species that adapt very well to North Sea conditions, and that reach high densities over large areas of the North Sea in summer and autumn.

For the present study, it was decided not to make an a priori selection of certain types of Atlantic species, but to include the whole range from strictly Atlantic to very tolerant species. The main feature selected for was an apparent transport of the species from the waters west of Scotland into the North Sea at some time of the year. The second criterion was that the species were fairly regular visitors to the North Sea. They had to occur at least in ten years during the period 1948-1996, and in at least 2 months during each of those ten years.

On the basis of a review of existing literature and consultations with scientists at SAHFOS, fourteen plankton species were selected that met these requirements. This group included six copepods, five diatoms, two molluscs, and one genus of annelid worms (Table 2.1). All the zooplankton species in this group (with the exception of *Calanus finmarchicus*) reach their maximum abundance in the North Sea in the second half of the year, and decline during the winter. These species apparently cannot survive the low winter temperatures in the North Sea. The diatoms, with the exception of *Dactyliosolen mediterraneus*, have a higher tolerance to low temperatures, and were about equally abundant in summer and winter.

The well-known Atlantic indicator species *Sagitta elegans* was not included in the list because the Chaetognatae in most of the CPR samples have not been identified to species level. For another Atlantic species, *Salpa fusiformis*, the identification in some periods was considered unreliable by SAHFOS experts, so this species was ignored as well.

A problematic case was the genus *Calanus*, which was not identified to species level in the years 1948-1957. The genus *Calanus* in the North Sea is composed of two species, *C. finmarchicus* and *C. helgolandicus*, the first of which presumably arrives in the northern North Sea with the inflowing Atlantic water (Backhaus et al., 1994). This species could thus be a potential indicator of Atlantic inflow. *Calanus finmarchicus* makes up the bulk of the *Calanus* population in the northwestern North Sea. The average for the period 1958-1979 was 97% in the first half of the year and 78% in the second half of the year. Therefore, the annual index for total *Calanus* in this area (which was available for the entire study period) was used as an approximation for the abundance of *C. finmarchicus*.

Taxon	Species	References
Algae, Bacillariophyceae	*Dactyliosolen mediterraneus*	7,12
	Rhizosolenia alata f. *indica*	7,12
	Rhizosolenia alata f. *inermis*	7,12
	Thalassiothrix longissima	7,12
	Nitzschia seriata	7,12
Annelida, Polychaeta	*Tomopteris* spp.	4,6,10
Copepoda, Calanoida	*Calanus finmarchicus*	4,6,7,9.11
	Candacia armata	1,4,6,7,8,9,11
	Eucalanus crassus	2,7,12
	Euchaeta hebes	7,12
	Metridia lucens	1,4,6,7,8,9,11
	Rhincalanus nasutus	2,7,12
Mollusca, Gastropoda	*Clione limacina*	2,4,6,7,12
	Limacina retroversa	4,6,7

Table 2.1. Atlantic indicator species in the northwestern North Sea.
Based on: (1) Rae and Fraser, 1941; (2) Fraser, 1952; (3) Rae, 1956; (4) Glover, 1957; (5) Williamson, 1963; (6) Bainbridge and Forsyth, 1972 ; (7) Oceanographic Laboratory Edinburg, 1973; (8) Lee and Ramster, 1977; (9) Fransz et al., 1991; (10) Reid et al., 1992; (11) Krause et al., 1995; (12) T. John and T. Jonas, pers. commun., 1998.

The study area in the North Sea was defined as the waters between 56° to 60°N and 3°W to 2°E. This area comprises the part of the North Sea that is directly influenced by the Atlantic inflow along the northwestern edge (Fig. 2.2). It is also the area were important changes in pelagic fish stocks were observed in recent decades. Within this area, monthly means of all sample values for each species were computed. These monthly means were then averaged to obtain annual indices for each species in each of the years 1948-1996. Data were available for all but three months during the entire study period.

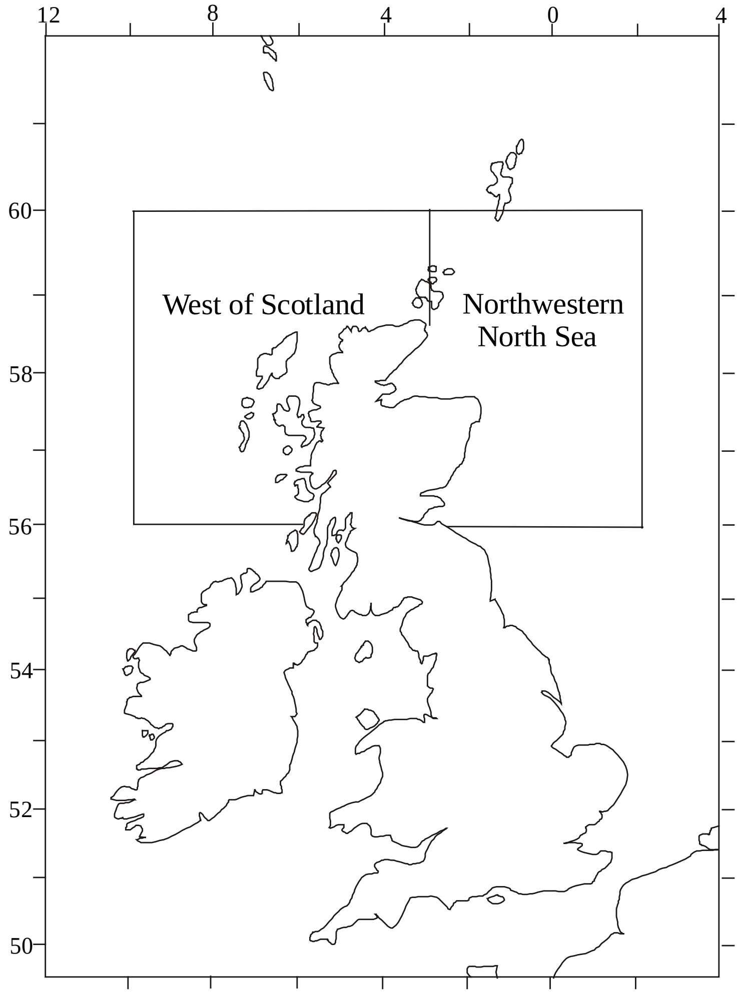

Figure 2.2. The two areas used for analysis of CPR data.

Variations in abundance of Atlantic species in the North Sea could be a function of the density of these organisms in the inflowing Atlantic water. To investigate this possibility, the abundance of Atlantic species was also calculated for the area from which the inflow into the northwestern North Sea originates. This source area was defined as the waters north and west of Scotland between 56° to 60°N and 3°W to

10°W (Fig. 2.2). For each of the Atlantic species listed in Table 2.1, an index series for this area was calculated in the same way as for the northwestern North Sea.

Another possible cause of variation in Atlantic species in the North Sea is the variation within the North Sea ecosystem itself. Atlantic species that easily adapt to North Sea conditions might reflect not only variations in Atlantic inflow, but also varying ecological conditions in the North Sea. In order to establish which of the variations in Atlantic species were presumably of North Sea origin, the index series of Atlantic species were compared to a similar series for the most common neritic species in the North Sea. Based on existing literature (Oceanographic Laboratory Edinburgh, 1973; Fransz et al., 1991), the species and genera selected as representative of the North Sea neritic community *were Temora longicornis*, *Acartia* spp., *Para-* and *Pseudocalanus* spp., and *Oithona* spp. Index series for these species were calculated in the same way and for the same areas as for the Atlantic species.

The existence of common trends within the group of Atlantic species in the North Sea was investigated by Principal Component Analysis (PCA). PCA is a multivariate technique that identifies axes of maximum variability in a multi-dimensional space of data points. Each axis (or principal component) represents a variance that is independent of the variance measured by the other axes. Species that show similar variations over time have high positive loadings on one or more of the principal components.

A common variation in one direction (i.e. a high positive or negative loading on one principal component) does not necessarily mean that this variation is caused by only one environmental factor. The group of species concerned may respond in the same way to a number of factors that work simultaneously. Conversely, groups of species that have high positive or negative loadings on different axes are not necessarily affected by different environmental factors. If two groups of species respond in different ways to the same environmental factor, they will have high positive or negative loadings on different principal components. It is dangerous, therefore, to relate individual principal components to individual environmental factors.

In this paper, PCA is used merely to identify sub-groups of species with a similar behaviour over time. For each sub-group, an index series is calculated by first standardising the annual abundance indices for each species, and then taking the means of the standardised indices. Differences and similarities between trends in various sub-group are then interpreted on the basis of the biological characteristics of the species within each group.

2.3. Results

Annual abundance indices for each of the Atlantic species listed in Table 2.1 are presented in Fig. 2.3 for the period 1948-1996. The values for the northwestern North Sea are shown together with those for the area west of Scotland, presented on the same scale. A corresponding set of graphs for neritic species is shown in Fig. 2.4.

The results of PCA indicate that the entire set of fourteen Atlantic species in the North Sea does not show clear common patterns (Fig. 2.5). The first principal component explains only 21% of the total variance in the data, and the second principal component only 19% (Table 2.2). The lack of a strong common signal in the Atlantic species indicates that the strength of the Atlantic inflow into the North Sea is not the dominating factor for all of them, or that different species may be affected by different spatial or temporal components of this inflow.

Table 2.2 . Results of a PCA for 14 Atlantic species or species groups in the northwestern North Sea: loadings on four axes (P1-P4).

Principal components	P1	P2	P3	P4
Percentage total variance explained	20.8	18.5	10.9	9.0
component loadings				
Limacina retroversa	0.797	-0.283	0.146	0.062
Candacia armata	0.695	0.508	0.185	-0.092
Calanus spp.	0.593	-0.468	0.123	0.220
Metridia lucens	0.589	0.341	-0.259	0.415
Tomopteris spp.	0.587	0.301	-0.008	-0.441
Clione limacina	0.562	-0.386	0.223	0.170
Euchaeta hebes	0.031	0.865	0.130	-0.142
Eucalanus crassus	0.081	0.596	0.314	0.030
Rhincalanus nasutus	0.219	0.584	-0.337	-0.015
Dactyliosolen mediterraneus	0.113	-0.004	-0.766	-0.092
Nitzschia seriata	0.041	0.130	-0.580	0.539
Rhizosolenia indica f. *indica*	-0.060	0.116	0.351	0.522
Rhizosolenia indica f. *inermis*	-0.479	0.099	0.052	0.005
Thalassiothrix longissima	0.368	-0.446	-0.236	-0.463

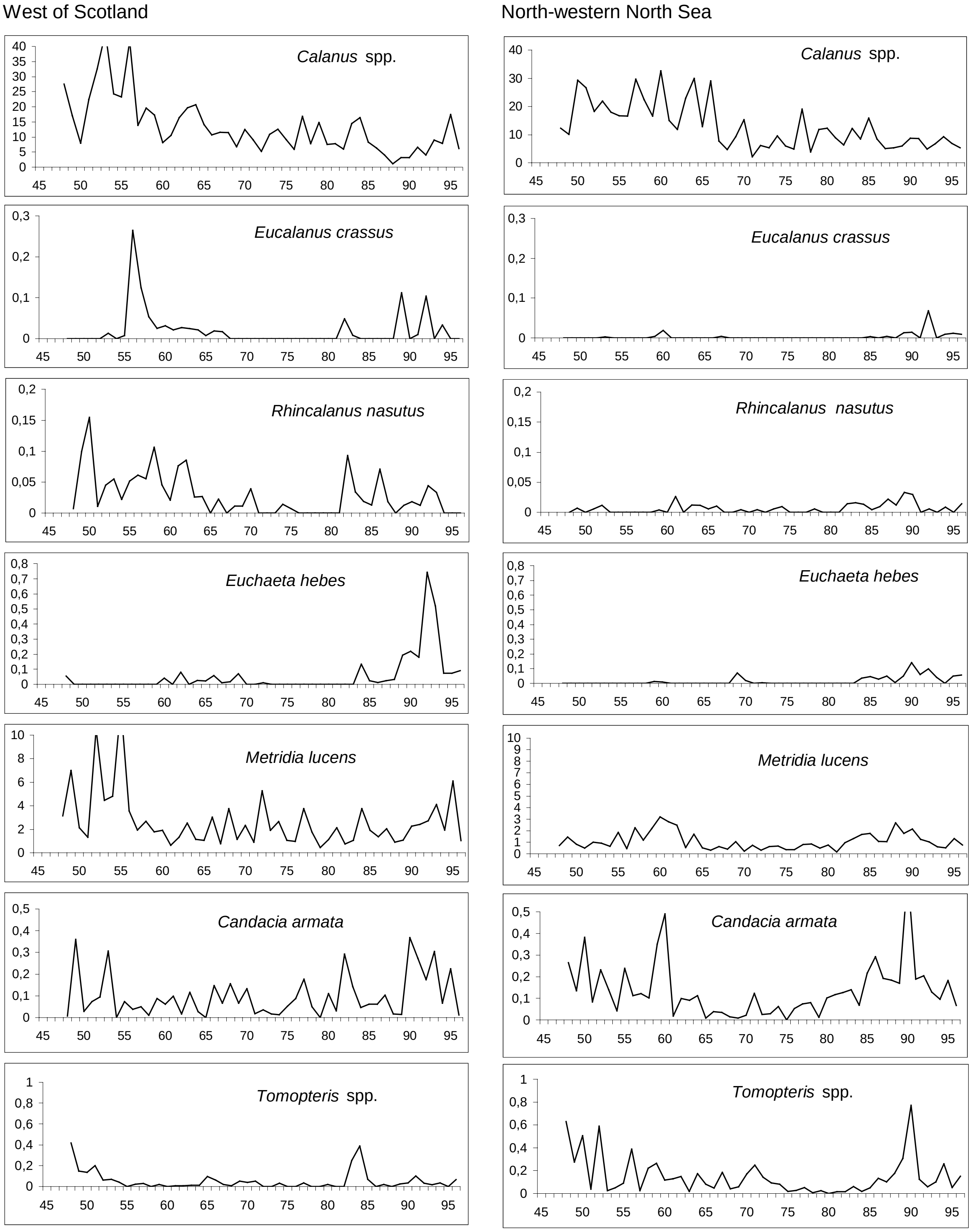

Figure 2.3. Long-term time series for fourteen Atlantic plankton species in the northwestern North Sea (right-hand column) compared to series for the same species to the west of Scotland (left-hand column). Abundances in mean numbers per sample.

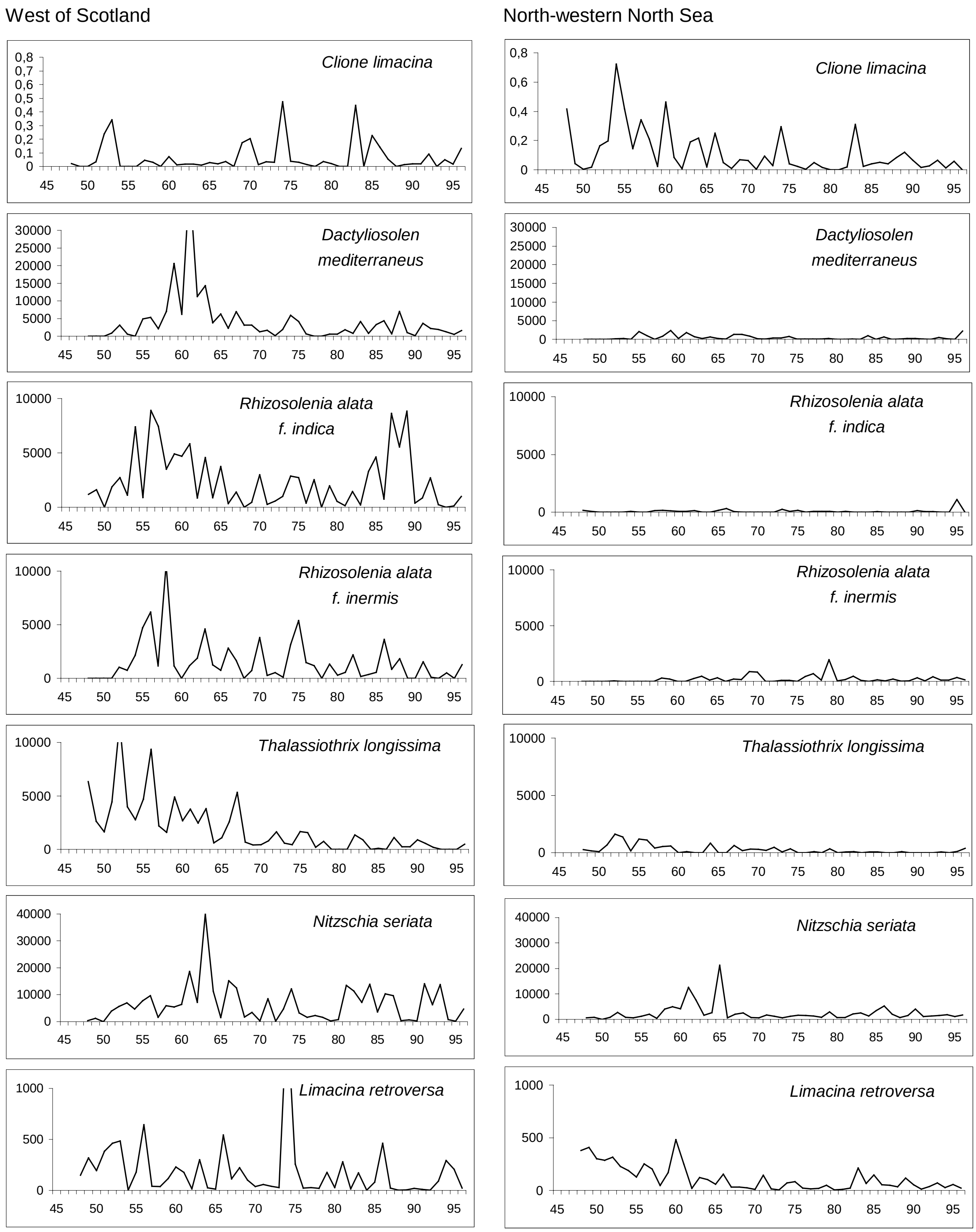

Figure 2.3. continued

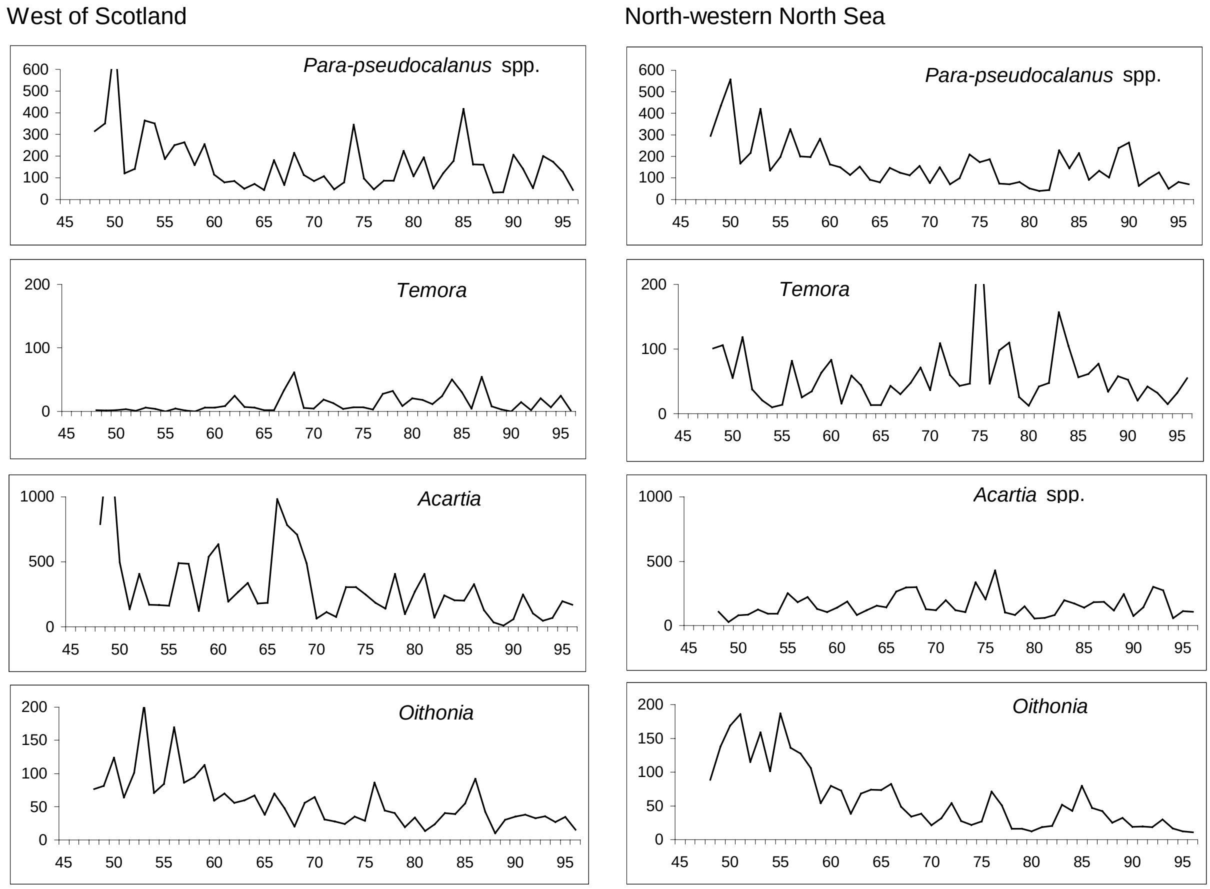

Figure 2.4. Long-term time series for four neritic plankton taxa in the northwestern North Sea (right-hand column) compared to series for the same species to the west of Scotland (left-hand column). Abundances in mean numbers per sample.

Although the total group of Atlantic species does not behave in a uniform way, the plot in Fig. 2.5 allows us to identify sub-groups that exhibit similar variations over time. These sub-groups, labelled after their most characteristic species, are the following.

(a) The "*Candacia armata* group" with high positive loadings on both axes: *Candacia armata*, *Metridia lucens*, and *Tomopteris* spp. The species in this group are restricted to areas in the northwestern and western North Sea that directly receive inflowing Atlantic water. They appear in the North Sea in the second half of the year, and they survive in this area for several months before they decline or even disappear at the beginning of the new year.

(b) The "*Calanus* group", with high positive loadings on P1, and negative loadings on P2. This group consists of *Calanus* spp., *Limacina retroversa*, *Clione limacina*, and

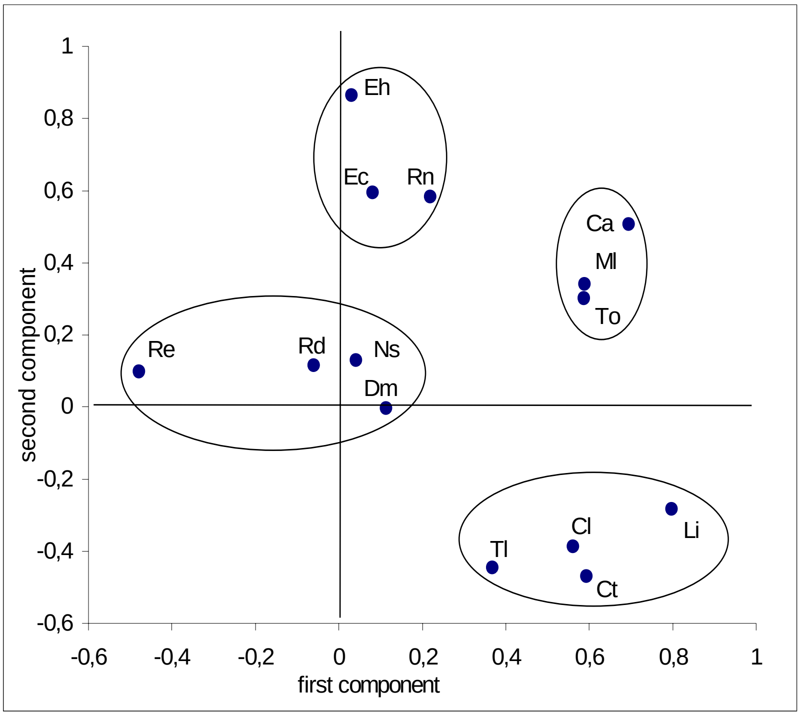

Figure 2.5. Results of a PCA for Atlantic species in the northwestern North Sea. The plot presents loadings of each species on the first two principal components. Eh = *Euchaeta hebes*, Ec = *Eucalanus crassus*, Rn = *Rhincalanus nasutus*, Ca = *Candacia armata*, Ml = *Metridia lucens*, To = *Tomopteris* spp., Li = *Limacina retroversa*, Cl = *Clione limacina*, Tl = *Thalassiothrix longissima*, Ct = *Calanus* total, Dm = *Dactyliosolen mediterraneus*, Ns = *Nitzschia seriata*, Rd = *Rhizosolenia indica* f. *indica*, Re = *Rhizosolenia indica* f. *inermis*.

Thallasiothrix longissima. This group consists mainly of zooplankton species with a wide distribution in the northern and central North Sea. Despite their Atlantic origin, these species appear to thrive in the North Sea, and their numbers in the North Sea are as high, or even higher, than to the west of Scotland. The exception is the diatom *Thalassiothrix longissima* which, like the other Atlantic diatoms, declines rapidly after entering the North Sea.

(c) The "*Euchaeta hebes* group", with high positive loadings on the second principal component. This group comprises *Eucheata hebes*, *Eucalanus crassus*, and *Rhincalanus nasutus*. In the North Sea, all three species are restricted to the regions of Atlantic inflow, and the densities in the North Sea are much lower than in the source waters to the west of Scotland. The first two members of this group are Lusitanian species that originate from the waters off the Iberian peninsula. The third one, *R. nasutus* has a wider Atlantic distribution, but it can also be considered as a typical southern species (Farran, 1910; Oceanographic Laboratory Edinburgh, 1973). The three species apparently can not adjust to North Sea conditions, and they disappear soon after entering the North Sea.

(d) The rest group, with small or negative loadings on the first and second principal components. This group consists entirely of diatoms: *Dactyliosolen mediterraneus*, *Rhizosolenia alata* f. *indica*, *R. alata* f. *inermis*, and *Nitzschia seriata*. All these species decline rapidly after they have entered the North Sea, and their numbers in the North Sea are very low compared to those to the west of Scotland. The short life span of these species reduces their significance as indicators of Atlantic influence. This probably explains the low co-variance between these species and the more long-lived Atlantic plankton species.

Within each of the above sub-groups, the annual indices for the northwestern North Sea show similar variations over the period 1948-1996. To illustrate these variations, an index series has been constructed for each of the groups (Fig. 2.6). The annual index for each group was calculated by first standardising the data series for each species, and then taking the mean of the standardised indices within each year.

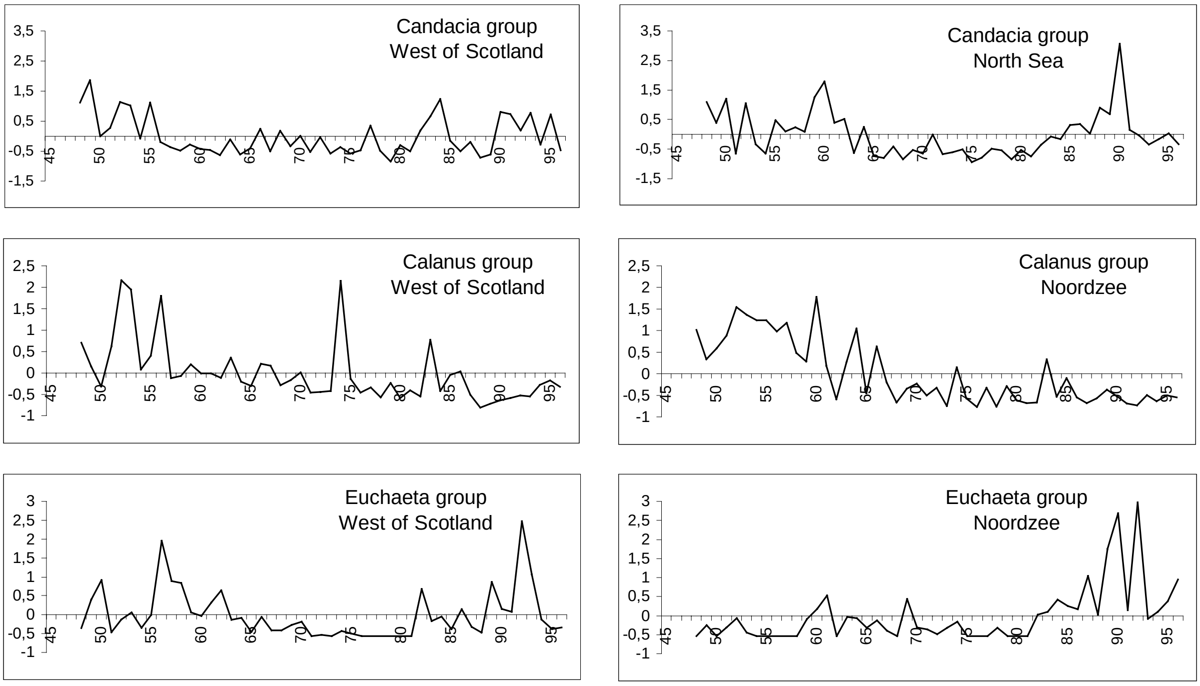

Figure 2.6. Long-term index series for three sub-groups of Atlantic species in the northwestern North Sea and to the west of Scotland. The index for each year is the mean of the standardised abundances of the individual species in that year.

The index series for each group in the northwestern North Sea is compared with the series for the same group to the west of Scotland, to investigate whether the variations in the North Sea are a reflection of similar variations in the area where the Atlantic water originates from.

The index for the *Candacia* group in the North Sea shows an oscillating pattern, with maxima around 1960 and 1990, and a minimum from 1965 to 1982. This pattern is not seen in the same group to the west of Scotland. Here the *Candacia* group, after starting at a high level in the early 1950s, is low from 1956-1981, and fluctuates without trend in later years. Neither is the pattern of the *Candacia* group encountered in any of the North Sea neritic species (Fig. 2.4). The changes in the North Sea *Candacia* group, therefore, are not related to variations of the same species to the west of Scotland, nor to variations in the North Sea ecosystem. The only group that shows resemblance with the *Candacia* group in the North Sea is the *Euchaeta* group to the west of Scotland. The latter has peaks in the late 1950s and early 1990s, and a period of low abundance from 1965-82. This could indicate some connection between the two groups.

The *Calanus* group in the North Sea shows a strong decline between 1952 and 1968, and a low level in subsequent years. The same group to the west of Scotland also shows a decline starting from 1952, but here the decline is more persistent, and continues until 1988. The *Calanus* pattern is also clearly seen in two of the neritic taxa within the North Sea, *Para-pseudocalanus* spp. and *Oithona* spp., and to a lesser extent in the same groups to the west of Scotland. It appears that the changes in the North Sea *Calanus* group reflect a widespread declining trend in zooplankton, which is seen in Atlantic and neritic species, both in the North Sea and to the west of Scotland.

The *Euchaeta* group in the North Sea shows a pattern which is nearly the opposite of the *Calanus* group. Here the indices are very low during the period 1950-1981, and they increase to a maximum around 1990. The same group to the west of Scotland also has a maximum in the early 1990s, but here we also see an earlier maximum in the late 1950s. The *Euchaeta* group in the North Sea thus partly reflects variations of the same group to the west of Scotland.

2.4. Discussion

2.4.1. Relation between plankton and Atlantic inflow

The various sub-groups of Atlantic species in the North Sea exhibit different patterns over time which may or may not be related to variations in Atlantic inflow. To interpret the differences between the sub-groups, we will consider the biological characteristics of each group, and also the relationship between the same groups in different areas, and between different groups in the same area.

The declining trend in the *Calanus* group in the North Sea is not restricted to the Atlantic species in this area, but it is also observed in some important neritic taxa. There is no reason, therefore, to assume a connection with the amount of Atlantic influence in the North Sea. The *Calanus* group (with the exception of *Thalassiothrix longissima*) consists of zooplankton species that strongly reproduce in the North Sea, and spread over large parts of it. In this respect, the species behave like indigenous North Sea species. The declining trend of the *Calanus* group in the North Sea thus seems to be a reflection of a change in the North Sea ecosystem, rather than a change in Atlantic inflow.

A declining trend in North Sea diatoms and zooplankton from 1950 to 1970-80 has been reported in many earlier studies based on CPR material (e.g. Colebrook, 1978; Reid, 1978; Radach, 1984; Colebrook et al., 1984; Aebischer et al., 1990; Fransz et al., 1991; CPR Survey Team, 1992). The supposed cause, a direct atmospheric effect on the surface waters, apparently also affected plankton production in the adjacent waters west of Scotland (Radach, 1984; Colebrook, 1986). The results presented here confirm the declining trend in some zoo- and phytoplankton species in the area west of Scotland (e.g. *Calanus* spp., *Limacina retroversa, Rhincalanus nasutus, Rhizosolenia alata* f. *inermis,* and *Thalassiothrix longissima*).

Contrary to the changes in the *Calanus* group, the variations in the *Candacia* group are more likely to reflect changes in Atlantic inflow in the North Sea. All species in this group have a strong Atlantic character. The species have different food requirements, so their parallel variations in the North Sea can not be a function of changes in food supply. This is confirmed by the observation that none of the North Sea neritic species in the area exhibits the pattern of the *Candacia* group. Neither are the variations in the North Sea a reflection of changes in the *Candacia* group to the west of Scotland. This leaves only one plausible explanation for the synchronous changes of the three species in the North Sea, namely a corresponding variation in Atlantic inflow.

The index for the *Candacia* group suggests that the Atlantic inflow in the northwestern North Sea was reduced from 1965 to 1982. A plot of monthly abundance indices of *C. armata* and *M. lucens* (Fig. 2.7) shows that during this period not only the annual abundance of the two species was reduced, but that also the time of appearance in the North Sea was delayed by one or two months. Data for *Tomopteris* spp. (not shown here) contain the same feature.

The variations of the *Euchaeta* group also seem to have an Atlantic origin. The species in this group have an even more pronounced Atlantic character than the

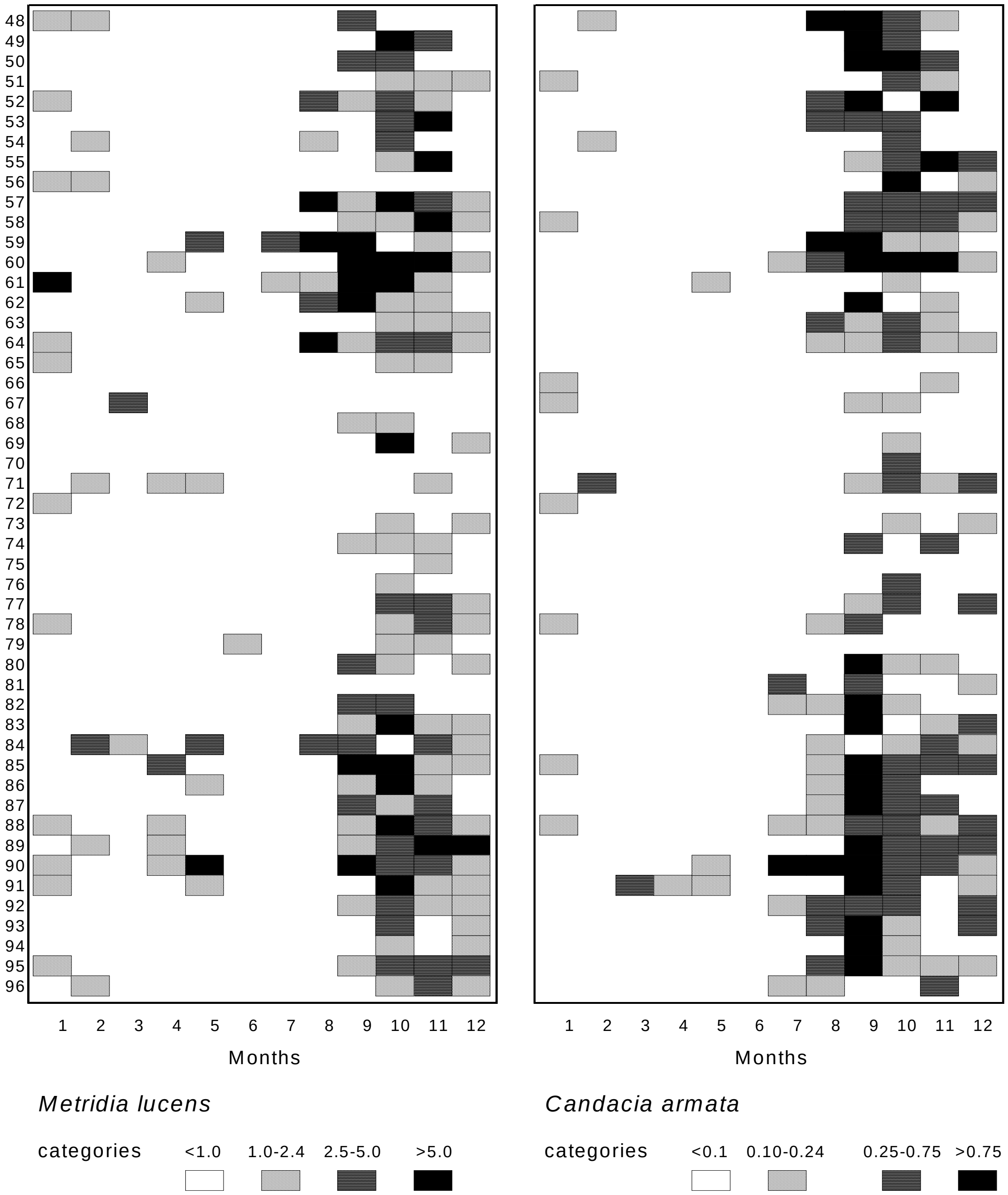

Figure 2.7. Monthly abundances of Metridia lucens and Candacia armata in the northwestern North Sea. Years are on the Y-axis and months on the X-axis. Values are mean numbers per sample.

species in the *Candacia* group. The pronounced maximum in this group after 1985 coincides with a similar maximum of the same species to the west of Scotland. This could indicate that the maximum in the North Sea is caused by a higher density of the species in the inflowing Atlantic water. However, the other maximum of the *Euchaeta* group to the west of Scotland, in the late 1950s, was not seen in the North Sea. This means that the density of these species in the North Sea is not simply a reflection of the abundance of the same group to the west of Scotland. If this is the case, the increased abundance in the North Sea after 1985 is probably caused by an increased Atlantic inflow in this area.

2.4.2. The best indicator species for Atlantic inflow

Summarising the above observations, it appears that variations of Atlantic inflow in the North Sea are most clearly expressed by species in the *Candacia* group. These species take an intermediate position between the *Calanus* group and the *Euchaeta* group. They are sufficiently "alien" to the North Sea not to be affected by the trends of the indigenous plankton in the area. At the same time, they survive long enough to mark the presence of Atlantic water in the northwestern North Sea. For this reason they are more suitable as indicators of Atlantic inflow than the extreme Atlantic species of the *Euchaeta* group. The species in the latter group normally decline very quickly in the North Sea, except in situations of an extreme inflow of (southern) Atlantic water.

Within the *Candacia* group, the two copepods *Candacia armata* and *Metridia lucens* already have a reputation as "classical" indicators of Atlantic inflow in the northwestern North Sea (Farran, 1910; Rae and Fraser, 1941; Rae and Rees, 1947; Glover, 1957; Bainbridge and Forsyth, 1972; Fransz et al., 1991; Krause et al., 1995). The third taxon in this group, *Tomopteris* spp. is probably a "less perfect" indicator of Atlantic influence because it is composed of more than one species. The genus occurs over a wider area in the North Sea than *Candacia armata* and *Metria lucens*, and is there is a suspicion that their survival and reproduction may be higher than in the truly oceanic copepods (H.G. Fransz, pers. commun., 1998). The best possible plankton index for Atlantic inflow in the northwestern North Sea, therefore, seems to be the combined index for *Candacia armata* and *Metridia lucens*. This index, presented in Fig. 2.8, has a more well-defined optimum around 1960 than the index for the total *Candacia* group.

It should be noted that the *Candacia/Metridia* index is only indicative of variations of Atlantic influence in the second half of the year. These variations may be independent of changes in Atlantic influence during the first part of the year. A second reservation to be made is that the variations in Atlantic influence do not necessarily indicate a variation of the volume of the inflow into the North Sea. Changes in Atlantic influence could also be caused by variations in the Atlantic component of the mixed water masses that enter the North Sea. Finally, as the CPR data refer only to the upper 10 m of the water column, caution should be used in extrapolating the findings to the entire water column.

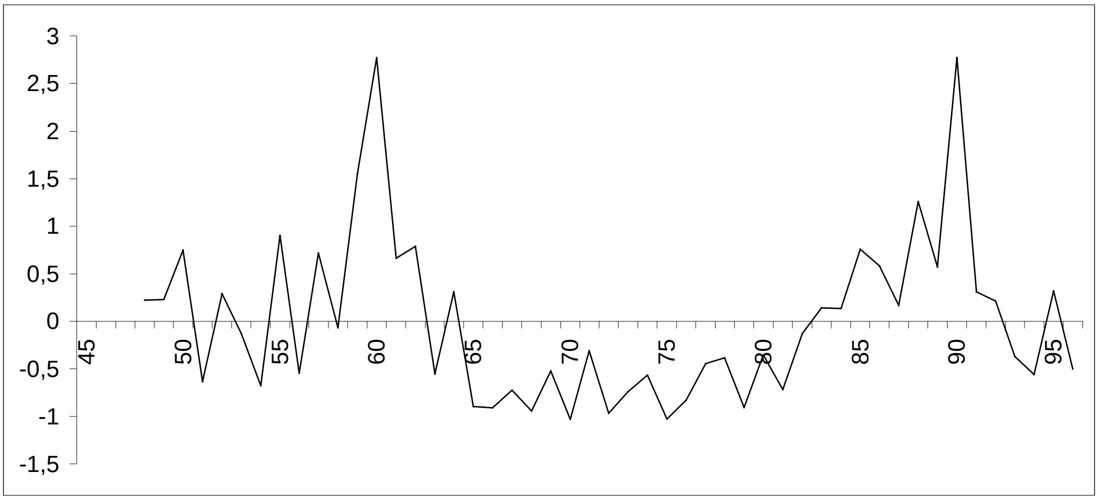

Figure 2.8. Long-term series of a combined index for Candacia armata and Metridia lucens in the northwestern North Sa. The index for each year is the mean of the standardised abundances of the individual species in that year.

2.4.3. *Candacia* pattern originates from outside the North Sea

Although the *Candacia* group to the west of Scotland does not exhibit the long-term variation seen in the North Sea, there are other species to the west of Scotland that vary in the same manner as the *Candacia* group in the North Sea. Examples are the species in the *Euchaeta* group, and also some Atlantic diatoms such as *Rhizosolenia alata* f. *indica* and *Dactyliosolen mediterraneus*. The fact that the *Candacia* pattern is also seen in some species to the west of Scotland indicates that the pattern probably originates from outside the North Sea.

An explanation for the absence of the long-term oscillation in the *Candacia* group west of Scotland, is that variations in transport of Atlantic water probably have the strongest effect on Atlantic species that are near the limit of their distribution. To the west of Scotland, the members of the *Candacia* group are well within the limits of their geographical range, so they will not be sensitive to variations in Atlantic transport. This situation is different for the members of the *Euchaeta* group, which reach the northern limit of their distribution to the west of Scotland. Variations in Atlantic transport will therefore have a stronger effect on this group than on the *Candacia* group in the same area. In the North Sea it is the *Candacia* group that reaches the limits of its distribution, and for this reason is most sensitive to variations of Atlantic influence. For the *Eucheata* group, the North Sea is already beyond the limits of its normal distribution. This group is of little use, therefore, to monitor normal variability of Atlantic influence in the North Sea. Only during episodes of exceptional input of (southern) Atlantic water will the species show up in the North Sea.

We may conclude that the episodes of increased Atlantic influence in the North Sea coincided with an increased occurrence of southern Atlantic water to the west of Scotland. The two maxima of the *Candacia* group (and even more so of the *Candacia/Metridia* index) in the North Sea are also seen in the *Euchaeta* group to the west of Scotland. In the North Sea, only the second maximum of the *Candacia* pattern is visible in the *Euchaeta* group. During this second maximum, the Atlantic water entering the North Sea probably was of a more southern origin than during the first maximum.

2.4.4. Comparison with hydrographic data

There are few hydrographic observations that can be used to validate the conclusions about variations of Atlantic influence, based on the changes in the *Candacia* group. However, the limited current measurements that do exist are in agreement with the plankton data. During the JONSDAP programme in 1976, no inflow of Atlantic water was measured to the east of Shetland (Riepma, 1980). This was a surprising outcome, as earlier work had suggested an important inflow of Atlantic water east of Shetland during summer and autumn (Turrell et al., 1992). The data presented in this paper show that JONSDAP'76 fell within the period of minimum abundance of the *Candacia* group, and thus in the period of presumed low Atlantic influence. Turrell et al. (1992) already suspected that the currents in the North Sea in 1975-1980 had been anomalous, and they suggested a reduction of the transport of Atlantic water into the North Sea at that time. The observations during JONSDAP'76 suggest that the reduced Atlantic influence during the 1970s was due to a reduced volume of the inflow into the North Sea, rather than to a reduction of the Atlantic content of the inflowing water.

The presence of Atlantic water of southern origin in the North Sea around 1990 is confirmed by observations of exceptionally high salinities, both in the northern North Sea (Heath et al., 1991) and in the southern North Sea (Becker et al., 1992). Apparently, the saline Atlantic water that had moved north from the Bay of Biscay entered the North Sea both from the north and from the south.

2.5. Conclusion

The minimum of the *Candacia/Metridia* index in1965-1980 corresponds to the period when Atlantic fish species in the northwestern North Sea declined and sprat, a neritic species, increased. The plankton data thus support the hypothesis that the long-term changes in pelagic fish stocks in the northwestern North Sea were caused by a sustained reduction of Atlantic inflow in this area.

Acknowledgments

I am greatly indebted to Chris Reid and the other members of the SAHFOS team for their help and encouragement during my work in Plymouth with the CPR data. Valuable comments on earlier versions of the manuscript were provided by George Fransz, Wim Wolff, Winfried Gieskes, Ger Jan Piet, and two anonymous referees. Financial support for the work at SAHFOS was provided by the Netherlands Organization for Scientific Research (NWO).

Chapter 3

The reappearance of spawning herring on Aberdeen Bank in 1983 and its relationship to environmental conditions

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Abstract

Evidence is presented in support of the hypothesis that the reappearance of spawning herring on Aberdeen Bank in 1983, after an absence of 16 years, was related to an increased Atlantic inflow in the area. Two Atlantic copepod species, *Metridia lucens* and *Candacia armata*, showed a simultaneous increase in the years when spawning herring returned to Aberdeen Bank. During the late 1960s, both species declined at the time when the spawning population on Aberdeen Bank disappeared. Earlier work has demonstrated that an increased Atlantic inflow results in a southward displacement of plankton concentrations and feeding herring in the northwestern North Sea. I hypothesise that such a southern distribution of the herring stock, caused indirectly by the increased Atlantic inflow, influenced recruit spawners to choose the nearby Aberdeen Bank as their spawning ground in 1983. Fluctuations of the spawning populations in the northern North Sea during earlier decades are explained by switches of recruitment between the northern and southern population, as a result of variations in latitudinal distribution of the recruiting year-class.

3.1. Introduction

During the annual herring larvae survey in the North Sea in 1983, large numbers of herring larvae were detected on Aberdeen Bank, an area where no spawning had been observed during the previous 16 years but where heavy spawning used to take place in the 1950s and 1960s. In these earlier years, the "Buchan" fishery for pre-spawning and spawning herring in the vicinity of Aberdeen Bank was one of the most important herring fisheries in the North Sea. The re-appearance of herring larvae on Aberdeen Bank in 1983 has been described in detail by several authors (Kiørboe and Johanson 1986, Munk et al. 1986, Richardson et al. 1986). None of these, however, addressed the question of the origin of the spawning herring on Aberdeen Bank, or what made them suddenly choose Aberdeen Bank as a spawning ground. The reappearance of larvae on Aberdeen Bank happened at a time when the North Sea herring stock was increasing after a period of stock depletion, and most scientists probably considered the spawning at Aberdeen Bank as a kind of “overflow” from the population at Shetland/Orkney, the spawning grounds of which are situated about 300 km further north (Fig. 3.1).

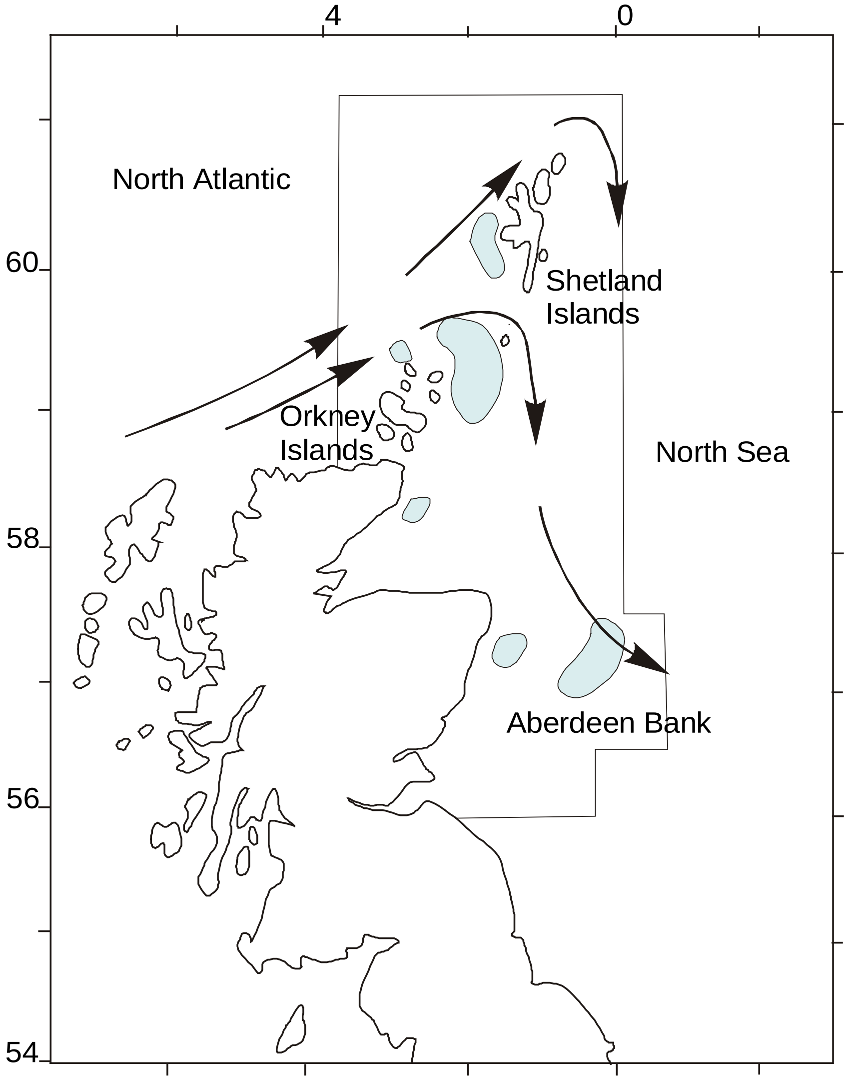

Figure 3.1. Herring spawning areas in the northwestern North Sea (adapted from Rankine 1986). Also indicated are the main inflows of Atlantic water. The sampling area for herring larvae is indicated by the box.

Observations on the Buchan population in earlier decades, however, indicated that this stock did not depend merely on an overflow of individuals from the Shetland/Orkney population. Although the two populations were very similar in their distribution and annual migrations (Fig. 3.2), their stock sizes had shown long-term variations that were independent, or even the opposite, of each other. Glover (1955, 1957) showed that the driftnet fishery for pre-spawning herring off the Scottish east coast shifted south between 1947 and 1954, causing prosperity to the southern (Buchan) ports of Peterhead and Fraserburgh, while the fishery at Shetland collapsed. The increased herring catches on the Buchan grounds coincided with an increased quantity of herring food in this area, and an earlier appearance of plankton species associated with oceanic water. After the boom of the 1950s, the Buchan fishery near Aberdeen Bank declined in the 1960s, while the fishery at Shetland recovered. Bainbridge and Forsyth (1972) and Bainbridge et. al (1978) showed that these developments coincided with a decline of the main food organisms of the herring, *Calanus finmarchicus* and *Spiratella (=Limacina) retroversa*, in the Buchan area after 1958. The virtual disappearance of the Buchan pre-spawning fishery from 1966 to 1969 coincided with an extreme scarcity of these food items in the Buchan area. The annual fluctuations in the abundance of *Calanus* and *Spiratella* in the Buchan area appeared to be largely determined by variations in the strength of Atlantic inflow into the northwestern North Sea.

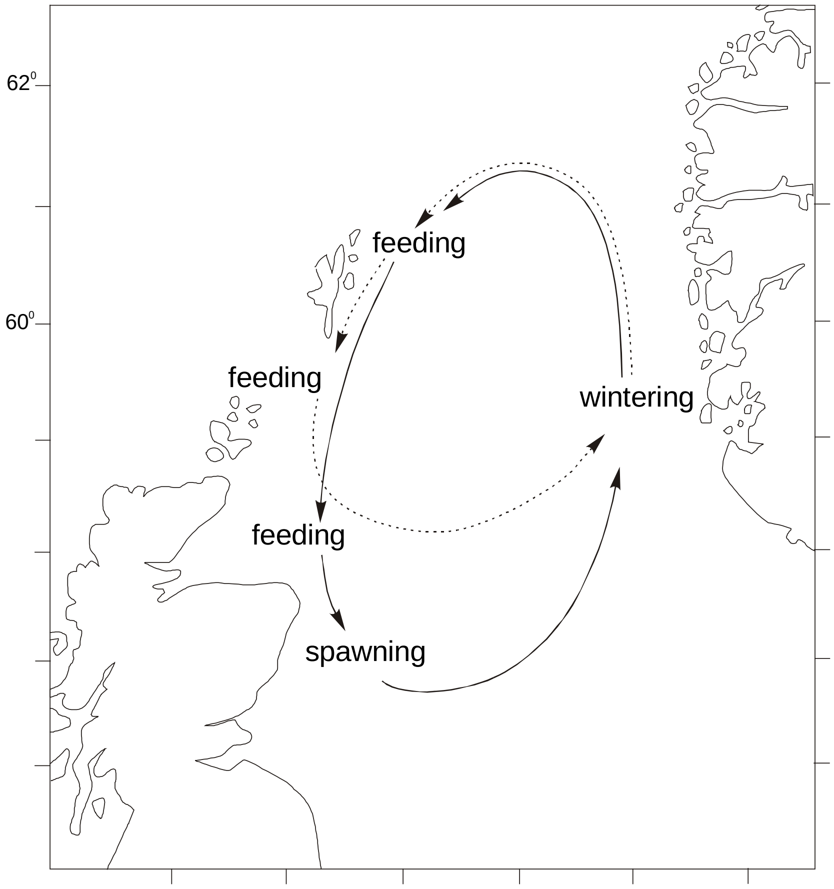

Figure 3.2. Seasonal migrations of the Buchan (solid lines) and Shetland/Orkney (broken lines) herring populations.

The decline of the fishery in the Buchan area was accompanied by a reduction of the larval production in this area. Saville (1971, 1978) presented the results of Scottish herring larvae surveys from 1951 - 1967, which showed that the abundance of larvae on Aberdeen Bank was high in the early 1950s, but gradually decreased to zero in

1967. At the same time, the abundance of larvae in the region of the Orkneys strongly increased.

The results of these investigations show that the Buchan population in earlier years changed independently from the Shetland/Orkney population. Spawning on Aberdeen Bank was at a maximum when the Atlantic inflow into the northwestern North Sea seemed to be strong, and when food abundance was high in the Buchan area in the months prior to spawning. This suggests that the intensity of spawning at Aberdeen Bank is a function, either directly or indirectly, of the Atlantic inflow into the northwestern North Sea.

If the spawning of herring at Aberdeen Bank is indeed dependent on the Atlantic inflow, the re-appearance of larvae in this area in 1983 must have been a symptom of increased Atlantic inflow into the northwestern North Sea. We shall investigate this hypothesis by looking at data on hydrography and the occurrence of plankton indicator species. Furthermore, the identity of herring populations in the northern North Sea is considered in the light of the re-appearance of larvae on the Aberdeen Bank. Was the reappearance due to the revival of a rudimentary population that had always persisted in this area, or was it due to colonisation by herring that came from elsewhere?

The question whether individual spawning populations represent self-contained stocks is important from a management point of view. It was discussed intensively in the North Sea area in the 1950s and 1960s (Postuma and Zijlstra 1958, Zijlstra 1958, 1964b, 1969, 1973, Parrish 1958, Kreft 1963, Schumacher 1963), but the interest in the subject declined in later years. In the meantime, North American scientists developed new concepts about stock structure in herring (Iles and Sinclair 1982, Smith and Morse, 1990, Stephenson and Kornfield 1990, McQuinn 1997). The reappearance of a spawning population at Aberdeen Bank provides an opportunity to apply these new concepts also to the North Sea situation.

3.2. Material and methods

3.2.1. Spawning grounds

The intensity of spawning on the various grounds in the northern North Sea was estimated from the abundance of small herring larvae, taken from ICES surveys conducted from 1972-1993 (Anon. 1985). A data base with the complete results of all surveys from 1972-1993 is kept at the Marine Laboratory in Aberdeen. The international sampling effort strongly declined in the early 1990s, and 1992 was the last year with a full coverage of the northwestern North Sea.

The distribution and abundance of herring larvae are only an indirect index of spawning intensity on the various spawning grounds. The survival of herring spawn and larvae is not constant from year to year, and also the distance that the larvae have drifted away from their hatching position may differ between years. To reduce the error introduced by differential mortality and drift, only the category of larvae <10 mm has been considered. Applying an average daily growth rate of 0.15 mm and a size at hatching of 6.7 mm, these larvae will be between 1 and 22 days old. Assuming a residual drift of 3.4 km/day, the larvae may have drifted up to 75 km away from their hatching ground (Munk et al. 1986). The majority of the larvae, however, will be less than 22 days old, and their position at the time of capture will be less than 75 km away from their hatching ground.

Data on numbers of larvae per square meter were extracted from the data base for all sampling stations in the north-western North Sea between 56°00’N and 62°00’N and between 4°00’W and 01°00’E (Fig. 3.1). This area, which includes the main spawning grounds at Orkney/Shetland and Aberdeen Bank, was covered each year between 1972 and 1992. For each year, mean densities per station were calculated for the first and second half of September, and then the values for both half-monthly periods were averaged. This procedure gives equal weight to both halves of the month, irrespective of sampling effort. Finally, the yearly values were averaged over 5-year periods.

3.2.2. Age distribution spawning herring

Age distributions of spawning herring taken on Aberdeen Bank were available from Dutch commercial catches in this area. During the first years when herring resumed spawning on Aberdeen Bank, the Dutch fleet apparently did not notice the concentrations of spawning herring, and no catches were taken. It was only from 1986 onwards that a fishery for spawning herring developed on Aberdeen Bank, and that samples of spawning herring from this region were collected under the routine sampling scheme for commercial catches of the Dutch fisheries research institute RIVO-DLO. Unfortunately, no samples of spawning herring were obtained from the Shetland/Orkney spawning grounds. In this area, the spawning grounds are situated mainly within the 12 mile fishing limit, and there was no Dutch fishery on spawning herring. The Marine Laboratory in Aberdeen could not provide age data for Shetland/Orkney spawners in the 1980s either.

3.2.3. Hydrographic data

Temperature and salinity data for the north-western North Sea were kindly provided by the ICES hydrographic service. Data were extracted for the month of August, which is the start of the spawning season in the northern North Sea. Sampling intensity was low during the period 1972-1992, and insufficient data were available to construct a time series for the Aberdeen Bank area. As a substitute, a series of surface temperature and salinity data was constructed for the entire northwestern North Sea, extending from 02°00'W to 02°00'E, and from 56°00'N to 61°00'N. Even for this larger area, the number of samples in August dropped below 50 in most of the years after 1980, and for the years 1989-1991 no samples were available at all.

3.2.4. Plankton indicator species

The oceanic influence in the north-western North Sea can also be estimated from the occurrence of plankton indicator species. A large amount of plankton data for the north-western North Sea has been collected over the years from ships of opportunity by the Continuous Plankton Recorder (COR) survey, presently operated by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in Plymouth. Data from all surveys since 1948 are accessible from a computerised data base. A full description of the methods used in the CPR programme is given by Warner and Hays (1994).

Based on the results of earlier studies (Rae and Rees 1947, Lee and Ramster 1977, Fransz et al 1991, Krause et al. 1995), two copepod species, *Metridia lucens* and *Candacia armata*, were selected as indicators of oceanic influence in the northwestern North Sea. These species enter the North Sea each year in late summer with the inflowing Atlantic water, and they disappear from the North Sea in the first half of the year.

Mean numbers per CPR sample (3 m^3) for *M. lucens* and *C. armata* were calculated for the northwestern North Sea for each month in the period 1948-1996. The northwestern North Sea was defined as the area between 56° and 60°N, and between 2°E and 4°W. The choice of a relative wide sampling area was necessary in order to obtain a sufficient number of samples in each month (15-20 on average). Annual values for both species were derived by taking the mean of the monthly indices. A combined index for *M. lucens* and *C. armata* was constructed by standardising the annual values for both species (subtracting the mean and dividing by the standard deviation), and taking the average of the two standardised values in each year.

3.3. Results

3.3.1. Larval abundance

After a period of complete absence from 1972-1982, herring larvae appeared again on Aberdeen Bank in 1983 and remained present in subsequent years (Figs. 3.3 and 3.4). The re-colonisation of the Aberdeen Bank spawning ground happened very abruptly. In the preceding year (1982) there had been some larvae at the inshore spawning area near Peterhead, but herring larvae had been found here during most of the earlier years, and their occurrence had never been followed by spawning at Aberdeen Bank. However, in 1983 and particularly in 1984, large numbers of larvae suddenly appeared on Aberdeen Bank, making this area as important as the more northern spawning grounds at Shetland/Orkney. The Aberdeen Bank spawning ground retained a prominent position at least until the last year of full survey coverage (1992).

The charts of larvae distributions show that the spawning on Aberdeen Bank in 1983 was not the result of a gradual build-up of a small resident population in the area. In the years 1972-1980, not a single larva was taken on Aberdeen Bank during any of the surveys. The adult herring that spawned on Aberdeen Bank in 1983, therefore, could not have been born at this locality.

To investigate whether the spawning at Aberdeen Bank in 1983 was due to an overflow of the existing spawning population at Shetland/Orkney, the temporal trend of total larval abundance in the Shetland/Orkney area is compared with larval abundance at Aberdeen Bank (Fig. 3.5). It is seen that the appearance of larvae on Aberdeen Bank in 1983 did not coincide with an increased abundance at Shetland/Orkney; in fact larval abundance in the latter area had declined between 1978-82. Consequently, the appearance of spawners on Aberdeen Bank in 1983 probably was not due to over-crowding of the existing spawning grounds at Shetland/Orkney. The later increase of larval abundance at Shetland/Orkney in 1988-1990 indicated that these grounds could in fact accommodate far more spawners than they did in 1983.

3.3.2. Age compositions spawning herring

Age compositions of spawning herring on Aberdeen Bank were available from 1986-1993 (Fig. 3.6). These age compositions show that the spawners in 1986-1988 were mostly young fish aged 3-5 years, with a small component of fish aged 6-7 years. Assuming that older herring return to their place of first spawning, the age compositions for 1986 and subsequent years provide indirect estimates of the age of the spawners in 1983-1985. The oldest herring sampled in 1986-1988 belonged to year-classes 1979 and 1980. This suggests that the spawning on Aberdeen Bank in 1983 was started by these two year-classes (aged 3 and 4 years at the time).

In the years 1989 - 1992, the proportion of 3 year-olds among the spawners sharply declined. The abundance of larvae at Aberdeen Bank in this period was not markedly different from the abundance during the preceding 6 years. This indicates that there was no major change in population size compared to the preceding period. The reduced proportion of 3 year-olds among the spawners therefore indicates a reduction of the number of herring recruiting at this age. All the year-classes recruiting during this period appeared in greater numbers from age 4 onwards. This means that the age of first maturity in the population was changing from age 3 to age 4 or older. Maturity distributions for the total North Sea stock show a delayed recruitment for the years 1992 and 1993, but not particularly for the years 1989-1991. Apparently, the changes in age at first recruitment at Aberdeen Bank were not representative for those in the entire North Sea stock.

During the period 1988 -1992, a series of strong year-classes (1985-1987) recruited to the overall North Sea stock (Fig. 3.7). Considering the large increase in larval abundance at Shetland/Orkney in 1988-1990, it is reasonable to assume that more herring of these strong year-classes recruited to Shetland/Orkney than to Aberdeen Bank.

3.3.3. Hydrographic data

Mean values of surface temperature and salinity for August in the northwestern North Sea are presented in Fig. 3.8. The data do not indicate a significant change in hydrographic conditions around 1983 that might explain the renewed attractiveness of Aberdeen Bank as a spawning ground for herring.

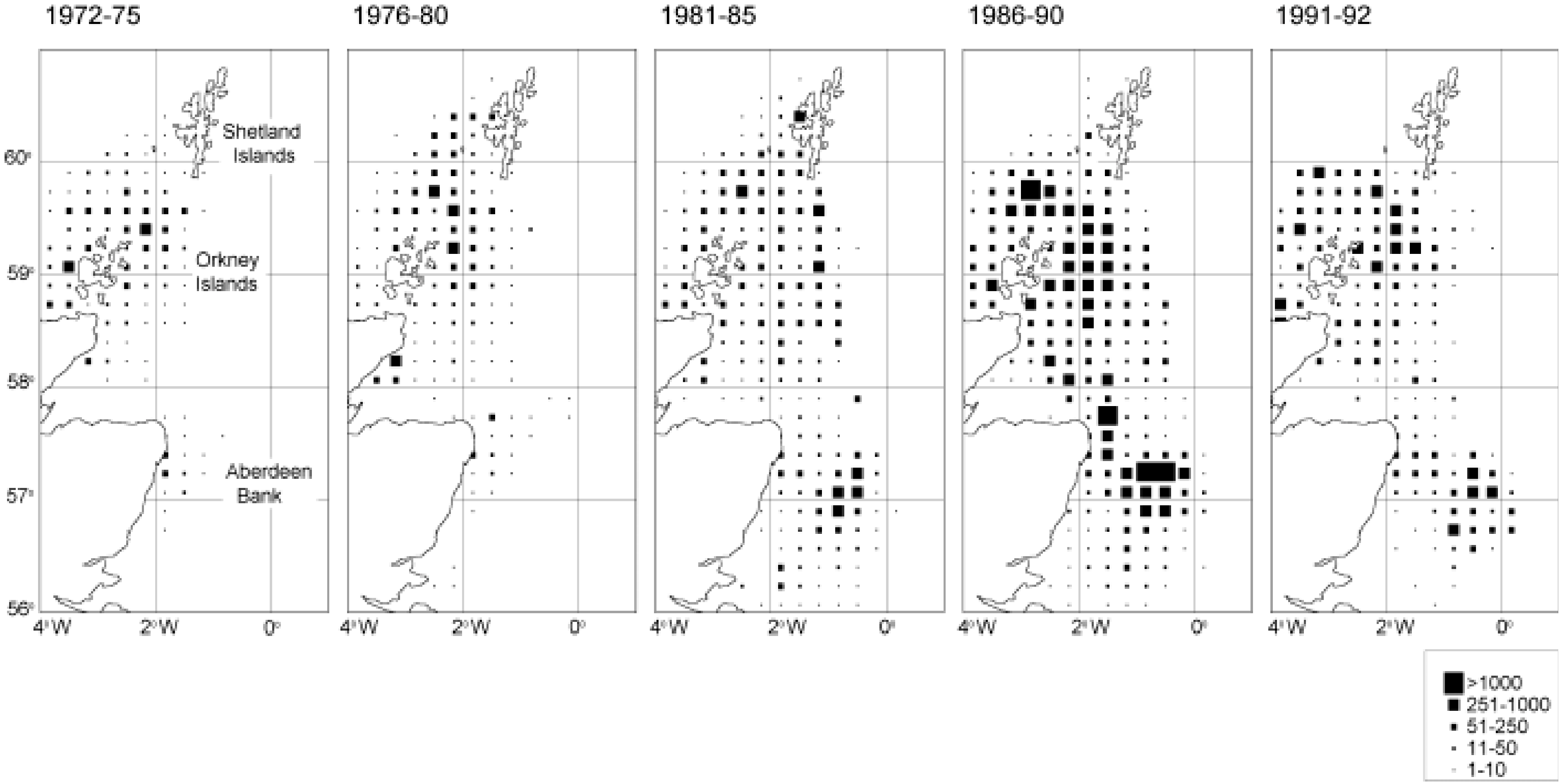

Figure 3.3. Mean distribution of herring larvae by periods of 5 years (except for the first and last period). The legend represent densities per square meter.

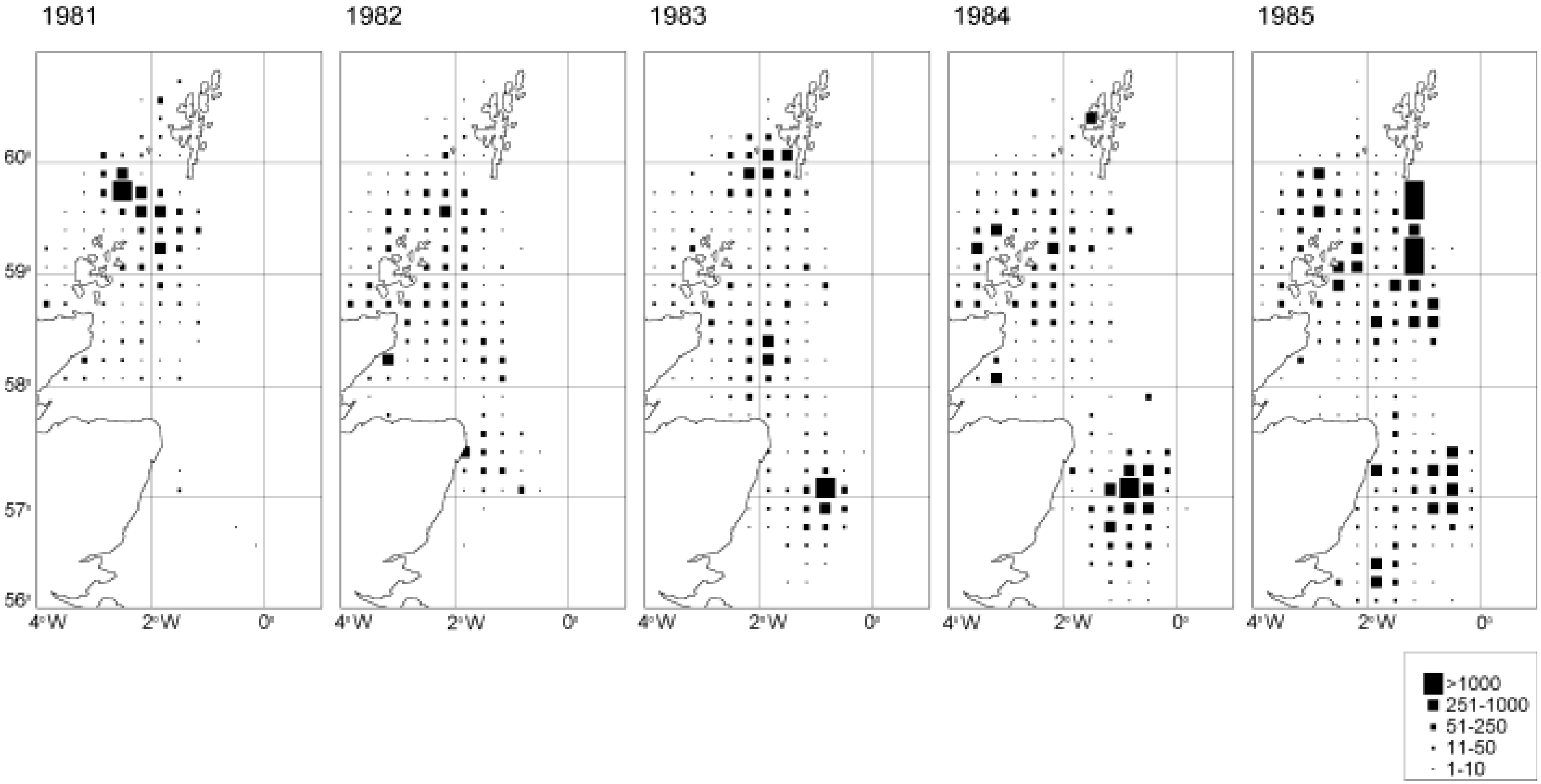

Figure 3.4. Annual distribution of herring larvae in the period 1981-1985. The legend represent densities per square meter.

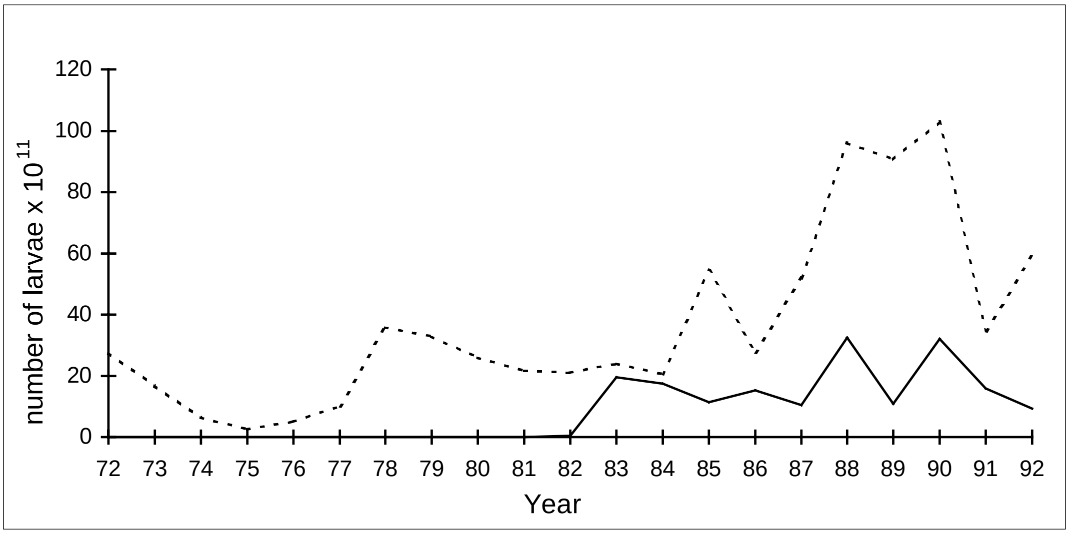

Figure 3.5. Total abundance of herring larvae at Aberdeen Bank (solid line) and at Shetland/Orkney (broken line). Aberdeen Bank has been defined as between 56°30'N and 57°30'N and between 00°20'E and 01°00W, and Shetland/Orkney as the area north of 58°N.

3.3.4. Plankton indicator species

Time series for the two Atlantic indicator species in the northwestern North Sea, *Metridia lucens* and *Candacia armata*, were constructed for the entire period (1948-1996) for which data were available (Fig. 3.9). During this period, *M. lucens* reached high values in the years 1955-1964, and also from 1982-1992. The period 1965-1981 was characterised by a marked scarcity of this species. The series for *C. armata* shows a similar pattern. Also in this species, two periods of relatively high abundance are separated by a period of low abundance during the second half of the 1960s and all of the 1970s.

In addition to the parallel trends in annual abundance, the species exhibit similar changes in seasonal occurrence in the North Sea. In the years 1965-1981, the appearance of both species in the North Sea was delayed by one or two months (Chapter 2, figure 2.7). Considering the fact that these species are recognised as indicators for Atlantic inflow in the northwestern North Sea, their parallel changes most likely signify multi-annual variations in the influx of Atlantic water into this area.

To compare the abundance of herring larvae on Aberdeen Bank with the occurrence of Atlantic plankton in the northwestern North Sea, the time series of larval

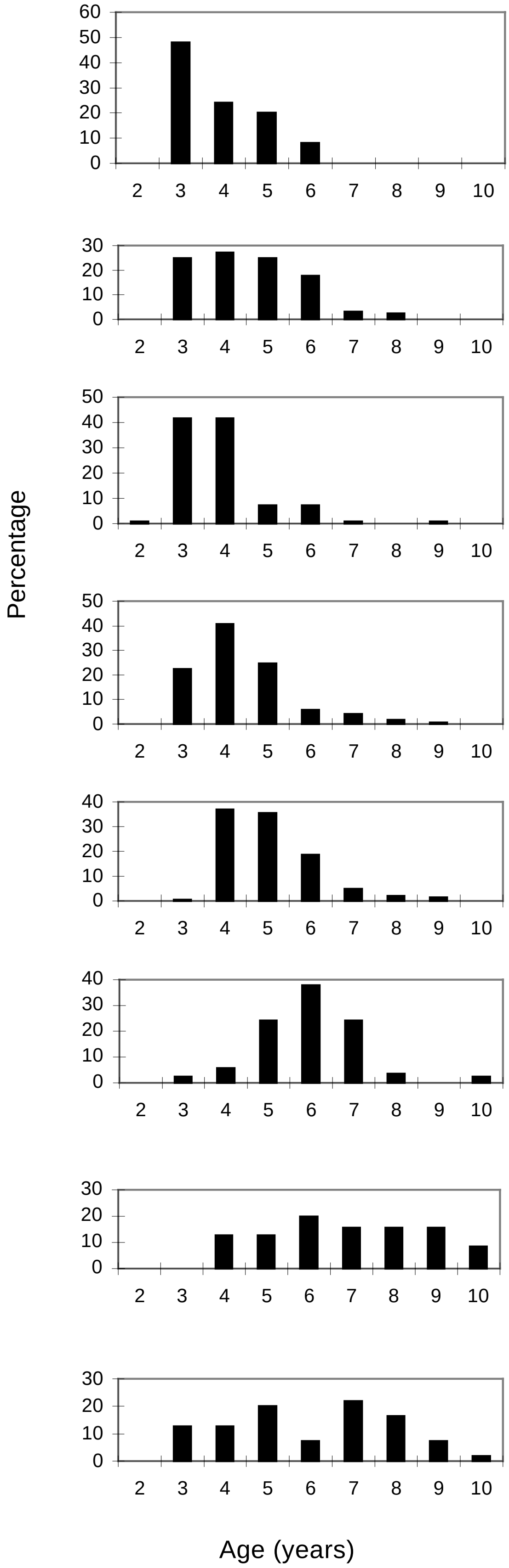

Figure 3.6. Percentage age compositions of spawning herring on Aberdeen Bank in 1986-1993.

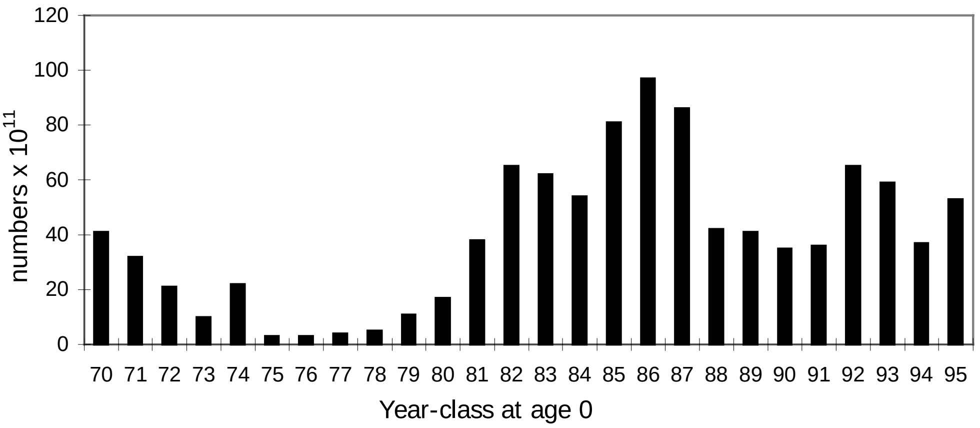

Figure 3.7. Recruitment to the total North Sea stock at age zero (data from Anon. 1998).

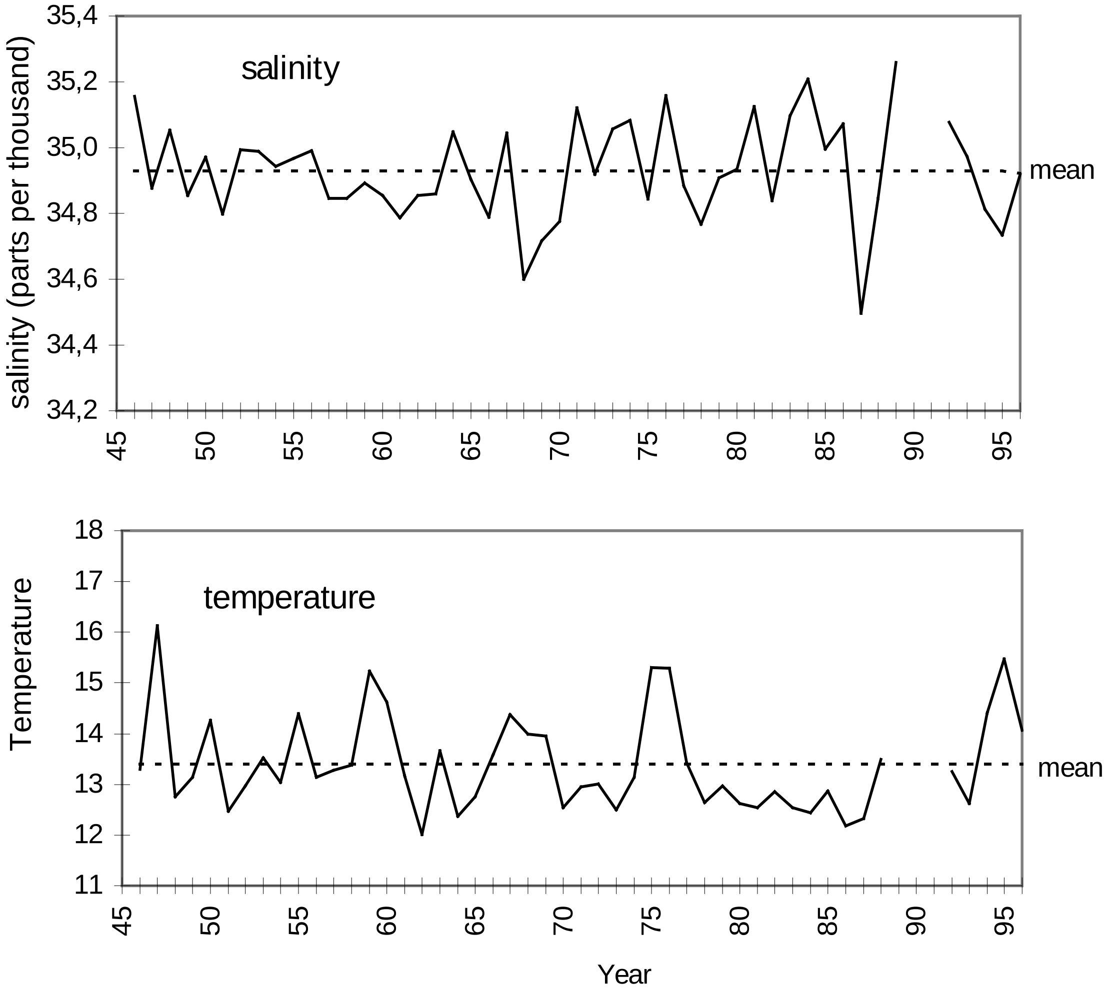

Figure 3.8. Surface salinity and temperature in the northwestern North Sea during August.

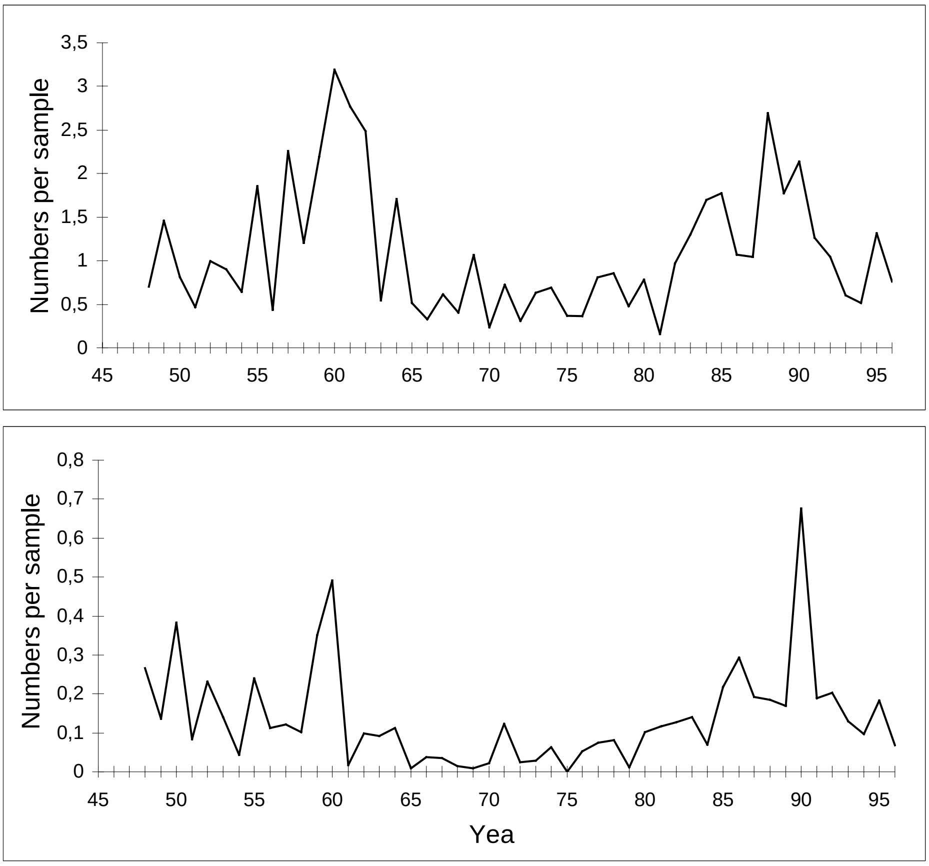

Figure 3.9. Mean annual abundance of *Metridia lucens* and *Candacia armata* in the northwestern North Sea.

abundance indices from the ICES surveys (1972-1992) was extended with Saville's (1971) data for the period 1951-1967. It is doubtful whether Saville's (1971) data are directly comparable with the later series from the ICES surveys in view of possible differences in survey coverage, sampling methods, and sampler efficiency. However, Saville's (1971) data at least provide a qualitative index of the abundance of larvae on Aberdeen Bank.

The comparison of the data series for herring larvae with the combined index for *Metridia/Candacia* (Fig. 3.10) shows that the period in which herring larvae were absent from Aberdeen Bank (1965 - 1982) coincided with the period of reduced abundance of the two Atlantic indicator species. Spawning at Aberdeen Bank was resumed in 1983; the first year in which the *Metridia/Candacia* index reached above-average values after 18 years.

3.4. Discussion

3.4.1. The environmental connection

Data on Atlantic plankton species presented in this report support the hypothesis that the revival of the Aberdeen Bank spawning population in 1983 was related to an increased Atlantic inflow in the northwestern North Sea. Other authors have described an earlier period of expansion of the Buchan population at a time of increased Atlantic inflow (Glover 1955, 1957), and a decline of the population at a time when the Atlantic inflow was reduced (Bainbridge and Forsyth 1972). We have evidence, therefore, that revival of the spawning population on Aberdeen Bank in the 1980s was another episode in a long-term cycle of expansion and contraction of the Buchan population in response to variations in Atlantic inflow into the area.

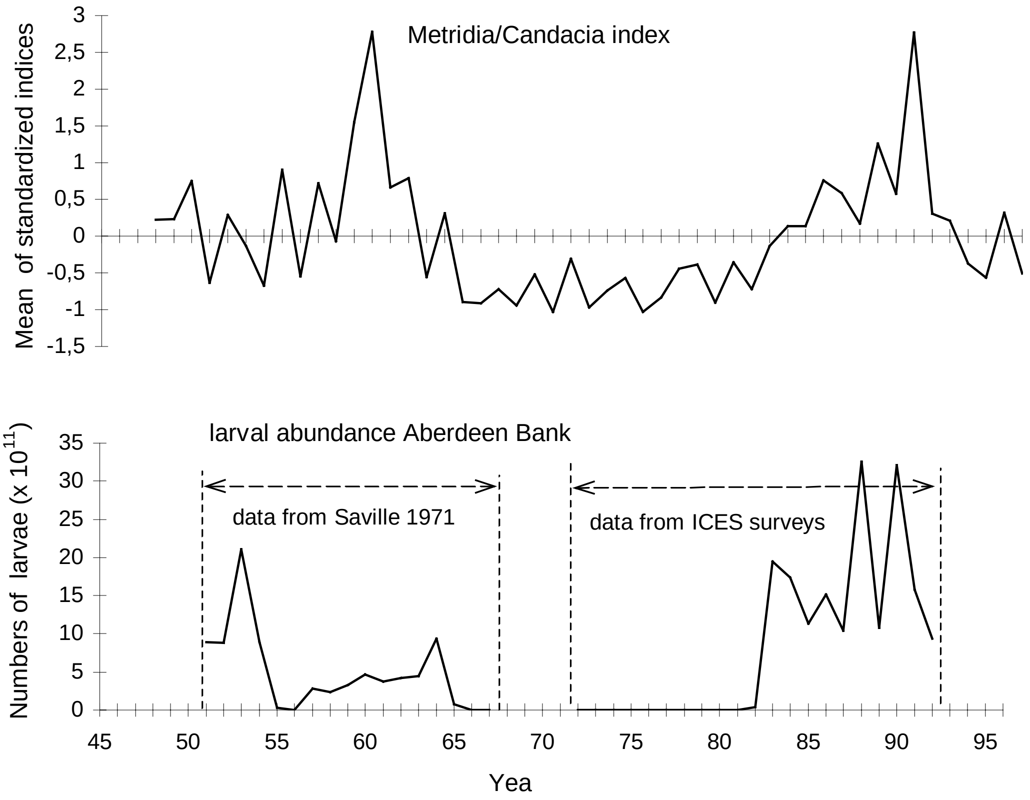

Figure 3.10. Abundance of herring larvae on Aberdeen Bank compared with a combined index for *Metridia/Candacia* , representing the strength of Atlantic inflow.

The lack of hydrographic evidence for the postulated changes in Atlantic inflow is probably due to the limited amount of data available. Earlier authors (Bainbridge and Forsyth 1972) found that variations of Atlantic inflow could be detected from salinity data only by looking at smaller areas within the northwestern North Sea. Hydrographic sampling in the post-1980 period was too limited to allow the calculation of mean salinities for these smaller areas.

The relationship between the Atlantic inflow and spawning at Aberdeen Bank could be either direct or indirect. A strong Atlantic inflow might affect temperature and salinity on Aberdeen Bank, thereby improving hydrographic conditions for spawning. However, it is hard to envisage how a change in hydrographic conditions on Aberdeen Bank would induce new herring spawn in this area. It is unlikely that pre-spawning herring each year make a quick survey of all available spawning grounds to determine where hydrographic conditions are optimal for spawning. More likely, a strong Atlantic inflow will affect the choice of spawning grounds indirectly by changing the geographical distribution of pre-spawning herring. Bainbridge et al. (1978) reported that the abundance of planktonic food in the Buchan area was partly dependent upon a strong Atlantic inflow in summer. The same applied to the latitudinal distribution of the herring, with a strong inflow resulting in a southern distribution of the herring. Apparently, a strong inflow of Atlantic water results in a southward displacement of the area of maximum plankton production, and hence in a similar displacement of the feeding herring. In years with a strong inflow, the herring will often find themselves in a relatively southern position at the end of the feeding season. As the spawning season in the northern North Sea follows immediately after the feeding season, recruit spawners will be inclined to choose a spawning ground which is not too far from the position where they stop feeding. In case of a southern distribution, the Aberdeen Bank is the most likely choice.

The strength of the Atlantic inflow, however, is not the only parameter that determines the latitudinal distribution of herring. In the summers of 1988-1990, herring in the North Sea had a very northerly distribution (chapter 5), despite a strong Atlantic inflow as indicated by the *Metridia/Candacia* index. The northerly distribution of the herring coincided with high water temperatures and scarcity of *Calanus finmarchicus*, the main food item of the herring. During these years, the distribution of *C. finmarchicus* was confined to the northern part of its normal range (Planque and Fromentin, 1996, Fromentin and Planque, 1996). The high temperatures and associated changes in plankton distribution appear to have had an overriding effect on the distribution of the herring in these years.

The northerly distribution of the entire herring stock during the summers of 1988-1990 may explain the relatively low recruitment of new spawners to Aberdeen Bank, despite the high Atlantic inflow. If the herring were distributed far north at the end of the feeding season, recruit spawners will have been inclined to choose Shetland/Orkney instead of Aberdeen Bank as their place of first spawning. Data on larval abundance suggest that the Shetland/Orkney area indeed received the bulk of the recruit spawners in these years.

3.4.2. Population identity

The reappearance of a spawning population on Aberdeen Bank, 16 years after the last herring larva had been caught in this area, has implications for our understanding of the stock structure of North Sea herring. In the North Sea area, scientists have long discussed the question whether the individual spawning populations were self-contained stocks, or whether they drew their recruits also from neighbouring populations. The hypothesis of self-contained stocks was advocated by Postuma and Zijlstra (1958) and Zijlstra (1958, 1964b, 1969, 1973), whereas Parrish and Sharman (1959), Kreft (1963), and Schumacher (1963) produced arguments for an exchange of recruits between populations. The discussion about the genetic identity of spawning populations was not restricted to the North Sea area. In North America, the main exponents of the theory of self-contained stocks were Iles and Sinclair (1982), whereas Smith and Jamieson (1986) refuted the evidence for genetic isolation of spawning populations. McQuinn (1997) gave an extensive review of the literature on the subject, both in Europe and in North America. The discussion in North America was stimulated by the reappearance of herring larvae on Georges Bank in 1986, nine years after these formerly important spawning grounds had been deserted. Stephenson and Kornfield (1990) argued that this was a case of resurgence, i.e. a revival of a rudimentary population that had never completely disappeared, whereas Smith and Morse (1990) suggested that the new spawners had no direct connection to the spawning population that formerly existed in this area.

Turning to our observations on Aberdeen Bank spawners, we come to the same conclusion as Smith and Morse did for the Georges Bank herring. The herring that spawned on Aberdeen Bank in 1983 can not have been descendants from a rudimentary population that always survived in this area. Extensive ICES larvae surveys in 1972-1981 found no evidence of any larvae production on Aberdeen Bank. Therefore, the herring that spawned in this area in 1983 must have been born elsewhere. The implication is that the Aberdeen Bank population is not (and has never been) a self-contained stock. Apparently, juvenile herring born at other localities in the North Sea can spawn at Aberdeen Bank and thereby become a member of the local population. If this applies to the Aberdeen Bank population, it is probably also true for other spawning population in the North Sea.

The apparent lack of "homing" in (at least some of the) recruit spawners raises the question how the identity of existing spawning populations is maintained. Some of these populations have been known for decades or even centuries, and there must be some mechanism by which new generations continue to recruit to these traditional spawning places. As early as 1962, Wynne-Edwards had drawn attention to the role of tradition in maintaining population identity in birds, mammals and fish. He identified the separate populations of North Sea herring as one of the examples in which the transmission of migration patterns by learning could play an important role in maintaining population identity (and success). Many years later, Corten (1993) arrived at the same conclusion as regards the maintenance of these populations.

Recently, McQuinn (1997) applied the principle of social transmission of migration patterns in his "adopted migrant" hypothesis. This theory postulates that individual spawning populations within a larger area all belong to one "metapopulation", and that the individual populations draw their recruits from a common pool of juveniles. Juvenile herring recruit to one of the populations by schooling with older, experienced herring, and by following these to one of the traditional spawning sites. When spawning in this locality for the first time, the recruit spawners become attached to the ground and return there in subsequent years. Spawning populations are thus perpetuated by the transfer of tradition from one generation to the next, and not by instinctive homing of first-time spawners.

Since older herring have already developed an attachment to one of the existing spawning sites, they will not be the ones that colonise new spawning areas. If spawners are found in a new area, these fish will normally belong to the recruiting year-class (McQuinn 1997). Our observations on the age composition of Aberdeen Bank spawners confirm this theory, as it appears that the first spawning in 1983 was conducted by recruit spawners. The same observation was made on Georges Bank, where the first spawners in 1986 belonged to the recruiting 1983 year-class (Stephenson and Kornfield, 1990, McQuinn 1997).

The adopted migrant theory predicts that colonisation of new spawning areas will occur when established populations become unstable following a population collapse or recruitment boom (McQuinn 1997). The case of the Aberdeen Bank spawners illustrates how the process might actually work. A relatively minor change in hydrography (only detectable from plankton indicator species) probably resulted in a southward displacement of feeding herring. The recruiting year-class, which is always distributed at the southern fringe of the population, lost contact with the older stock component that stayed behind in the Shetland/Orkney area ("knowing" that it had to spawn there within a few weeks). Without the guidance of older herring, the recruit spawners turned to the nearest place where bottom substrate and hydrographic conditions met their instinctive requirements for a spawning ground, and a new spawning population was established. The scenario illustrates that no large instability of the population was required, nor a major change in hydrography. All that was needed was the separation of a number of recruit spawners from the older stock component during the pre-spawning period. This is most likely to occur when the recruiting year-class is large in relation to the existing adult stock.

The colonisation of new spawning grounds illustrates that recruit spawners are free, within the limits of the metapopulation, to choose their own spawning ground. However, in most years this freedom will not be expressed in the establishment of new spawning sites, but merely in switches between existing spawning areas. Normally, the recruiting year-class will be mixed with herring 1-2 years older, that have already developed an attachment to one of the existing spawning areas. The choice of spawning area by recruit spawners will depend on the older herring that they associate with during the pre-spawning phase. If in a particular year recruit herring in the North Sea have a northerly distribution, they are likely to mix with experienced spawners from Shetland/Orkney, and consequently follow these fish to the Shetland/Orkney spawning grounds. Conversely, a southerly distribution of the recruiting year-class will mix them with members of the Aberdeen Bank population, and hence lead them automatically to the Aberdeen Bank spawning grounds. Shifts in recruitment between Shetland/Orkney and Aberdeen Bank, based on this mechanism, must have been responsible for the contrasting developments in both populations in earlier decades.

Acknowledgements

Kenneth Patterson kindly provided a copy of the herring larvae data base of the Marine Institute in Aberdeen. Chris Reid allowed me to use plankton data from the SAHFOS data base, and Harry Dooley provided me with hydrographic data from the ICES files. Stimulating comments on the manuscript were received from Ian McQuinn, Wim Wolff, Winfried Gieskes, Gert van de Kamp, and one anonymous referee.

Chapter 4

A proposed mechanism for the Bohuslän herring periods

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Abstract

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 wintering grounds of North Sea herring. In normal years North Sea herring winter in the adjacent waters of the northeastern North Sea. As yet there is no commonly accepted explanation for the occasional shifts of the 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 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 wintering area. It is shown that the two most recent episodes of Skagerrak invasions were indeed initiated by strong recruiting year-classes.

4.1. 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. 4.1), 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.

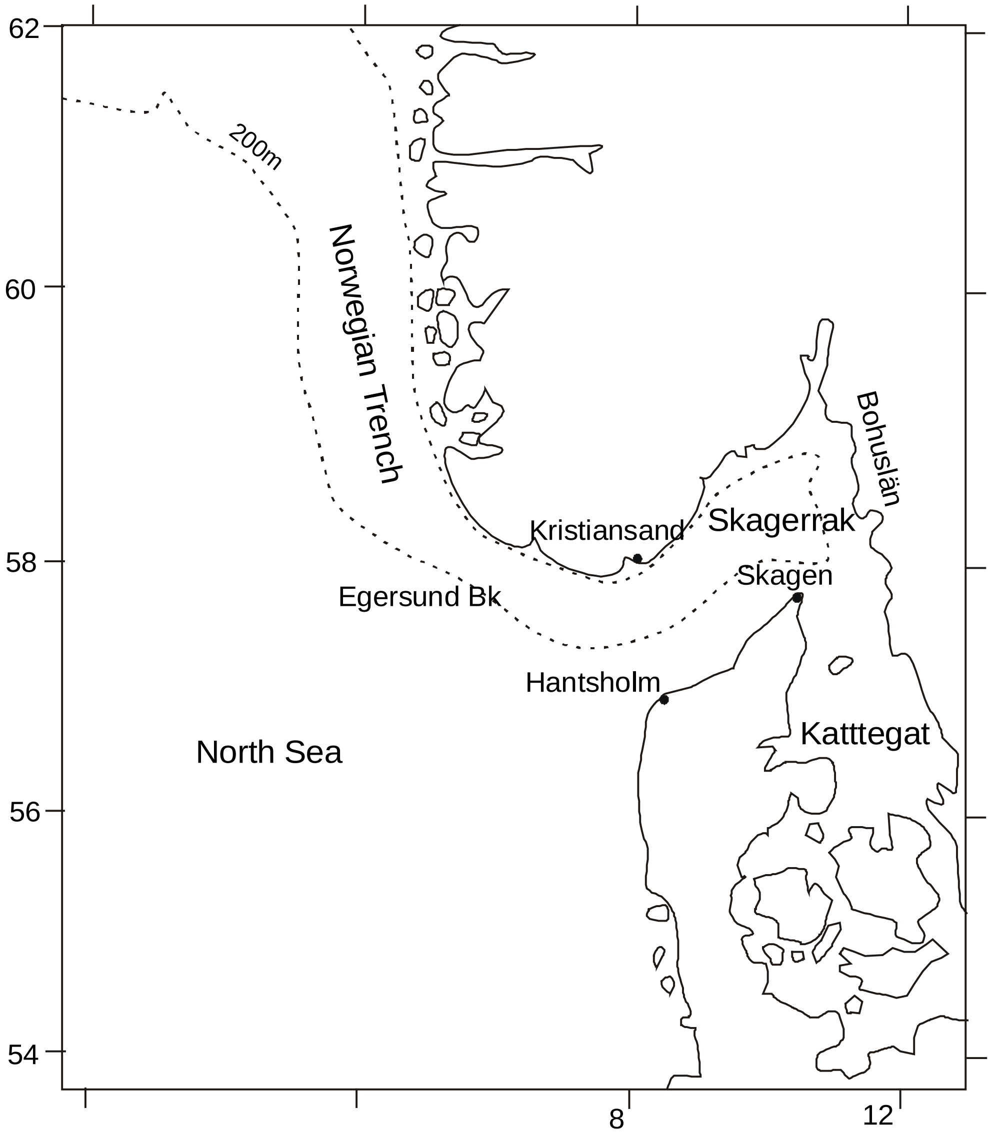


Figure 4.1. The Skagerrak and other localities mentioned in the text.

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 these 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 exploited only 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 18th 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 wintering North Sea herring can also be drawn from an inspection of the normal wintering grounds of North Sea herring in relation to the Skagerrak (Fig. 4.2). The main wintering grounds of North Sea herring 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. 4.3). The 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 at the end of the 19th century. 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 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

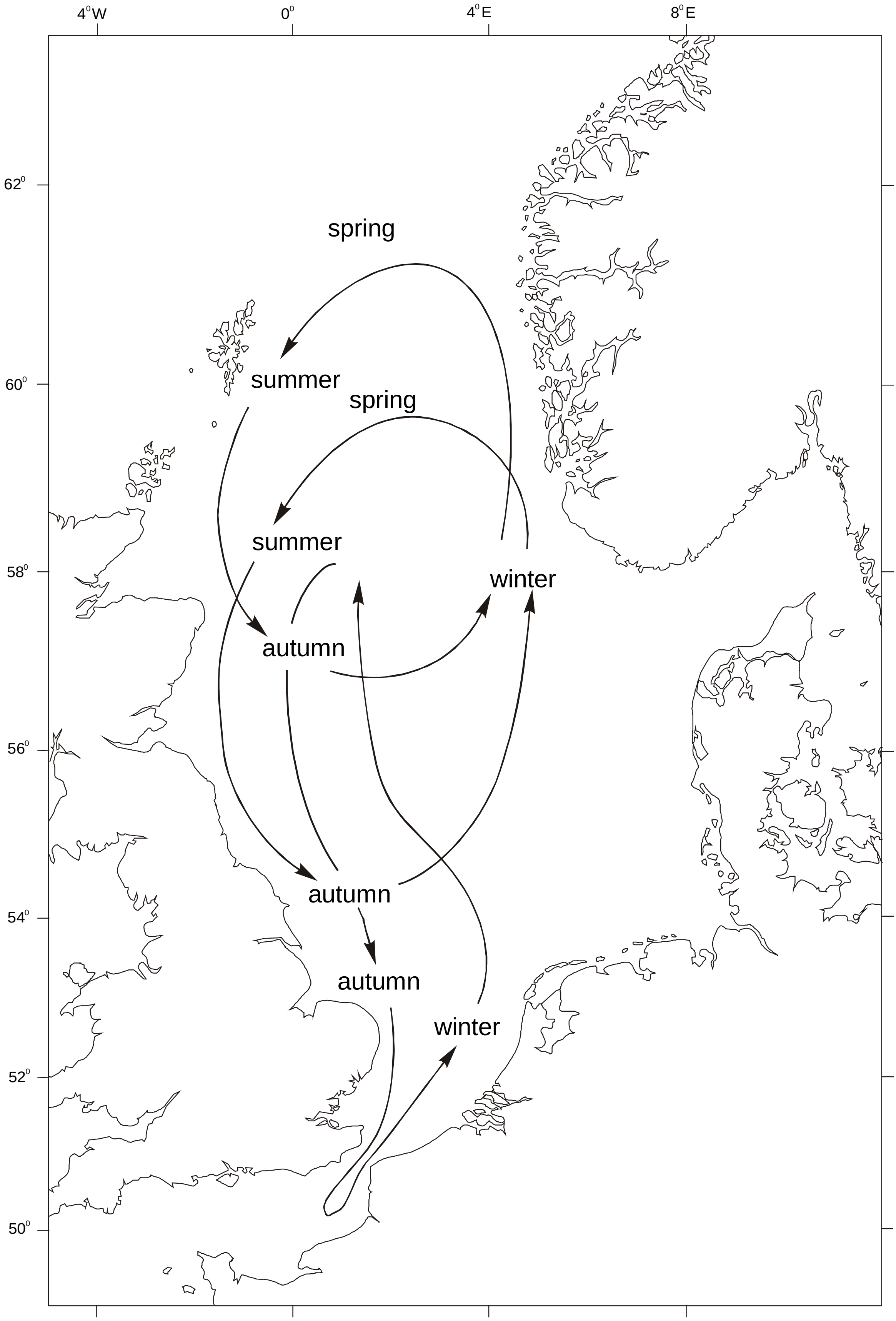


Figure 4.2. Annual migrations of adult North Sea herring. Adapted from Anon. 1965 and from Cushing and Bridger 1966.

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 alternation 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.

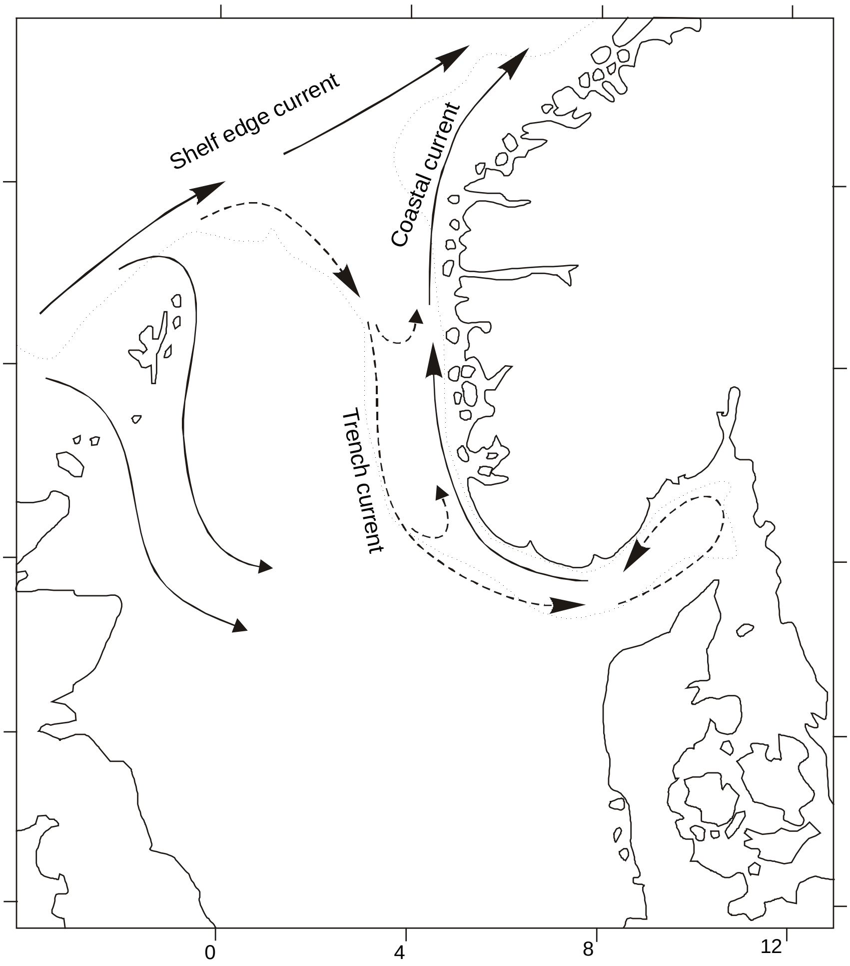


Figure 4.3. Currents in the northern North Sea and Skagerrak. After Svendsen *et al.* 1995b.

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 1962-65 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 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 Trench Current, resulting from a change in wind conditions over the entrance of the Skagerrak.

The first and second hypothesis 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.

4. 2. 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 1963/64 and 1964/65, and to a lesser extent already in the winter of 1962/63. As the invasions coincided with the introduction of mechanised 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 (Anon. 1971, Burd 1978). A few scientists, however, realised that the large catches in the Skagerrak might be also the result of a new migration of the herring, and that the new fishery 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, one 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 1962/63 (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 1964/65. 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 1962-65 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 1964/65 the herring approached the Bohuslän coast (Schubert 1966, Haraldsvik 1968), although they did not actually move into the inshore waters (Fig. 4.4).

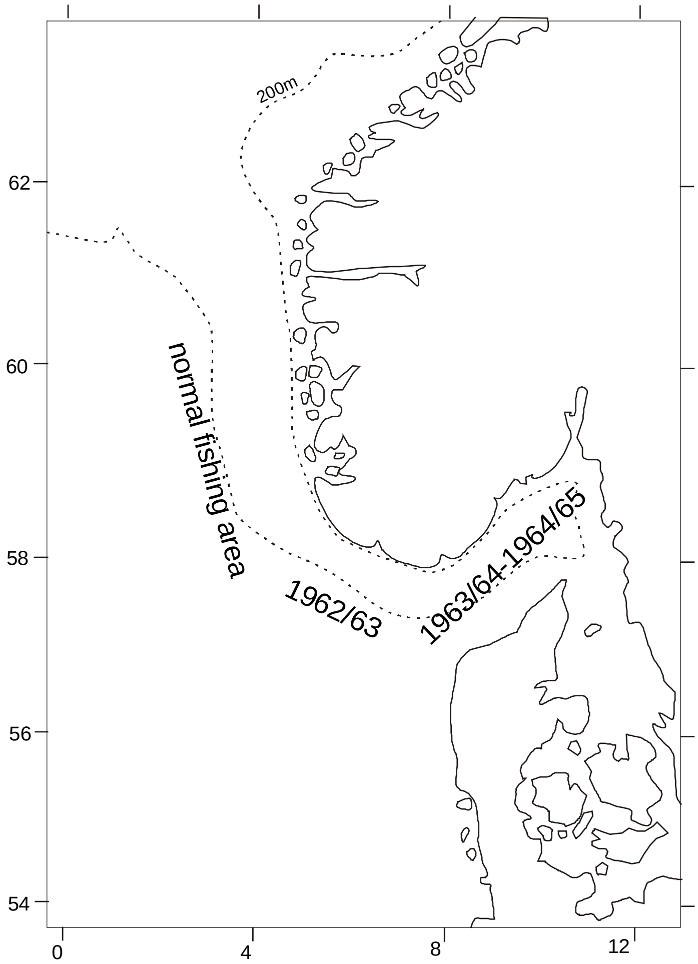


Figure 4.4. Main fishing areas of wintering North Sea herring in 1962-65 compared to the normal fishing areas in the 1950s and 1960s. Based on Furnestin 1956; Anon. 1964; Dutch catch statistics for 1957-1969; Höglund 1965, 1966, 1967; and Schubert 1965.

The main differences between the 1962-65 Skagerrak invasions and the former Bohuslän periods seem to have been the intensity and duration of the event. It is concluded, therefore, that the 1963-65 Skagerrak invasions were most likely were 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 1963/64 and 1964/65. Catch distributions for the Dutch trawl fishery in the north-eastern North Sea (Fig. 4.5) show that some of the herring must have retained their normal wintering position along the western edge of the Norwegian Trench.

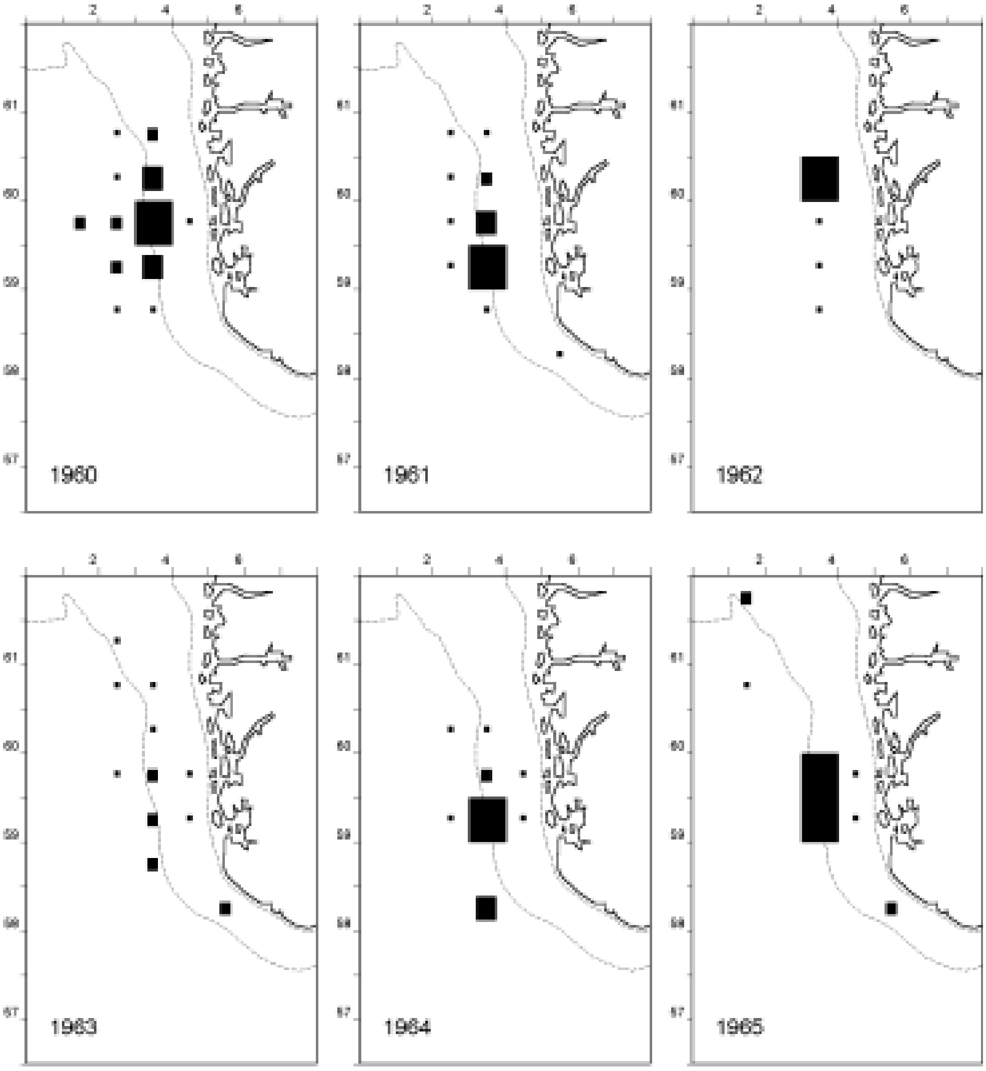


Figure 4.5. Herring catches by Dutch bottom trawlers along the Trench slope in January/February 1958-1965. Categories (lightest to darkest shade, respectively): 25-100, 101-500, 501-1000, and >1000 tonnes

4. 3. Material 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 northeastern 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, characterised by boreal plankton species, was investigated by looking at data from the Continuous Plankton Recorder (CPR) survey. The 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 (Oceanographic Laboratory Edinburgh 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 hour intervals, and grouped by 30° sectors. For each autumn (September to November) in the period 1960-65, the wind stress from various directions was estimated by summing the squared wind speeds per 6 hour 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 index has been used. The NAO index is the difference between the normalised 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 1864 (Hurrell 2000a,b). 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 north-western Europe (Alheit and Hagen 1997, Fromentin and Planque 1997). One may assume, therefore, that in general easterly winds will have prevailed over the Skagerrak during months with a negative NAO-index.

4. 4. Results

Water temperatures for October and November in the area where the herring assemble in autumn are presented in Figure 4.6. 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

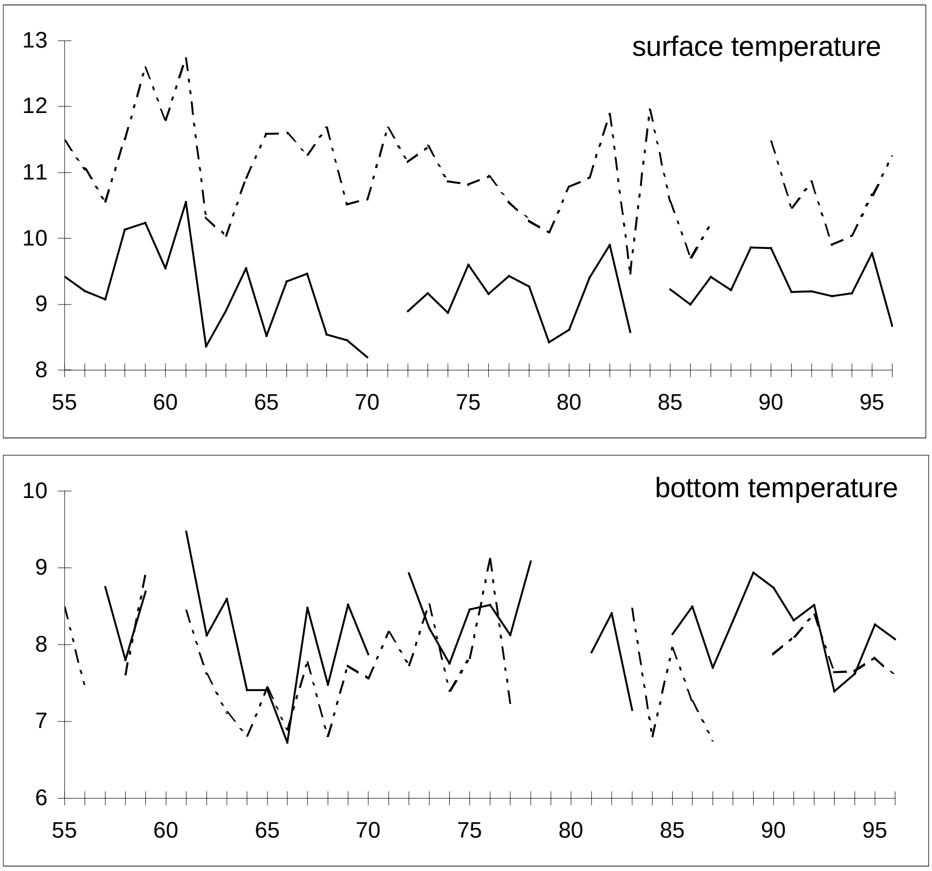


Figure 4.6. Mean surface (a) and mean bottom (b) temperature in October (broken line) and November (solid line) for the area 57°00’N to 61°00’N, and 02°00’E to 04°00’E.

bottom temperatures were about normal. On the other hand the herring invasions had stopped already in 1966 when the November bottom temperature reached a minimum.

The annual occurrence of three boreal copepods in the northeastern North Sea during the period 1950-96 is presented Figure 4.7. During the years of the Skagerrak herring invasions (1962-64), only one boreal copepod, *Euchaeta norvegica,* was present in some numbers in the northeastern North Sea. The abundance of this species in 1962-64, however, was by no means abnormally high. The two other boreal copepods considered, *Calanus hyperboreus* and *Metridia longa*, were completely absent from the north-eastern 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 Skagerrak herring invasions.

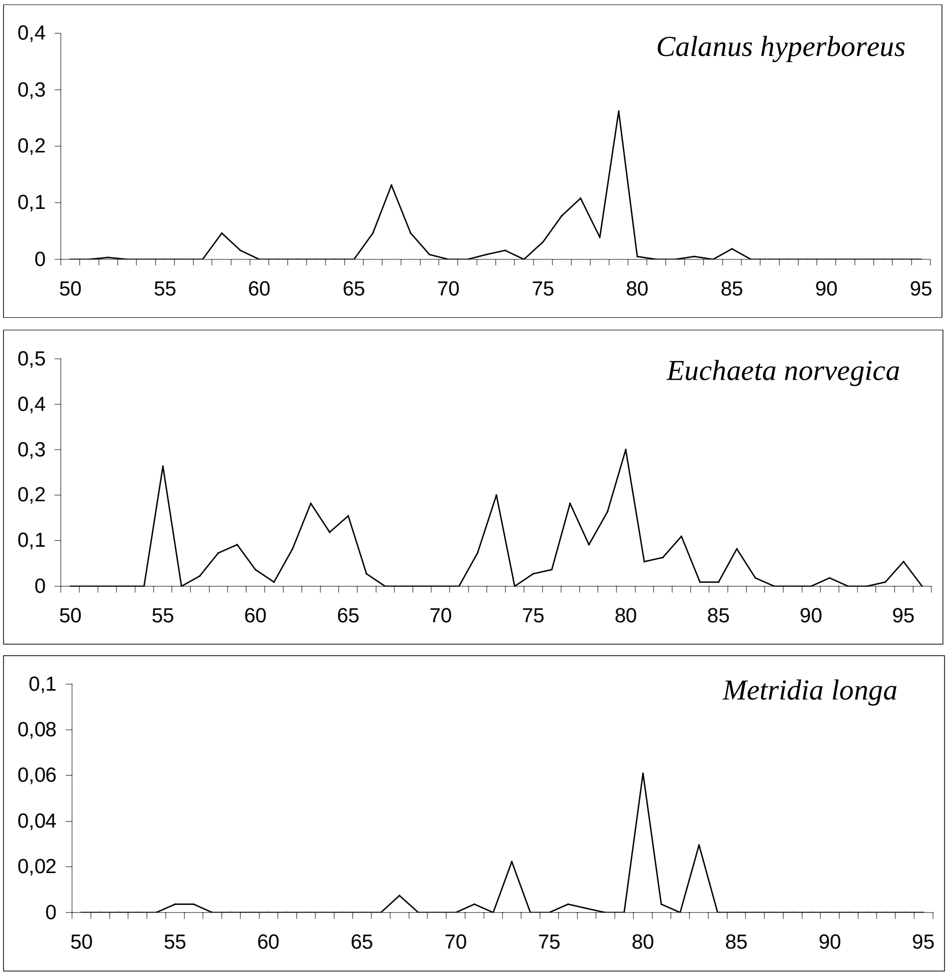


Figure 4.7. Annual abundance of 3 boreal copepods in the area 56°-60°N and 2°-8°E, 1948-1996.

Information on wind strength and direction over the entrance of the Skagerrak is presented in Figure 4.8. 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 4.9, 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

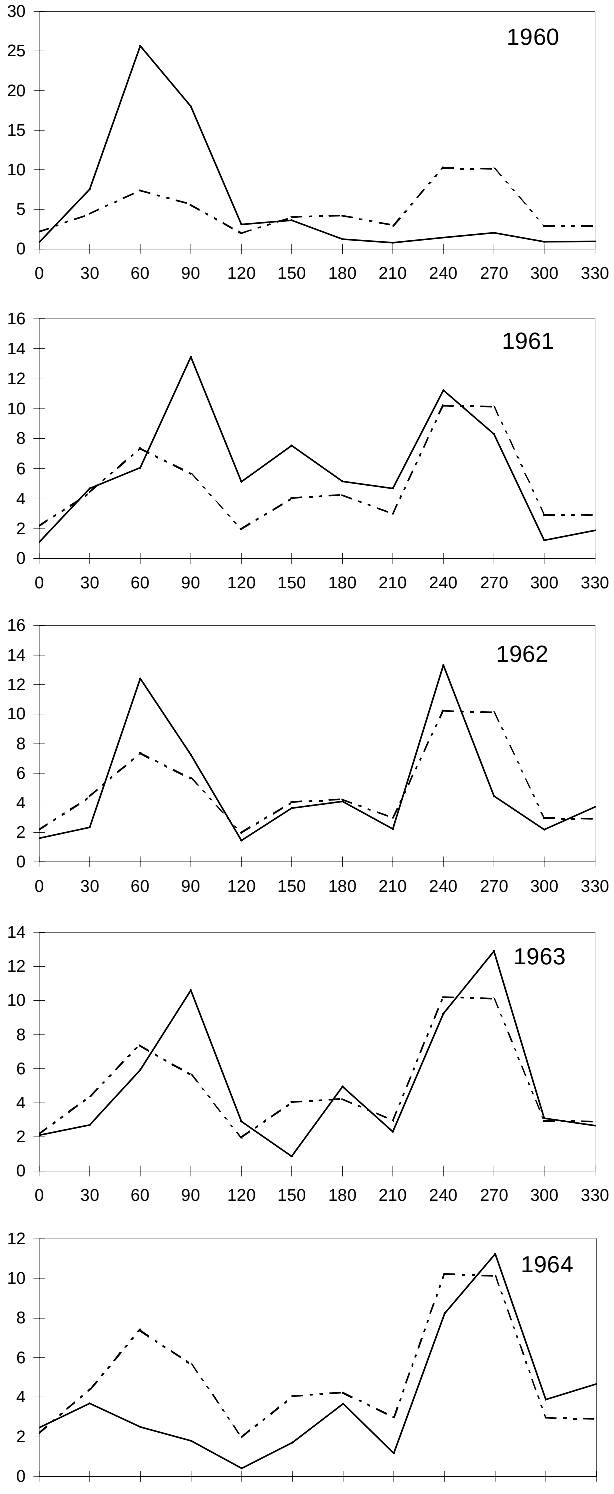


Figure 4.8. Average squared wind speed (m^2s^{-1}) per 6 h interval from different wind directions for the period September to November at Oksoy Fyr lighthouse, pos. 58°04’N, 8°03’E. Annual values for 1960-1964 compared to long-term mean for 1957-1975 (broken line).

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 proportionally between the size of the negative NAO-anomaly in autumn and the duration of the subsequent herring period in the Skagerrak.

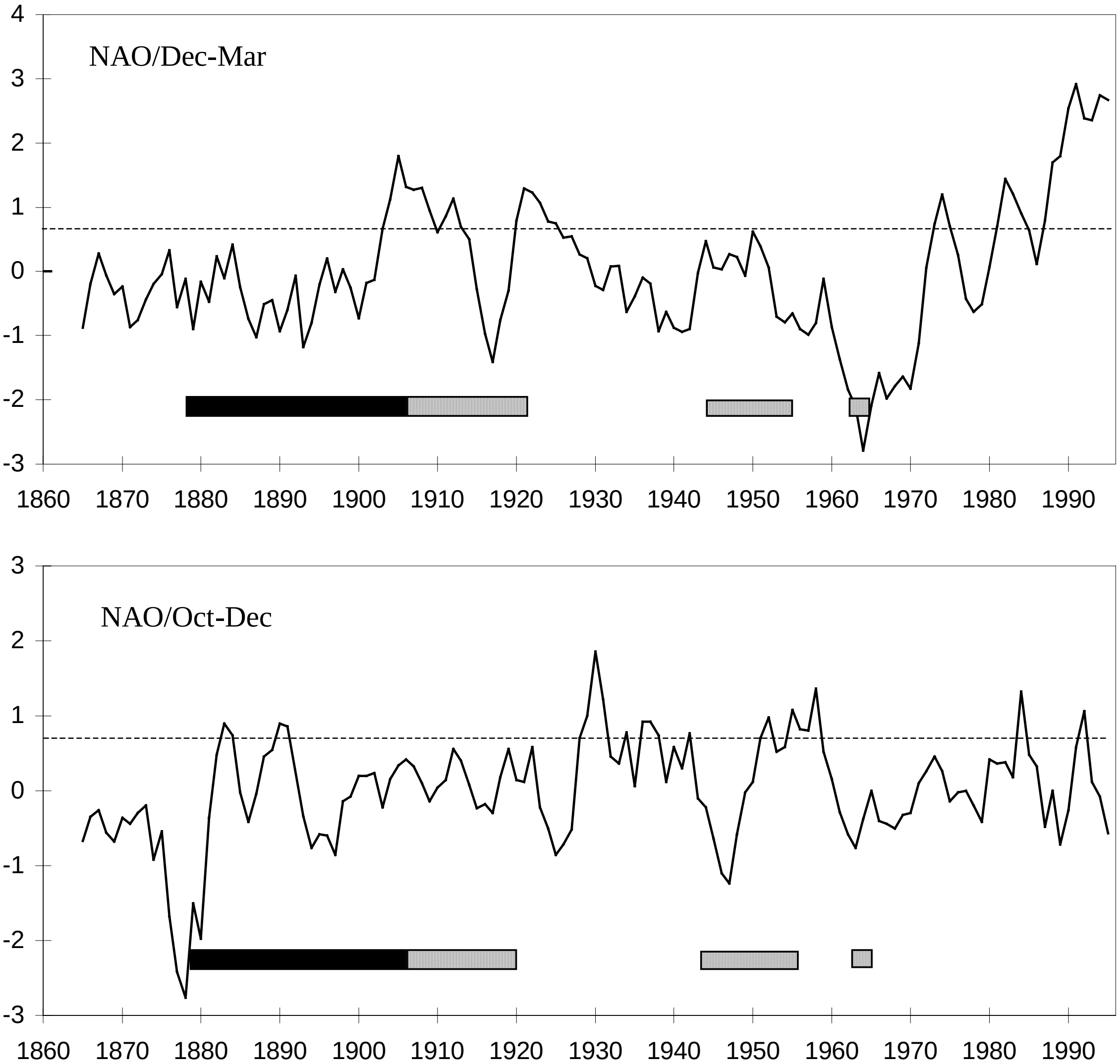


Figure 4.9. Wintering of North Sea herring in Skagerrak compared to NAO-indices (5-year running means) for winter (December to March) and autumn (October to December). Black bar indicates last Bohuslän herring period; shaded bars indicate Open Skagerrak periods. NAO data from Hurrell 2000a.

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.

4. 5. Discussion

The environmental data collected during the last episode of Skagerrak herring invasions (1962-65) 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 wintering area of the herring. The only anomalous environmental condition at the start of the invasions was the wind. In the first two 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 sub-surface, 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 know, 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 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 sub-surface 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 climate 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 his 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 sub-surface 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.

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 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 choose a spawning, feeding, or wintering area by themselves.

In the context of the present paper it is interesting to note the extreme conservatism in the choice of wintering area by Norwegian spring spawning herring. Dommasnes *et al*. (1994) described how the entire stock of these herring started to 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 wintering of North Sea herring in the Skagerrak is comparable to the wintering of Norwegian spring spawners in the Ofotfjord and Tyskfjord. Once the North Sea herring had spent one winter in the Skagerrak they returned there 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 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 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 1962-65 invasions this certainly was the case. In all the years of the herring invasions the catches in the Skagerrak consisted mainly of the strong year-class 1960. 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 (Anon. 1977).

Also the 1943-54 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 year-class 1939. 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 year-class 1939 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 north-eastern North Sea in 1962-65 showed that part of the population did not engage in the new migration, but stayed with the traditional 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 1963/64 and 1964/65 must have exterminated most of the 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 wintering in this area. This 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 (Anon. 1977). The recruiting year-class 1963 was more than three times as numerous as the surviving fraction of year-class 1960, and it was thereby in a position to make its own choice regarding its 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 characterised 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 or 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 of the larvae from their 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 wintering area.

4. 6. Conclusions

The start of Bohuslän herring periods is probably induced by an environmental factor. This factor is not a large-scale climate change but a variation in currents in the entrance of the Skagerrak as a result of easterly winds. A sub-surface, “compensation” current, induced by the easterly winds, could easily carry herring from their normal wintering area 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 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 wintering area. If this new year-class outnumbers the older fish in the population, it may "choose" a different 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.

Chapter 5

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

Fisheries Research 50 (2001): 189-204

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 Faeroe plateau. The anomalous distribution of the herring in 1988-1990 appears to be related to a short-term climate variation. The years were characterised 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 *Calanus 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.

5.1. 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 in the western and northwestern North Sea. Fig. 5.1 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 north-eastern 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 three 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.

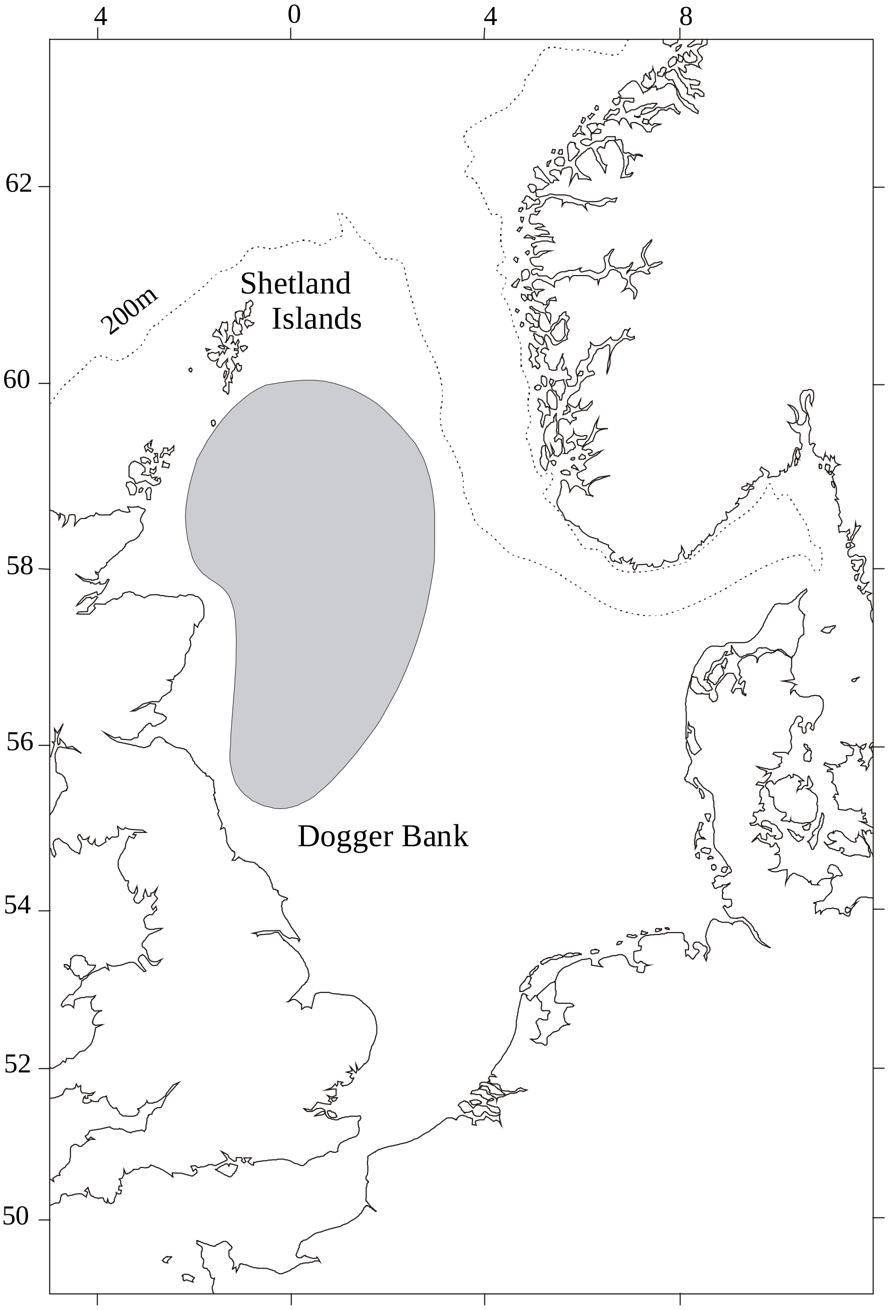


Figure 5.1. Traditional fishing areas for North Sea herring in June and July. Based on international catch data for 1955-1960.

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 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). *Calanus 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.

The annual migrations of the adult were already shown in Chapter 4, figure 4.2. The North Sea stock consists of three populations, each characterised 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 north-western 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.

5. 2. Data

5. 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 two 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 six sectors of the North Sea shown in Fig. 5.2.

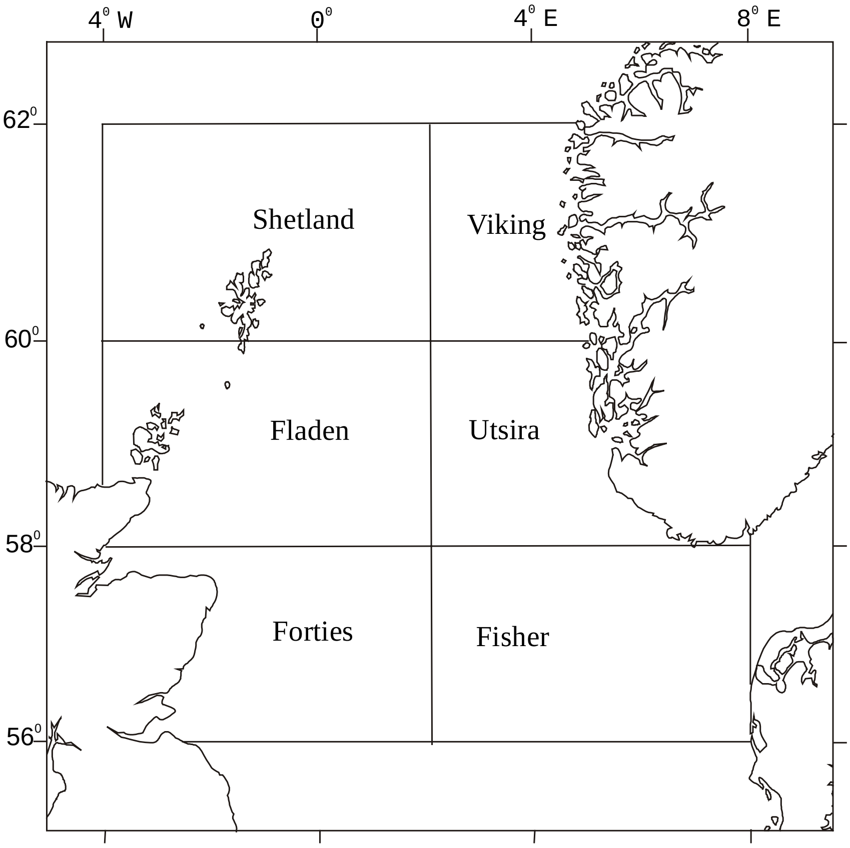


Figure 5.2. North Sea sectors used for analysis of catch data and acoustic surveys.

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.

5.2.2. 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 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 north-eastern 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 spawners. From 1990 onwards, participation in the surveys has stabilised, and results are considered to be more consistent.

5.2.3. Water temperature

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, 02°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 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.

5. 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.

5.3. Results

5.3.1. 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. 5.3. 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 eastern sector.

The development of catches by sector over the period 1985-1995 is presented in Fig. 5.4. 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 to the general northward shift in 1989-1990, but we shall return to this topic later. The data in Fig. 5.4 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. 5.5 shows that the combined catches for the two northern sectors increased from 1985-1989, 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. 5. 5).

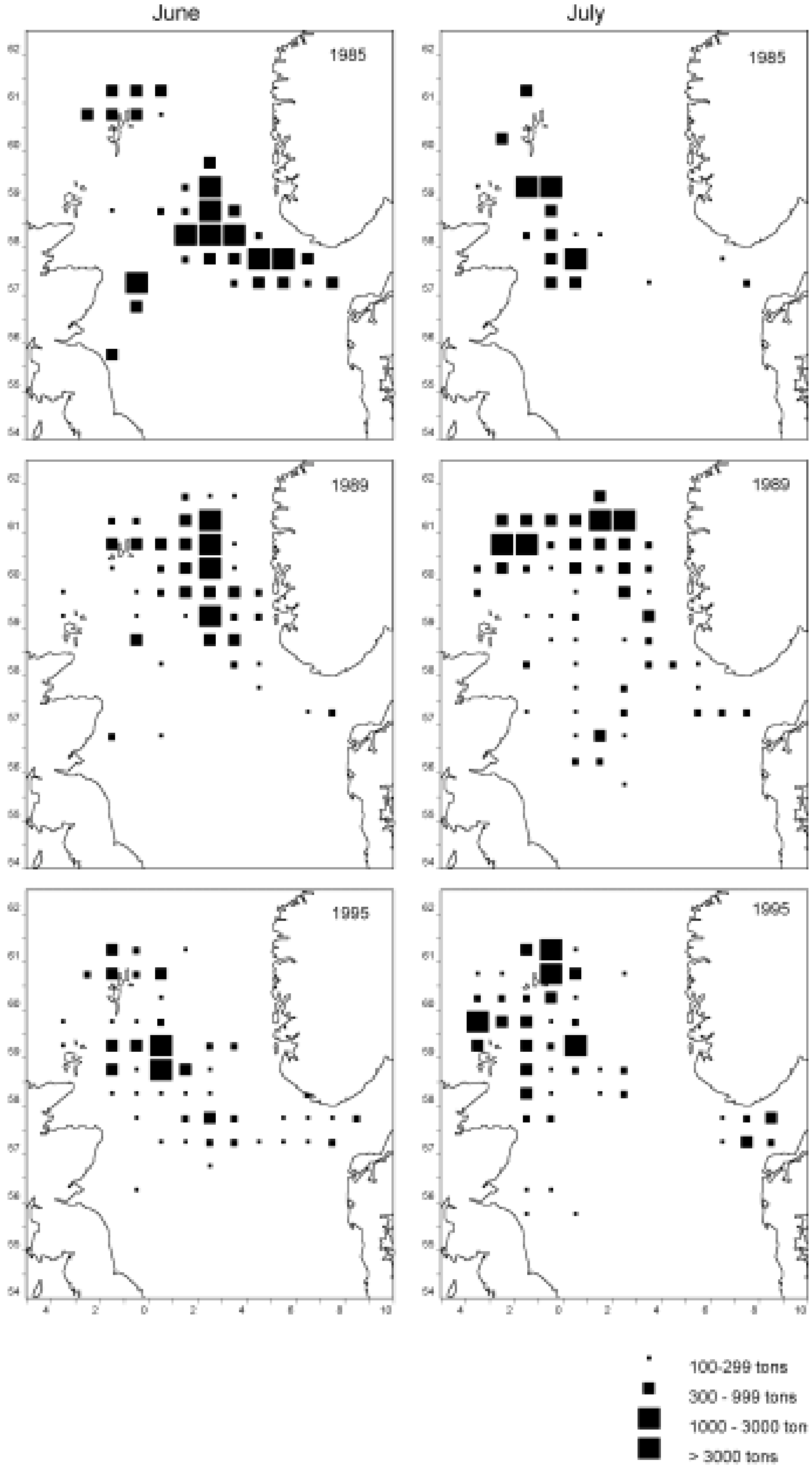
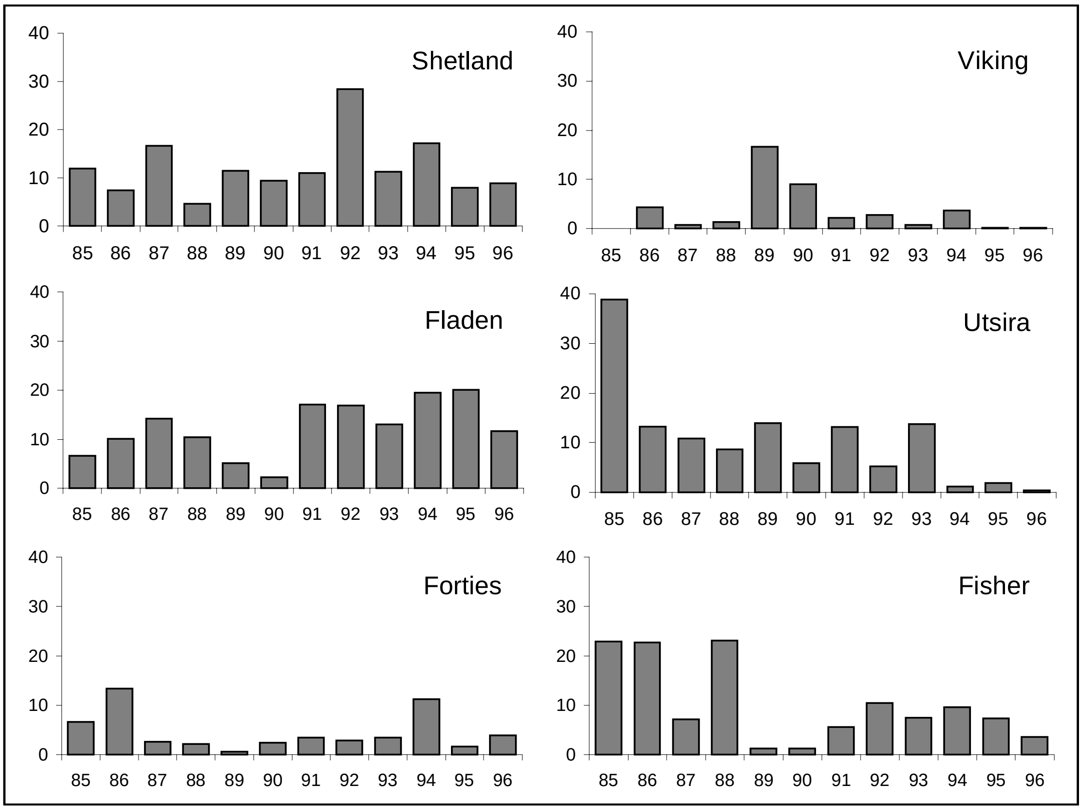


Figure 5.3. Variation in catch distribution illustrated by data for the years 1985, 1989 and 1995. Industrial catches of young herring omitted. Left hand June, right hand July.

JUNE



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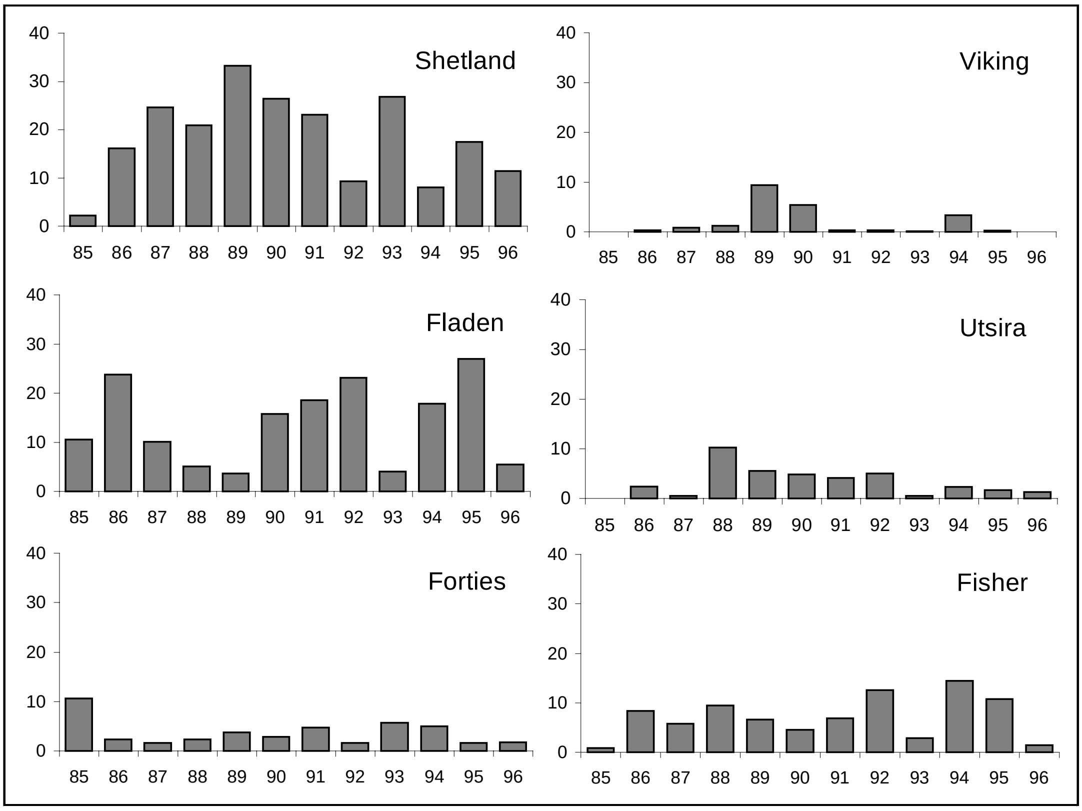


Figure 5.4. Catches in thousand tonnes by sector in June and July.

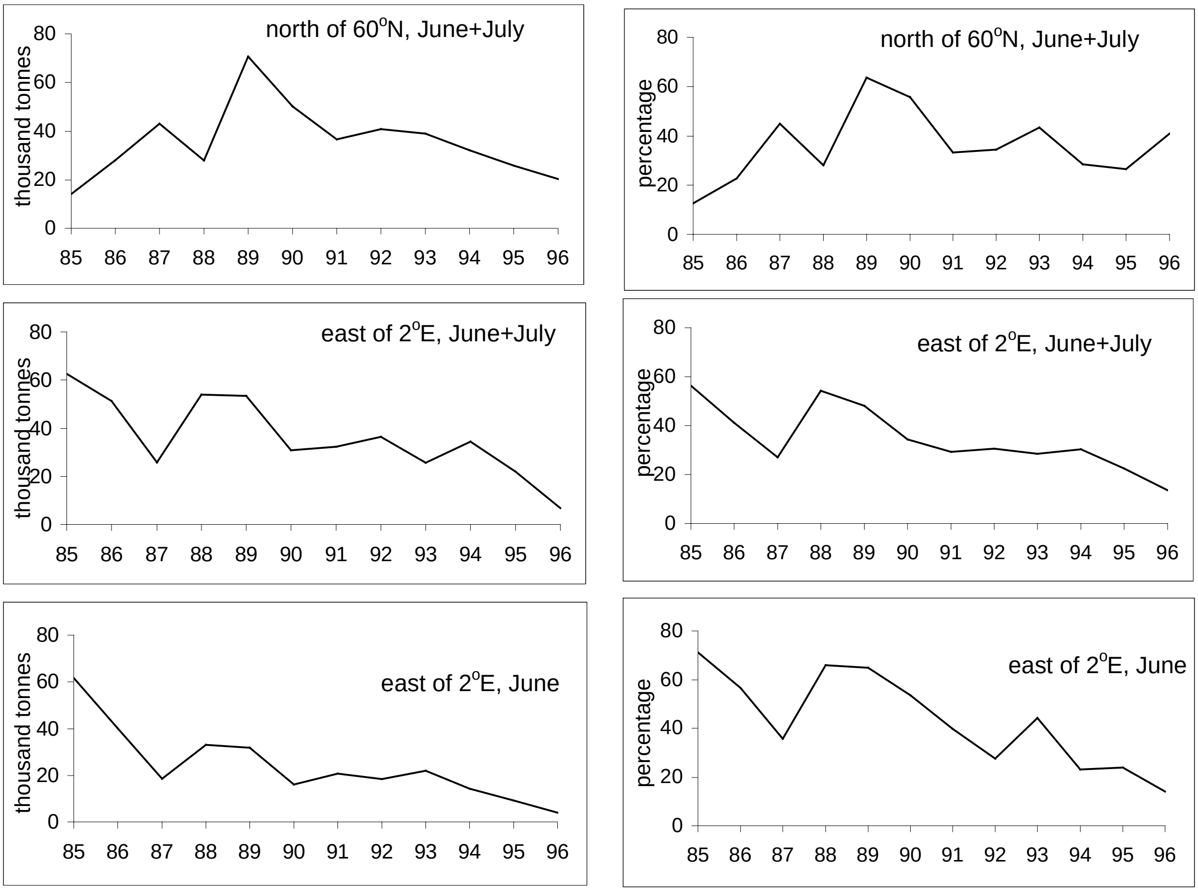


Figure 5.5. Catches in northern and eastern North Sea. Left-hand side graphs in 1000 tonnes, right-hand side graphs in percentage of total North Sea catch.

5.3.2. 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. 5.6. In the Shetland sector, acoustic abundance was high in the years 1988-1991, and also in 1996. The Shetland maximum in 1989-1990 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 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.

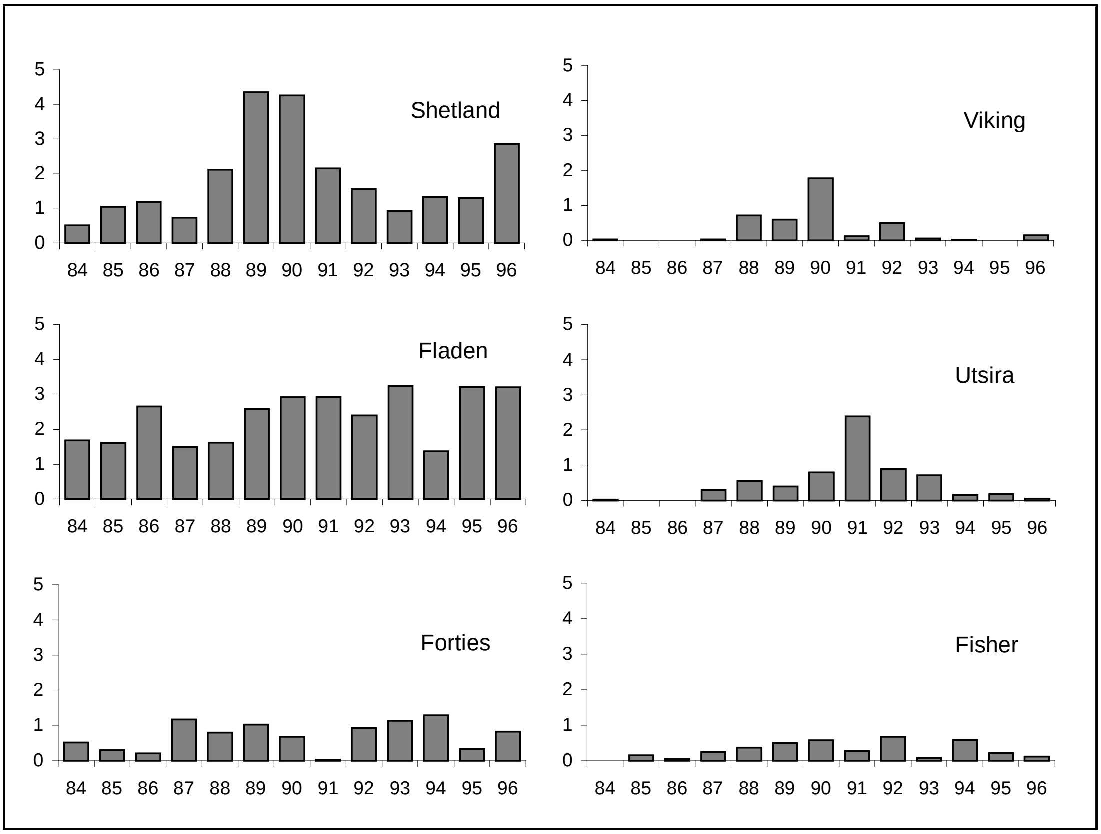


Figure 5.6. Acoustic estimates (numbers of fish x 10^9) by sector.

When the two northern sectors are combined (Fig. 5.7), the years 1988-1990 again have a high abundance in 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 - 1991, and then increased again in later years.

5.3.3. Relationship between northern distribution and water temperature

Bottom temperatures for position 60°N, 2°E in February are plotted in Fig. 5.8 for the years 1970-1996. It is seen that the temperatures reached their maximum values in the years 1988-1990, but stayed high also in 1991-1993.

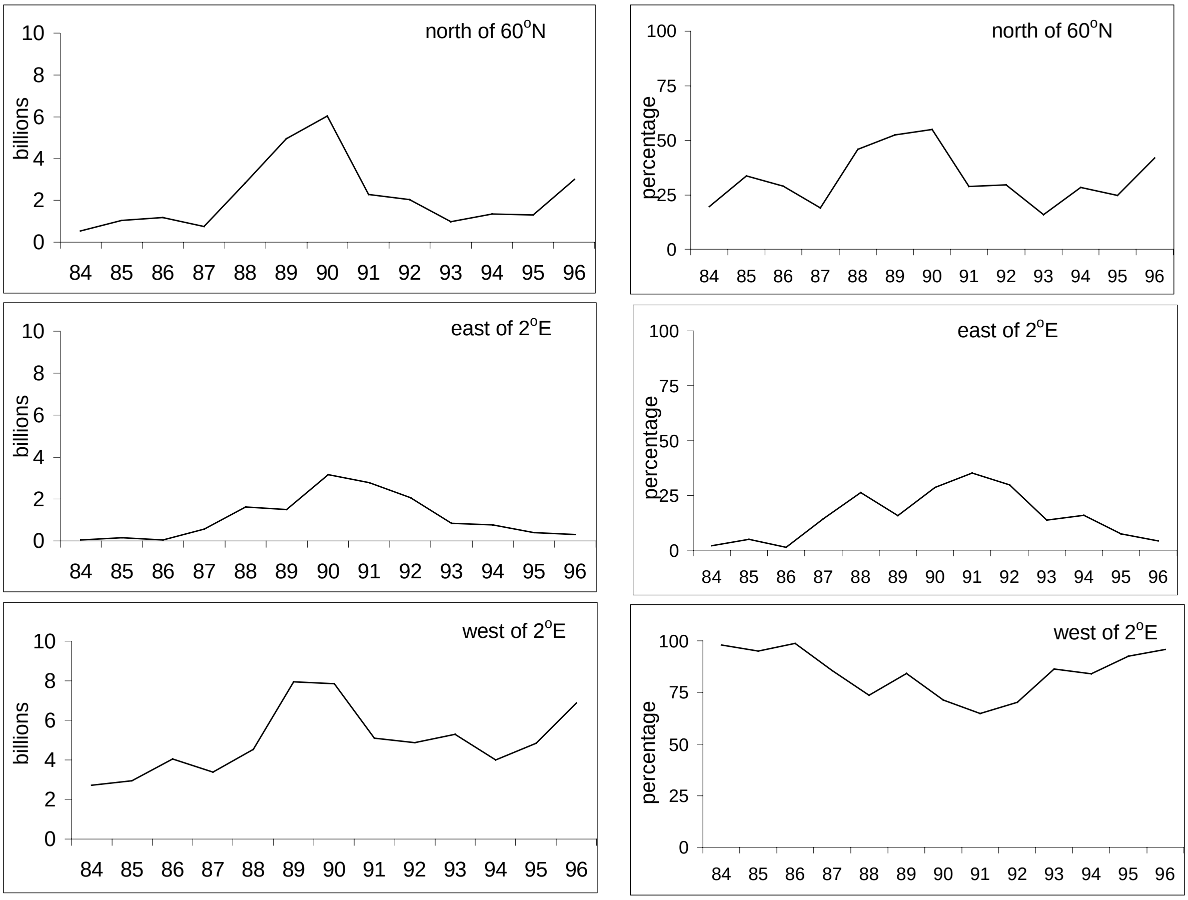


Figure 5.7. Acoustic estimates for northern, eastern and western North Sea. Left-hand side graphs in numbers of fish x 10^9, right-hand side graphs in percentage of total North Sea

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. 5.9, Table 5.1). 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 (> 500m) in Skagerrak was considered (Fig. 5.10). The data show that temperatures in the deep part 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 temperature 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 5.1. Correlation between northern distribution of the herring and two environmental variables.

Explanatory variable	Index northern distribution herring	r	p
Bottom temperature at 60°N, 02°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 Calanus 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

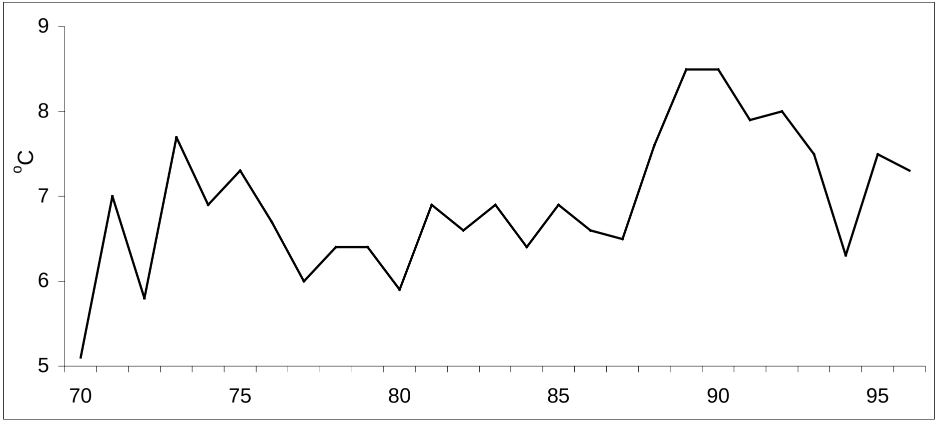


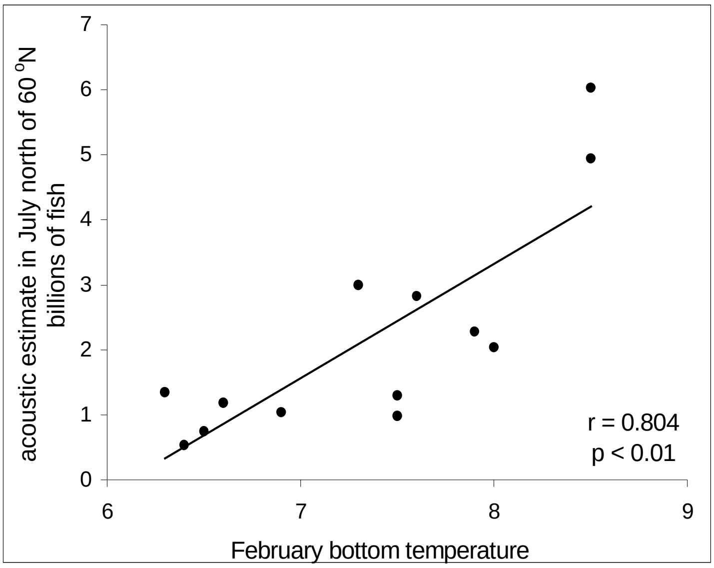
Figure 5.8. Bottom temperature at position 60°N, 02°E. Data from ICES Hydrographic Service.

5.3.4. 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. 5.11. 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 5.1, Fig. 5.12).

5.3.5. 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.



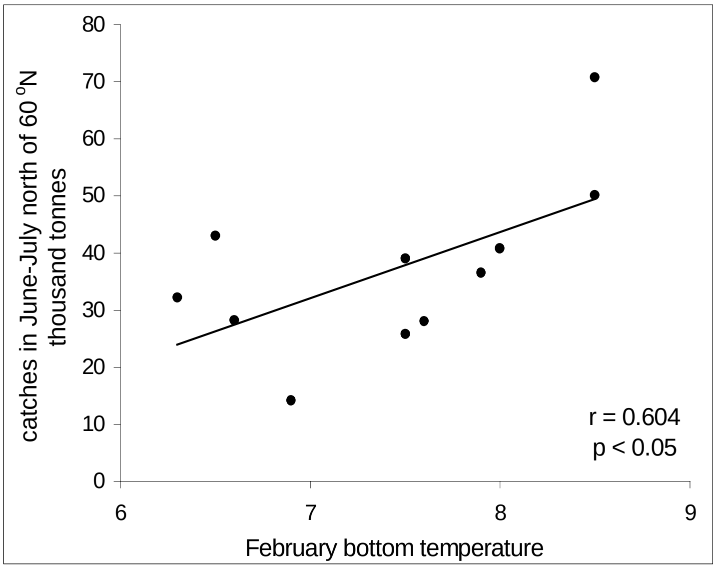


Figure 5.9. Correlation between bottom temperature in February and indices of northern distribution of herring during subsequent summer.

5.4. Discussion

5.4.1. 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.

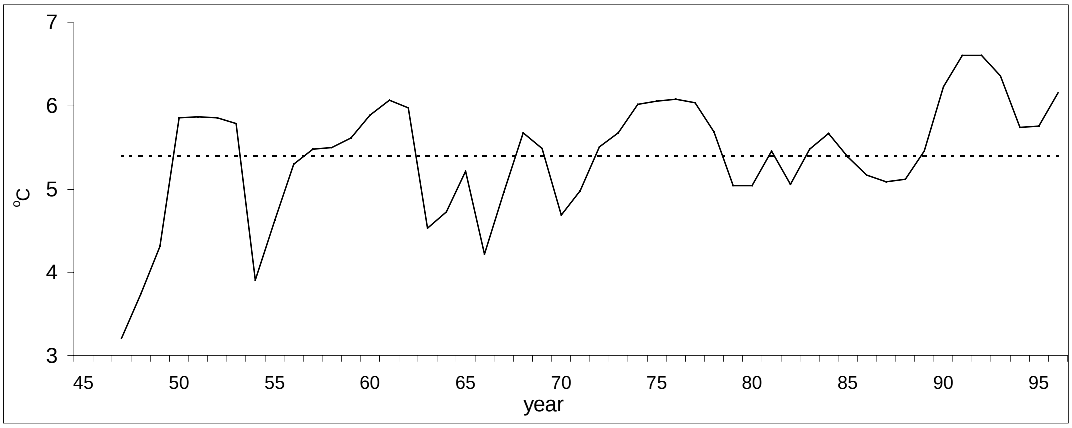


Figure 5.10. Annual average temperature in Skagerrak below 500 m compared to long-term mean. Data from ICES Hydrographic Service.

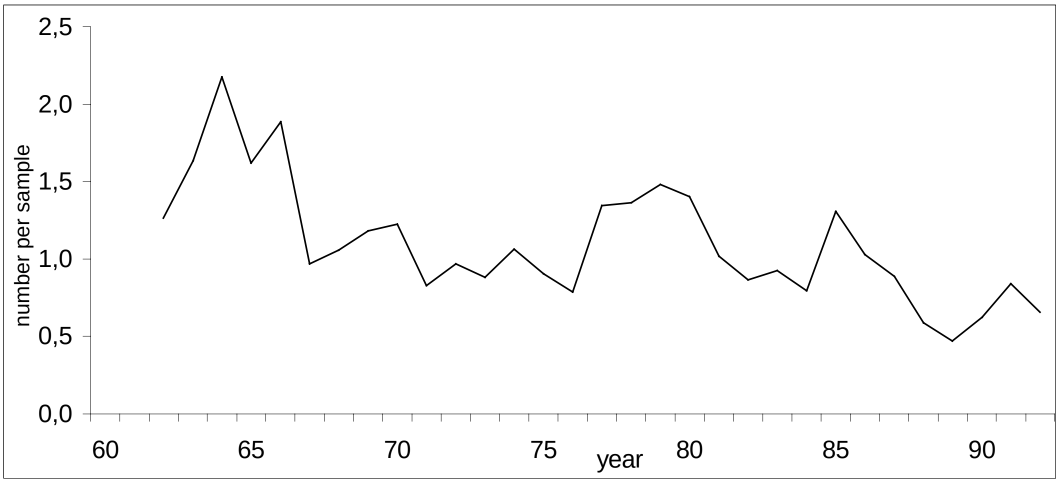


Figure 5.11. Annual average abundance *C. finmarchicus* in North Sea and adjacent part of North Atlantic, expressed in numbers of individuals per CPR sample. Data provided by

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

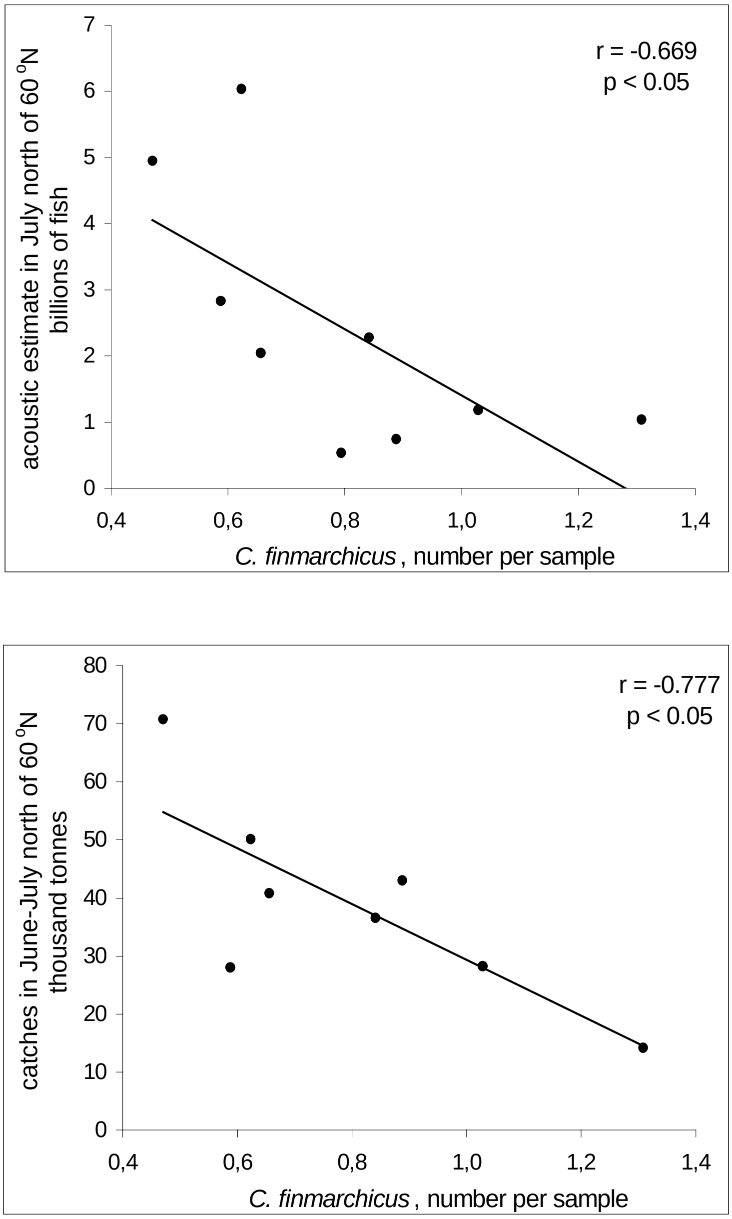


Figure 5.12. Correlation between annual abundance of *C. finmarchicus* and indices of northern distribution of herring during summer.

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 Faeroese waters during an acoustic survey in June 1990. Similar herring had been taken during exploratory fishing trips southeast of the Faeroes in June 1988 and 1989. The herring arrived in Faeroese waters in May, and they left the area in July in an easterly direction. The occurrence of these herring in Faeroese 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 Faeroese 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. 5.5), whereas this area made an insignificant contribution to the total North Sea catch in the years prior to 1960 (Fig. 5.1). 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. 5.1.

5.4.2. 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. finmarchicus* 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 Faeroes.

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 in their normal feeding areas, and this food shortage may have stimulated them to extend their feeding migrating 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.

5.5. 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 anomalous herring distribution 1988-1990, whereas their long-term trends could explain the sustained northward shift of herring since 1960.

If currents 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, and Gert van de Kamp. The study was part of the EU-sponsored SEFOS project.

Chapter 6

A possible adaptation of herring feeding migrations to a change in timing of the *Calanus finmarchicus* season in the eastern North Sea

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Abstract

During the first years after the re-opening of the North Sea herring fishery in 1983, a relatively high proportion of the catches in early summer was taken in the eastern North Sea. After 1986, the proportion of the catch in the eastern North Sea gradually declined. It is assumed that the high catches in the eastern North Sea in the early 1980s were due to a delayed migration of the herring from the eastern to the western part of the North Sea. This delayed departure of the herring from the eastern North Sea could have been caused by favourable food conditions in this area. Data on *Calanus finmarchicus* from the Continuous Plankton Recorder show that the seasonal cycle of this copepod in the eastern North Sea was delayed during the period 1976-1984, which resulted in an prolonged food supply for the herring in this area. It is likely that this extension of the feeding season induced the herring to delay their departure from the eastern North Sea. When the *Calanus* season shortened after 1985, the herring advanced their departure from the eastern North Sea. There was a delay of one or two years between the shortening of the feeding season and the earlier departure of the herring from the eastern North Sea. This suggests the existence of a certain conservatism in the migrations of the herring. It seems that the time of departure from the eastern North Sea is based not only on the food situation in the current year, but also on the average timing of food production in earlier years.

6.1. Introduction

When the fishery for North Sea herring was re-opened in 1983 after a ban of 6 years, the distribution of catches appeared to have changed in comparison to the years before the closure. This change in catch distribution was most pronounced during the month of June. Whereas in the years prior to the closure most catches in June were taken in the northwestern North Sea, the bulk of the catches in the first years after the re-opening came from the northeastern North Sea (Corten and Van de Kamp, 1992). This was the more surprising since herring catches in the eastern North Sea in the years prior to the closure (1971-1976) had been extremely low (ICES 1979). On the traditional fishing grounds in the northwestern North Sea, Dutch fishermen reported a scarcity of the herring in the first years after the re-opening of the fishery. The combination of high catches in the northeastern sector, and a low abundance of herring in the western area, suggested that the high catches in the northeastern sector were not merely due to an increased fishing effort in this area, but to a northeasterly shift in distribution of the stock.

In an analysis of the changes in catch distribution after 1983, Corten (2000) found that the northeasterly shift of catches was the combined effect of two separate trends; one working in a northerly direction and the other in an easterly direction. The northward shift, which had also been documented by Bailey *et al*. (1998) in an analysis of acoustic surveys, culminated in the years 1988-1990 and coincided with a succession of mild winters in the North Sea. There were two possible explanations for the northern distribution of the herring is these years: a direct effect of the high water temperature on the migratory behaviour of the herring, or an indirect effect of temperature through a change in food distribution. Planque and Fromentin (1997) had found that the main food item of the herring in the North Sea, *Calanus finmarchicus*, was sensitive to temperature. In years of high water temperature, the abundance of the species declined, particularly in the southern range of its distribution area. The feeding area of herring in the North Sea herring corresponds to the southern range of the distribution of *C. finmarchicus* in the North Atlantic region. A reduced abundance on the normal feeding grounds in the North Sea could have induced the herring to migrate north towards areas where *C. finmarchicus* was still abundant.

The temperature effect, however, could not explain the eastward shift of catches in the 1980s. This eastward shift did not coincide with the northward shift. It was most pronounced in the years immediately following the re-opening of the fishery in 1983, and it became less apparent in later years. Corten (2000) assumed that the easterly distribution of catches was not related to temperature, but to another, unknown environmental factor.

The purpose of the present study is to investigate the cause of this easterly distribution of catches in the early 1980s. From a preliminary analysis of catch distributions, it appeared that the easterly distribution occurred mainly in June; the first month of the fishing season. In July and August, the centre of the fishery shifted to the normal fishing grounds in the western North Sea. This suggested that the easterly distribution of catches in June was due to a delayed migration of the herring from the eastern to the western half of the North Sea. Herring spend the winter in the eastern part of the North Sea, in the vicinity of the Norwegian Trench (Parrish and Saville 1965). They normally leave this area in May or early June, and move over to the western half of the North Sea (Fig. 6.1). A low abundance of herring in the western North Sea in June, together with a high abundance in the eastern sector, could indicate a delayed departure of herring from the eastern North Sea.

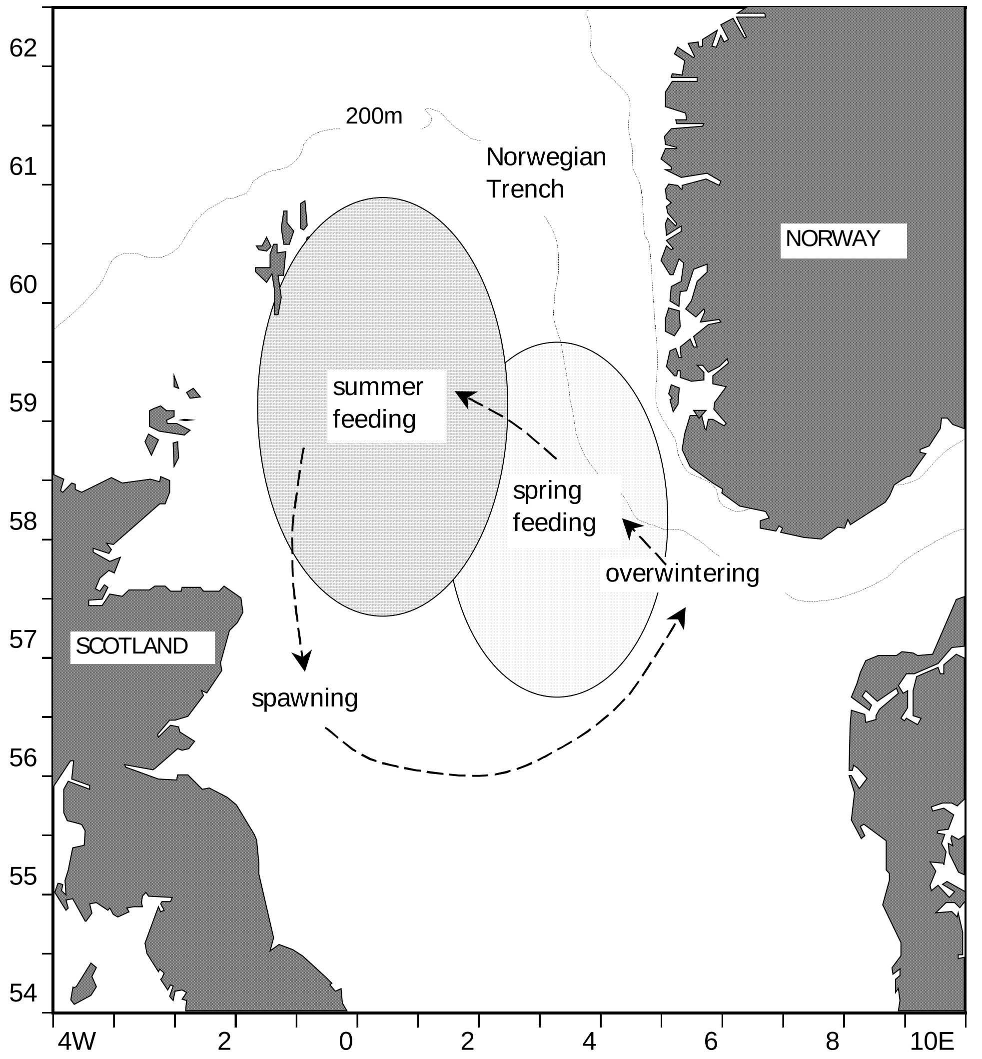

Figure 6.1. Schematic view of herring migrations in the northern North Sea, based on historical catch distributions in different seasons.

The cause of such a delayed departure could be an increased food supply in the eastern North Sea. It is in the eastern North Sea that the herring start feeding in March/April. By doing so, the fish take advantage of the fact that the spring bloom of *C. finmarchicus* occurs earlier in the eastern than in the western North Sea (Fransz *et al*. 1991). After *Calanus* starts to decline in the eastern North Sea, the herring move over to the western North Sea where the major plankton production occurs in June/July. The east/west migration of the herring in spring is presumably an adaptation to exploit the peak food production successively in the eastern and western North Sea. Such adaptations have also been noticed in other fish species. Harden Jones (1968) mentions that seasonal migrations are often a mechanism by which the population obtains the best part of the production cycle in different parts of its distribution area. In Norwegian spring spawning herring, the adaptation of feeding migrations to food distribution has already been described by Pavshtiks (1959), Østvedt (1965), Jacobsson (1969), Melle *et al*. (1994), and Holst *et al*. (1998). One may expect that North Sea herring, like Norwegian spring spawning herring, will also adapt their feeding migrations to changes in the distribution of their food. The delayed departure of the herring from the eastern North Sea in the early 1980s could thus have been an effect of favourable feeding conditions in the area. This is the hypothesis that will be tested in this paper.

6.2. Material and methods

6.2.1. Distribution of the herring stock

The distribution of the herring stock in different months and years has been estimated from the distribution of commercial catches and from the results of acoustic surveys. The distribution of commercial catches is of course only a rough approximation of the distribution of the stock and it would have been preferable to use catch per unit of effort (cpue). This index, however, is of little use in the highly directed herring fishery. The cpue of purse seiners and trawlers depends strongly upon the aggregation of the fish in schools, and therefore is no better index of stock abundance than the catch itself. Although the catches may not be directly proportional to fish abundance, they provide at least a qualitative index of stock distribution.

Detailed catch statistics for the entire North Sea are available only for the period after the fishing ban. From 1985 onwards, the ICES Herring Assessment Working Group compiled monthly charts of catches per statistical rectangle (ICES 1986 and subsequent reports). The figures reported in these charts were based on the best data available to working group members, and they may deviate from the catch data that were reported by the official statistical agencies in the various countries.

For the first two years after the re-opening of the fishery (1983 and 1984), no monthly charts of catches were published by ICES. In 1983 the fishery did not start until the second half of the year, due to problems in settling the quotas (ICES 1984). Because of the late start of the season, there was no fishery in the eastern North Sea in this year. In 1984 the fishery was conducted for the first time throughout the season. According to national statistics, the Norwegian fleet took 38,000 t in June and 16,000 t in July in the area east of 2°E (Aglen, pers. comm.). The corresponding monthly catches for the Scottish and Dutch fishery in the western half of the North Sea are not available; only the total annual catch. In order to obtain estimates for the monthly catches in the western sector in 1984, it was assumed that the distribution of the annual catch over the months was the same as in 1985; the first year for which monthly data for the western North Sea were reported.

Herring acoustic surveys provide a second source of information on the geographical distribution of the stock. These surveys, intended to monitor the development of total stock, were organised by a number of countries starting from 1983. The first full coverage of the North Sea was obtained in 1984, and the results were reported annually to the ICES Statutory Meeting (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 that was kindly provided by J. Simmonds and M. Bailey of the Marine Laboratory in Aberdeen. This set contained numbers per rectangle of adult, autumn spawning herring for the years 1984-1996, all calculated in a standard way.

6.2.2. Food abundance

Data on the abundance of planktonic food in the eastern North Sea were obtained from the Continuous Plankton Recorder (CPR) Survey. CPR samples are collected by ships of opportunity on standard shipping lines across the North Sea and the North Atlantic. A detailed description of the CPR sampling methods and data processing is given by Warner and Hays (1994). The CPR data base at the Sir Alister Hardy Foundation of Ocean Science (SAHFOS) in Plymouth holds computerised data for the North Sea back to 1948. The food items considered in this study were *Calanus finmarchicus*, Euphausiacea, and Larvacea. These three taxa are assumed to be the main food items for herring in the northern North Sea.

C. finmarchicus is the dominant copepod species in the northern North Sea and the main food item of the herring (Hardy *et al*. 1936, Parrish and Saville 1965, Dalpadado *et al*. 1996). After a rapid expansion in spring, the species can constitute more than 70% of the total zooplankton biomass in the northern North Sea in May/June (Fransz *et al*. 1991). In the CPR samples, *Calanus* has been identified to species level only from 1958 onwards. In earlier years, all *Calanus* species (mainly *C. finmarchicus* and *C. helgolandicus*) were lumped into one category “*Calanus* IV-V”. For these earlier years, the numbers of *C. finmarchicus* in the samples have been estimated by assuming that the ratio between *C. finmarchicus* and *C. helgolandicus* was equal to the mean ratio between these species in 1958-70.

The Euphausiacea are a group consisting of at least of five species, the most important of which is *Meganyctiphanes norvegica* (Lindley 1979, 1982a). In the routine analysis of CPR samples, the members of this group are not identified to species. Compared to other components of the plankton, Euphausiacea have a relatively long life span of one to two years (Lindley 1982b). Substantial stocks of these organisms overwinter in the northern North Sea, and Euphausiacea constitute the main food for herring at the beginning of the feeding season, before the *Calanus* bloom has started (Falk 1977, Dalpadado *et al*. 1996).

Larvacea, i.e. various species of *Oikopleura*, have sometimes been mentioned as an important food item for herring in the northeastern North Sea (Savage 1937). These organisms start to increase in May and June, and they reach their peak abundance in the eastern North Sea in July/August.

The abundance of each of these food items was considered for the entire period for which CPR data were available, i.e. the years 1948-1996. This was done in order to judge whether food conditions in the early 1980s deviated from the long-term mean. Samples were combined for the eastern North Sea, defined as the area east of 2°E between 56° and 60°N, and mean numbers per sample were calculated by month. Sampling intensity in the eastern North Sea was around 10-20 samples per month until the early 1980s, but it dropped to 5-10 samples per month after 1986. The monthly estimates of food abundance for these later years, therefore, are less accurate than for the earlier period.

6.3. Results

6.3.1. Distribution of herring catches

A global view of the changes in catch distribution in the northern North Sea during the period 1985-1996 is presented in Fig. 6.2. This Figure shows the average distribution of annual catches by statistical rectangle in three successive periods (1985-1988, 1989-1992, and 1993-1996). During the first period, most of the catches originated from the eastern North Sea south of 60°N. In the second period, the catches in the eastern area had declined, and the centre of the fishery had shifted north-west. A major part of the catch was taken north of 60°N. In the third period, catches north of 60°N had declined, and the fishery had shifted southwest. Over the whole period 1985-1996, one sees a continuous shift of catches to the west, and a temporary excursion to the north.

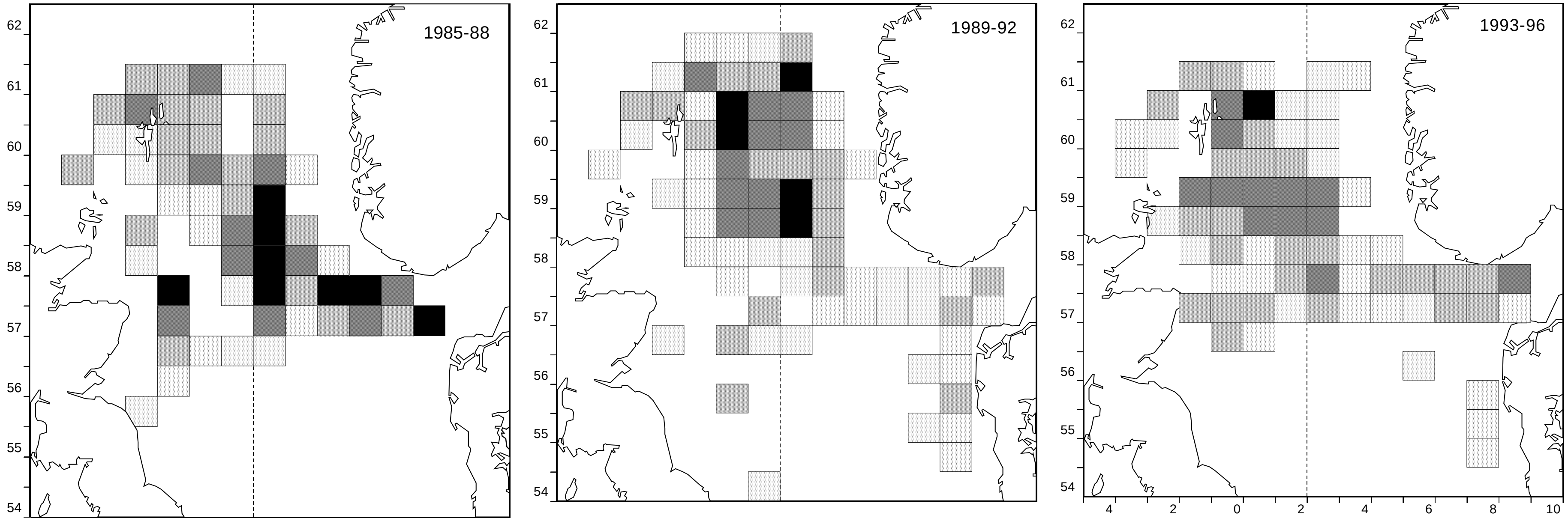

Figure 6.2. Mean distribution of herring catches by four-year periods. The 2° East meridian is shown to highlight the shift in catches from east to west. Categories: 100-500, 501-1000, 1001-2500, and >2500 t/yr. Based on data from the ICES Herring Assessment Working Group (ICES 1986 and subsequent reports).

The data in Fig. 6.2 refer to annual catches. Most of the catches in the northern North Sea are taken in June and July. In order to see which of these two months contributed most to the observed east/west shift in catch distribution, the catch data were grouped by month for the eastern and western half of the North Sea. The limits of these two subareas are shown in Fig 6.3.

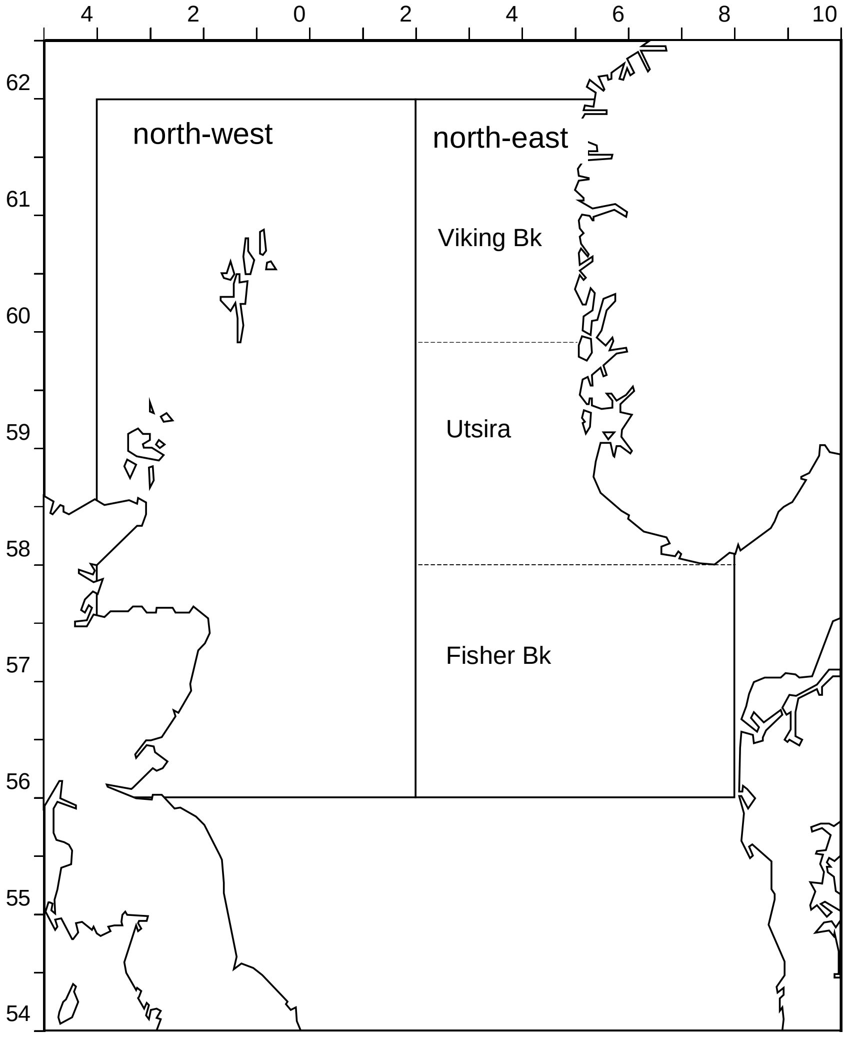

Figure 6.3. Definition of sub-areas for herring catch statistics.

The distribution of the total catch between the eastern and western half of the North Sea in June and July is shown in Fig. 6.4. In June, the catches in the eastern North Sea gradually declined over the period 1985-1996, both in absolute and relative terms. Expressed as a percentage of the total catch, the contribution of the eastern North Sea declined from 70% in 1985 to less than 20% in 1996. In July, the main part

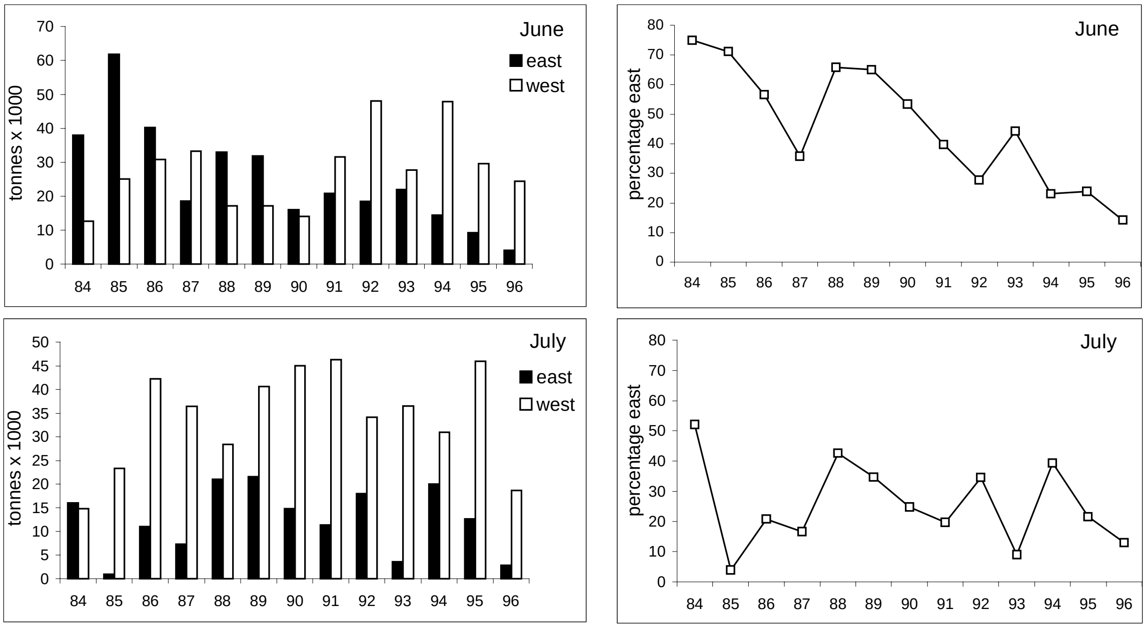

Figure 6.4. Herring catches for June and July in the eastern and western North Sea (left), and the percentage of the total catch in the eastern sector (right).

of the catch always came from the western half of the North Sea. The catches in the eastern half fluctuated around 25% of the total, without showing a trend over the years. It may be concluded, therefore, that the pronounced easterly distribution of the catches in the early 1980s occurred mainly during June; the first month of the fishing season.

Apart from the easterly distribution of catches in the early 1980s, the picture in Fig. 6.2 also shows a northerly distribution of catches around 1990, especially in the eastern half of the North Sea. This northerly distribution can be shown more clearly by plotting the June catches in the eastern North Sea by three smaller sub-areas shown in Fig. 6.3 (Viking Bank, Utsira, and Fisher Bank). The results (Fig. 6.5) show a marked increase in the northernmost area in 1989 and 1990, coinciding with a depression in the southernmost area.

6.3.2. Acoustic surveys

The results of acoustic surveys provide an independent estimate of the distribution of the stock in July. Numbers of fish per statistical rectangle were combined for the eastern and western North Sea in order to obtain acoustic estimates for each of the two areas (Fig. 6.6). The results show that the bulk of the stock was always found in the

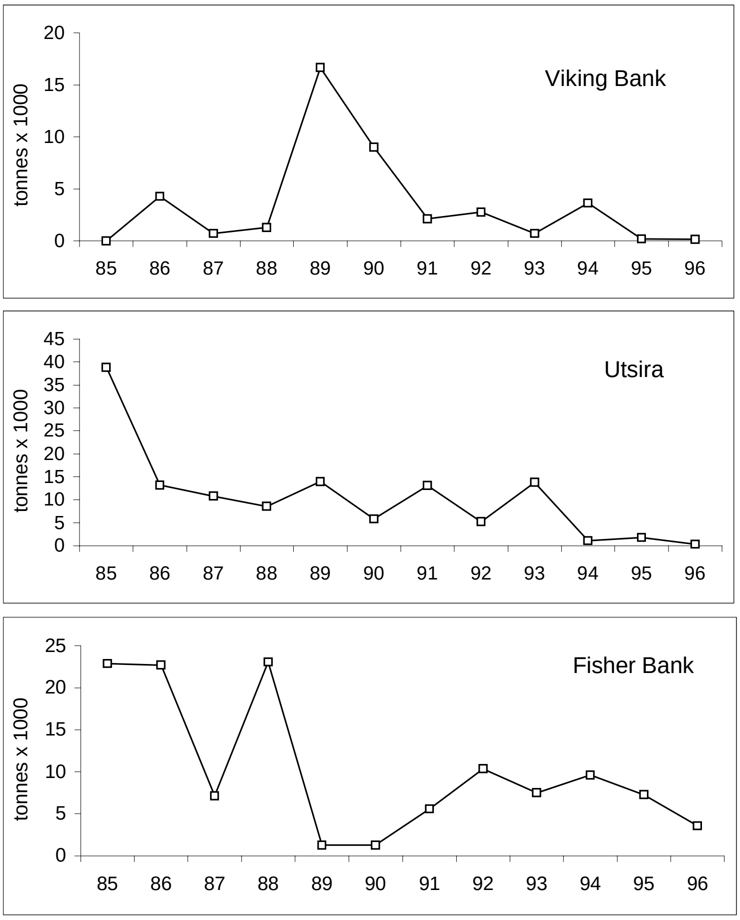

Figure 6.5. Herring catches in June in three sub-areas in the northeastern North Sea, showing the northern distribution of catches in 1989-1990.

western North Sea. This agrees with the results of the catch distributions, that also showed a predominance of the western area in July.

On a more detailed level, however, the results of the acoustic surveys deviate from the catch data in July. Whereas in the catch data, the contribution of the eastern sector fluctuated without trend, the acoustic estimates for this sector show a distinct pattern over the years. The proportion of the stock in the eastern sector gradually increased from 2% in 1984 to 30-35% in the years 1990-1992, and then decreased again to 4% in 1996. This marked pattern is not seen in the catch data for July.

There is a correspondence, however, between catch data and acoustic results with respect to the northern distribution of the stock in the years 1989-1990. When acoustic estimates for the stock north and south of 60°N are compared (Fig. 6.7), it appears that both the absolute and relative stock size north of 60°N was high in 1988-1990. In the catch data, a northerly distribution was noticed in 1989-1990 (Fig. 6.5).

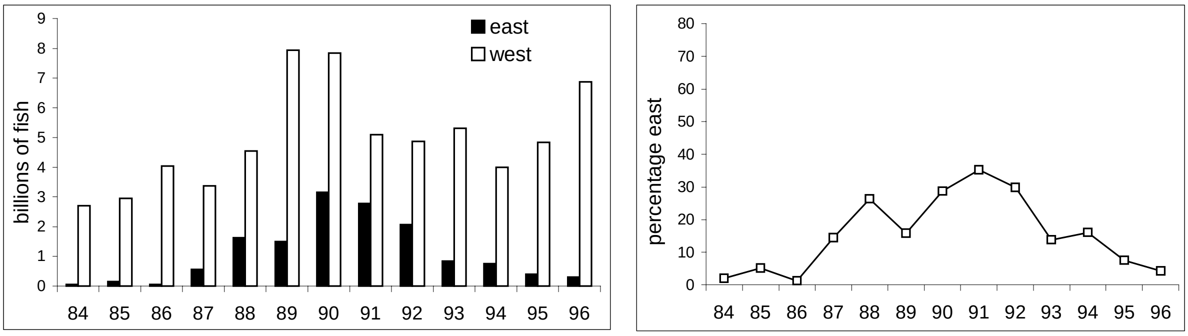

Figure 6.6. Acoustic stock estimates for the eastern and western North Sea (left), and the proportion of the stock in the eastern North Sea (right).

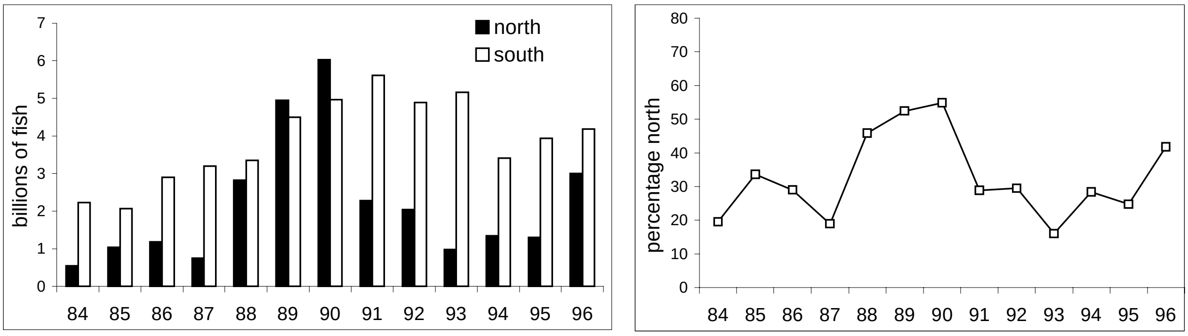

Figure 6.7. Acoustic stock estimates for the area north and south of 60°N (left), and the proportion of the stock in the northern part (right). Data exclude the survey area south of 56°N.

6.3.3. Food abundance

According to the hypothesis, the prolonged stay of the herring in the eastern North Sea must have been due to favourable feeding conditions in this area. These favourable conditions must have existed especially in June, the month during which the herring delayed their departure from the eastern North Sea. In order to test the hypothesis, therefore, we have to consider food conditions in the eastern North Sea specifically in June. Fig. 6.8 presents CPR data on the three main food items for the herring in this month. Data are shown for the entire period 1948-1996 in order to illustrate possible long-term trends in any of the three groups.

The main food item of the herring, *C. finmarchicus*, was unusually abundant during the period 1976 – 1984. This organism was far above the long-term average in

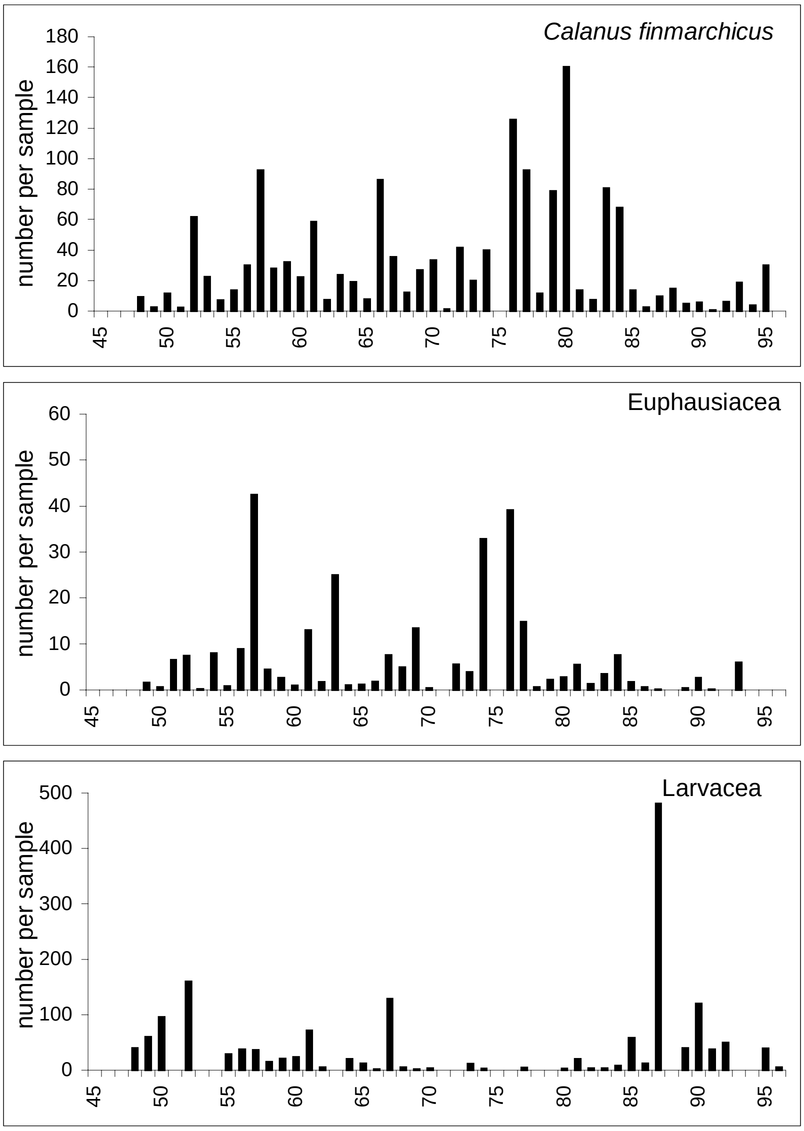

Figure 6.8. Abundance in June of the principal food components of herring in the eastern North Sea. Data for all years of CPR sampling. Values in numbers per CPR sample.

6 out of 9 years during this period. Starting from 1985, its abundance declined sharply. There seems to be a relation between the high abundance of *Calanus* in the period 1976 – 84, and the prolonged stay of the herring in the eastern North Sea at the time when the fishery was resumed in 1984 . We shall return to this subject later.

In order to see whether the changes of *C. finmarchicus* in June were caused by variations in total annual production or merely by changes in the timing of the production, the annual development of the *C. finmarchicus* season was investigated for a long series of years (1970-1996). The plot of monthly abundance indices in Fig. 6.9

shows that the variations in June were caused at least partly by a change in timing of the production cycle. In the years 1976-1984 the *Calanus* season in the eastern North Sea had a relatively long duration and extended into June or even into July. The peak abundance in this period occurred normally after May. Starting from 1985, the *Calanus* season shortened and the peak abundance advanced towards April or May. In the years 1988-1992, the abundance of *Calanus* was very low throughout the year. The changes of *Calanus* abundance in June, presented in Fig. 6.8, thus appear to be part of a larger pattern of change that affected both the timing and the size of the annual production.

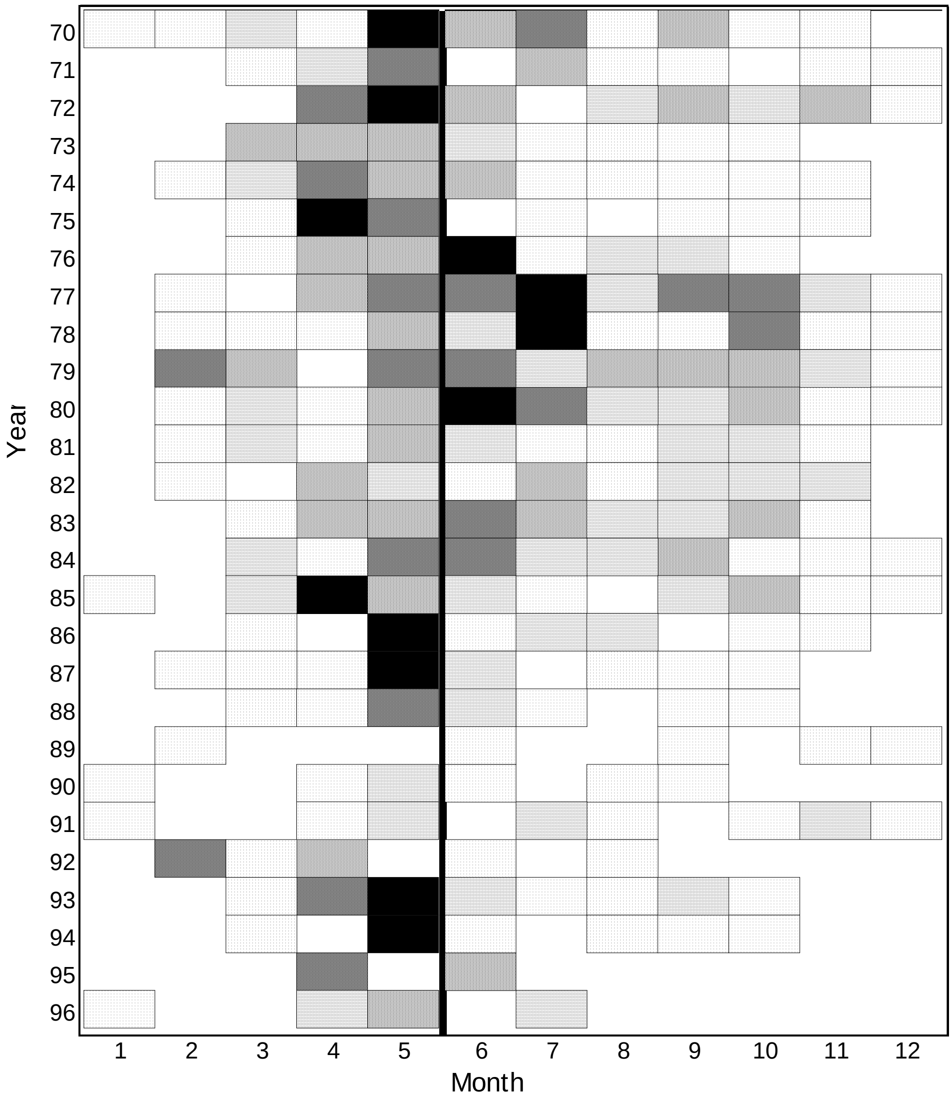

Figure 6.9. Monthly abundance of *C. finmarchicus* in the northeastern North Sea, expressed as numbers per CPR sample. The critical border between May and June has been highlighted by a black line. Shaded cells represent values of 3-9, 10-24, 25-49, 50-99, and >99 individuals per sample.

The abundance of the other two food items of the herring, Euphausiacea and Larvacea, also showed multi-annual variations in abundance during the month of June (Fig. 6.8). The Euphausiacea were relatively abundant in the mid-1970s and declined after 1977. The Larvacea were at a very low level between 1969 and 1984, and increased starting from 1985. Neither of the two groups shows a pattern, however, that corresponds in time and direction with the observed changes in herring abundance in the eastern North Sea.

6.4. Discussion

The hypothesis for the easterly distribution of herring catches in the mid-1980s consisted of two elements. Firstly, the easterly distribution of catches was assumed to be caused by a prolonged stay of the herring in the eastern area, prior to their departure to the western North Sea. Secondly, this prolonged stay in the eastern area was supposed to be due to favourable feeding conditions in this area.

Catch statistics and results from acoustic surveys show that the easterly distribution of herring in the mid-1980s was restricted to the month of June. In July, the distribution of catches had resumed its normal pattern, with the centre of gravity in the western North Sea. The results of the acoustic surveys in these years confirm that the stock in July had resumed its normal westerly distribution. It may be concluded, therefore, that the easterly distribution of catches in the mid-1980s was indeed due to a delay of about one month in the departure of the herring from the eastern to the western part of the North Sea.

The years in which the herring delayed their departure from the eastern North Sea followed a period of years in which the *C. finmarchicus* season extended into June. In order to compare the long-term changes in herring and *Calanus* in more detail, the proportion of the herring catch taken in June in the eastern sector and the abundance of *Calanus* in this area and month have been plotted on the same time axis in Fig. 6.10. The figure shows that the years of the extended *Calanus* seasons (1976-1984) largely coincided with the years of the fishing ban (1977-1983). Therefore, there are no data on herring distribution for most of the years in which the feeding season was prolonged. All we know is that the pattern of staying in the eastern sector in June had become firmly established when the fishery was re-opened in 1984 (judging from the repetition of this pattern in the next few years). This suggests that the population had started to prolong its stay in the eastern sector already some years prior to 1984.

The lack of data on herring distribution for the period 1977-1983 prevents us from demonstrating a statistically significant relationship between herring distribution and food. There is only one year of overlap (1984) between the period of extended *Calanus* seasons and the period for which we have data on herring distribution. Despite the lack of a statistical proof, however, one may conclude that the data support the hypothesis of a causal relationship between food abundance and the prolonged stay of the herring in the eastern North Sea. This conclusion is based on the general correspondence in time and direction of the observed changes in herring and *Calanus*. The herring started to prolong their stay in the eastern North Sea sometime between 1977 and 1984, following a marked extension of the *Calanus* season. When the *Calanus* season contracted after 1984, the herring gradually advanced their departure from the eastern North Sea. Considering the fact that *Calanus* constitutes the main food for herring at this time of the year, it is reasonable to assume that the changes in herring distribution were a consequence of the changes in *Calanus*.

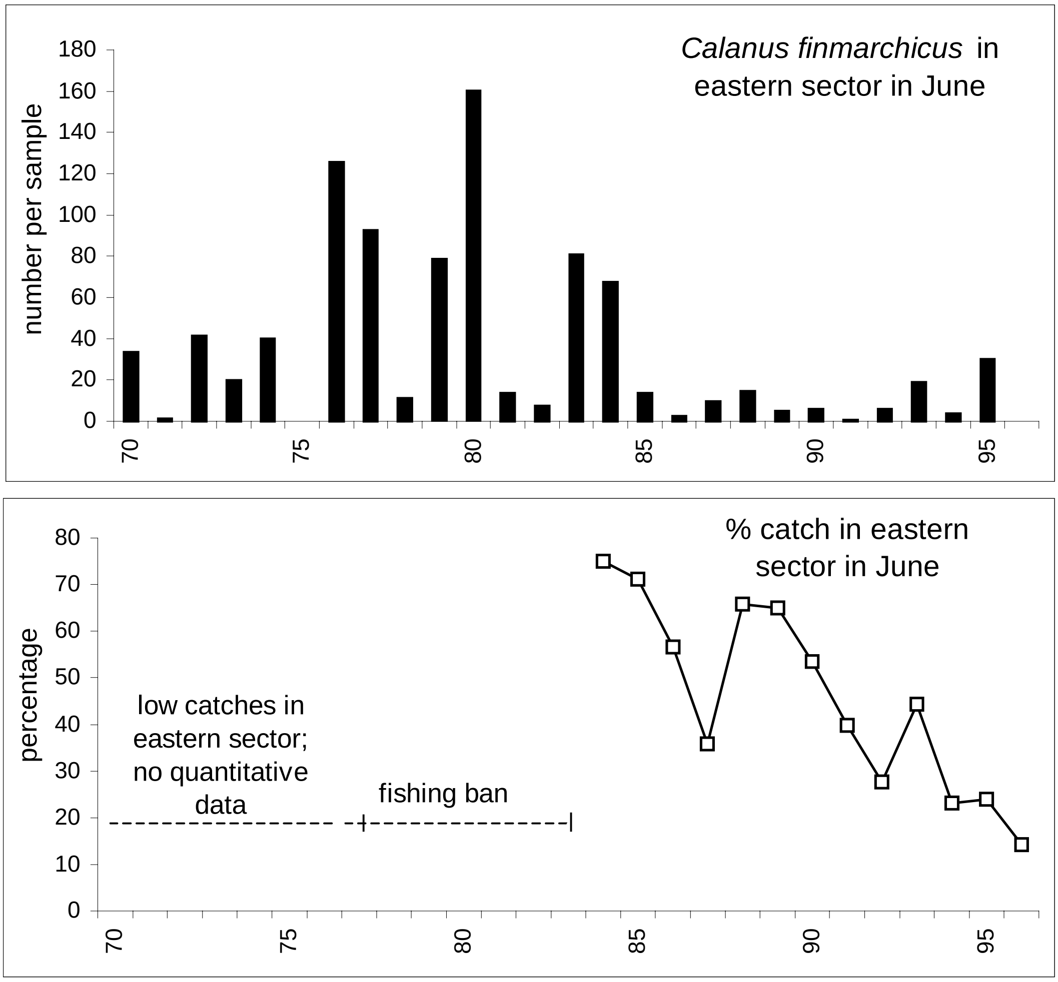

Figure 6.10. Comparison between *Calanus* abundance in the eastern North Sea in June and the relative contribution of the eastern North Sea to the total herring catch in that month.

The prolonged stay of North Sea herring in the eastern sector during years of high food abundance is comparable to the behaviour of Norwegian spring spawning herring. These fish were observed to delay their westward feeding migration in the spring of 1998 after they found unusually abundant food resources (again *C. finmarchicus*) in the eastern part of the Norwegian Sea (Holst *et al.* 1998).

In the North Sea herring, the pattern of staying in the eastern sector persisted for several years after the abundance of *Calanus* in June had declined (Fig. 6.10). In the years 1985-1990 (with the exception of 1987) herring catches in the eastern sector in June remained high, whereas *Calanus* abundance had already sharply declined. There are several factors that may have been responsible for slow response of the herring to the decline of *Calanus*.

For the first few years after the decline in *Calanus* (1985 and 1986), the continued presence of herring in the eastern sector could be due to conservatism in the behaviour of the herring. Although herring are capable of quickly adjusting their distribution to changes in food abundance on a small geographical scale (Cushing 1955), they may take more time to do so in case of changes on a larger geographical or temporal scale. If the herring had “learned” to stay in the eastern North Sea in June during the years of high *Calanus* abundance, it may have taken them a few years to “unlearn” this tradition after the abundance of *Calanus* had declined. Herring sometimes exhibit a certain conservatism in their migration patterns. This was noticed by Jakobsson (1969) in a study on the feeding migrations of Norwegian spring spawning herring. When food abundance on the traditional feeding grounds of these herring gradually declined in 1963-1965, the herring still continued to visit this area each year. Only when temperature conditions also deteriorated in 1965, the population finally changed its migrations and moved to a new feeding ground.

The conservative behaviour of herring could be an adaptation that prevents the population from overreacting to short-term variations in food abundance (Fernö *et al.* 1998). Although the spatial and temporal distribution of plankton is quite stable when considered on a multi-annual scale, the actual abundance in a given year may fluctuate strongly from one month to another (Fig. 6.9). It would be inefficient for the herring to adjust the timing of their long-range migrations to each of these short-term variation in food abundance. If food abundance in a normally rich feeding area temporarily drops, the fish will have a greater chance of finding food by staying in the same area and waiting for a new outburst of productivity, than by leaving the area prematurely. The best strategy for the fish would thus be to base the timing of their long-range feeding migrations on the average timing of the food production in the last few years, rather than on short-term fluctuations in the current year.

The hypothesis of conservative behaviour implies the existence of some kind of collective memory in the population. A certain number of fish in the population should be able to “remember” where and when they encountered favourable feeding conditions in previous years. Speculative as this assumption may seem to be, there is a growing amount of evidence that conservative behaviour indeed occurs in herring. This behaviour is observed not only in feeding migrations (Jakobsson 1969, Mysund *et al*. 1998, Fernö *et al*. 1998), but also in spawning and overwintering migrations (Wynne Edwards 1962, Røttingen 1992, Dommasnes *et al*. 1994, McQuinn 1997).

Although conservatism may thus have been responsible for the continued presence of the herring in the eastern North Sea in the first years after the decline of *Calanus* (1985 and 1986), it is unlikely that this factor would have affected herring behaviour for a much longer period. The decline of herring catches in the eastern sector in 1986 and 1987 indicates the disappearance of the new tradition, 1-2 years after the decline of *Calanus*. The proportion of the herring catch in the eastern sector, however, increased again in the years 1988-1990. It is unlikely that this phenomenon was connected to the high abundance of *Calanus* 4-6 year earlier. The high proportion of the catch in the eastern sector in 1988-1990 was probably due to a completely different cause, namely the anomalous northward migrations in these years, already mentioned in the introduction. The northward migrations in 1988-1990 will have affected the east/west distribution of the stock in June (and July), since by migrating north instead of west, the herring remained longer in the eastern sector than they would have done otherwise.

The two factors mentioned above, conservative behaviour and northerly migrations in 1988-1990, go a long way in explaining the time lag between the decline in *Calanus* and the reduction of herring catches in the eastern sector. The possibility remains, however, that in addition to temperature and *Calanus*, other factors affected the east/west distribution of the herring after 1984. These factors could include food items that were not considered in the present analysis (e.g. juvenile sandeel). An indication for the existence of such other factors is the trend in the acoustic data for July (Fig. 6.6). The acoustic surveys found a relatively high percentage (20-30%) of the stock in the eastern sector in July 1988-1992. For the first three years in this period (1988-1990) the easterly distribution in July was probably an effect of the anomalous northern migration of the herring; the same migration that affected the catch distribution in June (see above). For the next two years (1991 and 1992), however, the high proportion of the stock in the eastern sector in July can not be explained by northerly migrations, nor by the abundance of *Calanus*. Assuming that the acoustic estimates are correct, there must have been another factor in these two years that kept a significant fraction of the stock in the eastern North Sea until July.

Acknowledgements

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Chapter 7

The role of conservatism and tradition in stabilising migrations of herring

Abstract

Herring migrations often exhibit a remarkable stability from year to year. Spawning and wintering areas, and to some extent also feeding areas tend to remain constant over periods of decades or longer, despite annual changes in temperature, currents and food distribution. The mechanism behind this stability is investigated in this paper. Despite their stability under normal circumstances, herring migrations are sometimes observed to change abruptly. This indicates that the precise position of feeding, spawning and wintering areas is not genetically determined. Earlier authors have suggested that the stability of herring migrations under normal conditions is the result of conservatism: the fish would “remember” the places where they have been before, and have a tendency to return to these places in subsequent years. In this paper I review the evidence in support of this theory. Two types of conservatism are distinguished: habit formation and tradition. Habit formation is the simplest form of conservatism: the fish repeat a migration which they have performed by chance the first time. A more sophisticated form of conservatism is tradition. In this case young fish learn a migration route from older herring, adhere to it for the rest of their life, and pass the habit on to the next generation. It is difficult to prove the existence of habit formation or tradition in herring populations by experimental means because the populations involved are very large and the migrations take place in the open sea. The study of this phenomenon, therefore, has to be based on observations of herring populations under natural conditions. In this paper, several observations on the behaviour of North Sea herring and Norwegian herring are presented that support the hypothesis of habit formation and tradition. The strongest support is provided by cases in which the herring adapt their migration in response to a change in currents or food distribution, and adhere to the new migration even after the original stimulus has disappeared.

7.1. Introduction

Migrations of herring (*Clupea harengus*) usually show a very stable pattern from year to year. This stability is normally taken for granted; scientists become interested in herring migrations only when there is an occasional change. In such cases, they try to find an explanation for the change by relating herring distribution to a variety of environmental factors, such as temperature (Jakobsson 1969), food (Bainbridge and

Forsyth 1972), water type (Storrow 1932), meteorological conditions (Alheit and Hagen 1997), combinations of different hydrographic factors (Maravelias 1997) or even extraterrestrial influences (Ljungman 1880, Pettersson 1926).

The papers dealing with changes in herring migrations far outnumber the papers that deal with the stability of them. Yet, the question what makes the herring change their migrations in exceptional circumstances is directly related to the question what makes them adhere to the routine pattern under normal conditions. If we understand the mechanism behind the normal stability of herring migrations, we are in a better position to address the question why these migrations occasionally may be altered.

The mechanisms that govern the distribution of herring (and animals in general) can be divided into reactive and predictive mechanisms (Neill 1979, Dodson 1988, Fernö et al. 1998). Reactive mechanisms make the fish respond to changes in its direct environment. It is these mechanisms that are supposed to be responsible for the annual, or even multi-annual variations in the distribution of the fish. All the above studies on changes in herring distribution deal with reactive mechanisms.

If we want to study the stability of the distribution and migrations, we have to concentrate on the second type of mechanisms, i.e. the predictive ones. A predictive mechanism controls the distribution of the fish irrespective of environmental stimuli. Therefore, it is this class of mechanisms that must be responsible for the stability of fish distributions, even in situations where the environment changes.

Predictive mechanisms fall into two categories: genetic control and learnt behaviour (Fernö et al. 1998). Most of the studies on fish behaviour (and animal behaviour in general) have so far concentrated on genetic control. It has been demonstrated that innate factors are responsible for the general timing and orientation of the migration in a large number of animals, particularly birds (Perdeck 1958, Berthold and Querner 1981, Helbig 1991), but also mammals, fish and even insects (Dingle 1996). In salmon, genetic factors control both the timing of migration in smolts and the direction of their migration (see review by Smith 1985).

In view of the widespread occurrence of genetic control in animal migrations, it is likely that these factors also play a role in herring migrations. However, in herring migrations we sometimes observe that not only the timing and general direction are constant from year to year, but also the small details of the migration route. The best example are the spawning migrations. Herring are known to spawn each year in very specific localities, often only a few kilometres in extent, to which they migrate over distances of several hundred kilometres (Harden Jones 1968). It is hard to imagine that the return of the fish to such specific localities, i.e. the fine tuning of the migrations, is also a matter of genetic control.

The question whether or not migration routes are genetically determined is related to the question whether or not individual populations are genetically distinct. The discussion on this subject has gone on throughout most of the 20th century. Some scientists showed that adjacent spawning populations differed in meristic and morphometric characteristics, and they considered this as evidence for a genetic separation of the populations (Zijlstra 1958, 1969, Postuma and Zijlstra 1958). This implied that recruit spawners would return to the spawning ground where they were born, and that this homing to a particular spawning ground was most likely genetically controlled.

However, other scientists questioned the assumption that spawning populations constituted self-contained, genetically distinct stocks. Hodgson (1929) found different otolith types among herring spawning at the same time on the same spawning ground. This suggested the herring were not all born in the same season, and that the spawning population concerned, therefore, did not constitute a self contained stock. Reviews of the extensive discussion on this subject are presented by Harden Jones (1968), Smith and Jamieson (1986), and McQuinn (1997). Smith and Jamieson (1986) presented a review of the earlier studies on tagging, spawning time, morphometric and meristic characteristics, and allozyme data, and they concluded that the majority of the results did not support the hypothesis of a genetic distinction between neighbouring spawning populations.

The conclusion of Smith and Jamieson (1986) that there was no evidence for genetic differences between neighbouring spawning populations, had important implications for the migration mechanism. If the different populations had no separate genetic identity, the homing of herring to specific spawning grounds could not be genetically determined either. Later authors tried to identify another predictive mechanism that could explain the observed stability in the herring migrations. If the position of the spawning ground was not coded in the genome, an alternative explanation for the return the fish to the same position would be that the fish had learnt this position during an earlier stage of their life. This explanation was suggested by Røttingen (1992), Corten (1993) and McQuinn (1997). The last author pointed out that the same theory had already been presented many years before by Wynne-Edwards (1962), a fact that had been overlooked by most contemporary herring workers.

Learnt behaviour plays a role in the distribution of many animals. Several species of birds and mammals return each year to exactly the same place to feed, reproduce or over-winter, apparently because they have "learnt" these places during an early stage of their life (see reviews by Wynne-Edwards 1962, Bonner 1980, Sutherland 1996). The animals may have learnt this behaviour either from their own experience, or they may have learnt it from their parents or other individuals in the population. In the case of a transfer of migration habits between successive generations, we speak of "tradition" or even "culture" (Galef 1976, Mainardi 1980, Bonner 1980).

In fish the ability to learn has been well established in laboratory experiments (Beyer 1976, Bitterman 1984). Also under natural conditions, learning appears to play an important role in many aspects of the behaviour of fish (Kieffer and Colgan 1992). The marked tendency of many fish to stay within a restricted range, and to return to this "home range" when they are displaced some distance away from it (Gerking 1959) is probably also based on the learning capability of the fish.

The fact that fish under natural conditions can indeed "learn" certain localities and the way to get there, was demonstrated in a series of experiments by Helfman and Schultz (1984). These authors worked with French grunts (*Haemulon flavolineatum*), a species of coral reef fish in which the juveniles perform daily migrations between feeding and resting places. By transplanting young individuals to a new locality where resident fish were either left in place or were removed, the authors demonstrated that newcomers within two days learned the existing migration routes by copying the behaviour from experienced resident fish.

In the experiments of Helfman and Schultz (1984), learning occurred on a relatively small temporal and spatial scale. The fish learned a migration pathway over a few hundred meters, on a bottom that had a variety of landmarks, and they had to retain this memory only for one day. It is a long way to extrapolate these findings to the annual migrations of marine fish over distances of hundreds of kilometres, in an ocean without landmarks. Yet, the hypothesis that learning also plays a role in these long-distance migrations is attractive. It has been proposed not only for herring, but also for cod (Rose et al. 1993), and for walleye, a freshwater species (Olsen et al. 1978). In salmon, the importance of learning in migratory behaviour is already widely accepted (see review by Dittman and Quinn 1996)

The purpose of the present paper is to further investigate the role of learning in the case of herring migrations. It starts from the conclusion by Smith and Jamieson (1986) that herring spawning populations are not genetically distinct, and that population-specific migrations, therefore, can not be explained by genetic factors (Corten 1993, McQuinn 1997). The alternative hypothesis I want to investigate is that population-specific migrations are based on acquired behaviour. According to this hypothesis, herring develop an attachment to areas where they have been feeding, spawning or wintering, and they have a tendency to return to these areas in subsequent years in the same season. The inclination of the fish to adhere to a migration pattern (or any other behaviour pattern) that it has established earlier in its life, may be called “conservatism” (Jacobson 1969).

In the case of conservatism, the return of the fish to the same area is a form of learnt behaviour. However, there are two ways in which the fish may have learnt a certain behaviour: from its own experience or from other individuals. The fish (or year-class) may arrive in a certain area by chance and develop an attachment to it. In this case, the “habit” of returning to that place is restricted to the particular fish or year-class. This relatively simple form of learning is termed “habit formation”, to distinguish it from the more sophisticated form in which the habit is copied from older fish in the population. In the latter case, the habits are passed down from one generation to the next, and they may be called “traditions”. Hence this form of conservatism is called “traditional behaviour”.

In the following sections, my first hypothesis is that the conservative behaviour of herring is based on habit formation. This is the most simple hypothesis, requiring the smallest number of assumptions. In cases where habit formation appears to be insufficient to explain the observed stability of migration patterns, I will investigate a second hypothesis, namely that young generations of herring copy their migration pattern from older ones; in other words, that the stability of migration patterns is based on tradition.

The study of habit formation and tradition in herring has to be based on indirect evidence. So far, it has been impossible to conduct experiments with natural herring populations, mainly because of the very large numbers of individuals involved, and the problems in observing and following the fast moving fish. The only way to gather insight in the existence of learning mechanisms is to compare the behaviour of populations from year to year, identify the constant patterns under normal conditions, and investigate under what conditions these normal patterns change.

For the present study, I have used material that was derived from North Sea herring and from Norwegian spring spawning herring. The study is based mainly on a review of published data, but for North Sea herring also some new data are presented. The role of learning will be considered successively for spawning, overwintering and feeding migrations. For each type of migration, first the evidence is considered for stability in the annual migrations, in particular the homing of fish to the same place from year to year. The second step is to investigate the mechanism behind this homing behaviour.

The question how the fish are able to find back the same locality year after year will not be addressed in the present study. The study of navigation mechanisms in fish is a subject on its own, the discussion of which is outside the scope of this paper.

7.2. Spawning migrations

7.2.1. Homing to spawning areas

Spawning migrations provide the most pronounced examples of homing behaviour in herring. Atlantic herring deposit their eggs on the bottom in small, well defined areas, that are visited year after year (Harden Jones 1968). Within the overall distribution area of a herring stock, there may be several distinct spawning places that maintain their identity over the years. Although the groups of herring that spawn at the various spawning sites probably do not constitute genetically distinct populations (Smith and Jamieson 1986, McQuinn 1997), they appear to consist of the same individuals that return to these sites year after year. In the North Sea, the evidence for the return of herring to the same spawning sites is mainly based on the stability of meristic and morphometric characters within the same year-class on the same spawning ground (Postuma and Zijlstra 1958, Zijlstra 1958, 1964b, 1969, 1973). Further evidence for the return of herring to the same spawning ground is based on the constant ratio between different age groups on a spawning ground, and (for Canadian herring) on the results of tagging experiments (see reviews by Harden Jones 1968, Hourston 1982, Burd 1985, Smith and Jamieson 1986, and McQuinn 1997).

The fact that each spawning ground in the North Sea represents the “home” of a separate spawning population was clearly illustrated during the period of stock depletion in the 1960s and 1970s. From 1950 to 1976, heavy exploitation reduced the total North Sea stock from an original level of 3 million tons to only 53,000 tons (Anon 1997). During this period, a number of spawning populations apparently became extinct, since the fishery on their spawning grounds ceased to exist, and no larvae were detected in the vicinity anymore. Following the introduction of a fishing ban in 1977, the stock gradually recovered, and by 1989 a level of 1.3 million tonnes was reached. Yet, despite the growth of the stock, there was no increase in the number of spawning populations (Fig. 7.1). Spawning remained restricted to the few spawning sites that still existed at the time when the stock reached its minimum (with one exception to which I shall return later). Apparently, the spawning sites of the populations that had been exterminated, were not utilised by members of the surviving populations, despite the expansion of these populations.

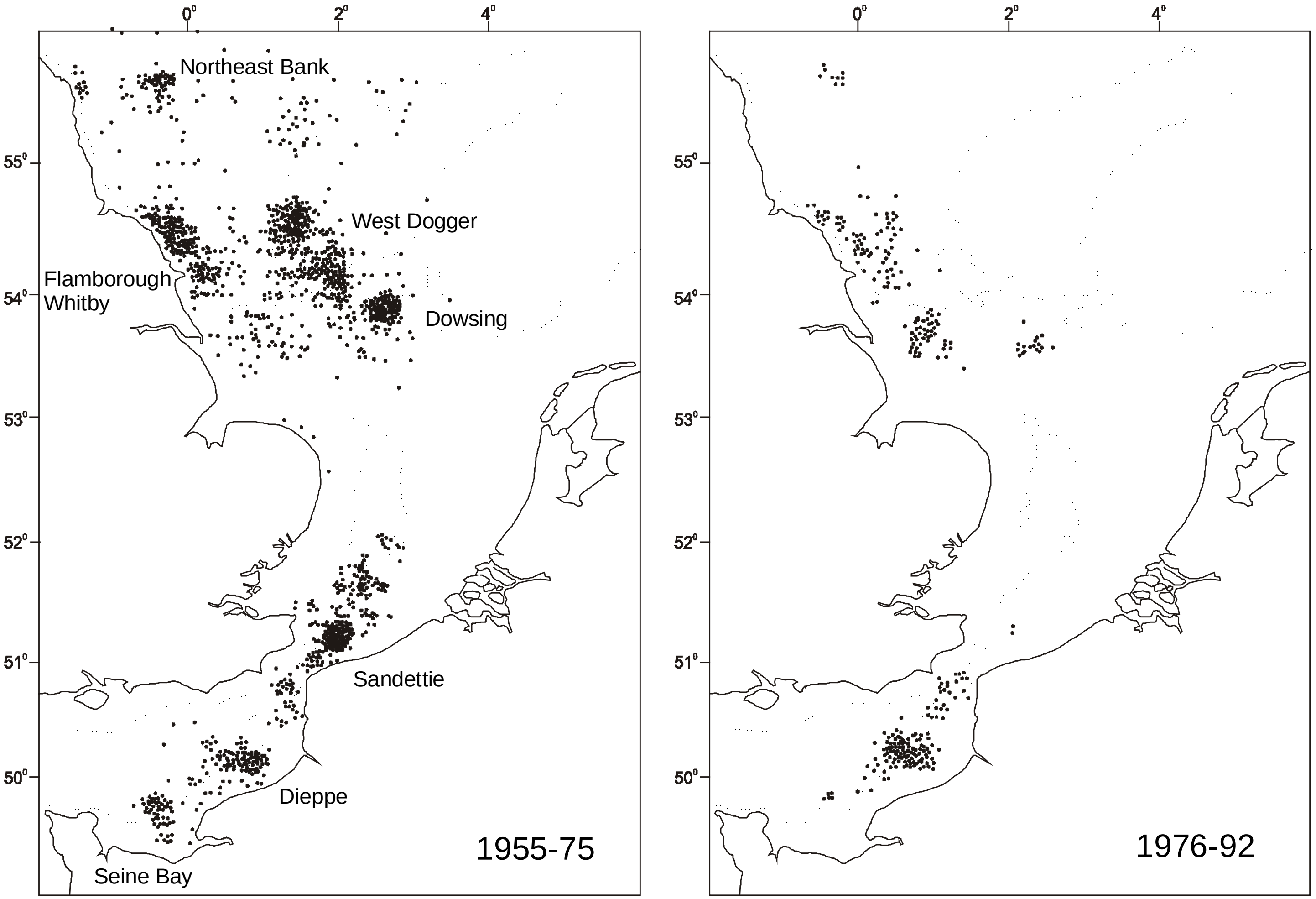

Figure 7.1. The lasting reduction of the number of spawning grounds in the central and southern North Sea, following the depletion of the stock in the early 1970s. Each dot represents a catch of spawning herring from which a sample was obtained by the Dutch fisheries research institute. Data combined for the years before the stock collapse (1975-75) and for the period of the recovery (1976-92).

7.2.2. Changes of spawning area

Although homing to specific spawning areas appears to be the rule, there are examples of an occasional change of spawning ground, either by individuals or by an entire year-class. The tagging experiments by Hourston (1982) on Canada's west coast herring demonstrated that not all herring returned to the same place for spawning, but that a certain percentage (from 4% to 34%) strayed to other areas. The lack of genetic differences between North Sea populations (Smith and Jamieson 1986) is a strong indication that straying from one population to another also occurs in the North Sea. Another argument for the exchange of individuals between populations was the gradual change in otolith characteristics within the same year-class on the Buchan spawning ground over a number of years, reported by Parrish and Sharman (1959).

In rare situations, herring appear to colonise entirely new spawning grounds, or re-occupy spawning grounds that were deserted many years before. The most recent example of re-colonisation in the North Sea is the emergence of a new spawning population on Aberdeen Bank in 1983 (Chapter 3, Fig. 3.3 and 3.4). This locality used to be an important spawning ground in the 1950s, but larval production in this area gradually declined in the 1960s, and came to a complete stop in 1967 (Saville 1971). For the next 17 years, no herring larvae were detected, despite an intensive sampling effort. However, during the routine ICES larvae survey in 1983, a sudden outburst of new spawning activity was found in the area. Since then, this spawning has been repeated every year. Similar examples of re-colonisation of old spawning grounds have been recorded from the Norwegian coast (Bergstad et al. 1991) and from the east coast of the United States (Stephenson and Kornfield 1990, Smith and Morse 1990).

An interesting example of the adoption of a new spawning ground was provided by the 1959 year-class of Norwegian spring spawning herring (Jakobsson 1968, 1969, Devold 1968). It is worth considering this case in some detail, since I shall return to it in the next sections. In the years prior to 1963, nearly the entire stock of Norwegian herring used to spawn off southern Norway, feed north-east of Iceland, and overwinter south-east of Iceland (Fig. 7.2). This situation changed drastically with the recruitment of the strong year-class 1959; a year-class that had been transported far north during the larval stage, and that had grown up in the Barents Sea. Due to its northern distribution, this year-class had remained separated from the adult stock in the summer prior to its first spawning. When it first spawned in February 1963, the main part of this year-class chose an area off the Lofoten Islands in northern Norway as its spawning ground. Although some spawning had been recorded in this area before, it had never been a major spawning area for the stock. After spawning in the Lofoten area, a large fraction of year-class 1959 remained in the northern Norwegian Sea, and

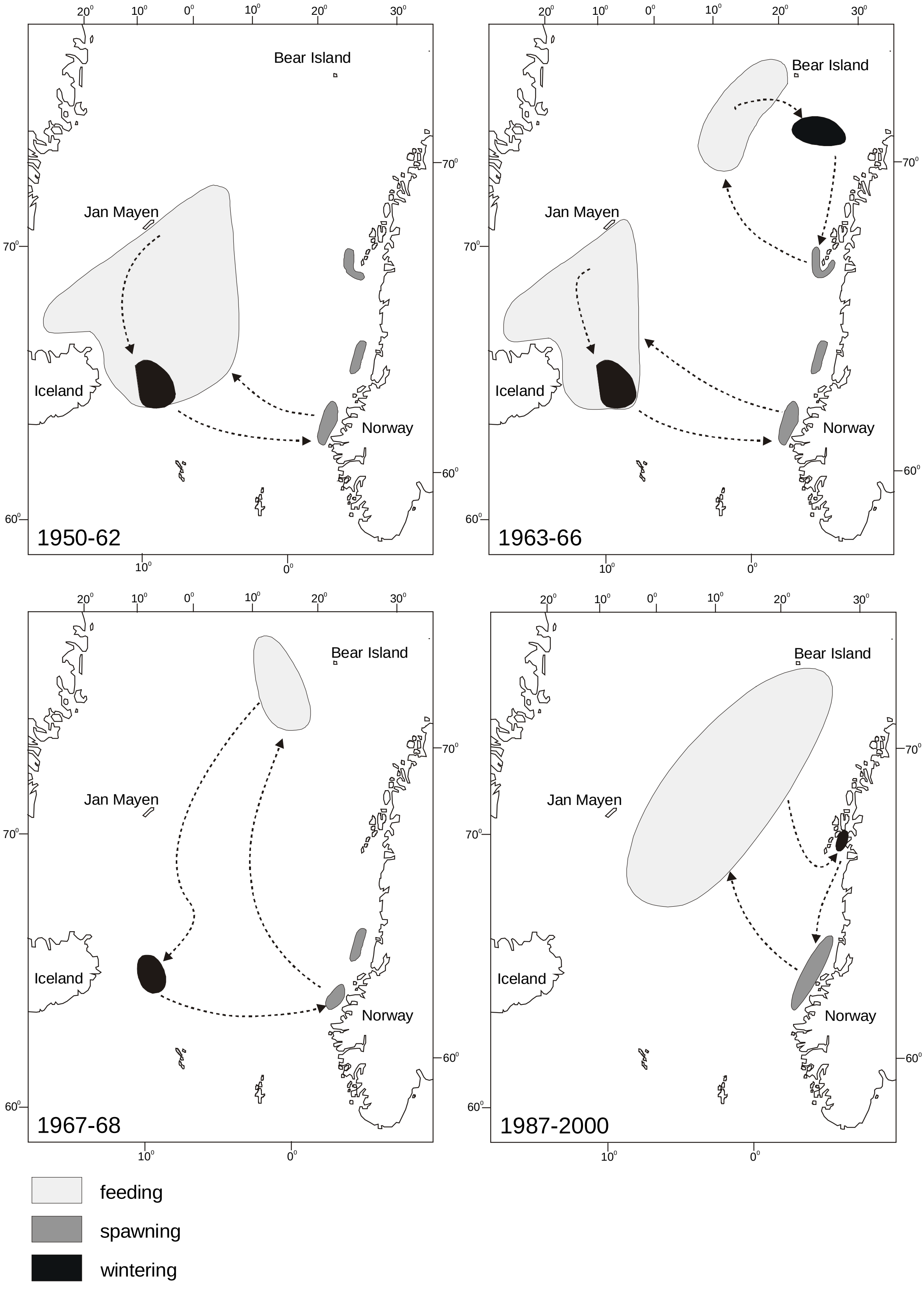

Figure 7.2. Migrations of Norwegian spring spawners in different periods. Adapted from Dragesund et al. 1980, Holst et al. 1998, and Fernö et al. 1998.

adopted a feeding and overwintering area in the vicinity of Bear Island, far away from those of the older stock (Fig. 7.3). For 3 years, this fraction of year-class 1959 (followed by younger herring of year-classes 1960 and 1961) stuck to these new spawning, feeding and overwintering areas, and the stock of Norwegian herring in fact consisted of two components that remained separate throughout the year (Devold 1968). This situation ended in the autumn of 1966, when the separate fraction of 1959 year-class no longer moved to its own overwintering area south of Bear Island, but instead migrated to the traditional overwintering area of the old stock near Iceland. During the subsequent winter, both stock components overwintered in the same area, and at the end of the winter the population as a whole migrated to southern Norway to spawn on the traditional spawning grounds. From this time onwards, the stock again behaved as one unit, and used only the traditional spawning grounds off southern Norway, and the traditional overwintering grounds south-east of Iceland. As for feeding, the whole population from 1967 onwards migrated to the northern feeding grounds near Bear Islands, that until then had been used only by the separatists of year-class 1959 and the subsequent age groups (Jakobsson 1969).

The possible explanation for the division and subsequent unification of the stock of Norwegian spring spawners will be further discussed in the next section. At this stage, the main point to note is the fact that a fraction of year-class 1959 originally chose a spawning area that was different from the one where it had been born, spawned there in three consecutive years, and then changed its own spawning area for the traditional one off southern Norway.

In the Norwegian herring stock, the new (temporary) spawning colony was established by a recruiting year-class. This appears to be the case also in other examples of the establishment of new spawning populations. The herring that re-colonised the Georges Bank spawning ground off the east coast of the United States all belonged to the new year-class 1983 (Stephenson and Kornfield 1990). Also the re-colonisation of the Aberdeen Bank spawning ground in the North Sea is attributed to a recruiting year-class (chapter 3).

7.2.3. The mechanism of homing in spawning migrations

Based on the lack of genetic differences between neighbouring populations and the evidence for a substantial interchange of individuals between such populations, Smith and Jamieson (1986) and McQuinn (1997) concluded that individual spawning populations do not have a separate genetic identity. A further argument against the genetic discreteness of spawning populations is the observation that new spawning populations may occasionally appear out of nowhere (McQuinn 1997). Some authors have argued that the appearance of such populations is due to the resurgence of a rudimentary population that has always existed in the area (Stephenson and Kornfield 1990). However, in the case of the Aberdeen Bank spawning grounds, the results of larvae surveys demonstrate that prior to the revival of the population in 1983, no spawning occurred in the area for a long period. Finally, the changes in spawning grounds of the 1959 year-class of Norwegian herring, described above, indicate that herring do not necessarily always spawn at the position where they were born, and that they may change their spawning ground during their lifetime (Devold 1968, Dragesund et al. 1980).

Since the position of the spawning ground appears not to be genetically determined, I conclude that the return of the fish to the same spawning ground in successive years has to be an effect of learning or “habit formation”. I hypothesise that the fish have learnt the position of a particular spawning ground sometime during their early life, and developed an attachment to this site.

The simplest explanation of the attachment of herring to a particular spawning site would be that the fish have been born at this location, and that they remember the position from the first days of their life. However, although homing to native spawning grounds has been well-established for salmon (Hasler et al. 1978, Hasler and Scholtz, 1983), it is unlikely that this mechanism also exists in herring. Whereas salmon may spend up to one year in the stream where they were born, herring larvae stay near their hatching site only for a few hours, and are then transported hundreds of kilometres away by the currents. It is unlikely that the newly born herring larva, without a developed sensory system, can already determine its position and retain the memory of it for the next three years (Harden Jones 1968, Corten 1993).

Hence, I reject the hypothesis that the learning process or “habit formation” occurs immediately after hatching, i.e. at the first time when the (larval) fish finds itself on the spawning ground. For the next three years, the juvenile herring grows up in a nursery area far away from the spawning grounds, and it can not possibly learn the position of a spawning ground during this period. The next chance for the herring to learn the position of a particular spawning ground is when it spawns for the first time itself, at an age of 3 years (in North Sea herring). My hypothesis, therefore, is that the habit of spawning at a particular place is not formed until this moment of first spawning. This implies that until the moment of first spawning, recruit herring are basically free to choose any of the existing spawning places.

Although habit formation can explain the return of the same (adult) generation of herring to a particular spawning ground, it does not explain the appearance of successive generations of herring on the same spawning ground. If the continuity of spawning at a particular site was caused merely by habit formation within a single year-class, the spawning at that site would last only for the lifetime of that year-class. What we see in reality is that spawning sites are visited by a succession of year-classes, and thereby continue to exist for many years, sometimes even many decades. The formation of exactly the same habit by a series of successive generations is unlikely to be a matter of chance. We need a second hypothesis to explain the continued spawning on specific sites by subsequent generations. This second hypothesis, earlier formulated by Wynne-Edwards (1962), Corten (1993), and McQuinn (1997), is that in most cases recruit spawners do not select their first spawning site at random, but that they learn the position of an existing spawning site from older herring. According to this theory, recruit spawners school with older herring, and these older herring lead the school to the place where they have spawned themselves in the previous year. By also spawning at this place, the recruit herring develop a site attachment to this particular spawning area, and thereby become members of the spawning population. The continued existence of the spawning site, therefore, is caused not only by habit formation, but also by tradition.

The second hypothesis, i.e. that new year-classes learn the position of existing spawning grounds from older herring, is based mainly on the elimination of other possibilities. It is difficult to obtain positive evidence for the existence of this mechanism. Still, the following observations appear to support the theory.

The first observation is lasting reduction of the number of spawning sites in the North Sea after the temporary depletion of the total North Sea stock in the 1970s (see above). When the North Sea stock increased again in the 1980s, many of the earlier deserted spawning grounds remained unoccupied. Assuming that spawning populations do not constitute genetically distinct units (our first hypothesis), the only explanation for the fact that spawning herring have not returned to these places, is that there were no old herring left that could “teach” these places to new generations.

The second observation concerns the establishment of a new spawning ground by Norwegian herring of year-class 1959 of the in the Lofoten area in 1963. It is assumed that this happened accidentally, due to the northern distribution of the year-class during the preceding feeding season (Devold 1968). When year-class 1959 returned to this spawning ground in the following two years, it was followed by younger herring of year-classes 1960 and 1961 (Devold 1968). These two year-classes apparently followed the herring that was one or two years older, instead of migrating to the spawning area of the older (main) population.

The last example also concerns the 1959 year-class of Norwegian herring. After this year-class had established a new spawning ground in the Lofoten area and spawned there for 3 years in succession (later joined by younger year-classes), they did not return to this area in 1967, but instead migrated to the spawning area of the main population off southern Norway. This happened presumably because the fish had mixed with herring of the main population during the winter of 1966/67, and at the end of the winter followed these (mainly older) herring to the traditional spawning grounds.

These three cases suggest that one generation of herring learns the position of a specific spawning place from another, normally older generation of herring. These observations thus support the hypothesis that the continuity of spawning grounds is due not only to habit formation within one year-class, but also to the social transmission of migration patterns between generations, in other words to tradition.

7.3. Overwintering migrations

7.3.1. Homing to overwintering areas

In overwintering migrations, the word "homing" is used less frequently than in the context of spawning migrations. Maybe this is due to the fact that overwintering grounds are generally less clearly defined than spawning grounds, which makes homing to overwintering grounds more difficult to observe. Also, the word "home" seems to be associated more with the place where an animal reproduces than with the area where it spends the winter. Still, the definition of "homing" given by Gerking (1959) includes the return of fish to all kinds of places formerly occupied, including overwintering and feeding grounds.

In the North Sea, the overwintering grounds of the central and northern herring populations are found in the region of the shelf edge, and particularly along the western slope of the Norwegian Trench (which may be considered as a continuation of the shelf edge) (Fig. 7.3).

Herring occur widespread throughout this area during the winter, and at first sight there seems to be no reason to assume that individual fish or groups of fish home to a particular locality within the total range. However, a number of observations indicate that the herring are not distributed randomly throughout the overwintering area, and that certain fractions of the stock have a preference for particular sections of the area.

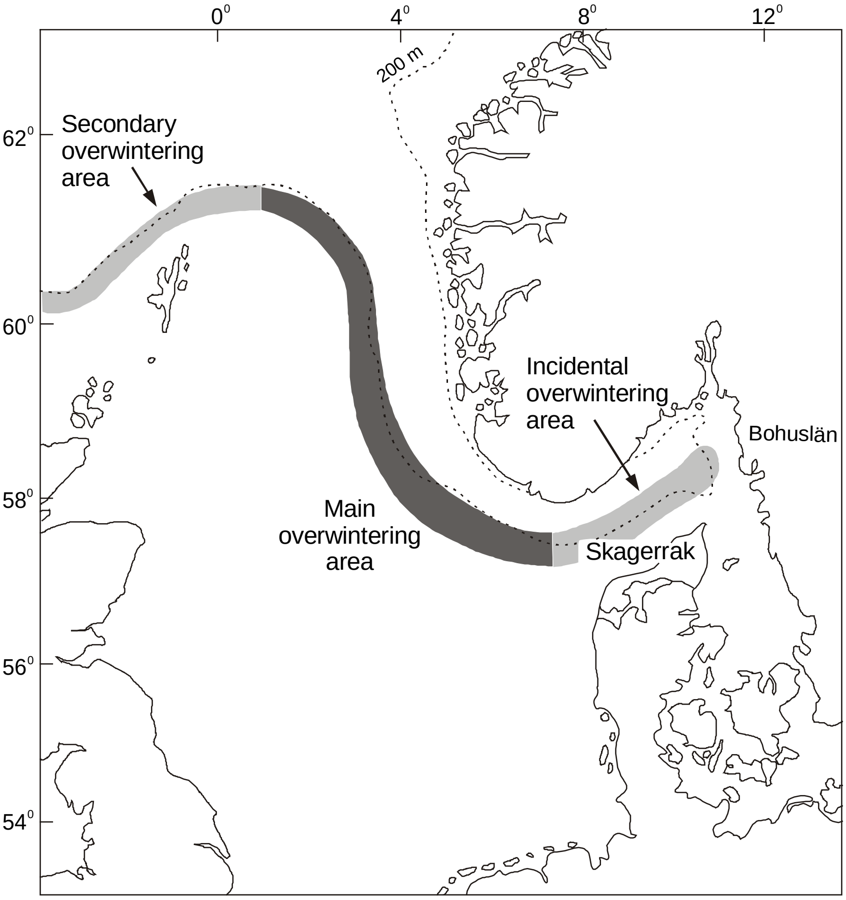

Figure 7.3. Schematic presentation of the overwintering grounds of the central and northern North Sea populations.

The first evidence for this was provided by Swedish tagging experiments in the Skagerrak in 1949-1953 (Höglund 1955). Herring tagged in March-April 1953 close to the Swedish coast migrated out into the open North Sea in summer, but exactly one year later a relatively large number of recaptures (45 out of a total of 2000 tagged fish) was taken within 100 km from the original tagging position in the Skagerrak (experiment 9, table 8).

The Skagerrak plays an interesting role in the overwintering of North Sea herring. Normally, the fraction of the total North Sea stock that overwinters in this area is small or negligible. This situation, however, may suddenly change, and large numbers of herring may invade the Skagerrak during winter, making this area the main overwintering ground of the North Sea stock. These winter invasions will be repeated for a number of years, until the population reverts to the old migration pattern, and starts overwintering in North Sea again. Episodes of regular, large-scale migrations of North Sea herring into the Skagerrak during winter are called "Bohuslän herring periods", after the Swedish coastal area where the herring appear (Devold 1963, Höglund 1978, Alheit and Hagen 1997). In the past, Bohuslän herring periods occurred with a frequency of about once a century, and one period could last from 20 to 60 years (Alheit and Hagen 1997).

The last real Bohuslän herring period ended in 1906, but since then there have been several shorter episodes in which North Sea herring overwintered in the open Skagerrak but did not approach the Swedish coast . The last of these “Open Skagerrak periods” started in the autumn of 1963, when the recruiting year-class 1960, instead of choosing the normal overwintering area for adult herring in the north-eastern North Sea, migrated into the Skagerrak and spent the first winter of its adult life (1963/64) in this area. In the following spring, the year-class moved out into the North Sea to feed and spawn, but it returned to the Skagerrak in the autumn of 1964, to spend its second winter again in this area. By this time, the news of herring concentrations in the Skagerrak had spread, and a large international fleet concentrated in the area to exploit the herring. In the third winter (1965/66), some herring were still observed near the entrance of the Skagerrak, but the fish did not seem to cross the border between North Sea and Skagerrak. In subsequent years, no adult North Sea herring were observed anymore inside or near the Skagerrak.

The invasion of herring into the Skagerrak in autumn 1963 coincided with the occurrence of strong north-easterly winds. These winds must have forced surface water out of the Skagerrak, and thereby strengthened the sub-surface counter-current that normally runs into the Skagerrak. The recruiting year-class 1960, distributed near the entrance to the Skagerrak, was probably caught by this increased sub-surface current, and swept passively into the Skagerrak (chapter 4). Such a passive transport, however, can not explain the invasion in the second year. In the autumn of 1964, there were no strong winds from the north-east, and there was probably no particularly strong sub-surface current into the Skagerrak. This time, the fish must have migrated actively into the area. The return of the fish to the Skagerrak in 1964, therefore, is probably an example of homing; the fish supposedly migrated towards the area because they had been there before. The fact that the invasions were discontinued after 1964 was possibly due to the heavy fishing in Skagerrak during the two winters when the herring were found this area. Höglund (1978) thought that under normal conditions the herring would have returned for many more years.

The herring that overwinter along the slope edge in the northern part of the North Sea also seem to home to specific parts of the area. This was demonstrated by the depletion of the overwintering population in the north-eastern part of the North Sea. From 1960 – 1969, the overwintering herring in this area were heavily exploited by a newly developed purse seine fishery. This fishery each winter took catches between 200,000 and 600,000 tonnes, representing 38% to 51% of the total annual North Sea catch. However, after 1970 the overwintering population in the north-eastern sector appeared to have been depleted, and the contribution of this area to the total North Sea catch dropped to an average of 4% in the years 1970-1976 (Anon. 1979). In these years, however, overwintering herring were still taken in significant quantities the north-western part of the North Sea (Anon. 1979). This showed that there was no random movement of herring along the shelf edge during winter. Apparently, the fraction of the population that used to overwinter along the western part of the shelf edge had survived the heavy exploitation of the late 1960s. These fish continued to overwinter in the north-western area after 1970, and they did not seem to spread to the eastern North Sea where the resident overwintering population had been removed.

Examples of homing to overwintering grounds are also known from Norwegian spring spawning herring. In the previous section, a short overview of the migrations of this stock in the 1950s and 1960s was presented (Fig. 7.3). The traditional overwintering area of this stock was found to the east of Iceland, in the cold waters of the East Iceland Current (Jakobsson 1969, Dragesund et al. 1980). In the winter of 1963/4, a large fraction of the new year-class 1959 did not join the adult stock on the normal overwintering grounds, but instead overwintered in a new area south-east of Bear-Island. In the following two winters, the fish returned to this area, thereby exhibiting homing to an overwintering ground that it had occupied before.

The stock of Norwegian spring spawners became depleted by the end of the 1960s, and at that time the remaining fish apparently stopped making their long-distance migration into the open Norwegian Sea (Røttingen 1992). The adult herring were observed to remain in the vicinity of the Norwegian coast all year round, and to overwinter in scattered locations along this coast. It was not until 1986, with the recruitment of the strong 1983 year-class, that the population in spring moved out again into the open Norwegian Sea. (Røttingen 1992). However, although the population resumed its oceanic feeding migration, it did not re-occupy the former overwintering grounds near Iceland. In the autumn of 1987, the entire population entered two fjords in northern Norway, the Ofotfjord and Tysfjord, and spent the whole winter in this confined area (Dommasnes et al. 1994). This was the first time in recent history that overwintering adult herring had been recorded in this area. In subsequent years, the population returned each winter to these fjords, despite the fact that the oxygen level in the area dropped significantly due to the metabolic activity of the herring. Until the present (2000), these fjords in northern Norway remain the only overwintering area for the entire herring stock, which has now grown to 10 million tonnes (Toresen, pers. comm.).

7.3.2. The mechanism of homing in overwintering migrations

The previous examples have shown that herring may have specific overwintering areas, and that the fish tend to return to the area where they spent the previous winter. In this respect, overwintering migrations bear a remarkable resemblance to spawning migrations. The main difference with spawning migrations is that overwintering migrations seem to be more flexible. In the North Sea, the overwintering grounds of part of the stock shifted temporarily in 1963–1964 whereas the spawning areas remained constant.

As in spawning migrations, we can rule out a genetic coding of the exact overwintering positions. The migrations of both the North Sea herring and the Norwegian spring spawners have shown drastic changes from one period to another; changes which can not have been caused by a corresponding change in the genetic composition of the entire stock.

The main factor involved in homing to overwintering grounds appears to be conservatism. If a recruiting year-class by chance spends the winter in a new area, it has a tendency to return there in subsequent winters. This behaviour was observed in North Sea herring in the Skagerrak in 1963-64, in Norwegian spring spawners near Bear Island in 1963-65, and again in Norwegian spring spawners in the Ofotfjord and Tysfjord since 1987. In all cases, there was no hydrographic reason why the herring should return to the same place where they had been the previous winter. The only plausible hypothesis is that the fish had learnt the position where they were the year before, and that their return to this place was due to habit formation.

As in spawning migrations, however, habit formation by itself can not explain the appearance of a succession of year-classes on the same overwintering ground. When North Sea herring of year-class 1960 returned to the Skagerrak in the winter of 1964/65, it was followed by younger herring of year-class 1961 (Höglund 1967). The same phenomenon was observed in Norwegian herring, when year-class 1959 established a new overwintering area near Bear Island in 1963, and younger herring of year-class 1960 and 1961 appeared in this area in subsequent years. Also the new overwintering area of the 1983 year-class of Norwegian herring in the Ofotfjord and Tysfjord, established in 1987, was visited in subsequent years by younger generations of herring. In all these cases, it appeared that new year-classes followed older herring to an existing overwintering ground, and thereby learnt the position of this location from the older herring. I therefore hypothesise that the continuity of overwintering grounds is based not only on habit formation within a single year-class, but also on the transfer of habits between successive year-classes, i.e. on tradition.

Indirect evidence for the existence of tradition is provided by the observation that changes in overwintering areas seem to occur only when a recruiting year-class lacks the guidance of older herring. North Sea herring of year-class 1960 were presumably transported into the Skagerrak before they had a chance to follow the older herring to the traditional overwintering grounds along the western edge of the Norwegian Trench. The 1959 year-class of Norwegian herring did not make contact with the older stock component because of its northern distribution. And the 1983 year-class of Norwegian herring could not learn from older herring, simply because there were no survivors left that knew the old tradition.

In two of the above examples, the new migration did not turn into a tradition. The North Sea herring that migrated into the Skagerrak in 1963 and 1964 abandoned this habit in 1965, after a large part of the overwintering population in the Skagerrak had been removed by the fishery. And the Norwegian herring of year-class 1959 eventually adopted the traditional overwintering area of the main population in 1966, possibly after this year-class during the preceding summer had come into contact with the rest of the stock (Jakobsson 1969). However, in the third example (the overwintering of Norwegian herring in the Ofotfjord and Tysfjord in 1987), the new migration pattern was copied by subsequent generations, and the population has continued to overwinter in this area until the present (1999/2000). In this case, we can clearly speak of the establishment of a new tradition.

The establishment of a new tradition may also be the explanation for the historic Bohuslän herring periods in the Skagerrak. In chapter 4 it was suggested that these periods started in the same way as the 1963 Skagerrak invasions, i.e. by the chance displacement of a recruiting North Sea year-class into the Skagerrak. It appears that the start of earlier Skagerrak herring periods also coincided with periods of easterly winds in autumn, and thus presumably with an increase of the sub-surface current into the Skagerrak. According to my theory, a new year-class that had accidentally been transported into the Skagerrak during the first winter of its adult life would return there in subsequent winters due to habit formation (hypothesis 1), and this new migration pattern would be copied by subsequent year-classes (hypothesis 2). When the tradition of overwintering in Skagerrak had become established, the Bohuslän period could continue for decades, regardless of hydrographic conditions. A Bohuslän period in North Sea herring would thus be the equivalent of the current tradition of inshore overwintering in Norwegian spring spawning herring.

7.4. Feeding migrations

7.4.1. Homing to feeding areas

The feeding areas of most herring stocks are large in comparison to their spawning grounds, and even to their overwintering grounds. Within the overall feeding area, the distribution of the food is changing from year to year, and the herring seem to be actively searching for the areas with the highest food density (Cushing 1955). Herring thus appear to adapt their own distribution to the variable distribution of their food (Pavshtiks 1959). Homing to pre-determined positions seems to be in conflict with this adaptation to the distribution of food. It is surprising, therefore, to find that also in the case of feeding migrations there are examples of herring returning to the same area where they were the year before.

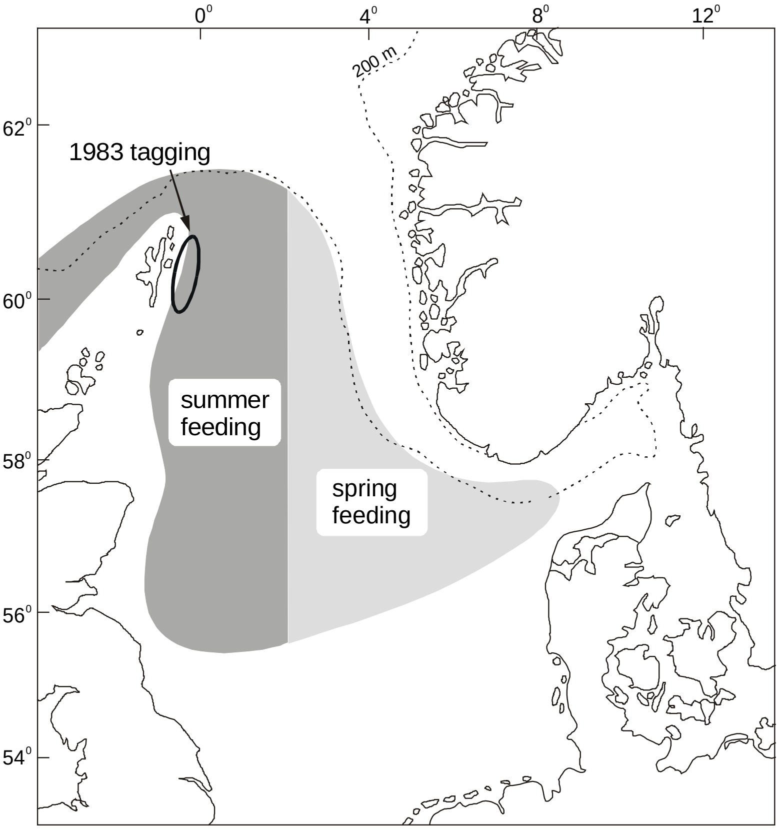

Figure 7.4. Feeding grounds of adult North Sea herring. Also indicated is the position of the tagging and recapture experiment near Shetland in 1983-1985.

We start the review of homing in feeding migrations with an example from North Sea herring. The feeding grounds of this stock are spread over a wide area in the central and northern North Sea (Fig. 7.4). Catches in any part of this area seem to consist of a mixture of herring belonging to different spawning populations (Parrish and Sharman 1958, Schumacher 1963), and it is normally assumed that the North Sea stock behaves more or less as a homogeneous mixture at this time of the year. This assumption was also the basis of a large international tagging experiment in 1983-1985, aimed at estimating the total stock size of North Sea herring (Morrisson and MacDonald 1986). The plan was to release a large number of tagged herring during summer, wait for one year until the herring would have mixed randomly throughout the population, and then estimate total stock size from the percentage of tagged fish in the catches.

In the summer of 1983, a total of 48,000 herring was tagged with internal microwire tags and released in the vicinity of the Shetland Islands (Fig. 7.5). Because detection of the microwire tags required special electronic equipment on board the fishing vessel, recaptures had to be obtained from experimental fishing with a chartered purse seiner. This experimental fishing was conducted in the vicinity of the Shetland Islands in June and July 1984, and again in June and July 1985. In both years the rate of recovery in June was much lower than in July, as can be seen from the following text table.

Year	month	Tonnes of fish screened for tags	Number of tags recovered	Tags per 1000 tonnes
1984	June	666	9	13.5
	July	475	13	27.4
1985	June	342	0	0
	July	917	28	30.5

The difference in tags density between June and July was significant at the 0.001 level ($X^2 = 35.2$, $\varphi = 2$), and this difference remained if the recaptures were calculated by age group.

Morrison and MacDonald (1986) concluded that both in June 1984 and 1985, an additional stock component occurred in the Shetland area which was not part of the tagged population. This implied that the tagged fish had not mixed randomly throughout the whole stock. Considering the complete absence of recaptures in June 1985, one could also conclude that the tagged fish belonged to a stock component that used to feed in the Shetland area only in July, and apparently had a different feeding area in June. The results of the tagging experiment suggest the existence of sub-groups within the total North Sea stock during the feeding season, and the homing of such sub-groups to specific areas at specific times.

Another, possibly related example of homing during the feeding season was observed during the same years in the eastern part of the North Sea. This is the area where the feeding season of North Sea herring normally starts. The herring utilise the early production of food in this area, mainly *C. finmarchicus*, before they move over to the western half of the North Sea (Fig. 7.4). When the North Sea herring fishery was re-opened in 1983 (after a fishing ban of 6 years), the herring appeared to stay longer in the eastern area than they used to do before the closure (Corten and Van de Kamp, 1992). Whereas in earlier years the fishery would shift to the western North Sea in June, the fishery now continued in the eastern North Sea throughout this month. In the years after 1985, the new pattern gradually disappeared, and the herring resumed their old habit of leaving the eastern North Sea already in early June.

The prolonged stay of the herring in the eastern North Sea in the early 1980s was possibly related to an extended feeding season in the area. This hypothesis was tested by investigating plankton data from the Continuous Plankton Recorder Survey (chapter 6). The results showed that the main food item of the herring, *Calanus finmarchicus*, had an extended season in the eastern North Sea in most of the period 1976-1984 (Chapter 6, Fig. 6. 8 and 6.9). Whereas in normal years the abundance of *C. finmarchicus* dropped sharply after May, the abundance during the years 1976-1984 generally remained high during June and even July. In these years, which coincided largely with the period of the fishing ban, the herring seemed to have developed the habit of postponing their departure from the eastern North Sea until July. After the *Calanus* season in the eastern North Sea shortened again starting from 1985, the herring reverted to their old pattern of leaving the eastern North Sea in early June. There seemed to be a time lag, however, between the shortening of the *Calanus* season and the adaptation of the feeding migrations of the herring (Chapter 6, Fig. 6.10). After 1985, catches in June in the eastern North Sea declined less rapidly than the abundance of *C. finmarchicus*. In chapter 4, I attributed this slow response to conservatism in the behaviour of the herring.

Maybe “homing” is not the best word to describe the prolonged stay of the herring in the eastern North Sea in the early 1980s. The new migration pattern involved a change in time, rather than in space, of the distribution of the fish. However, if we incorporate the factor time in Gerking’s (1959) definition of homing, we may define homing also as the return of the fish to a place that was formerly occupied *at the same time of the year*.

Homing to specific feeding grounds has also been observed in the stock of Norwegian spring spawning herring (Jakobsson 1969, Dragesund et al. 1980, Jakobsson and Østvedt 1996, Fernö et al. 1998). In the 1950s and early 1960s, the fish used to migrate from their spawning grounds along the Norwegian coast to the waters north-east of Iceland where good feeding conditions prevailed during summer (Fig. 7.2). In the years 1963 – 1964, the abundance of food (mainly *C. finmarchicus*) in this area declined, due to the south- and eastward extension of the polar front. The herring, however, continued to visit the area in search for food, apparently following an established tradition. It was not until 1965, when the traditional feeding grounds were covered by polar water of less 0°C, that the herring abandoned this area and migrated further north-east along the edge of the polar front, in search of a new feeding area. They did so only after they had first attempted to penetrate into the polar water mass on their old feeding ground, and were forced to give up this attempt (Jakobsson 1969).

The last example of homing to feeding grounds concerns the 1959 year-class of Norwegian herring. As described in section 2, a large fraction of this year-class constituted a separate stock component during the first years of its adult life, with its own feeding, spawning and overwintering areas in the northern Norwegian sea (7.2). After the separate component during the winter of 1966/67 had merged with the main part of the stock, it continued to home to its own feeding area in the Bear Island region, taking the rest of the stock along as well (Jakobsson 1969).

7.4.2. The mechanism of homing in feeding migrations

Like in other types of herring migrations, homing to feeding areas can not be based solely on innate behaviour since the timing and routes may change from one period to another. Examples are the changed timing of the westward migration in North Sea herring in the early 1980s, and the changes of feeding area in the Norwegian herring in 1965 and again in 1967. The Norwegian herring even seem to have completely stopped their oceanic feeding migrations by the end of the 1960s, when the stock had become very small (Røttingen 1992).

In the case of feeding migrations, the herring actively search for concentrations of food. The return of the herring to the same place in successive years might be due to the fact that the herring each year find the highest food abundance in the same area. In this case, the observed “homing” would simply be a function of food distribution. However, there are observations of a return of herring to certain areas, irrespective of food abundance. The Norwegian herring kept returning to the old feeding grounds north-east of Iceland in 1963-65, despite the fact that food abundance in the area had declined. Another example was the prolonged stay of North Sea herring in the eastern North Sea in early summer, some years after the *Calanus* season had shortened again.

These observations suggest that the distribution of the herring during the feeding season is not solely determined by the distribution of food in the current year, but that the fish also have a tendency to go back to the area where they were feeding the year before. It was in relation to the feeding migrations of Norwegian herring to Icelandic waters that the word “conservatism” was used for the first time in the context of herring migrations (Jakobsson 1969).

In feeding migrations, we thus seem to find the same kind of habit formation that was earlier observed in spawning and overwintering migrations. If the herring encounter good feeding conditions in a particular area in one year, they appear to remember this position, and return there in subsequent years. This hypothesis of habit formation can explain the continued stay of herring in the eastern North Sea in the mid-1980s, and the continued migration of Norwegian herring to the old feeding grounds north-east of Iceland in 1963-1965.

However, also in feeding migrations we observe that young herring seem to copy migration routes from older herring. After Norwegian herring of year-class 1959 had temporarily established a new feeding ground west of Bear Island (presumably as a result of its northern distribution during the preceding adolescent phase), the subsequent year-classes 1960 and 1961 also appeared on this new feeding ground (Devold 1968). This phenomenon can not be explained by habit formation. It would have been too much of a coincidence if these two younger age groups had by chance ended up in the same new feeding area as year-class 1959. Presumably the two younger year-classes followed the herring of year-class 1959 to its new feeding ground near Bear Island.

Thus, I hypothesise that social transfer of migration routes also occurs in feeding migrations. Like in spawning and overwintering migrations, the continuity of existing feeding migrations is caused not only by habit formation within a single year-class but also by tradition, i.e. the transfer of habits from one generation to the next.

The hypothesis that tradition creates continuity in feeding migrations is supported by observations that this continuity may break down in situations where no older fish are left to “teach” new generations. When the stock of Norwegian herring was severely reduced by the end of the 1960s, the population stopped making its oceanic feeding migrations and stayed near the Norwegian coast all year round. This situation lasted for nearly two decades, until in 1987 the stock had grown to such an extent that food in the coastal zone became scarce, and the fish had to move out into the open Norwegian Sea again. This time, however, the migration pattern did not resemble the classical pattern from the 1950s and 1960s. Instead of migrating directly towards the polar front, the herring were feeding in scattered locations in the eastern Norwegian Sea and the overall direction of their migration was clockwise instead of anti-clockwise. Røttingen (1992) assumed that the stock did not resume the old migration pattern, partly because there were no older herring left to "teach" the new year-class 1983 the traditional migration. The same suggestion has been made more recently by Fernö et al. (1998) and Misund et al. (1998).

It is possible that the social transfer of migration habits was also the cause of the switch in feeding area of the main population of Norwegian herring in 1967. After this population had become mixed with the separate component of year-class 1959 during the winter of 1966/67, it did not migrate to its usual feeding grounds near Jan Mayen, but instead migrated together with year-class 1959 to the new feeding grounds near Bear Island (Jakobssen 1969). This may have been a (rather unusual) case of the transfer of habits from a young generation to an older one.

7. 5. Discussion

7.5.1. The role of learning in herring migrations

In the previous sections, examples were presented of homing in spawning, overwintering, and feeding migrations of herring. In each case, it was concluded that the observed homing was most likely based on learnt behaviour. This was the only theory that could explain both the homing under normal conditions, and the occasional change of migration pattern under special circumstances. The learning hypothesis presented in the earlier sections consisted of two components. The first hypothesis was that adult herring have a tendency to habit formation, i.e. to repeat the migrations that they have performed during the first year of their adult life. The second hypothesis was that recruit herring, in the first year of their adult life, learn existing migration routes from older herring. The combination of the two mechanisms could explain the observed long-term stability of herring migrations.

Of course the role of learning should not be over-emphasised. The actual behaviour of the herring will be determined by a combination of genetic control, environmental conditions, and learnt behaviour. In this respect, herring migrations resemble the migrations in some species of birds, in which the same combination of mechanisms appears to be at work (Sutherland 1998). The resemblance between herring and birds may not be entirely coincidental. In both cases, a number of similar conditions exists:

- the animals perform long-distance migrations to very specific locations;
- the migrations are performed in social groups;
- the groups contain individuals of different ages, some of which have performed the migration before.

If these three conditions are conducive for the development of traditions in migratory behaviour, such traditions might also exist in other fish species that perform long-distance migrations in schools consisting of several age groups. One could think for instance of pelagic species that perform long distance migrations several times during their life, such as mackerel, horse mackerel, and tuna.

7.5.2. Changing the tradition

Although herring migrations normally tend to be stable from one year to the next, the patterns are not fixed forever. Once in a while the population, or a certain segment of it, may change an existing migration habit. The examples presented in the previous sections suggest that changes of migration pattern may occur in at least four different situations:

(a) a recruit year-class starts a new migration because it does not catch up with the adult part of the population;
(b) a recruit year-class starts a new migration because there are no adult herring left that can show them the traditional pattern;
(c) adult herring change their migration in response to a strong or sustained environmental (c) stimulus;
(d) adult herring get in contact with another stock component and adopt the tradition of these other herring.

Changes of type (a) seem to be the most common. According to our hypothesis, the recruiting year-class has no previous attachment to a particular spawning, feeding or overwintering area, so it is not bound by tradition. If the year-class somehow fails to make contact with the adult part of the population at the time when it has to start its first migration, it will have to choose a spawning, overwintering or feeding area by itself.

The mismatch between the distribution of a recruiting year-class and the older stock component will often be due to some environmental factor that affects the distribution of the recruits more than that of the adults. The recruiting year-class that started the spawning on Aberdeen Bank in 1983 had probably been feeding further south than the rest of the population, due to an increased inflow of Atlantic water into the North Sea (chapter 3). In the case of the Skagerrak invasion of 1963, the recruiting year-class was probably affected more by the subsurface current into Skagerrak than the older generations that were distributed further north (chapter 4). And the northern distribution of year-class 1959 of the Norwegian herring was due to an unusually strong transport by the Norwegian Coastal Current during the larval stage. In all these cases, there was a special environmental condition that probably caused the separation between the recruiting year-class and the older stock component, and thereby forced the new year-class to adopt its own migration pattern. However, once the new migration pattern had become adopted, it was perpetuated in subsequent years, regardless of the environmental factor that had sparked it originally.

Changes of type (b) require no further explanation. If the older stock component has become extinct, there is no way in which the recruiting year-class can learn the old tradition anymore. In this case, the recruiting year-class has no choice but to invent a new migration route by itself. This is probably what happened when the Norwegian herring of year-class 1983 established a completely new overwintering area, and also a new feeding migration.

In practice, the influence of the old stock component may already be reduced if its numbers are low in relation to the recruiting year-class. In all examples of the establishment of new migrations by a recruiting year-class mentioned above, the recruiting year-class was large in relation to the preceding ones. This means that the recruit herring will have outnumbered the herring of one and two years older. Even with a partial overlap of distribution between the recruiting year-class and the older herring, the influence of the older age groups will have been lower than usual.

Whereas our observations show that recruit herring can easily start a new migration pattern, it appears to be more difficult for older herring to do so. Presumably, this is due to the fact that conservatism refrains them from changing the existing routine, even if the environment changes. Changes of type (c) will therefore require a relatively strong, sustained change of environment. The shift of feeding grounds by Norwegian herring in 1965, only after the traditional feeding area had become completely uninhabitable, is the best example in this category. Also North Sea herring proved to be reluctant to change a well-established feeding migration. It took these herring several years after 1985 to adapt their distribution to the shortened *Calanus* season in the eastern North Sea.

Changes in migration of adult herring, due to mixing with other populations (type d) are the least common and also the most difficult ones to explain on the basis of our hypotheses. The only example presented above is the change of spawning and overwintering area by Norwegian herring of year-class 1959 at an age of 7 years, after they had come into contact with the main population in the summer of 1966. The fish had already for three years established their own spawning and overwintering areas, and one would expect that they had developed an attachment to these areas. It is remarkable, therefore, that in the end they abandoned their own migration pattern in favour of the traditional pattern of the old stock. This could suggest an innate preference for the general direction of the traditional migrations.

7.5.3. The adaptive advantage of conservatism and tradition

Without going into a full discussion on the evolutionary significance of conservative and traditional behaviour, it is interesting to briefly consider the possible advantages of this behaviour for the herring. There must be some reason why during the evolution this species in particular has developed such a pronounced tendency to stick to existing migration patterns.

At the least, conservative behaviour will reduce the risk of running into unexpected problems (Fernö et al. 1998). If a certain behaviour has not resulted in serious problems in the past, there is a fair chance that it will not do so at present either. The behaviour may not be the optimum choice from all the options that exist, but it is not the worst one either. In the case of migrations, sticking to a well established route will reduce the risk of unpleasant surprises.

In some types of herring migration, this risk-avoiding aspect seems to be the main justification of the conservative behaviour. In overwintering migrations for instance, there is no inherent advantage of overwintering in any particular fjord or part of the shelf edge. If herring return each year to the same place, they probably do so simply because they have successfully overwintered there the year before. Sometimes, the area that the fish choose for overwintering is clearly not the most suitable place (e.g. the fjords in northern Norway with their reduced oxygen content). Yet, as long as the population is not confronted with serious problems in their existing overwintering area, they do not change their habit.

In addition to reducing the risk of negative events, conservatism may also increase the chances of positive events. This occurs by consolidating behaviour that by chance has turned out to be successful. If the population in one year by chance has discovered a high food abundance in a particular area, it may be worthwhile to return to this place next year. Plankton production tends to show multi-annual trends both in time and in space (section 4), and therefore the chances of finding food in the current year will be greatest in those areas that have shown a high abundance last year. After the Norwegian herring in 1965 had discovered more productive feeding grounds near Jan Mayen, it went directly to this area in 1966 and 1967 (Jakobsson 1969). North Sea herring started to prolong their stay in the eastern North Sea after they had experienced a few years with an extended *Calanus* season in this area (section 4). In this way, conservatism is a way of conserving experience that has been acquired by trial and error.

If it is advantageous for a year-class to turn behaviour, which by chance has proven to be successful, into a habit, it will be equally advantageous for younger generations to copy this successful habit from the older fish. By adopting the habits of older generations, new year-classes can benefit directly from experience that was gained by trial and error by these older generations. In the years prior to 1965, the migration route of Norwegian herring to their feeding grounds was probably passed on from one generation to the next. By following experienced older fish, recruit herring would directly find their way to the most productive feeding areas along the polar front north-east of Iceland. When the tradition had died (along with the old stock), later year-classes had to re-invent the system of oceanic feeding migrations (Røttingen 1992, Fernö er al. 1998, Misund et al. 1998).

The possibility to transfer newly developed, adaptive behaviour from one generation to the next is generally considered to be the main advantage of tradition (Bonner 1980, Mainardi 1980, Helfman and Schultz 1984, Dodson 1988). Mainardi (1980) and Bonner (1980) use the term “cultural evolution” for the transfer of new behaviour by tradition, instead of by genes. The advantage of the “cultural” transfer of new behaviour is that it allows a much more rapid adaptation to changes in environment than the genetic evolution.

7.5.4. Spawning migrations as a special case

Whereas the advantages of habit formation and tradition for the population are easy to understand in the case of feeding and overwintering migrations, it is more difficult to see their benefit with respect to spawning migrations. Yet it is in spawning migrations that we find the most pronounced examples of conservatism and tradition. What advantage does it have for an individual herring to return to a fixed position for spawning each year, and what benefit does this behaviour have to the population as a whole?

Contrary to feeding and overwintering migrations, spawning migrations do not provide feedback to the individual fish. A herring has no way of evaluating whether its spawning has been successful, i.e. whether it has resulted in the production of offspring. Therefore, it has no incentive to change its spawning ground, even if none of the larvae it has produced will survive.

The same situation exists at the population level. Spawning populations will continue to spawn at their traditional locality, no matter what the fate of their offspring will be. We can illustrate this problem with a theoretical population that has two spawning areas, A and B (Fig. 7.5). The larvae born at location A are always transported to a suitable nursery area where they will grow up to become recruits. The larvae born at location B, in contrast, are always swept out into the open ocean and perish. First-time spawners, (descendants of course from population A), may either follow experienced spawners from population A or from population B to their respective spawning grounds. They have no means of finding out which choice will be "best" for the benefit of the total stock. If they opt for population B, they will spawn faithfully at location B for the rest of their lives, without contribution a single recruit to the overall stock.

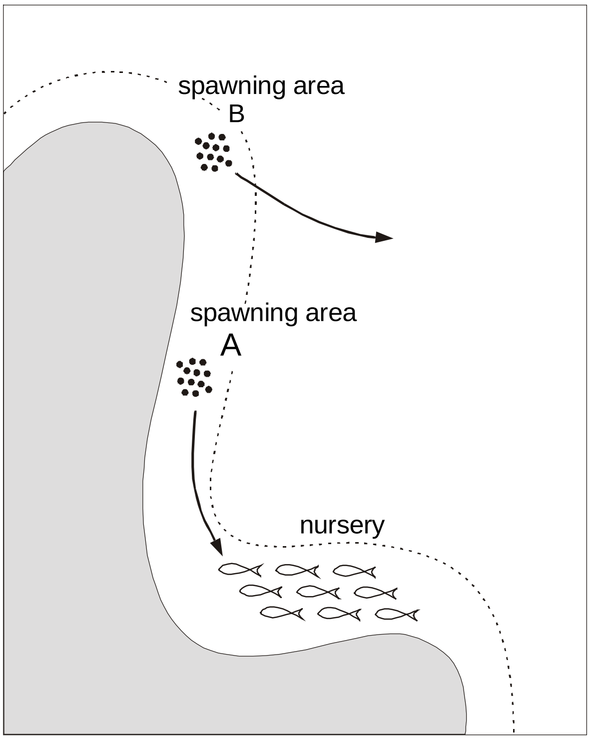

Figure 7.5. Hypothetical example of a herring stock composed of two spawning populations, A and B.

At first sight, habit formation and tradition do not seem to serve a useful purpose in spawning migrations. There is no feedback of results to the individual herring, nor to the individual spawning population. Hence the population can not adjust its migration to obtain better results. The main advantage of tradition, i.e. the possibility to transfer adapted behaviour, does not exist in spawning migrations.

However, even if conservative behaviour has no benefit to the individual fish, or even to the individual spawning population, there may still be a benefit to the species at a higher stock level. If spawning populations do not constitute self-contained stocks, the offspring they produce will not be channelled directly back to them, but will be added to a pool of recruits that they share with a number of neighbouring populations. Such a group of populations that share a common pool of recruits is termed a meta-population (McQuinn 1997). Maybe it is at this meta-population level that we have to look for the significance of tradition in spawning migrations.

Within the meta-population, each spawning population produces recruits (with more or less success) that are added to the common pool. The recruits from this pool are re-distributed among the various spawning populations, without necessarily returning to their parent population. From a meta-population point of view, it does not matter which spawning population has contributed most to the overall recruitment in a given year. Presumably the relative contribution of the various spawning populations will vary from year to year. The main point is that the combined recruitment, derived from all populations together, remains at a high level.

This brings us to the question what factors influence the overall recruitment success of the stock. To address this question, we briefly have to consider the peculiar spawning habits of the herring. Herring are unique among most other marine fish in their habit of depositing their eggs on the bottom, rather than dispersing them throughout the water column. This concentration of eggs on the bottom greatly increases the risk of predation by demersal fish and invertebrates. In order to reduce the risk of predation, the herring concentrate their eggs in a very small location. The resident predators in this location will be soon be saturated, and predation mortality will stay within acceptable limits. This strategy has been termed “predator swamping” (Lambert 1990).

The concentrated spawning will result in a simultaneous hatching of all eggs, and a concentration of larvae within a small area. If the environmental conditions at the time and place of hatching are unfavourable, the whole generation of larvae will perish. By "putting all its eggs into one basket”, the stock takes a large gamble with its future recruitment. In this situation, it may be advantageous for the stock to adopt a bet-hedging strategy (Lambert 1990). If the larvae are born in a series of separate batches, chances will increase that one of the batches will meet a suitable “environmental window” (Cury and Roy 1989). Lambert (1990) showed that recruitment success in Norwegian spring spawners was probably related to the number of separate spawning waves (at intervals of some weeks) on the same spawning ground.

The bet-hedging strategy can also be applied on a spatial scale. By increasing the number of separate spawning sites, chances are increased that somewhere a batch of larvae will meet a suitable environmental window. The precise position of the sites is not important, since the drift of the larvae to the nursery areas is variable anyway. The essential point is to have a number of different starting positions for the larvae.

It is in this respect that tradition assumes a role in the spawning strategy of the herring. Without tradition, the herring would be guided only by their tendency to join other herring at the time of spawning, and to concentrate their spawning products within a narrow area. This would easily lead to an over-concentration of spawning in a limited number of places, and a low chance that one of the few batches of larvae would survive. Tradition is the mechanism that counteracts this trend to over-concentration. It allows the total stock to split up into a number of separate components, each with its own traditional spawning ground and spawning time. In this way, tradition ensures that the number of spawning events is increased, and that there is a greater chance that somewhere within the meta-population, a batch of larvae will meet suitable environmental conditions. I conclude that tradition in spawning migrations does not serve to maintain spawning grounds that are particularly suitable, nor to transfer newly acquired behaviour to future generations. Its only use is to maintain a “cultural diversity” within the total stock, and thereby a diversity of spawning grounds.

7.5.5. Implications for research

In studying the relationship between herring distribution and environment, one has to be aware of the possible existence of habit formation and tradition. If (adult) herring have got used to a certain migration pattern, they tend to adhere to it, even if the environment gradually changes. The fish may wait to adapt their migrations until a certain environmental threshold has been reached. This means that in some cases the response of the fish to an environmental change will not be linear but stepwise. The delayed response of the fish may create a time lag between the environmental change and the change in fish migration.

Once the fish have changed their migration, they may be reluctant to reverse the change again, even if the environmental cause has disappeared. In this case, the distribution of the fish will not reflect the environmental conditions of the moment, but of those in some period in the past.

We may expect that the conservative behaviour becomes stronger with the age of the fish. Older herring may be the most reluctant to adapt their migrations to changing environmental conditions. Recruit herring, on the other hand, are not yet influenced by conservatism, and they will probably respond most readily to changes in the environment. In studying the response of herring to environmental change, one should therefore take the age structure of the population into account.

7.5.6. Implications for management

When property rights for herring stocks are divided between countries on the basis of “zonal attachment”, it is important to realise that the distribution of adult herring is at least partly determined by habit formation and tradition. The traditional migration pattern may change sometime in future, which will affect the distribution of the stock over the various national economic zones.

A second aspect to notice, is the existence of separate units within the stock, each with their own traditional migration patterns. If the fishery is concentrated too much in one particular area, it may exterminate one of these separate components. This may lead to the temporary disappearance of herring from this area.

In the case of feeding or overwintering migrations, the herring seem to be rather flexible, and they will re-occupy an abandoned area again after some time. This is much less the case in spawning migrations. If a spawning population has become extinct, the corresponding spawning site may not be re-occupied for several decades. This seems to be related to the very strong traditional element in this type of migrations.

Earlier authors have already advocated the protection of individual spawning populations. Wynne-Edwards (1962) did so because he assumed that the tradition on which spawning migrations were based, contained accumulated knowledge that would be lost if the population was exterminated. Other authors (Hourston 1982, Burd 1985, Stephenson 1998, 1999) assumed that spawning populations constituted self-contained stocks, that should be protected because they were irreplaceable. However, Smith and Jamieson (1986) rejected the need for separately managing individual spawning populations, arguing that these merely constituted “transient subdivisions of the total stock”.

Although Smith and Jamieson (1986) were probably right in their opinion about the genetic status of the spawning populations, they may have drawn the wrong conclusion with regard to the management implications. Even if spawning populations derive their identity only from a special tradition instead of from a special genetic constitution, their separate identity may still be meaningful from a biological point of view. As discussed above, the diversity of spawning populations within a stock may increase the chances of successful recruitment to the stock as a whole. This is a good argument for the conservation of individual spawning populations.

Chapter 8

General discussion and outlook

8.1. Outline of the chapter

The work presented in this thesis was aimed at finding the environmental cause(s) of some long-term, natural changes in the distribution of North Sea herring during the last decades. As explained in the introduction of this thesis, herring research during the past 40 years had been focussed almost exclusively on fishery induced changes. Yet it appeared that a number of long-term changes in the herring stock could not be explained by fishery effects. For that reason I expected that such long-term changes in the stock would have been caused by equally long-term changes in its natural environment. Such multi-annual variations in atmospheric or hydrographic conditions are commonly referred to as climate variations. The ultimate goal of the study, therefore, was to link long-term changes in herring to climate variations.

In the previous chapters a number of long-term changes in the distribution of North Sea herring was described, and an attempt was made to link these changes to environmental causes. I will now review the results of these case studies, and see whether they support the original hypothesis that long-term changes in herring stocks were caused by equally long-term changes in the environment. To start with, a review will be presented of all environmental variables that were found to be associated with changes in herring distribution. In this review the various ways are described in which the environmental factors were found (or supposed) to affect the distribution of the herring.

The second section deals with the interrelationship between the different environmental variables. Can the changes in water temperature, currents and food distribution that affected the herring, all be related to a common climate variation? To be more specific, could the North Atlantic Oscillation (NAO) be the ultimate cause of all environmental variations that affected the herring? The North Atlantic Oscillation is the main climate variation in our part of the world, and it is the principal candidate for the cause of naturally induced changes in herring distribution.

Section 2 will lead to the conclusion that some of the environmental variations that affected the distribution of the herring were not directly related to the NAO. The most important variation in this category is a presumed long-term variation of Atlantic inflow into the northwestern North Sea. The existence of this variation was demonstrated on the basis of the presence of Atlantic plankton in the northwestern North Sea. The plankton data, however, provide only indirect evidence for the existence of the inflow variations. Since the variations of Atlantic inflow are a key element in the explanation of changes in herring in the northwestern North Sea, further (indirect) evidence for their existence is provided in section 3 by reviewing a number of synchronous changes in other components of the ecosystem, described by other authors.

After the analysis of historic changes, possible scenarios for future change are discussed in section 4. Starting from current predictions of climate change in the North Sea during the next decades, possible changes in distribution of North Sea herring during this period are considered.

An unexpected outcome of my study was the observation that the response of herring to environmental variation seemed to be suppressed by conservatism. The fish tend to adhere to habits that they have established in the first year of their adult life. They will change these habits only if the environmental stimulus is strong. This phenomenon was observed in spawning, feeding and wintering migrations. Conservatism may complicate the relationship between the behaviour of the fish and environmental variation. This subject is discussed in more detail in section 5. Due to conservatism, the herring in some cases do not respond to an environmental variation at all, whereas in other cases their response lasts longer than the environmental variation itself. To explain the complicated response of herring to environmental variation, a conceptual model for the migratory behaviour of herring is presented in section 6. This model describes how the behaviour of the fish is the result of a combination of innate preferences, environmental stimuli, and acquired habits.

In section 7 the conclusions of the present study are summarised. Do the results obtained support the hypothesis that long-term changes in herring distribution are caused by equally long-term environmental variations, or has this hypothesis to be rejected?

8.2. Environmental factors associated with long-term changes in North Sea herring

In the previous chapters, I concluded that changes in distribution of North Sea herring were related to a number of different environmental variables. These included:

- Atlantic inflow into the northwestern North Sea as reflected by the *Metridia-Candacia* index for this area
- water temperature in February in the northeastern North Sea;
- annual abundance of *Calanus finmarchicus* in the total North Sea;
- abundance of *C. finmarchicus* in the northeastern North Sea in June;
- northeasterly winds over the Skagerrak in autumn.

In the following paragraphs, a review is presented of the ways in which each of these environmental variables was assumed to affect herring distribution.

8.2.1. Atlantic inflow into the northwestern North Sea as reflected by the *Metridia/Candacia* index for this area

The work on plankton indicator species described in chapter 2 was carried out in order to test the hypothesis of a sustained reduction of Atlantic inflow into the northwestern North Sea in the 1970s. Such a reduction had been postulated by Corten (1986) to explain changes in the distribution of herring larvae during this period. Earlier, Bainbridge and Forsyth (1972) had already suggested that the northward shift of herring fisheries in the western North Sea in the 1960s was related to a reduction of Atlantic inflow in that period.

Analysis of CPR plankton data showed that two “classical” indicator species for Atlantic water in the northwestern North Sea, *Candacia armata* and *Metridia lucens*, were below average from 1965 –1980, and increased after 1980. These results provide evidence that the Atlantic inflow into the northwestern North Sea had indeed been reduced in the 1960s and 1970s, and that it had increased again after 1980.

Long-term variations of the Atlantic inflow into the northwestern North Sea may affect the herring population in a number of ways. A direct effect may occur on the transport of herring larvae that are born in the northwestern North Sea in autumn. These larvae have to drift across the North Sea during winter in order to reach the nursery areas along the eastern border of the North Sea in spring. The residual current in the vicinity of the hatching places probably depends on the strength of the Atlantic inflow in this area (chapter 1, figures 1.2 and 1.3), and consequently the initial transport of the larvae would be a function of the Atlantic inflow. A reduced Atlantic inflow will cause a stagnation of the larvae in the vicinity of their hatching areas, and this will reduce the number of larvae that reach the nursery areas in the eastern North Sea, and hence subsequent recruitment. Corten (1986) showed that during the period of recruitment failure in 1972-1979, most herring larvae in February were still found in the western half of the North Sea instead of in the eastern half. This suggested that a sustained hydrographic change had taken place in the northwestern North Sea, which had reduced the eastward transport of the larvae.

A second effect of variations of Atlantic inflow may occur through changes in the distribution of food for the herring. Bainbridge and Forsyth (1972) reported multi-annual shifts in the latitudinal distribution of the summer herring fishery in the western

North Sea. These shifts appeared to be related to the distribution of food organisms. They found that the area of maximum food abundance occurred relatively south (off Aberdeen) in years with a strong Atlantic inflow. In years of low Atlantic inflow, the maximum food abundance (and the centre of the fishery) shifted north towards the Shetland area.

Finally, variations in Atlantic inflow may affect the choice of spawning area by recruit spawners (chapter 3). This effect occurs through the distribution of the herring during the feeding season. The spawning season in the northwestern North Sea follows directly after the feeding season, and recruit spawners will be inclined to choose a spawning ground not too far away from the area where they have last been feeding. In the above paragraph we saw that the strength of the Atlantic inflow probably determines the latitudinal distribution of food, and thereby of the feeding herring. Through its effect on the distribution of feeding herring, the strength of the Atlantic inflow will thus influence the choice of spawning ground by recruit herring.

8.2.2. Water temperatures in February in the northeastern North Sea

The northern distribution of herring during the summers of 1988-1990 was found to be associated with high water temperatures (about 2ºC above average) in the northeastern North Sea in February (chapter 5). It was assumed that the high temperatures found in February persisted in the following months (there were no accurate temperature data available for the northeastern North Sea in March and April), and thereby were representative for the water temperature at the start of the spring feeding migration.

I have presented two possible explanations for the correlation between temperature and northerly distribution. The first explanation is that herring responded directly to a higher temperature by moving northward. The reason for doing so would be to control temperature-dependent physiological processes, such as gonad maturation and metabolic rate (chapter 5). As water temperature in the North Sea normally has a north/south gradient, the herring could reduce their ambient temperature by moving north. The northward extension of the feeding migrations in 1988-1990 can well have been an attempt of the herring to maintain an optimum ambient temperature.

A second explanation for the correlation between temperature and herring distribution may be that temperature affected the herring indirectly through changes in the distribution of its food. This theory is further discussed below.

8.2.3. Annual abundance of *Calanus finmarchicus* in the total North Sea

The northerly distribution of herring in 1988-1990 coincided with a reduction of the mean abundance of *Calanus finmarchicus* in the North Sea (chapter 5). Since *C. finmarchicus* is the main food item of the herring in the first half of the year, the reduced abundance of this copepod on the normal feeding grounds may have stimulated the herring to search for food elsewhere.

C. finmarchicus is a cold water species, which has the centre of its distribution in the Norwegian Sea (Planque and Fromentin, 1996). The North Sea constitutes approximately the southern limit of its distribution. High temperatures in the North Sea will therefore have a negative effect on the abundance of this copepod. Fromentin and Planque (1996) found a negative correlation between the (winter) NAO index and the abundance of *C. finmarchicus* in the North Sea and adjacent waters. The reduced abundance of *C. finmarchicus* during years with a high NAO-index was attributed both to a stronger mixing of the water by westerly winds (delaying the onset of the spring phytoplankton bloom), and to the higher water temperatures. During (warm) years with a positive NAO-index, the distribution of *C. finmarchicus* was confined to the northern part of its distribution area.

In the spring following a mild winter, the herring in the North Sea will thus be confronted with a shortage of its main food item. This may trigger a genetically determined reaction to migrate further north, to colder waters where *C. finmarchicus* still occurs in high densities. The northward extension of the herring feeding migrations in the springs of 1988-1990 may thus have been caused primarily by a shortage of food on the normal feeding grounds, and only indirectly by the higher water temperatures (see previous section).

8.2.4. Abundance of *C. finmarchicus* in the northeastern North Sea in June

The easterly distribution of herring catches in June during the first years after the re-opening of the herring fishery in the North Sea (1984-86) followed, and partly coincided with, a period of prolonged *Calanus* seasons in the eastern North Sea. Whereas the abundance of *C. finmarchicus* in this area normally declines by the end of May, the season continued until June or July in most of the years 1976-1984. The prolonged *Calanus* season in these years is reflected by the high NAO- index for June.

It is likely that the easterly distribution of herring catches in the years 1984-1986 was directly related to the prolonged *C. finmarchicus* season in the eastern North Sea. Most of the North Sea herring start their feeding season in the northeastern North Sea, and migrate towards the western North Sea by the time food supply in the eastern North Sea (mainly *C. finmarchicus*) starts to decline. The migration from the eastern to the western half of the North Sea normally takes place late May - early June. During the period of extended *Calanus* seasons in the eastern North Sea, the herring probably continued to feed in this area longer than they used to do before. This explains the easterly distribution of herring catches during June in these years (chapter 6). After the *Calanus* season shortened again from 1985 onward, the easterly distribution of herring catches persisted for two more years. This persistence was attributed to conservatism in the behaviour of the herring (see also chapter 7).

8.2.5. Northeasterly winds over the Skagerrak in autumn

In chapter 4 it was concluded that the invasion of North Sea herring into the Skagerrak in the autumn of 1963 was probably caused by a passive transport of the fish by a sub-surface current. This conclusion was based on the observation of strong northeasterly winds over the Skagerrak at the time when the invasion took place. It was assumed that the northeasterly winds had driven surface water out of the Skagerrak, and thereby increased the existing sub-surface current into the Skagerrak. A strong recruiting herring year-class (1960) happened to be distributed off the entrance of the Skagerrak at the time when the sub-surface current presumably increased. Since these were recruit herring, they had not yet developed a site-attachment to the normal overwintering area of adult herring in the North Sea. Therefore, they would not resist the passive transport into the Skagerrak by an increased sub-surface current. I hypothesised that by spending the first winter of their adult life in the Skagerrak, the herring developed a site attachment to this area. This would explain the return of the year-class to the Skagerrak in the following winter, at a time when meteorological conditions were normal.

I suggested that earlier invasions of North Sea herring into the Skagerrak (the historic Bohuslän herring periods) started in the same way as the 1963 invasion. Once a new year-class had been drawn into the Skagerrak by a strong subsurface current, it would spend the first winter of its adult life in this area, and thereby develop a site attachment to it. In subsequent winters, the fish would return to the Skagerrak, regardless of meteorological conditions. This time, the year-class would be followed by younger herring, which would copy the new migration pattern. In this way, anomalous weather conditions during one year might cause a sequence of year-classes to overwinter in the Skagerrak during a much longer period. The Skagerrak herring period of 1963-65 ended already after two winters, presumably due to the intensive fishing effort in the area (Höglund 1978). I assume that under normal conditions the fish would have returned to the Skagerrak for several more years (chapter 4).

According to the above theory, the start of a Bohuslän herring period is triggered by a period of sustained northeasterly winds over the Skagerrak at the time when a new herring year-class has to choose its first overwintering ground. Such a period of northeasterly winds is most likely to occur during a negative phase of the NAO. However, the local weather in a small area such as the Skagerrak shows large random fluctuations, superimposed on the NAO pattern. Therefore, a negative phase of the NAO does not immediately result in a period of northeasterly winds over the Skagerrak, and thereby in the start of a Bohuslän period. It merely increases the chances that the necessary conditions for the start of a Bohuslän period will sometime occur.

8.3. The relationship between the different environmental factors

The ideal of a scientist is to explain the world by as few rules or principles as possible. In the case of natural changes in herring, it would be attractive, therefore, if in the end one could attribute all observed changes to a single climate variation. In this section, I shall make an attempt at doing so by comparing the different environmental parameters that were associated with changes in herring distribution, and see whether they share a common denominator.

As mentioned in chapter 1, the main climate variation in Western Europe is the North Atlantic Oscillation. The NAO affects atmospheric circulation, and thereby water temperature, wind-driven currents, density driven currents, and vertical mixing of the water column. In view of its profound hydrographic effects, the NAO could be the common cause of all environmental variations that were found to affect the herring. In the following paragraphs, I will investigate whether this indeed is the case.

8.3.1. Environmental variations that are related to the NAO

To allow a comparison between the various environmental parameters and the NAO, all have been plotted on the same time axis in Figure 1. Two NAO-indices have

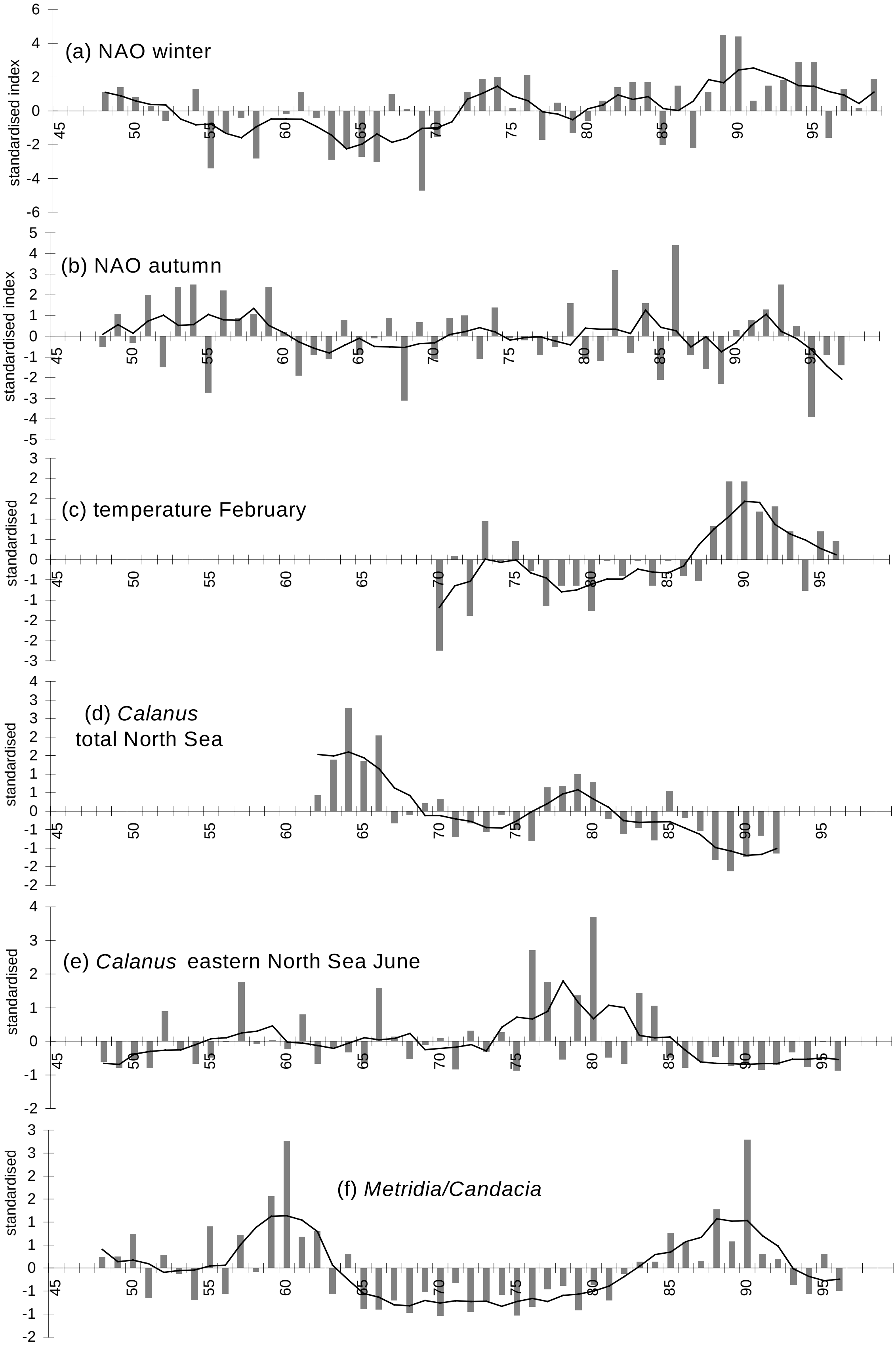

Figure 8.1. Time series of environmental parameters that were related to changes in North Sea herring. All parameters have been presented as standardised indices. Drawn line represents 5-year moving average.

been presented, one for the autumn (October-December) and one for the winter (January-March). These are the seasons when the wind speed over the North Sea reaches its maximum, and when the NAO is expected to have its strongest effect on the North Sea. The seasonal indices have been calculated using monthly indices provided by Hurrell (2000b).

Surprisingly, the autumn and winter NAO-indices appear to fluctuate independently from one another (Fig. 8.1). One would have expected that a climate variation which persists on a time scale of decades, would also persist throughout the year, or at least throughout the autumn/winter period. This does not appear to be the case: the NAO-index for the autumn is not correlated with the index for the winter (Fig. 8.2).

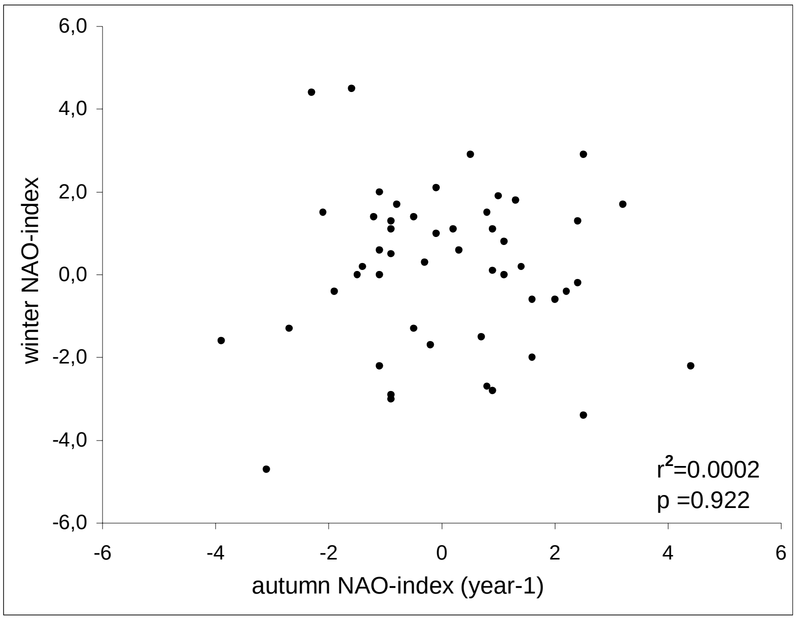

Figure 8.2. Comparison between autumn and winter NAO-index.

Because the autumn- and winter NAO-indices vary independently from one another, the comparison between NAO and environmental parameters was made separately for the autumn and winter NAO-index (Fig. 8.3). For the winter index, the comparison was made within the same year, but in the case of the autumn index, a time lag of one year was applied to the environmental parameters. The reason for this is that the environmental parameters concerned (winter temperature, *Calanus* abundance for the total North Sea, and *Calanus* abundance in June in the eastern North Sea) refer to the first half of the year, and a relationship with the autumn NAO-index was more likely to exist for the preceding autumn. An exception was the

Metridia/Candacia index, which refers mainly to the second half of the year, and for which the comparison with the autumn NAO-index was made within the same year.

Only two of the four environmental factors appeared to be correlated with the NAO. These were bottom temperature in February and mean annual abundance of *Calanus finmarchicus* in the total North Sea. The correlation existed only with the winter NAO-index.

The bottom temperature in February was positively correlated with the winter NAO-index (Fig. 8.3). This correlation may be explained by the reduced cooling of the North Sea during years with a positive NAO index (chapter 1). Because of the vertical mixing of North Sea water during winter, a reduced cooling at the surface will result in a relatively high bottom temperature at the end of the winter.

The annual abundance of *C. finmarchicus* in the total North Sea was negatively correlated with the winter NAO-index. This negative correlation was already found by Fromentin and Planque (1996). These authors attributed the reduced abundance of *C. finmarchicus* during a positive phase of the NAO to the low tolerance of the (boreal) copepod to high water temperatures, and also to the increased mixing of the water column by westerly winds, resulting in a delayed onset of the spring phytoplankton bloom.

The main effect of the NAO on North Sea herring thus occurs through variations in winter temperature and/or annual *Calanus* abundance. These effects can explain the northern distribution of herring following winters with a high NAO index.

Another effect of the NAO on North Sea herring may occur through changes in the current system near the entrance of the Skagerrak (not included in Figures 8.1 and 8.3). During a negative phase of the NAO, there will be an increased frequency of northeasterly winds over the Skagerrak. Such winds are expected to strengthen the sub-surface current into the Skagerrak, and thereby cause a drift of recruit herring into this area. This may trigger the start of Skagerrak or Bohuslän herring period, as already discussed in section 8.2.5.

8.3.1. Environmental variations that are not related to the NAO

Two environmental parameters associated with herring changes did not appear to be related to the NAO. These were the *Calanus* abundance in June in the eastern North Sea, and the *Metridia/Candacia* index in the northwestern North Sea (Fig. 8.1 and 8.3).

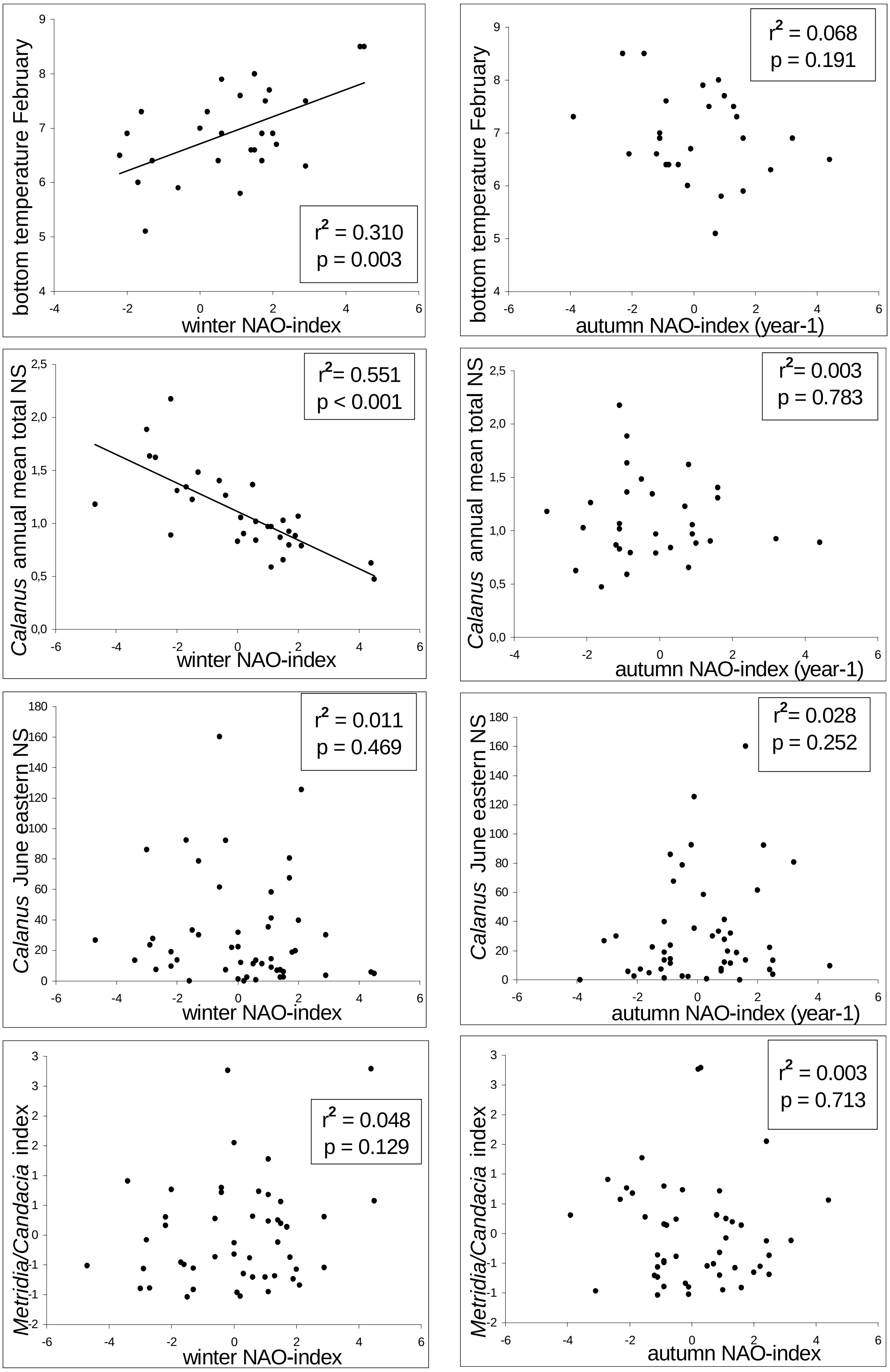

Figure 8.3. Correlation between different environmental parameteres and NAO-index for autumn and winter.

The *Calanus* abundance for June in the eastern North Sea is an index for the duration of the *Calanus* season in this area, with a high index representing an extended season. The absence of a correlation between this index and the NAO indicates that the duration of the *Calanus* season in the northeastern North Sea is not related to local meteorological conditions. The actual factor that determines the duration of the *Calanus* season remains unknown for the time being.

The *Metridia/Candacia* index for the northwestern North Sea is assumed to reflect variations of Atlantic inflow into this area (chapter 2). Since the *Metridia/Candacia* index does not show a correlation with either of the two NAO indices, the postulated variations of Atlantic inflow are not related to the NAO either. The NAO is the dominant long-term variation in meteorological conditions in this area. If the inflow variations are not correlated with the NAO, they must be independent of local meteorological conditions. This leads to the conclusion that the inflow variations probably originate from the North Atlantic, and that they must be driven by long-term changes in the strength or density of the ocean currents. An investigation of the oceanographic causes of the inflow variations was outside the scope of this study, but the biological results reported here raise an interesting oceanographic question.

The conclusion that variations of Atlantic inflow into the northwestern North Sea may stem from wider changes in the current system of the North Atlantic implies that neighbouring areas along the periphery of the ocean might be affected by these changes as well. In this respect it is interesting to note the existence of long-term hydrographic and ecological changes in the western English Channel, which are sometimes referred to as the “Russell cycle”. The author after whom these changes were named (Russell 1935, 1973) assumed that they were caused by variations of Atlantic inflow into the western Channel. Although other authors have presented alternative explanations for the observed changes (see review by Southward 1980), the Atlantic inflow hypothesis remains one of the most plausible theories. It would be interesting to investigate the possible connection between the *Metridia/Candacia* variations in the North Sea and the Russell cycle in the English Channel. A link between the variations of Atlantic inflow into the North Sea and those into the English Channel was already suspected by Russell (1935) himself.

8.4. Changes in other biotic components of the ecosystem in the northwestern North Sea that support the hypothesis of long-term changes of Atlantic inflow

The results of the plankton study presented in chapter 2 supported the hypothesis of long-term variations of Atlantic inflow into the northwestern North Sea. However, in the absence of firm evidence from actual current meter measurements, the existence of these variations remains a theory that requires further testing. One possibility of doing so is to compare the postulated changes in Atlantic inflow with ecological changes in the northwestern North Sea reported by other authors, and see whether the changes coincided in time and direction. In the following paragraphs, some long-term changes in other fish species and benthos in the northwestern North Sea will be considered that could be related to the same variations in Atlantic inflow that are presumably reflected by the *Metridia/Candacia* index.

As described in chapter 1, the sprat stock in the northwestern North Sea increased sharply in the 1970s, at the time when herring recruitment declined. Corten (1990) described how variations of Atlantic inflow into the northwestern North Sea could have opposite effects on the stocks of herring and sprat in this area. Both species spawn in late summer/early autumn, and a reduction of Atlantic inflow will slow down the eastward drift of the larvae of both species. In the case of herring this reduced drift is detrimental since it will prevent the larvae from reaching the nursery areas in the eastern North Sea. For the sprat stock in the northwestern North Sea, however, the stagnation of the eastward transport of larvae is advantageous. The recruitment to this population consists of juveniles that have grown up in the northwestern North Sea. Larvae that drift away to the eastern North Sea will probably not return to the northwestern North Sea. A retention of larvae in the northwestern North Sea will thus increase recruitment to the stock in this area. The strong increase in sprat recruitment in the northwestern North Sea in the 1970s, followed by the sharp decrease at the end of the decade, thus supports the hypothesis that the inflow of Atlantic water was low in the 1970s, and increased at the end of this decade.

A similar conclusion can be drawn from the observed changes in the sandeel stock around the Shetland Islands. This stock also depends for its recruitment on larvae that are retained in the area. Turrell (1992a) assumed that the high abundance of young sandeels in the inshore waters around Shetland in the mid- and late 1970s might have been the result of a reduction or cessation of the inflow of Atlantic water in this area. Starting from 1983, recruitment to the sandeel stock sharply declined. This decline in recruitment occurred at a time when the spawning stock was relatively high, and the decline in recruitment must therefore have been caused by environmental factors

(Kunzlik 1989, Bailey 1989). If the high recruitment in the 1970s was due to a retention of larvae in the area, the reduced recruitment after 1983 may have been caused by an increased transport of larvae out of the area. These results are consistent with the hypothesis that the Atlantic inflow was low during the 1970s, and increased in the early 1980s.

A third case that supports the hypothesis of variations of Atlantic inflow, are the long-term variations in growth of the bivalve *Arctica islandica*, reported by Witbaard (1996). The growth of this mollusc on the Fladen Grounds, the central part of the northwestern North Sea, showed various multi-annual cycli, the longest of which had a period of 33 years (Witbaard *et al*. 1997). The variations in growth rate of the mollusc were assumed to be caused by changes in the sedimentation rate of organic matter, which depends on the current velocity in the area. The long-term variations in the growth of the mollusc were therefore concluded to reflect long-term variations in the position or strength of the Atlantic inflow (Witbaard *et al*. 1997).

The maximum cycle of 33 years, found in the growth rate of *A. islandica*, roughly corresponds to the time interval between the two maxima of the *Metridia/Candacia* index (1960 and 1990) found in chapter 2. This suggests that the long-term variations in both the mollusc and the copepods might be related to the same variation of Atlantic inflow. Further support for this theory is provided by the synchrony of the variations in both data series, with the *Metridia/Candacia* index reaching a maximum around 1960, at the same time when the growth of *A. islandica* dropped to a minimum. If the sedimentation rate of organic matter is inversely related to current velocity in the area, as Witbaard *et al*. (1997) assumed, a high Atlantic inflow would reduce the sedimentation rate, and thereby reduce the growth rate of *A. islandica*. The observed minimum in the growth of *A. islandica* at a time when the *Metridia/Candacia* index reached a maximum, thus supports the assumption that both the growth rate of the mollusc and the abundance of the Atlantic copepods were influenced by the same long-term variations of Atlantic inflow.

8.5. Outlook for future changes in the herring stock

One of the reasons to study natural changes in the herring stock in the past is that it may allow a better understanding of changes that are occurring at present, and possibly even a prediction of changes that will occur in the future. Now that the present management strategy for North Sea herring is aimed at harvesting a constant, low proportion (20%) of the stock each year (chapter 1), future changes in stock size and distribution will be caused mainly by environmental variability.

The climate variations that affected North Sea herring in the past 50 years will probably continue to do so in the near future. This means that the distribution of herring during the next decades will be influenced by the North Atlantic Oscillation and by the presumed variations of Atlantic inflow into the northwestern North Sea.

So far, the NAO is unpredictable (KNMI 2000). Therefore, we do not know when the current positive phase will change into a negative phase. However, assuming that the NAO continues to behave as it has done in the past century, a phase shift should occur sometime within the next one or two decades. Once this has happened, water temperatures in the North Sea at the end of the winter will generally be lower than at present, and the herring will be less likely to migrate far north during the feeding season (chapter 5). Another consequence of a negative phase of the NAO is that the chances of a new Skagerrak herring period will be increased (chapter 4).

The presumed variations of Atlantic inflow, reflected by the *Metridia/Candacia* index, can not yet be predicted either. The present time series (50 years) is too short to decide whether there is a *Metridia/Candacia* “cycle” with a period of about 30 years (the time span between the two observed maxima), or whether the variations of the *Metridia/Candacia* index represent fluctuations that occur at random intervals in time. One indication that the variations of Atlantic inflow might adhere to a cyclic pattern, is the 33-year cycle found in the growth rate of *Arctica islandica* during the last 100 years (Witbaard *et al*. 1997).

In addition to the environmental variations that we have seen in the past, the next decades may also show symptoms of a new climatic phenomenon: global warming due to the accumulation of greenhouse gases in the atmosphere. The likely consequences of this climate change have been the subject of intensive study (Anon. 2000), but much uncertainty still remains as to the ultimate effects. The main effects expected on a global level during the present century are an increase of mean temperature by 1.4° - 5.8°C, an increase of mean sea level by 0.1 – 0.9 m, and an increased precipitation at high latitudes (IPCC 2001). The increased fresh water input in the sub-polar areas (resulting from higher precipitation and melting of polar ice) may affect the thermohaline circulation (THC), and thereby the currents in the whole of the North Atlantic. The changes in the THC resulting from global warming, however, can not yet be modelled accurately (Stocker and Schmittner 1997).

While much uncertainty exists as to the effects of climate change at a global level, the effects on a relatively small area such as the North Sea are even more unpredictable. No models are yet available that can estimate future changes in temperature in this area with any reasonable degree of precision. A personal estimates of one of the scientists working in this field is that the average temperature of the North Sea during the next 50 years will increase by 0.5 – 1.0°C (A. Kattenberg, pers. comm.). This estimate is based on the assumption that neither the current system of the North Atlantic, nor the amplitude and geographic pattern of the NAO will change as a result of rising greenhouse gas concentrations. A rise of water temperature by 0.5 – 1.0°C is small in comparison to the variations of about 2°C caused by the NAO in the past (Fig. 8.1). Hence it is expected that the northward extension of herring feeding migrations, resulting from such a temperature rise, would be smaller than those observed in 1988-1990.

However, the situation would be quite different in case the NAO would change as a result of the accumulation of greenhouse gases (KNMI 2000). Some model simulations indicate that rising greenhouse gas concentrations could lead to a change in the geographical pattern of the NAO, and an increased storm track activity over the eastern Atlantic and western Europe (Ulbrich and Christoph 1999). If the climate in western Europe changes according to this scenario, the increase in average water temperature in the North Sea during winter will be greater than the 0.5 – 1.0°C mentioned above. A more pronounced increase in winter temperature is expected to result in a more northward migration of the herring in spring (chapter 5), and extreme northern distributions like the ones observed in 1988-1990 could become the rule instead of the exception.

8.6. Conservatism: a complicating factor in the relation between herring and its environment

8.6.1. Herring behaviour changes more slowly than the environment

Although herring are observed to adapt their migration patterns to long-term variations in the environment, they do not react immediately to every short-term variation. It sometimes takes a fairly drastic or sustained environmental change to make the population change its normal migration pattern (chapter 7). Once the fish have changed their migration pattern in response to such an environmental change, they sometimes adhere to the new pattern even after the original environmental cause has disappeared. Examples of this conservative behaviour were noticed in the winter migrations into the Skagerrak in 1963-65 (chapter 4) and in the prolonged feeding period in the eastern North Sea in the early 1980s (chapter 6). In both cases, the fish started a new migration pattern in response to an environmental change, but continued to perform the new migration for some time after the environmental conditions had returned to the original condition. I describe in chapter 7 a number of other cases, both in North Sea herring and in Norwegian spring spawning herring, in which conservatism apparently affected the behaviour of herring.

Conservatism creates a certain inertia in the behaviour of the fish. This inertia tends to make changes in behaviour last relatively long, sometimes longer than the environmental changes that caused them. This is a surprising outcome, as the original assumption in the present study was that sustained changes in herring migrations were driven by equally sustained changes in the environment (chapter 1). The results of the case studies presented in chapters 3, 4, and 7 have shown that this assumption sometimes is false. Long-term changes in herring behaviour may actually result from shorter environmental changes. The behaviour of the herring sometimes is more stable than the environment.

The conservatism of the herring complicates the relationship between the behaviour of the fish and its environment. Due to this conservatism, the distribution of the stock in a given year may not only be a function of current environmental conditions, but also of those in previous years. Until now, this aspect of herring behaviour has never been considered in studies on the relationship between herring and its environment. It explains some of the problems that earlier authors had in relating long-term changes in herring migrations (e.g. the Bohuslän herring periods) to environmental factors.

As described in chapter 7, the changes of migration pattern adopted by one year-class may be copied by subsequent year-classes. This makes the relationship between herring and its environment even more complicated. A certain migration pattern may be the result of an environmental change that did not occur during the life-time of the current generation, but during the life of its ancestors. Amazing as this theory may seem, there are several observations to support it (chapter 7). Particularly in the case of spawning and overwintering migrations, the transfer of migration patterns from one year-class to the next appears to be a common phenomenon.

8.6.1. The role of conservatism from a biological point of view

Apart from its direct relevance for understanding the behaviour of herring, the existence of conservatism is interesting from a general biological point of view. Conservatism is a strategy that allows the population to adapt to medium-term variability in its environment. To see this point, one may first consider environments that change either very rapidly or very slowly. In an environment that changes rapidly from one year to another, the distribution of food and temperature in the current year will not be predictable on the basis of the distribution in the last few years. Hence, the behaviour of the fish has to be adaptive rather than conservative. On the other hand, if the population lives in an environment that changes only at time scales of centuries or longer, the necessary adaptation of its behaviour may occur through selection and genetic modification. In this case, there is no need for conservatism either. Conservatism is useful only in situations where the environment shows medium-term changes. In this case, the environmental conditions in the current year are likely to resemble those in the last few years. It will be advantageous for the population, therefore, to adapt its behaviour to the environmental conditions in those last few years. The environment changes too rapidly, however, to allow a genetic adaptation of the population's behaviour. In this case, the population can adapt its behaviour only by using learned information, i.e. by behaving conservatively.

North Sea herring live in an environment that appears to be conducive to the development of conservative behaviour. Although considerable variations in the distribution of temperature and food occur from year to year, certain patterns appear to persist on a time scale of several years or even decades. Examples are the prolonged *Calanus* season in the eastern North Sea in 1976-1984 and the long-term changes of Atlantic inflow into the northwestern North Sea. These patterns presumably reflect long-term oceanic or climate variations. The existence of these multi-annual patterns increases the chance that the environment next year will behave the same way as it did this year. In this case, it is advantageous for the population to migrate directly to the area where it has found optimum food or shelter conditions in previous years (thus behaving conservatively), rather than spending much energy in a random search of the entire distribution area.

From a wider biological point of view, it is interesting to note the similarity between the learning behaviour in herring, found in the present study, with learning behaviour reported earlier for salmon (Dittman and Quinn, 1996) and for some species of birds (chapter 7). The similarity between the behaviour of herring and migratory birds is especially striking. Like in these birds, a new herring year-class apparently "learns" the places that it visits during the first year of its adult life, and it tends to return to these places in subsequent years. Even the phenomenon of "culturally" determined migrations routes, in which new generations learn existing migration routes from older generations, is found in herring too. In birds, migration routes appear to be culturally determined in species with extended parental care, in which the young migrate with their parents (Sutherland 1998). In herring the transfer of "traditional" migration routes must occur in schools in which recruit migrants are mixed with older herring. In both cases, the collective migratory behaviour provides an opportunity for recruit migrants to supplement their innate knowledge of migratory direction and distance with an additional amount of information that is obtained by learning.

8.7. A conceptual model for herring migrations

The objective of the present study was to investigate the causes of natural, long-term changes in the migrations and distribution of the herring. It was expected that such changes in the distribution of the herring would be caused by equally long-term changes in the environment. The results of this study, however, have shown that the relationship between the herring and their environment is not straightforward. Sometimes the herring respond to an environmental change, and sometimes they don't. In cases where they do react to an environmental change, their response sometimes lasts longer than the environmental change itself. This complicated nature of the response of herring to environmental variation tends to obscure the causes of the observed changes in behaviour.

The response of the herring to environmental variation can only be understood in the context of other factors that determine the behaviour of the fish. These factors are innate behaviour, habit formation (conservatism), and imitation of behaviour from older herring (tradition). Each of these factors has a varying influence, depending on the age of the fish, the type of migration, and the strength of the environmental stimulus. This results in a behaviour that is sometimes dominated by innate preferences, sometimes by environmental stimuli, and sometimes by conservatism. In order to describe the role of these individual factors and their interaction, I propose the following conceptual model for the migratory behaviour of the herring. This model is based on existing knowledge about the distribution of herring at different stages of its life (e.g. Parrish and Saville 1965, Harden Jones 1968), on earlier theories about herring migration (Wynne-Edwards 1962, Corten 1993, McQuinn 1997), and on the findings of the present study.

During the first two years of their life, the distribution of the herring is determined by their place of birth, and by the passive transport of the larvae in the first months after hatching. The fish may grow up in nursery areas that are situated hundreds of kilometres away from the spawning, feeding, and wintering places of the adult stock. During their third year of life the young herring reach maturity, and by this time they have to catch up with the adult population in its feeding, spawning and wintering migrations.

The recruit herring have a genetically determined preference for the approximate time and direction of the various migrations they have to undertake as adult fish. However, the precise timing and routes of these migrations are not genetically determined. The herring have to learn these during the first year of their adult life. When the herring start to mature in the summer of their third year, they leave the nursery areas and migrate offshore into deeper water (an innate behaviour). Here they will join schools of other herring (also genetically determined behaviour) and follow these to the summer feeding grounds. The schools of feeding herring will normally contain a certain percentage of herring that have already spawned the previous year. At spawning time, the recruit spawners will follow the “experienced” spawners to one of the existing spawning sites (imitation). By spawning at a particular site, the recruit herring will develop an attachment to this site, and as a result return there again in subsequent years (habit formation). By this time the herring have become experienced spawners, and they will pass the habit of spawning at this particular site on to a new generation of herring (tradition). After their first spawning, recruit herring will follow older herring to one of the traditional wintering grounds, and develop an attachment to this wintering ground in the same way as they developed an attachment to a particular spawning site.

Environmental variations will affect the distribution of adult herring primarily through changes in food distribution. The production of planktonic food for the herring depends strongly on the availability of nutrients, which in turn is determined by currents and stratification of the water column. Changes in currents or stratification will lead to changes in the distribution of food. Although the adult herring will have developed an attachment to a certain feeding area, they will be forced to change if this traditional area for some years in succession does not provide sufficient food. Conversely, the fish will learn to stay longer in a certain area if the period of food production in this area is extended. Environmental variations that affect food abundance and distribution will thus affect the distribution of feeding herring, but they may do so with a certain delay, due to the conservatism of the fish.

The effect of environmental variation on spawning migrations is more complicated. Unlike in feeding migrations, the herring can not “judge” whether an environmental change has made an existing spawning ground unsuitable (except in case the temperature has changed). The final result of its spawning will largely depend on the later transport of the larvae; something the herring can not possibly foresee. It seems therefore that herring do not easily change their spawning migrations; they simply return to the same site where they have spawned the first time. This is a position which they normally have learned from the older herring in the population. The position of the spawning grounds, therefore, is not directly influenced by environmental variation. The only instance in which a new spawning site may be established, is when a recruiting year-class for some reason lacks the guidance of older herring. This may be due to a scarcity of older herring in the population, to an abundance of recruits, or to a special environmental condition that affects the distribution of the recruiting year-class more than that of the older herring (e.g. an abnormal distribution of food). In the absence of the guidance of older herring, the recruiting year-class (or part thereof) chooses a new spawning ground. After having spawned at this site once, the herring develop a site attachment and return to this same place in subsequent seasons. This time they will also lead the way to herring of the next generations. The establishment of a tradition to spawn at the new site is not due to a permanent change of the environment, but merely to the chance occurrence of a special environmental condition at the time when the first year-class had to choose its first spawning site.

A similar mechanism exists in wintering migrations. Also in this case, recruit herring follow older herring to one of the existing wintering sites, develop an attachment to this area, and return there in subsequent years regardless of environmental conditions. Only if the recruiting year-class looses contact with the older herring, will it be forced to choose a wintering area by itself. Like in spawning migrations, the recruiting year-class will develop an attachment to this new site, return there in subsequent winters, and lead new year-classes along to this new site. The permanent establishment of a new wintering site will create the impression that a permanent change has occurred in the environment. However, the new tradition is based merely on the chance occurrence of a special environmental condition in the first year that the new wintering site was established.

8.8. Conclusions

The objective of this study was to identify the environmental factors that caused long-term, natural changes in the migrations and distribution of North Sea herring during the last 50 years. It was expected that these changes would have been caused by environmental variations of an equally extended duration; in other words by climate variations.

The results of the study have shown that in some cases the observed changes in herring distribution could indeed be linked to a climate variation: the North Atlantic Oscillation. The NAO appeared to be the indirect cause of a northward shift of feeding grounds in 1988-1990, and a shift in wintering grounds in 1963-65. Other changes in North Sea herring, however, were not correlated with the NAO. These were the prolonged feeding seasons in the eastern North Sea in the early 1980s, and the changes in spawning area in the western North Sea.

In the western North Sea, the herring appeared to be affected by long-term variations of the inflow of Atlantic water. Evidence for the existence of these inflow variations was provided by a study of plankton indicator species. The variations of Atlantic inflow affected the distribution of the food for the herring, and thereby of the herring themselves. Through their effect on the distribution of feeding herring, the inflow variations also affected the choice of spawning sites. This, however, only applied in the case of recruiting year-classes.

The response of the herring to environmental variation appeared to be more complicated than expected. Older herring exhibit conservatism, and they have a tendency to repeat the same migration regardless of environmental variation. Young herring copy migratory habits from older herring and thereby continue the tradition. This conservatism tends to suppress the response of the population to environmental variation, especially in spawning and wintering migrations. Existing traditions are changed only if a recruiting year-class establishes a new spawning or wintering site. This may be the result of an unusual environmental condition that prevails only in the year when the new spawning or wintering site is first selected. Due to habit formation, the year-class returns to this position in subsequent years and passes the habit on to new generations.

As a result of conservatism, an environmental variation that lasts only for one year may affect the behaviour of the population for a much longer period. The original assumption that long-term changes in the behaviour of the herring were always caused by equally long-term changes in the environment, thus turned out to be false. Sometimes, the behaviour of the herring is more stable than the environment.

Summary

Natural variation in the distribution and abundance of North Sea herring used to be a well-known phenomenon in the days of the traditional driftnet fishery. With the advent of modern fishing methods after World War II, however, the effects of fishing started to outweigh the changes in stock size and distribution caused by variations in the environment. As a result of over-fishing in the 1960s and 1970s, the North Sea population was reduced to 1% of its original level by 1975. Rebuilding of the stock necessitated a closure of all directed herring fisheries from 1977 – 1983 and a tight system of quotas in subsequent years.

During the years of over-exploitation, research on North Sea herring was focused entirely on the effects of fishing. This pre-occupation with man-induced changes was understandable under the given circumstances. However, it led to a reduced attention for, or even a complete neglect of, the natural variability in the stock. In recent years fishery managers have started to rebuild the herring stock by stabilising fishing mortality at a low, constant level. It is unlikely, however, that such a management regime will ultimately lead to a stable stock situation. Once the man-induced effects have been brought under control, natural variation will regain its former importance. Hence it is important to re-direct part of the research on North Sea herring at natural variability. Only by recognising and understanding natural variation will we be in a position to separate fishery effects from natural variations, and to recommend appropriate management measures.

The general objective of this study, therefore, was to investigate natural variability in North Sea herring. Natural variability is a broad subject which encompasses changes in growth, survival and distribution of the fish at various stages of its life. Moreover, variability may be considered at time scales from days to decades. For practical reasons, my study had to be restricted to variability during a particular life stage, and at a particular time scale. The adult phase of the life cycle was chosen because this is the stage that is studied most easily. Commercial fisheries normally target adult herring, and changes in distribution of adult herring can be studied on the basis of catch statistics for these fisheries. As regards the time scale, the study focused on multi-annual variations, ranging from several years to several decades. These long-term variations are more important from a fisheries management perspective than short-term variations. Natural changes may occur at an even longer time scale (centuries) but such secular changes can not be studied on the basis of the data presently available.

When herring change their distribution independently from changes in the fishery or changes in stock size, they probably do so in response to a change in the

environment. If we can identify this environmental cause, we may be able to understand why the herring have changed their behaviour, and possibly even predict how long this change will last. My original assumption was that the response of the herring to an environmental variation would be proportional in time and strength to this variation. Thus, long-term changes in the distribution of the herring would have to be caused by environmental variations of an equally long duration. This was the basic assumption in the present study. Long-term changes in the hydrography of the North Sea may stem either from changes in the atmosphere or from changes in the North Atlantic. Changes in mean atmospheric conditions ("weather") that last more than a few years are called climate variations. Multi-annual changes in mean oceanic conditions are called variations in ocean climate. The specific objective of the study, therefore, was to test the hypothesis that long-term variations in the distribution of North Sea herring are caused by long-term variations either in atmospheric climate or in ocean climate.

Several natural changes in the North Sea herring during the last 50 years were investigated in detail in order to identify their environmental cause. These case studies are summarised below.

(a) Shifts in the position of spawning grounds in the western North Sea and variations in the transport rate of herring larvae in this area had earlier been ascribed to variations in Atlantic inflow into this area. However, in the absence of adequate hydrographic data on the Atlantic inflow, this hypothesis had not been tested. Using data from the Continuous Plankton Recorder Survey, I tested the hypothesis that the Atlantic inflow into this area was subject to long-term variations. I found that the abundance of two "classical" Atlantic plankton species, *Candacia armata* and *Metridia lucens*, showed variations that corresponded in time and direction with the changes in Atlantic inflow postulated to explain the shifts in spawning grounds and transport rate of herring larvae. The plankton data, therefore, support the hypothesis that long-term variations in Atlantic inflow do indeed occur. A theory was formulated that explains how variations in the strength of the Atlantic inflow, through their effect on the distribution of pre-spawning herring, can influence the position of herring spawning grounds in the western North Sea.

(b) Shifts in the position of wintering grounds from the eastern North Sea to the Skagerrak have been documented for many centuries. The periods when North Sea herring used to winter very close to the Swedish coast, sometimes for up to several decades, are known as "Bohuslän" herring periods. The last period when North Sea herring spent the winter in the Skagerrak was from 1963 to 1965. Environmental conditions during this period were analysed in order to find the factor that caused the migration into the Skagerrak. The only anomalous condition during these years was a period of sustained easterly winds at the time when the first invasion took place. This observation led to the formulation of a theory that explains both the 1963-65 Skagerrak invasion and the earlier ones. According to this theory, a period of Skagerrak invasions starts with the chance displacement of a recruiting year-class into the Skagerrak. This happens when strong easterly winds in autumn or winter drive surface water out of the Skagerrak and thereby strengthen the sub-surface counter-current into this area. If a recruit year-class is distributed near the entrance of the Skagerrak at that time, it may be transported passively into the Skagerrak. Once this has happened the year-class spends the first winter of its adult life in this area and develops a site-attachment to it. The next autumn it will return actively to the Skagerrak because of its attachment to the area. This time it will be followed by younger herring that will also develop a site attachment to the Skagerrak. By this mechanism, an anomalous condition during one autumn or winter may trigger the start of a Skagerrak herring period in which the herring for a number of years return to the Skagerrak each winter.

(c) A northward shift of herring feeding grounds was noted in the years 1988-1990. This shift coincided with a period of very mild winters. The extended northward migration of the herring was probably caused either directly or indirectly by the increased water temperatures. A direct effect may have occurred through the preference of the herring for a specific water temperature. In “warm” years, the herring will find its optimal temperature at a higher latitude than in cold years. Another explanation is that temperature affected the herring indirectly through the distribution of its food. The main food item of the herring, *Calanus finmarchicus,* is known to contract its distribution area to the north in years following mild winters. This could have forced the herring to migrate further north in search of sufficient food. On the basis of the available data it has not been possible to choose between the two explanations.

(d) An eastern distribution of feeding herring was observed in the first years after the re-opening of the fishery in the North Sea in 1983. The eastern North Sea is the normal feeding area for herring in the first months of the year before they migrate towards the western half of the North Sea. An analysis of the food supply in the eastern North Sea, based on data from the Continuous Plankton Recorder Survey, showed that the *Calanus finmarchicus* season in this area lasted longer than usual in the years 1976-1984. Instead of ending in May, the season continued until June or

July. The herring apparently had responded to the extension of the *Calanus* season by delaying the onset of their westward migration. When the *Calanus* season in the eastern North Sea shortened again after 1985, the herring responded after 1-2 years by advancing their departure from the eastern North Sea. The delayed response of the herring was attributed to the tendency of the fish to adhere to a well-established migratory habit. The hydrographic cause of the changes in the duration of the *Calanus* season could not be identified.

In only two of the four case studies above, the change in herring distribution could be attributed to a change in atmospheric conditions and thus to climate variation. The series of mild winters suggested to cause the extended northward feeding migrations in 1988-1990 was an effect of the North Atlantic Oscillation (NAO), a multi-annual variation in the mean atmospheric pressure distribution over the North Atlantic. The NAO was in an extreme, positive phase during these years, which resulted in an increased westerly circulation during winter, and a reduced cooling of surface waters. The winter invasions of herring into the Skagerrak in 1963-1965 were attributed to strong easterly winds during autumn. These winds were probably associated with the extreme, negative phase of the NAO prevailing at that time. Also the earlier periods of herring migrations into the Skagerrak since 1876 appear to have started during a negative phase of the NAO.

Although the NAO, through its effect on air circulation over the North Sea, seems to be at the root of some of the observed variations in herring distribution, it is not the sole cause of natural variability in the herring stock. Indeed, the changes in spawning area in the western North Sea were not correlated with the NAO. These changes appeared to be related to long-term variations of Atlantic inflow into the North Sea. The inflow variations were not generated by local wind stress, so they probably originated from processes elsewhere in the North Atlantic. It is possible that these distant oceanic processes are also somehow related to the NAO, but this possibility could not be further investigated within the scope of the present study. Because of their external origin, the variations in oceanic inflow cannot be simulated by hydrodynamic models of the North Sea. However, the evidence for their existence, derived from plankton indicator species, is quite strong, and it would be interesting to study them thoroughly in future by collecting more hydrographic observations.

A striking outcome of the study was that adult herring do not automatically respond to every environmental variation. Instead, they exhibit “conservatism”, i.e. they tend to adhere to routine migration patterns that were established in earlier years. Only in cases when the environmental stimulus is sufficiently strong will the fish change an existing migration pattern. After such a change, the new migration will become the standard pattern. In this way, a short but strong variation in the environment may lead to a longer change in the migratory behaviour of the fish. In many instances, recruit herring appear to copy existing migration patterns from older herring. By doing so, they turn the migratory habits of these older herring into "traditions". A new migration pattern, adopted by one year-class in response to a strong environmental stimulus, may thus be copied by subsequent generations and continue to exist after the original environmental cause has disappeared.

The conclusion of my study is that several long-term changes in the distribution of North Sea herring, recorded during the last 50 years, were related to climate variations. The herring responded to variations in atmospheric climate as well as to variations in ocean climate. The sensitivity of herring to climate variability has important implications for fisheries management. Even under conditions of constant fishing mortality, the stock will continue to show pronounced changes as a result of environmental variation. Fisheries managers have to take this natural variability into account when deciding on optimum harvest strategies and the allocation of quotas to different fleets and areas.

Haring en klimaat; veranderingen in de verspreiding van Noordzeeharing tengevolge van klimaatschommelingen

Samenvatting

Natuurlijke veranderingen in de verspreiding van Noordzeeharing zijn van oudsher een bekend verschijnsel. Vóór de Tweede Wereldoorlog, toen de visserij nog werd uitgeoefend met de traditionele vleet, verdween de haring soms jarenlang uit een bepaald gebied zonder dat dit toegeschreven kon worden aan de visserij. Omgekeerd verscheen de vis soms plotseling in een nieuw gebied, wat dan leidde tot de opbloei van een nieuwe visserij. Algemeen werd aangenomen dat deze verschijnselen veroorzaakt werden door natuurlijke veranderingen in watertemperatuur en zeestromingen, en veel onderzoekers hielden zich bezig met de speurtocht naar deze natuurlijke oorzaken.

Met de komst van moderne visserijmethoden na de Tweede Wereldoorlog begonnen de effecten van de visserij de natuurlijke veranderingen van het bestand te overschaduwen. Als gevolg van overbevissing daalde het bestand aan Noordzeeharing gestaag in de jaren 60 en 70. In 1975 werd een dieptepunt bereikt, waarbij de totale haringstand minder dan 2% bedroeg van zijn omvang kort na de oorlog. Het is begrijpelijk dat in deze jaren de onderzoekers hun aandacht bijna uitsluitend gingen richten op de effecten van visserij. Door deze eenzijdige oriëntatie op visserijeffecten verloren zij de rol van natuurlijke veranderingen echter geleidelijk uit het oog. Zelfs nadat de haringstand midden jaren 80 weer uit de gevarenzone was geraakt, bleef het onderzoek bijna uitsluitend gericht op het kwantificeren van visserijeffecten.

Nu de effecten van overbevissing de laatste jaren zijn teruggedrongen, is te verwachten dat de relatieve betekenis van natuurlijke variaties weer gaat toenemen. Deze overweging was voor mij aanleiding het onderzoek naar natuurlijke variabiliteit in Noordzeeharing nieuw leven in te blazen. Ook in de afgelopen decennia van overbevissing had de haring een aantal gedragingen vertoond die veroorzaakt leken te zijn door natuurlijke veranderingen in zee. Door hun eerdergenoemde preoccupatie met de effecten van visserij hadden onderzoekers echter weinig aandacht besteed aan deze verschijnselen. Mijn doel was een aantal van deze onverklaarde verschijnselen onder de loep te nemen en te trachten hun hydrografische oorzaak te achterhalen.

Het onderzoek richtte zich speciaal op meerjarige verschuivingen in de verspreiding van volwassen haring. Deze verschuivingen kunnen van grote invloed zijn op de visserij, en een begrip van hun oorzaken is daarom van praktisch belang. Mijn hypothese was dat veranderingen in de verspreiding van de haring, die niet toegeschreven konden worden aan effecten van de visserij, een reactie moesten zijn op hydrografische veranderingen. Verder nam ik aan dat de reactie van de haring op een hydrografische verandering evenredig zou zijn aan de duur en sterkte van die verandering. Volgens deze laatste aanname zouden meerjarige verschuivingen in de verspreiding van haring veroorzaakt moeten worden door hydrografische veranderingen die eveneens meerdere jaren besloegen. Veranderingen in de hydrografie van de Noordzee kunnen hun oorsprong vinden in de Noord-Atlantische Oceaan of in de atmosfeer boven de Noordzee. Meerjarige variaties in gemiddelde atmosferische omstandigheden (het “weer”) worden klimaatschommelingen genoemd. Analoog hieraan noemen we variaties in gemiddelde oceanografische condities schommelingen in oceanisch klimaat. Het specifieke doel van mijn onderzoek was dus het toetsen van de hypothese dat meerjarige veranderingen in verspreiding van Noordzeeharing veroorzaakt worden door schommelingen in atmosferisch of oceanografisch klimaat.

Diverse verschuivingen in de verspreiding van Noordzeeharing gedurende de afgelopen 50 jaar werden nader onderzocht met het doel hun oorzaak vast te stellen. Hieronder volgt een kort overzicht van de afzonderlijke studies.

(a) Het vermoeden bestond dat verschuivingen in de positie van paaigronden in de westelijke Noordzee samenhangen met variaties van de instroom van Atlantisch water in dit gebied. Een bewijs voor het bestaan van deze variaties was echter nooit geleverd. Gebruikmakend van gegevens van de “Continuous Plankton Recorder Survey” heb ik de hypothese getoetst dat de instroom van Atlantisch water in de noordwestelijke Noordzee onderhevig is aan meerjarige schommelingen. Het bleek dat de dichtheid van twee Atlantische planktonsoorten in dit gebied, *Candacia armata* en *Metridia lucens*, meerjarige veranderingen vertoonde die zowel in tijd als in richting overeenkwamen met de eerder op grond van haringgegevens gepostuleerde variaties van Atlantische instroom. De planktongegevens ondersteunen daarmee de hypothese dat de waargenomen verschuivingen van haringpaaiplaatsen samenhangen met variaties in sterkte van de Atlantische instroom. Het effect van de Atlantische instroom op de positie van haringpaaiplaatsen wordt verklaard door aan te nemen dat de sterkte van deze instroom de verspreiding van het voedsel in de westelijke Noordzee bepaalt, en daarmee de verspreiding van haring kort voor het paaiseizoen.

(b) Verschuivingen van het overwinteringgebied van Noordzeeharing tussen de oostelijke Noordzee en het Skagerrak zijn al eeuwenlang bekend. De tijden waarin Noordzeeharing in het Skagerrak dicht onder de Zweedse kust overwintert, staan bekend als “Bohuslänperiodes”. Dergelijke episodes duurden in het verleden gemiddeld enkele decennia. De laatste keer dat Noordzeeharing in de winter het Skagerrak binnentrok, was in de jaren 1963 tot 1965. Ik heb de hydrografische omstandigheden tijdens deze jaren onderzocht om te zien welke factor de immigratie in het Skagerrak veroorzaakte. De enige bijzonderheid die ik kon vaststellen, was een periode met abnormaal frequente oostelijke winden in het najaar van 1963; het moment dat de haring voor de eerste maal het Skagerrak binnentrok. Op grond van deze observatie werd een theorie ontwikkeld waarmee zowel de invasies in de jaren 1963-1965 als die tijdens eerdere Bohuslänperiodes verklaard kunnen worden. Aangenomen wordt dat een dergelijke episode begint doordat een nieuwe haringjaarklas tengevolge van een bijzondere samenloop van omstandigheden de aansluiting mist met het oudere deel van de populatie dat in de noordoostelijke Noordzee overwintert. Dit gebeurt doordat in de herfst, op het moment dat de nieuwe jaarklas zich nabij de ingang van het Skagerrak bevindt, een sterke oostenwind het oppervlaktewater van het Skagerrak naar buiten drijft waardoor er onder de oppervlakte een stroming ontstaat naar het Skagerrak toe. De nieuwe jaarklas wordt met deze stroming passief het Skagerrak binnengevoerd en verblijft hier vervolgens gedurende de eerste winter van zijn volwassen leven. Ik neem vervolgens aan dat de vis in deze winter een gehechtheid aan het Skagerrak ontwikkelt als gevolg waarvan hij de volgende winters actief naar dit gebied terugkeert. Het derde element in mijn theorie is dat er in deze volgende jaren ook jongere haringen van volgende jaarklassen mee zwemmen, die vervolgens ook weer een gehechtheid aan het Skagerrak ontwikkelen. Op deze wijze kan een afwijkende hydrografische situatie gedurende een enkele herfst of winter een Skagerrakperiode op gang brengen tijdens welke de haring gedurende een reeks van jaren iedere winter naar dit gebied terugkeert.

(c) In de jaren 1988-1990 werd een noordwaartse verschuiving van de voedselmigraties van de haring waargenomen. Dit verschijnsel viel samen met enkele opeenvolgende extreem zachte winters. De noordelijke trek van de haring was waarschijnlijk het directe of indirecte gevolg van de relatief hoge watertemperatuur aan het eind van de winter. Een direct effect kan veroorzaakt zijn door een voorkeur van de haring voor een bepaalde watertemperatuur. In warme jaren zal de haring deze voorkeurstemperatuur op een hogere breedtegraad aantreffen dan in koude jaren. Een andere verklaring is dat de temperatuur de verspreiding van de haring indirect beïnvloedt via de verspreiding van zijn voedsel. Het verspreidingsgebied van *Calanus finmarchicus,* het voornaamste voedsel van de haring, krimpt naar het noorden in seizoenen volgend op zachte winters. Dit kan de haring gedwongen hebben om verder naar het noorden te trekken. Op basis van de beschikbare gegevens was het niet mogelijk om een keuze te maken uit beide verklaringen.

(d) In de eerste jaren na de heropening van de haringvisserij in 1983 bleek de haring in de zomer vooral gevangen te worden in het oostelijk deel van de Noordzee. Dit is het gebied waar de haring overwintert en waar hij normaal alleen gevangen wordt in april – mei. Vanaf juni verschuift de visserij gewoonlijk naar de westelijke Noordzee, de trek van de haring volgend. Een analyse van het voedselaanbod in de oostelijke Noordzee, gebaseerd op gegevens van de Continuous Plankton Recorder Survey, liet zien dat het *Calanus finmarchicus*-seizoen in dit gebied abnormaal lang duurde in de jaren 1976-1984. In plaats van te eindigen in mei, zoals gebruikelijk is, duurde het seizoen nu tot juni of juli. Blijkbaar was dit voor de haring aanleiding zijn vertrek naar de westelijke Noordzee uit te stellen, en tijdens de maand juni te blijven foerageren in de oostelijke Noordzee. Toen het *Calanus*-seizoen in de oostelijke Noordzee vanaf 1985 weer korter werd, hield de haring nog 1-2 jaar vast aan het latere tijdstip van vertrek uit dit gebied. Deze trage aanpassing van het migratiepatroon werd toegeschreven aan conservatisme in het gedrag van de vis. De hydrografische oorzaak van de veranderingen in de duur van *Calanus*-seizoen kon niet worden achterhaald.

In slechts twee van de vier bovenbeschreven studies kon de verandering in de verspreiding van de haring worden toegeschreven aan een verandering in atmosferische condities. De serie zachte winters die beschouwd wordt als oorzaak van de noordelijke verspreiding in 1988-1990 hing samen met de Noord-Atlantische Oscillatie (NAO); een meerjarige variatie in gemiddelde luchtdrukverdeling boven de Noord-Atlantische Oceaan. De NAO verkeerde in een extreme, positieve fase gedurende deze jaren, wat leidde tot een sterke westelijke luchtcirculatie over de Noordzee en een verminderde afkoeling van het oppervlaktewater in de winter. Het binnentrekken van haring in het Skagerrak in de winters van 1963-1965 werd toegeschreven aan het frequent voorkomen van oostenwind in de herfst van 1963. Deze hoge frequentie van oostenwind hield waarschijnlijk verband met de extreme, negatieve fase van de NAO in die periode. Ook de eerdere Bohuslänperiodes sinds 1876 bleken begonnen te zijn tijdens een negatieve fase van de NAO.

Hoewel de NAO, via zijn effect op de luchtcirculatie over de Noordzee, de achterliggende oorzaak blijkt te zijn van sommige veranderingen bij de haring, is hij waarschijnlijk niet de enige klimatologische factor die het gedrag van de vis beïnvloedt. De verschuivingen van paaigronden in de westelijke Noordzee houden kennelijk verband met meerjarige variaties van de Atlantische instroom in dit gebied. De planktonindices die verondersteld worden deze instroomvariaties te weerspiegelen, zijn niet gecorreleerd met de NAO. Op grond hiervan wordt aangenomen dat deze instroomvariaties onafhankelijk zijn van de atmosferische condities boven de Noordzee en dat ze vermoedelijk gedreven worden door processen elders in de Atlantische Oceaan.

Een verrassend resultaat van het onderzoek was dat volwassen haring niet automatisch reageert op elke verandering in zijn milieu. In plaats daarvan vertoont hij “conservatisme”, d.w.z. de neiging om vast te houden aan een bestaand migratiepatroon dat in eerdere jaren is vastgelegd. Pas bij een sterke verandering in het milieu wijzigt de vis het bestaande patroon. Na zo'n aanpassing wordt de nieuwe migratie het standaardpatroon. Op deze wijze kan een korte maar intense verandering in het milieu leiden tot een langdurige verandering in het migratiegedrag van de vis. In veel gevallen blijken jonge haringen het bestaande migratiepatroon van oudere haring over te nemen. Zo kunnen migratiegewoontes van oudere haring worden omgezet in “tradities”. Een nieuw migratiepatroon, ingevoerd door een bepaalde jaarklas als reactie op een sterke, kortstondige verandering in het milieu, kan dus worden overgenomen door volgende generaties en blijven bestaan lang nadat de oorspronkelijke oorzaak verdwenen is.

De conclusie van mijn onderzoek is dat verschillende meerjarige veranderingen in de verspreiding van Noordzeeharing gedurende de afgelopen 50 jaar verband hielden met klimaatschommelingen. De haring reageerde zowel op veranderingen in atmosferisch als in oceanisch klimaat. Door conservatisme in het gedrag van de haring verliepen de aanpassingen van de migraties niet altijd synchroon met de hydrografische veranderingen. De gevoeligheid van haring voor klimaatschommelingen heeft consequenties voor het visserijbeheer. Zelfs bij constante visserijdruk zal de verspreiding van haring veranderingen blijven vertonen als gevolg van hydrografische variabiliteit. Dit kan gemakkelijk aanleiding vormen tot politieke conflicten omtrent de verdeling van de quota. Vooral nu ons klimaat de komende jaren niet alleen onderhevig zal zijn aan de gebruikelijke schommelingen maar misschien ook aan een meer permanente verandering, dienen visserijbeheerders rekening te houden met de mogelijkheid van aanzienlijke verschuivingen in de verspreiding van haring over de verschillende economische zones van landen rond de Noordzee.

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Curriculum Vitae

Adrianus Antonius Hendrikus Maria Corten werd op 17 juni 1944 in Oosterhout geboren. Na het behalen van zijn diploma hbs-B aan het Mgr. Frenckencollege te Oosterhout (1961) volgde hij een studie biologie aan de Rijksuniversiteit te Utrecht alwaar hij in 1967 zijn doctoraaldiploma verkreeg. Van 1968 tot 1971 werkte hij als assistent-deskundige voor de FAO in Sierra Leone (West Afrika). Hier deed hij onderzoek naar de omvang van pelagische visbestanden. In 1971 trad hij in dienst van het Rijksinstituut voor Visserijonderzoek (RIVO) te IJmuiden, waar hij gedurende 24 jaar de leiding had van het onderzoek aan haring en andere pelagische vissoorten. Sinds 1998 verricht hij namens het RIVO onderzoek aan pelagische vissoorten in het West-Afrikaanse land Mauritanië.