SPAWNING MIGRATION OF NORWEGIAN SPRING SPAWNING HERRING (*CLUPEA HARENGUS* L.) IN RELATION TO POPULATION STRUCTURE

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Where and when do they spawn?

DR. SCIENT. THESIS

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PREFACE

The fishery and its management is like all other catch activities dependent on knowledge of the animal's mode of living. The questions of where and when to find the fish have circulated for centuries. In earlier periods the fishermen were prevented from exploring the open seas, due to the condition of their boats and fishing equipment. Thus, during these periods it was particularly important for them to know the times and areas at which fish were occurring in coastal waters. Throughout centuries the coastal communities in Norway developed based on the knowledge of where and when the herring and other fish occurred along the coast. In general, the herring aggregated in certain areas along the Norwegian coast and at certain times of the year, especially in connection with the spawning in winter. However, the migration patterns of the herring was not always to be relied on, as indicated by the following quotations (after Rollefsen 1966).

> *'It comes up to the shore here from the great fish pond which is the Icelandic Sea, towards the winter when the great part of other fish have left the land. And the herring does not seek the shore along the whole, but at special points which God in his Good Grace has found fitting, and here in my days there have been two large and wonderful herring fisheries at different places in Norway. The first was between Stavanger and Bergen and much further north, and this fishery did begin to diminish and fall away in the year 1560. And I do not believe there is any man to know how far the herring has travelled. For the Norwegian Books of Law show that the herring fishery in the most northern part of Norway has continued for many hundreds of years, although it may well be that in punishment for the unthankfulness of men it has moved from place to place, or has been taken away for a long period.'*
>
> **Clergyman Peder Claussøn Friis (1545-1614)**

> *'This fish is also very often used for fodder for cattle, which eat of it with great appetite, and has thus in many ways done more for the prosperity of the land than might readily be imagined. But as the herring now begins to fall away, and comes each year later than the year before, it is to be feared that it will with time desert our coast completely, and will find another way.'*
>
> *'This prophecy has since been fulfilled, as there has been no spring herring in this place since the year 1756. It is true that is has been seen in later years in the sea and off the coast, but it has been unwilling to turn into our shores, and has passed us and gone further to the south. After visiting our shores each year for twenty years it has taken leave of us and turned to our neighbours.'*
>
> **Clergyman and naturalist Hans Strøm (1726-1797)**

During the present century it was confirmed that the herring aggregating along the Norwegian coast in winter belong to the Norwegian spring spawning herring stock, which together with the Icelandic spring and summer spawners form the Atlanto-Scandian herring group. The Norwegian spring spawning herring is known as one of the largest fish stocks in the world, which may cover large parts of the north-eastern Atlantic migrating between nursery areas, feeding areas, wintering areas and spawning areas. However, the stock size has fluctuated and the migration pattern has varied over the years. One may say that this herring stock moves in mysterious ways. Despite extensive research efforts on this stock in the past, there exist no definite explanations to its migration behaviour. Thus, studies on the migrations of Norwegian spring spawning herring are still relevant, and will probably be so for many years ahead.

In the present thesis I aim to increase the knowledge of factors influencing the spawning migration of Norwegian spring spawning herring. I hypothesise that both the time and location of spawning is influenced by the following aspects of population structure: the age and length composition, the composition with respect to nursery area of origin, and composition with respect to body condition (amount of energy reserves). The main period of my analyses is the 1990s, when spawning migration have commenced from the wintering area in the Vestfjord system, northern Norway (68°N), towards the spawning grounds situated between 58°and 70°N.

I thank the Norwegian Research council for funding my work. I also thank the Institute of Marine Research (IMR), Bergen for providing a nice environment for work, for providing help from permanent staff and for additional economical support. I thank all the staff at the Pelagic Division for their friendship and support.

Due to the needs of my study the number of biological herring samples was increased significantly compared to IMR's regular sampling. In addition, weighing of gonads was included as a new measure. Consequently this resulted in a significant amount of extra work for the technicians involved in the measurements of the data. Nevertheless, these people did an amazing job, and they showed an interest, support and encouragement, which I really admire. Thus, I would like to emphasise that this thesis is a product of the efficient and accurate work of IMR's skilled technicians, to whom I am most grateful.

I thank my supervisors Arne Johannessen at the Department of Fisheries and Marine Biology, University of Bergen, and Ingolf Røttingen and Olav Sigurd Kjesbu at IMR, for their valuable help and support during my study period. I am especially grateful to Arne Johannessen who has been my supervisor since I started my Cand. Scient. studies in 1991. He has always kept his door opened and

been very supportive with respect to my work in all these years. In addition he encouraged me during a period of unemployment, and I was dependent on his help to get funding from the Norwegian Research Council.

I thank my co-authors Jens Christian Holst and Øyvind Fiksen. I also thank Jens Christian Holst and Reidar Toresen for comments in connection with the synthesis of my work.

I am also indebted to 'Skaarfish Group A/S' for providing data on herring fat content and for collecting samples of herring from commercial catches, and to 'The Norwegian Sales Organisation for Pelagic Fish' for providing data on herring fat content and fishery statistics with respect to size group composition.

Finally, I thank my family for the support and understanding during this period. I especially thank my wife, Kjersti, who has been alone with family obligations in periods, particularly during the last year of my thesis, when I worked at all days and at all hours.

Bergen, October 1998

Aril Slotte

Aril Slotte

TABLE OF CONTENTS

LIST OF PAPERS

This thesis is based on the following six papers, which will subsequently be referred to by their Roman numerals.

Paper I. Slotte, A. Differential utilisation of energy during wintering and spawning migration in Norwegian spring spawning herring (*Clupea harengus* L.). *Journal of Fish Biology*. In press.

Paper II. Slotte, A., Johannessen, A. & Kjesbu, O. S. Effects of fish size on spawning time in Norwegian spring spawning herring (*Clupea harengus* L.). Submitted manuscript.

Paper III. Holst, J. C. & Slotte, A. Effects of juvenile nursery on geographic spawning distribution in Norwegian spring spawning herring (*Clupea harengus* L.) *ICES Journal of Marine Science*. In press.

Paper IV. Slotte, A. & Johannessen, A. Biological characteristics of Norwegian spring spawning herring (*Clupea harengus* L.) south of N°61. Submitted manuscript.

Paper V. Slotte, A & Fiksen, Ø. The spawning migration of Norwegian spring spawning herring (*Clupea harengus* L.): a state-dependent trade off? Submitted manuscript.

Paper VI. Slotte, A. Effects of fish length and condition on spawning migration in Norwegian spring spawning herring (*Clupea harengus* L.). Submitted manuscript.

INTRODUCTION

IDENTIFICATION OF NORWEGIAN SPRING SPAWNING HERRING

This thesis addresses the Norwegian spring spawning herring stock (*Clupea harengus* L.), which together with the Icelandic spring and summer spawning herring form the Atlanto-Scandian herring group (JOHANSEN 1919; DRAGESUND & al. 1980). The Norwegian spring spawning herring is known as one of the largest fish stocks in the world, which may cover large parts of the north-eastern Atlantic migrating between nursery areas, feeding areas, wintering areas and spawning areas. However, the herring fishery has fluctuated since the 15th century corresponding with fluctuations in stock size (LØBERG 1864; BOECK 1871; SARS 1879; HJORT 1914; LEA 1930), and also the migration pattern has varied with years. Spawning has occurred at a variety of locations along the Norwegian coast at a range of approximately 1500 km from 58°N to 70°N (RUNNSTRØM 1941a, b; DEVOLD 1963, 1968; DRAGESUND 1970a; DRAGESUND & al. 1980, 1997; RØTTINGEN 1990, 1992; JOHANNESSEN & al. 1995; SLOTTE & DOMMASNES 1998). The larvae hatched along the Norwegian coast will drift northwards along with the coastal current to nursery areas in fjords and in the Barents Sea, and the adolescent herring leave the nursery areas and enter the Norwegian Sea 1-2 years prior to first spawning, generally at age 2-4 years dependent on the growth rate (LEA 1929 a, b; RUNNSTRØM 1936; DRAGESUND 1970a, b; DRAGESUND & al. 1980). Feeding has occurred off the Norwegian coast and westwards into the Norwegian Sea and into Icelandic waters at high stock levels, and in Norwegian coastal waters at low stock levels (DEVOLD 1963; DRAGESUND & al. 1980, 1997). The known wintering areas of the present century have been situated in open waters of the Norwegian Sea prior to 1970 (DEVOLD 1963, 1968; DRAGESUND & al. 1980), and in Norwegian coastal waters and fjords in subsequent years (DRAGESUND & al. 1997; HAMRE 1990; RØTTINGEN 1990, 1992). During summer feeding in the Norwegian Sea the Norwegian spring spawners may mix with Icelandic spring spawners (FRIDRIKSON & AASEN 1952). However, due to different growth patterns (FRIDRIKSSON 1944, 1958), age composition (JAKOBSSON 1965; ØSTVEDT 1965) and spawning areas (FRIDRIKSON & AASEN 1950, 1952; FRIDRIKSSON 1955) the Norwegian spring spawners and the Icelandic spring spawners have been separated and regarded as two distinct stock units. In addition, Norwegian spring spawning herring differ phenetically (JOHANNESSEN & JØRGENSEN 1991) and genetically (JØRSTAD & PEDERSEN 1986) from local Norwegian fjord herring stocks. It differs phenetically (RYMAN & al. 1984; JOHANNESSEN & JØRGENSEN 1990) from populations in the North Sea, Skagerak, Kattegat and the Baltic Sea, whereas there appears to be little genetic difference between these stocks based on electrophoretic analyses (RYMAN & al. 1984; JØRSTAD & al. 1991). However, JØRSTAD & al. (1991) suggest that genetic differences are likely to be found if more comprehensive studies with use of new techniques, as mitochondrial DNA analysis, are carried out in the future.

FLUCTUATIONS IN FISHERY AND ABUNDANCE

For centuries one of the mysteries in Norwegian waters was the unforeseen fluctuations in the winter fishery of herring along the Norwegian coast. Løberg (1864) summarised the fluctuations in the fishery from the 15th century to the 18th century. He also referred to reports of herring fisheries from the 9th century throughout the 14th century. However, it was first during the 15th century, when the process of salting and storing of herring became common, that the herring fishery started to progress significantly. Løberg reported that the herring disappeared from the coast from after 1567, and that the fishery didn't start until the first part of the 17th century. The herring disappeared again during the period 1650-1700. There was a significant fishery from the beginning of the 18th century, and the years between 1740 and 1760 were particularly rich, but after 1784 the herring were once more absent at the coast. The subsequent herring period was between 1808 and 1873 (LØBERG 1864; BOECK 1871; SARS 1879; HJORT 1914). In 1904 a large year class of herring was born (HJORT 1914), which contributed to a very rich herring fishery in the years to come (LEA 1930; RUNNSTRØM 1941a; Devold 1963) (Fig. 1). The spawning stock biomass during the 1930s and 1940s was between 10 and 20 million tonnes (Reidar Toresen, Institute of Marine Research Bergen, Norway, unpublished data). However, in the late 1960s there was a severe decline in stock abundance of Norwegian spring

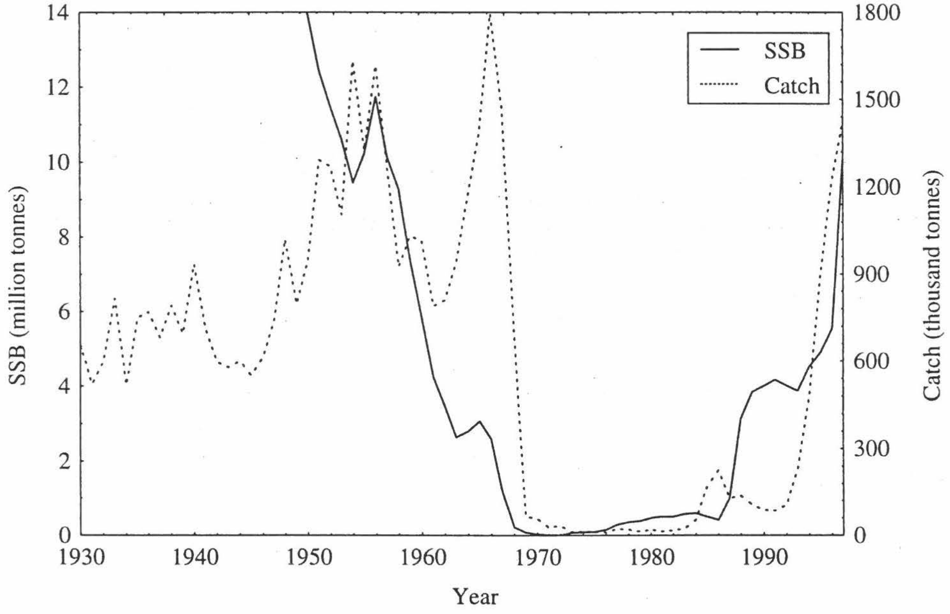

Fig. 1. Total catch of Norwegian spring spawning herring during 1930-98, data from DRAGESUND & al. (1980) ANON. (1998), and spawning stock biomass (SSB) during 1950-98, data from ANON. 1998.

spawning herring due to high fishing pressure and low recruitment (DRAGESUND & al. 1980). The development of the stock was closely monitored after 1970, with use of tagging experiments and research surveys. In 1970 the fishery of small herring was banned, and also in 1972 a total ban on the fishery of adult herring was introduced. The stock remained at a low level until a new strong year class was born in 1983 (HAMRE 1990; RØTTINGEN 1990). Based on this year class the strong 1991 and 1992 year classes developed (DRAGESUND & al. 1997), and the present spawning stock has once again reached a level of 10 million tonnes in 1997 (ANON. 1998).

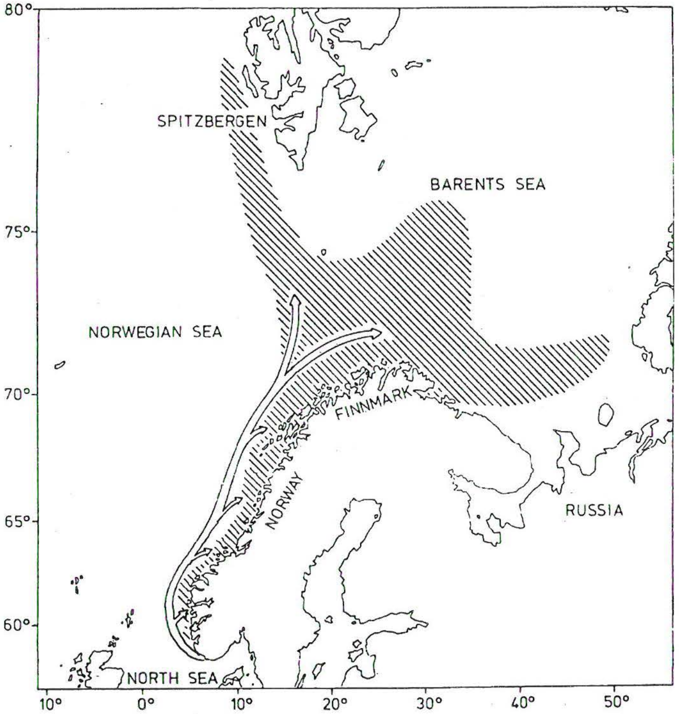

Fig. 2. Drift routes of Norwegian spring spawning herring larvae and adjacent nursery areas (hatched areas). Modified from DRAGESUND & al. (1980).

LIFE HISTORY MIGRATIONS

SARS (1879) was the first to succeed in describing the life history migrations of the herring found along the Norwegian coast. He suggested that these herring stayed in areas of the open sea between Norway, Iceland and Scotland and fed mainly on copepods until they became mature at about 6 years of age, after which they would migrate to the spawning grounds along west coast of Norway. He further suggested that the larvae drifted northwards with the current. LEA (1929b) made new discoveries in the life history of the herring. He found that the herring progeny grew up in coastal waters to the north of the spawning grounds, and at a certain age they left the nursery grounds to go through an oceanic stage prior to the first spawning. Later studies have proved that not all of Lea's conclusions were correct, i.e. the distribution of the 0-group herring is more widespread, ranging from fjords and coastal areas to the open ocean of the Norwegian Sea and Barents Sea (DRAGESUND 1970a, b; DRAGESUND & al. 1980; HAMRE 1990) (Fig. 2). However, these authors agree with Lea that the herring leave the nursery areas to enter the Norwegian Sea 1-2 years before it spawns for the first time, generally at age 2-4 dependent on the growth rate.

The spawning of Norwegian spring spawning herring has traditionally occurred along the Norwegian coast from 58°N to 70°N within five major areas: Lofoten (area 05), Træna-Haltenbanken (area 06), Møre (area 07), Sogn-Hordaland (area 28) and Rogaland (area 08) (Fig. 3). However, the relative importance of the different grounds has changed with time. RUNNSTRØM (1941a) regarded the grounds south of Møre, particularly the ones to the west and south off the island of Karmøy, as the most significant in the 1930s and also in former periods of rich herring fisheries. Between 70 and 80 % of the landings during the first three decades of this century came from the southern grounds (RUNNSTRØM 1941b; RØTTINGEN 1990). Spawning grounds off the Møre district were used regularly during this period, whereas grounds north of Møre seemed to be used for few seasons only and were considered insignificant. The southern grounds were also important in the late 1940s and onwards, but gradually the spawning moved more northwards in the last years of the period 1946-1958 (DEVOLD 1963). After 1959 the southern grounds were not utilised, whereas significant numbers of yolk sac larvae north of the main fishing areas at Møre indicated that banks north of Møre and even off the Lofoten islands were important in the early 1960s (DRAGESUND 1970a). In 1963 a stock unit commenced spawning off Lofoten, and feeding and wintering in open seas to the north of Lofoten close to Bear Island (DEVOLD 1968; JAKOBSSON 1968). However, in summer 1966 this unit joined the main part of the stock wintering to the east of Iceland and spawning off Møre (Fig. 4a).

Corresponding with the severe stock decline in the late 1960s, the herring changed its feeding and wintering areas and hence migrations. Oceanic nursery, feeding and wintering areas were abandoned and the entire life cycle was spent in Norwegian coastal waters and fjords (DRAGESUND & al. 1980; RØTTINGEN 1990; HAMRE 1990). When the strong 1983 year class recruited to the spawning stock the herring commenced wintering in the Vestfjorden area (area 00), northern Norway (RØTTINGEN 1992), while the feeding area was extended westwards in the Norwegian sea (DRAGESUND & al. 1997) (Fig. 4b). When spawning for the first times in 1987 and 1988, the 1983 year class mainly utilised the grounds off Møre (RØTTINGEN 1990). In 1989 a small fraction of the spawning stock, predominated by the 1983 year class, appeared at the spawning grounds off Karmøy for the first time in 30 years (RØTTINGEN 1989). A fishing ban for herring was introduced in the areas south of 61°N in1989, as the reappearance of Norwegian spring spawning herring at the southern grounds was considered important with regard to rebuilding of the stock (RØTTINGEN & SLOTTE 1998). However, the fraction spawning at the southernmost grounds remained at a low level (< 4 % of the spawning stock) in the period 1990-98 (JOHANNESSEN & al. 1995; RØTTINGEN & SLOTTE 1998). When the spawning stock increased with the recruitment of the strong 1991 and 1992 year classes, spawning herring were also distributed at the northernmost grounds off Lofoten (DOMMASNES & HAMRE 1996a, b; SLOTTE & DOMMASNES 1998). In addition, the feeding areas was extended further westwards in the Norwegian Sea towards Icelandic waters (Fig. 5).

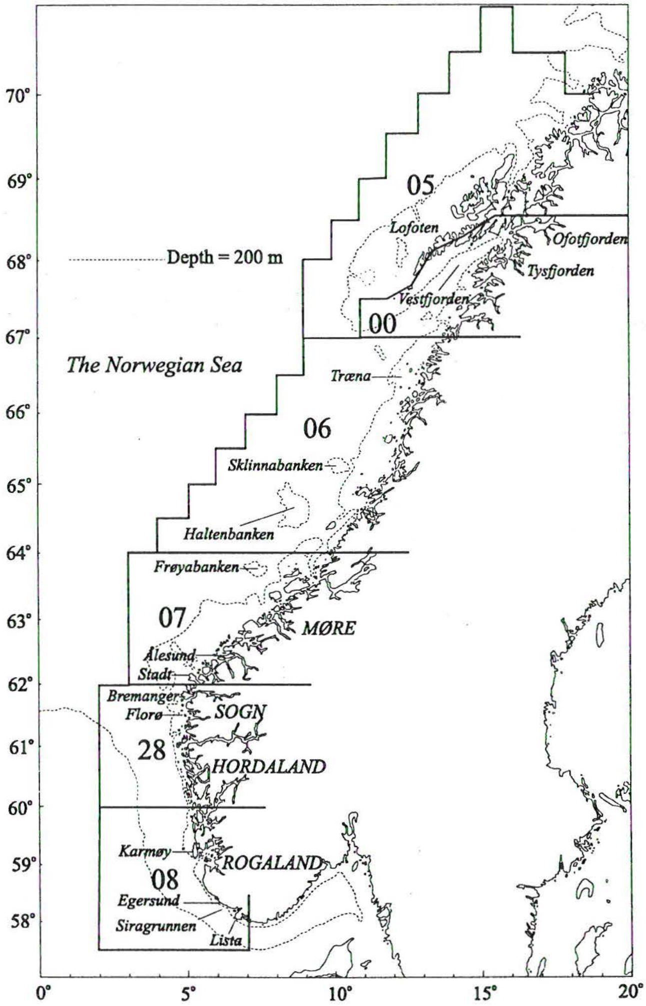

Fig. 3. Map of the Norwegian coastline with statistical areas (two digits), and important herring districts (capitals) and locations.

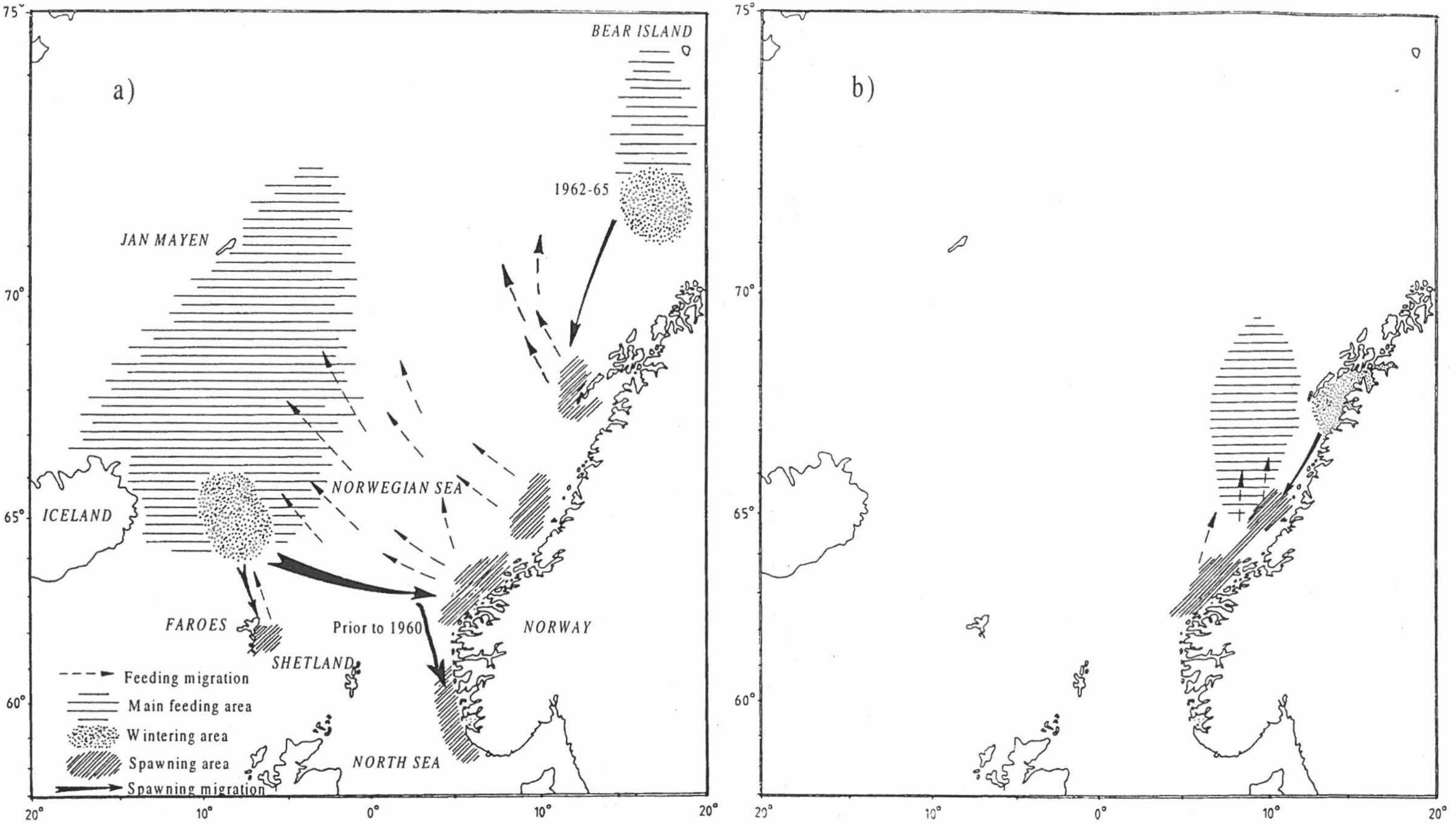

Fig. 4. a) Migration pattern 1950-1970, modified from Dragesund & al. (1980). b) Migration pattern of the 1983-year class in 1988, modified from Røttingen (1990).

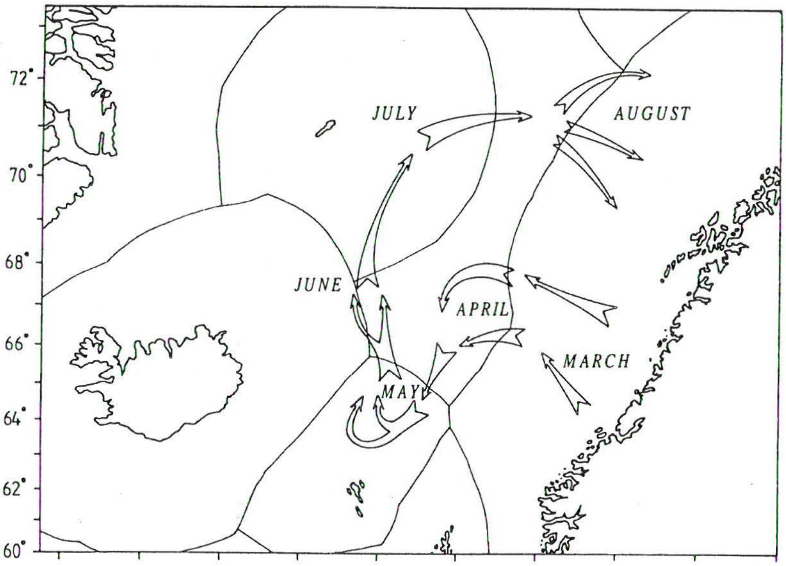

Fig. 5. Feeding migration of Norwegian spring spawning herring in 1995. Modified from ANON. (1995). A similar migration pattern was observed in 1996 (ANON. 1996).

SPAWNING MIGRATION IN RELATION TO ENVIRONMENTAL CONDITIONS

Herring have demersal eggs laid during all months of the year in a wide range of environments from the deeper part of the continental shelf to the intertidal zone and in a wide range of salinities and temperatures between latitudes 35°N and 70°N (BLAXTER 1985). However, within a population the environmental preferences favouring the survival of eggs and larvae may be specific, leading to spawning at specific times and locations (HAEGELE & SCWEIGHERT 1985). Correspondingly, the maturation rate or spawning time is found to increase with observed temperatures in herring, which is suggested to be an adaptive characteristic selected to provide the best match of emerging larvae to available food organisms in spring plankton blooms (HAY 1985; WARE AND TANASICHUCK 1989) in accordance with the match-mismatch hypothesis (CUSHING 1990). Also the spawning time in herring may be influenced by tidal and lunar phases, which could have selective advantages (HAY 1990).

In Norwegian spring spawning herring, stony or rocky bottom and depths less than 250 m are preferred for spawning (RUNNSTRØM 1941b; DRAGESUND 1970a). Such suitable locations are distributed at a range of approximately 1500 km along the Norwegian coast between 58°N and 70°N. Traditionally, the most important spawning grounds are banks and shelf areas from north towards south at Lofoten, Træna, Sklinnabanken, Haltenbanken, Frøyabanken, and off the districts of Møre, Sogn, and Rogaland (see Fig. 3). All these spawning grounds are located within the coastal current allowing larvae to drift northwards to nursery areas along the coast and in the Barents Sea (DRAGESUND 1970a).

For centuries the relative importance of the different spawning grounds of Norwegian spring spawning herring has varied. This is evident from fluctuations in fisheries along the coast from the 15th century to the 1920s (LØBERG 1864; BOECK 1871; SARS 1873; HJORT 1914; LEA, 1930) and from more direct investigations on the spawning grounds in the 1930s and onwards (RUNNSTRØM 1941a, b; DEVOLD 1963; DEVOLD 1968; DRAGESUND 1970a; DRAGESUND & al. 1980; RØTTINGEN 1990; DRAGESUND & al. 1997; SLOTTE & DOMMASNES 1998). In addition the time of arrival and spawning has also varied between periods and spawning areas (RASMUSSEN 1939; RUNNSTRØM 1941a, b; AASEN 1962; DRAGESUND 1970a; JOHANNESSEN & al. 1995). These variations in location and time of spawning were to some extent influenced by variations in temperature and salinity (JENSEN 1881; BUCH 1883; HJORT 1895; RUNNSTRØM 1941b; DEVOLD 1963). However, the environmental factors do not entirely explain the dynamics of the spawning migration.

SPAWNING TIME IN RELATION TO POPULATION STRUCTURE

In previous times the herring along the Norwegian coast were separated into two groups based on arrival time and maturity. BOECK (1871) was the first scientist assigned by the government to study the herring along the Norwegian coast. He found that there were two main categories of herring: the "large herring" with maturing gonads, occurring at the west and north coast in November-December and leaving in January, and the "spring herring" with running gonads, occurring at the south western coast in February. This suggestion was later supported by race investigations performed by BROCH (1908), JOHANSEN (1919), SCHNAKENBECK (1931), RUNNSTRØM (1933, 1937, 1941a), who found that the "large herring" and "spring herring" differed in vertebral number. While Scnakenbeck came to the conclusion that these were two distinct races, Runnstrøm suggested that these were components of the same stock which simply had different spawning areas. However, as the "large herring" arrived later each year from the beginning of this century and onwards, the "large herring" and "spring herring" became more and more mixed to the extent that they were impossible to distinguish (AASEN 1962; DEVOLD 1963), and since the 1950s these terms have not been used.

On the other hand several studies on both Norwegian spring spawning herring and other herring stocks have demonstrated that the time of arrival at spawning grounds and spawning time are influenced by the population structure. Based on data of Norwegian spring spawning herring collected prior to the severe stock decline in the late 1960s, the recruits were found to spawn progressively later in the season than the older repeat spawners (LEA 1929a; RASMUSSEN 1939; RUNNSTRØM 1941a, b; DRAGESUND 1970a). After reanalysing data from RUNNSTRØM (1941a, b), LAMBERT (1987) concluded that herring spawned in a decreasing order of age, suggesting that also among repeat spawners there was a difference in spawning time between age groups. LAMBERT & MESSIEH (1989) found a similar relationship between fish length and spawning time in Atlantic herring from Canadian waters. Studies of WARE & TANASICHUK (1989, 1990) gave more support to the hypothesis of herring spawning in a decreasing order of size. They claimed that Pacific herring (*Clupea harengus pallasi*) initiate maturation at the same time regardless of fish weight, while the instantaneous maturation rate increases with fish weight and thus resulting in earlier spawning in larger fish. WARE & TANASICHUK (1989) also concluded that wave spawning in the Pacific herring is based upon the size dependent maturation rate. Both Atlantic (LAMBERT 1987 and references therein; LAMBERT & MESSIEH 1989) and Pacific (HAY 1985; WARE & TANASICHUK 1989) herring are observed to spawn in up to four waves. LAMBERT (1987) and LAMBERT & MESSIEH (1989) found also that the number of spawning waves is reflected by the number of age modes or length modes in the reproductive stock. WARE & TANASICHUK (1989) concluded that size-dependent maturation rate will result in a progressively earlier spawning as a herring ages. They suggested that this may enhance an individual's fitness over its reproductive life-span, because of interannual uncertainties in food supply, predation pressure and density-dependent interactions. This is analogous to the hypothesis that the recruitment success is likely to improve if the fish spawn in waves (HAY 1985; WARE & TANASICHUK 1989; LAMBERT 1990).

SPAWNING MIGRATION IN RELATION TO JUVENILE NURSERY

Another aspect of population structure that may influence the spawning time and spawning distribution of Norwegian spring spawning herring, is the composition of growth components. The distribution of the 0-group herring is widespread, ranging from fjords and coastal areas to the open ocean of the Norwegian Sea and the Barents Sea (DRAGESUND 1970a, b; DRAGESUND & al. 1980; HAMRE 1990; DRAGESUND & al. 1997). The large range of temperature and ecological regimes experienced by the juveniles is reflected in differences in growth patterns throughout their geographic range. As a rule, the growth rate decreases northwards, and consequently individuals from the coastal nurseries mature at a younger age than individuals from the Barents Sea. The heterogeneous growth structure of the Norwegian spring spawning herring stock was subject to investigations early in this century (LEA 1929a, b; OTTESTAD 1934; RUNNSTRØM 1936). These studies indicated that the herring leave the nursery areas to enter the Norwegian Sea 1 or 2 years prior to first spawning, generally at age 2-4 years dependening on the growth rate. LEA (1929a, b) found that the herring along western Norway left the coastal waters at a mean age of 3 years in order to recruit to the adult stock feeding offshore, whereas the mean age at recruitment exceeded 4 years farther north. RUNNSTRØM (1936) studied the spawning rings in herring scales and found that herring of the southern type spawned for the first time at age 3-6 years with the main proportion spawning at age 4-5 years, while the ages of the northern type was 4-8 years and 5-6 years, respectively. In addition, RUNNSTRØM (1941a) found that the immature herring of northern Norway (north of 64°N) mainly comprised herring of the northern type, and that this proportion decreased southwards along the coast. Similarly, within the mature and spawning herring, he found that the northern type was more predominant in the northern districts, while both growth types were more equally represented in the southern district.

REPEAT SPAWNING AT SAME SPAWNING GROUNDS (HOMING)

If the environmental conditions are satisfactory for a given range of spawning grounds, then homing is generally accepted as the main factor influencing the geographical spawning distribution in herring (HOURSTON 1982; WHEELER & WINTERS 1984). Tagging experiments on Pacific herring (HOURSTON 1982) and Atlantic herring (WHEELER & WINTERS 1984) have demonstrated high return rates to specific spawning grounds. This has led to a general consensus that the herring maintains population integrity and persistence by repeatedly returning to spawn (i.e. home) with high precision at specific spawning grounds (MCQUINN 1997). Tagging experiments on two spawning components at low stock levels in the 1970s, also indicated that Norwegian spring spawning herring may have high homing rates (DRAGESUND & al 1980; HAMRE 1990; HOLST 1991). However, the overall impression is that the geographical spawning distribution of this stock is highly dynamic and involves a considerable degree of straying between spawning grounds along the Norwegian coast (RUNNSTRØM 1941a, b; DEVOLD 1963; DEVOLD 1968; DRAGESUND 1970a; DRAGESUND & al. 1980; DRAGESUND & al. 1997; HAMRE 1990; RØTTINGEN 1990, 1992). In fact from tagging experiments there is also evidence of some trans-oceanic straying from spawning grounds off western Norway to south west Icelandic spawning grounds and vice versa (FRIDRIKSON & AASEN 1950, 1952; FRIDRIKSSON 1955), and from spawning grounds off western Norway to spawning grounds off the Faroes (JAKOBSSON 1970). In addition, herring tagged off the west coast of Norway have been recovered in the North Sea and Skagerak (FRIDRIKSON & AASEN 1952; AASEN 1954). Thus, the precision of homing to particular spawning grounds does not appear to be a crucial factor in the life history strategy of this stock. This is also emphasised with respect to the relation between geographical spawning distribution and stock size.

RELATIONS BETWEEN STOCK SIZE AND STRAYING

There is a clear relationship between stock level and straying in Norwegian spring spawning herring. When the stock increases, the feeding areas and spawning areas are expanded (DEVOLD 1963; DRAGESUND 1970a; DRAGESUND & al. 1980; DRAGESUND & al. 1997; HAMRE 1990; RØTTINGEN 1990, 1992). LINDSEY & al. (1959) suggested that some straying in fish may have selective advantages, since individuals invading new areas may obtain more resources and thereby have more viable offspring. The importance of straying for colonisation of new habitats has later been emphasised in other studies (QUINN 1984; OLIVIERI & al. 1990; QUINN & DITTMAN 1990). There is an inverse relationship between survival of eggs and egg density in herring (RUNNSTRØM 1941b;

TAYLOR 1971; GALKINA 1971; HOURSTON & ROSENTAL 1981), and also reduced density of spawning products may reduce competition for food among larvae (KIØRBOE & al. 1988). Thus, when the size of a herring stock increases, straying to other spawning grounds should be advantageous.

THE STATE-DEPENDENT MIGRATION HYPOTHESIS

In life history theory it is assumed that the process of selection favours those genotypes which have age-specific schedules of growth, fecundity and mortality that generate the highest lifetime reproduction (lifetime fitness) (SHAFFER 1979; CHARLESWORTH 1980; SIBLY & CALOW 1986), i.e. variable or unpredictable adult mortality rates select for reproduction early in life, while high, variable or unpredictable juvenile mortality rates select for delayed reproduction and longer adult life. However, there are constraints that limit the capacity of the fish to achieve these demographic characteristics simultaneously. The resources available for allocation are finite and limited, as the feeding processes and structures themselves are limited. The resources used in one aspect of metabolism will not be available for use in others; the concept of trade-off constraints (SIBLY & CALOW 1983). For example, energy used to improve locomotion, which should improve the ability to escape from predators or the migration potential, will not be available for reproduction. This could have negative effects on maturation and fecundity. The incorporation of the trade-off constraint concept was important in the development of life history theory (SCHAFFER 1974 a, b, 1979; SCHAFFER & ROSENZWEIG 1977). The extended theory assumes that at each age, an individual fish can allocate a part of its total energy resources to reproduction; the reproductive effort. It is assumed that an increase in reproductive effort will result an increased number of progeny, whereas the probability of surviving until next spawning will decrease. Thus there must be trade-offs between reproductive investment and survival. The traditional life-history theory do not account for changes in the motivation of organism, it is only based on the animals age or size. MCNAMARA & HOUSTON (1986, 1996) and MANGEL & CLARK (1986, 1988) introduced dynamic modelling, which made it possible to model behaviour that depends on the internal state of the animal, suggesting that animals have state-dependent life history strategies. The approach assumes that the differences in behaviour over a time period result in different values of the state variable at the end of the period, which in turn result in different levels of reproductive success in the future.

In anadromous fish there is a link between homing and life history strategy. Anadromous fish are found to home to natal rivers with high precision (HARDEN JONES 1968; NORTHCOTE 1984; THORPE 1988). The upstream migrations involve significant energy losses, and the rate of tissue depletion (relative energy loss) is generally highest in smaller individuals (GLEBE & LEGGETT 1981a, b; JONSSON & al., 1997). GLEBE & LEGGETT (1981a, b) found that semelparous shad use 70-80% of their total energy resources (including release of spawning products) during a spawning run, while iteroparous shad use only 40-60%. A similar pattern was found in other anadromous species (several salmon and shad stocks), in which semelparous fish use more than 70 % of their energy resources, while iteroparous fish use less than 60 %. The significant energy loss involved in upriver migrations is reflected in the life history strategies of these fishes. The largest individuals of the American smelt, (*Osmerus mordax*) (MCKENZIE 1964), Atlantic salmon (*Salmo salar* L.) (KALLIO-NYBERG & PRUUKI 1990) and anadromous brown trout (*Salmo trutta*) (L´ABÉE-LUND 1991) are observed to travel further upstream to spawn than smaller conspecifics. In addition fish size and age have been observed to correlate with the total length of the home river in both salmon (SCHAFFER & ELSON 1975; POWER 1981; THORPE & MITCHELL 1981; SCARNECCHIA 1983) and anadromous brown trout (L´ABÉE-LUND 1991). The fish size is also found to increase with river harshness in salmon (SCHAFFER & ELSON 1975), American shad, *Alosa sapidissima,* (GLEBE & LEGGETT 1981b) and brown trout (JONSSON 1985). Obviously migration distance and river discharge are two major factors determining the energy used to reach the spawning grounds. Thus, SCHAFFER (1979) suggests that increasing rivers lengths and increasing current velocities would favour the selection of larger fish with a high amount of energy reserves. In other words, fish homing to these harsh and large rivers, spend more years in the sea before maturing. Similarly, migratory Arctic charr, *Salvelinus alpinus*, mature at older ages, have higher fecundity and greater longevity than stationary charr (TALLMAN & SAURETTE 1996).

A possible strategy in herring towards repeat spawning at the same spawning grounds every year, seems to be in conflict with life history theory. With respect to the above mentioned studies of life history strategies in anadromous fish and of state-dependent life history strategies in general, such a strategy is not likely to increase the lifetime fitness of an individual. Norwegian spring spawning herring are highly iteroparous fish, which may live for more than 20 years and spawn up to 15 times. Thus, in order to secure a high lifetime fitness, these herring must utilise the available energy in a more conservative way than do anadromous fish. This, could imply trading off energy by reducing the distance migrated to a spawning ground and/or reducing gonad investment. In principle the present spawning migration of Norwegian spring spawning herring is analogous with the upriver spawning migration of freshwater and anadromous fish. The herring may choose between suitable spawning grounds located in the vicinity of the starting point of the migration, the wintering area in northern Norway, and southwards along the coast at a range of approximately 1500 km. In addition, the track of the southward spawning migration of this stock follows the topography of the Norwegian continental slope, while the large scale direction of the Norwegian coastal current is in the opposite direction at depths down to 150 m, at a maximum speed of up to 100 cm $\cdot$ sec^{-1} and at an average speed of 15-40 cm $\cdot$ sec^{-1} (AURE & ØSTENSEN 1993). Given the significant differences in migration distance to the different spawning grounds, it seems likely that the migration behaviour of herring, analogous to fish migrating in rivers, also could be influenced by energetic constraints, i.e. state dependent migrations. This is consistent with the fact that the metabolic rate in general decreases with body size (WINBERG 1956, 1961) and that optimal swimming speed, defined as the velocity at which the total energy expenditure per unit distance travelled is minimal, increases with the fish size (Ware 1975, 1978). In addition herring commonly do not feed throughout the wintering and spawning season (Iles 1964; Parsons & Hodder 1975; Crawford 1980; Bradford 1993a), thus during this period they suffer a distinct energy depletion (Milroy 1906; Bruce 1924; Channon & Saby 1932; Lovern & Wood 1937; Leim 1957; Wood 1958; Iles & Wood 1965; Ackman & Eaton 1976; McGurk & al. 1980; Almatar 1989; Henderson & Almatar 1989). State-dependent migration constraints could cause deviation from homing in Norwegian spring spawning herring in two major ways. First, small fish or fish in bad condition may not be able to home to a particular spawning ground, and instead spawn in suitable areas within a shorter migration distance from the wintering grounds. Second, large fish and fish in good condition are better fit for long migrations and are therefore more likely to stray towards grounds at a farther migration distance from the wintering area, in search for areas with lower fish densities or more profitable environmental conditions.

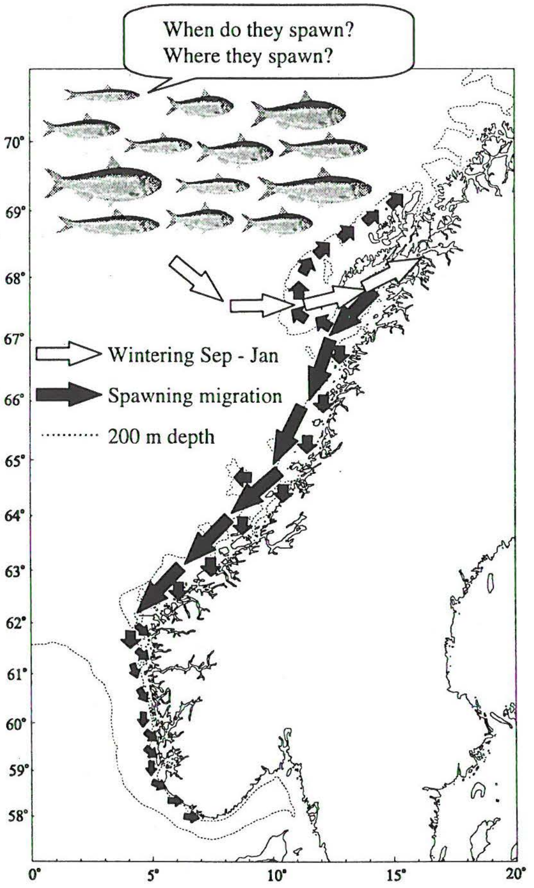

Fig. 6. Illustration of the spawning migration of Norwegian spring spawning herring in the 1990s and the main questions of the present thesis.

OBJECTIVES

Based on the previous mentioned studies it is hypothesised that both the spawning time and selection of spawning grounds in Norwegian spring spawning herring are influenced by the following aspects of population structure: the age and length composition, the composition with respect to nursery area of origin, and composition with respect to body condition (amount of energy reserves). Data utilised to test for relations between spawning migration and population structure are related to the present migration pattern (Fig. 6), although I do take advantage of some historical data. The thesis has 6 main objectives, which all are dealt with in separate papers.

Paper I. The main objective of this paper was to examine energy depletion during wintering and spawning migration in relation to gonad development and fish length. The paper evaluates whether: 1) herring feed during the wintering and spawning migration, 2) the energy expenditure increases during the migration period compared to the stationary wintering period, and 3) relative energetic costs decrease with body length. An additional purpose of this paper was to produce an estimate of energetic costs per distance migrated (km) towards the spawning grounds. Such an estimate should form the basis for a model of the spawning migration (**Paper V**).

Paper II. The main objective of this paper was to examine the effects of fish length and condition on spawning time. The paper evaluates whether: 1) onset of maturation (initiation of vitellogenesis and spermatogenesis) in autumn commences simultaneously regardless of fish length, 2) the instantaneous maturation rate increases with fish length leading to spawning in a decreasing order of size, and 3) the herring will spawn in waves related to the number of age or length modes in the spawning population.

Paper III. The main objective of this paper was to examine the effect of juvenile nursery on geographic spawning distribution. The paper evaluates whether: 1) changes in stock size systematically effect the recruitment pattern of two components from different nursery areas; coastal nurseries and Barents Sea nurseries, 2) an asynchronous maturity schedule of the two components results in different recruitment patterns, and 3) juvenile area is a factor determining the geographic spawning distribution of fully recruited components (age ≥ 6 years).

Paper IV. The main objective of this paper was to examine the biological characteristics of the small fraction spawning at the southernmost grounds in comparison with the main stock. The paper evaluates whether: 1) this fraction undertakes the same seasonal migrations as the main stock with feeding in the Norwegian Sea, wintering in Vestfjorden, northern Norway, and a southward spawning migration, 2) this fraction differs from the main stock with respect to age and length composition, meristic characters and spawning period.

Paper V. The main objective of this paper was to construct a model, which would predict the optimal spawning migration for fish of different lengths. The paper evaluates whether the spawning migration could be a state-dependent trade off between the costs and benefits of migration.

Paper VI. The main objective of this paper was to test the constructed model (**Paper V**) by examining the effects of fish length and condition on the selection of spawning grounds. The paper evaluates whether herring of larger size and/or better condition will tend to migrate farther south to spawn.

METHODOLOGY

FIELD STUDIES VERSUS EXPERIMENTAL STUDIES

The present thesis is entirely based on field data. Some research scientists may have the view that some of the proposed hypotheses also should have been studied under more controlled experiments on captive herring, especially the relation between maturation (onset of maturation, maturation rate, gonad investment) and fish length/condition. On the other hand, wild herring are influenced by many other factors than captive herring (differential environments, antipredator behaviour, vertical migrations, horisontal migrations etc.), which are likely to influence the maturation process. Thus, ideally a combination of field studies and experimental studies would have been preferred to give the best knowledge of these relationships. However, the maturation has already been studied experimentally both in Pacific herring (HAY & BRETT 1988; HAY & al. 1988) and in Atlantic herring (MA & al. 1998), supporting the present field data. The experimental study by MA & al. (1998) was carried out at IMR supervised by Olav Sigurd Kjesbu. Kjesbu and his colleges are presently doing experimental research on maturation in captive Norwegian spring spawning herring, and these studies are combined with field studies. Such combined studies are planned in the years to come, and hopefully they will provide new and valuable knowledge on the herring maturation and other aspects of herring physiology.

SAMPLING DESIGN

In order to fulfil the objectives of this thesis the biological samples were collected regularly from the period of onset of wintering until the time of spawning. Obviously the data collected should be representative for the target population. This may in many cases be difficult, but the present situation of Norwegian spring spawning herring has been particularly suitable in this respect. The stock appears as a relatively homogenous mass within the Vestfjorden system during the wintering period (September-January). During the spawning season it distributes at several locations along the coast, but the main spawning takes place off Møre and so does the fishery (SLOTTE & JOHANNESSEN 1997). Thus, with respect to field studies of maturation, energy loss etc., it would be possible to collect rather representative samples for the entire stock during the wintering period, and for the main part of the stock during the spawning season.

One objective of this thesis was to estimate the costs of spawning migration from the wintering grounds to the spawning grounds off Møre. This was done by comparing length specific energy of herring in the wintering area with herring from the spawning grounds, analogous to similar investigations in anadromous fish (GLEBE & LEGGETT 1981a, b; JONSSON & al. 1997). In this respect, representative samples are more difficult to obtain than during a stationary wintering period, since the herring are more wide spread during the spawning season. Ideally one should be able to estimate the energy content of live herring in the wintering area, tag the fish, then recapture them at the different spawning grounds and analyse the energy loss. This would, however, demand instrumental technology for energy measures of the live fish, and a large amount of tagged fish in order to have a relative high recapture probability. Such studies could be possible in a future perspective, but presently one has to rely on the present sampling design, taking into account the uncertainty of such estimates.

MEASURES OF MATURATION

One objective of the present thesis was to study the relation between maturation and fish length or fish condition. In this respect the gonads of the fish were weighed, and the increase in gonad weight was assumed to reflect an increase in maturity level. However, this may not always be the truth. Fish at the same maturity level may have different length specific gonad weights due to differential gonad investment as indicated by egg size or fecundity (Hay & BRETT 1988; HAY & al. 1988; BRADFORD & ILES 1992; BRADFORD & STEPHENSEN 1992; MA & al. 1998). HAY & BRETT (1988) suggested that a reduction in the number of maturing oocytes occurs naturally and reflects a mechanism that allows herring to adjust their egg size and egg number according to available energy resources and environmental conditions. Thus, even though oocyte diameter may be a good maturation criterion in herring (HAY & al. 1987), the intracellular characteristics of oocyte morphology should be studied in a more detailed way (GILLIS & al. 1990) in order to be certain about maturity level. This uncertainty was taken into account in relation to the present thesis. The gonad weights were measured in thousands of fish, and sub-samples of ovaries were collected during the wintering and spawning migration for further analyses. These ovaries were analysed by OSKARSSON (1998) with respect to fecundity, atresia, oocyte diameter and detailed oocyte histology (diameter of yolk granules, volume fraction of yolk granules and chorion thickness).

SOURCES OF ERRORS

Although the present migration pattern of Norwegian spring spawning herring has been advantageous with respect to representative sampling, there may be sources of errors connected to the actual sampling of the stock with different types of catch gears. These errors have not been fully addressed in my papers as they to my knowledge should not have any major influence on the conclusions drawn. Anyway, I appreciate that these uncertainties exist, and therefore I give an overview of the most important and relevant sources of errors in the following.

Numerical underestimation of smaller fish compared with their larger conspecifics is not uncommon in pelagic trawls due to a tendency for the smaller herring to escape through the meshes in the upper rear part of the trawl (LARSEN 1985). On the other hand, this effect may be to some extent be counteracted by size specific swimming speed (BLAXTER 1969; WARDLE 1993). Herring infested with *Ichthyophonus hoferi* usually have low condition and are less able to avoid pelagic trawls (KVALSVIK & SKAGEN 1995), i.e. herring with low condition may be overestimated by this gear. Swimming speed increases with temperature, and trawl catchability of the herring may therefore be reduced in warm Atlantic water compared to colder water bodies (MOHR 1969). During spawning the escape capability of herring is close to zero (MOHR 1969). After spawning, emigrating and feeding schools are more dynamic in shape, density and movements than prespawning schools and harder to catch (MOHR 1969; NØTTESTAD & al. 1995). Vertical distribution of the fish may also influence the catchability, as the fish size is shown to increase with increasing swimming depth in herring distributed in vertical layers at the wintering grounds (FOOTE & al. 1996).

Purse seines are supposed to be nonselective. However, the vertical distribution of herring by size could also affect the composition in purse seine samples. More important is the fact that the purse seine fishery itself is selective, as there is a commercial motivation for catching the largest, better paid herring (SLOTTE & JOHANNESSEN 1997). Thus, the year class composition as measured by purse seine samples may be biased by having a larger proportion of older fish than actually present in the area. However, in the present thesis this problem was only relevant during the spawning season, which period the herring in the trawl samples from IMR's regular surveys comprised herring of similar sizes as the purse seine catches within the same areas (own unpublished data). Thus, such errors are not supposed to have any significant influence on the latitudinal and temporal variations presented.

SYNOPSIS

ENERGY UTILISATION DURING WINTERING AND SPAWNING MIGRATION

Paper I demonstrated that the herring, with few exceptions, did not feed during the wintering and spawning season 1994-95 and 1995-96, as also shown elsewhere (ILES 1964; PARSONS & HODDER 1975; CRAWFORD 1980; BRADFORD 1993a). Instead the energy utilised for gonad development and metabolism was drawn from reserves stored during the summer feeding period. Throughout the wintering and spawning migration the storage lipids in whole herring were depleted, whereas the proteins remained relatively constant. This is in accordance with other studies suggesting that storage lipids mainly support the routine and active metabolism, whereas the chief function of storage proteins is gonad development (ILES 1984; BRADFORD 1993a), i.e. the loss of proteins in the soma is approximately balanced by the gain in gonads. On the other hand, **Paper I** demonstrated an inverse relationship between mesenteric fat amount and maturity level as found also in Baltic herring (RAJASILTA 1992), which indicate that gonad development could involve some fat depletion.

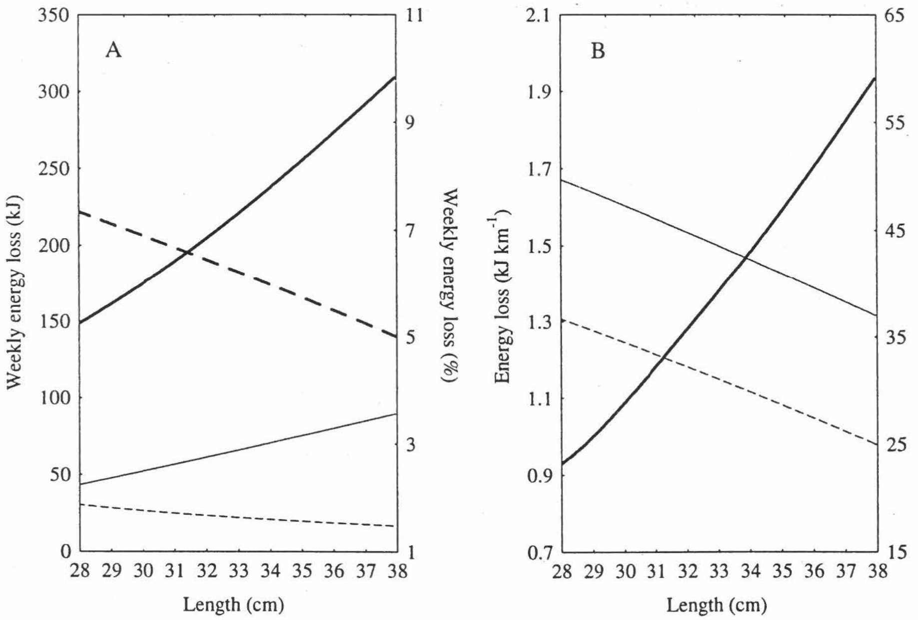

Fig. 7. A) Model of length specific relative (%) (dotted line) and absolute (kJ) (whole line) weekly energy loss. Comparison between the wintering (thin line) and migrating (thick line) herring in 1995-96. B) Model of absolute length specific energy loss (kJ) per km (whole thick line), and relative length specific energy loss prior to (thin dotted line) and after (whole thin line) spawning, during an 800 km migration distance from the wintering area Vestfjorden to the main spawning area off Møre in 1996. Adapted from **Paper I**.

The main result of **Paper I** was, however, the difference in energy depletion found between periods of wintering and migration. The data were fitted with models to demonstrate the length specific differences in energy utilisation (Fig. 7). The absolute and relative weekly energy loss was 2-3 and 3-4 times higher respectively during spawning migration than during wintering. In addition the absolute weekly energy loss increased, whereas the relative energy loss decreased with fish length during both the wintering and migration period. The absolute migration costs per km migrated ($kJ \cdot km^{-1}$) varied from 0.9-1.5 kJ in 1995 and 0.9-1.9 kJ in 1996 in 28-38 cm herring. The relative cost of the 800 km spawning migration from Vestfjorden to Møre in 28-38 cm herring, including the release of spawning products, varied from 46-32 % and 49-36 % in 1995 and 1996 respectively. These results clearly demonstrate the benefits of being large and/or in good condition with respect to the spawning migration in this stock.

EFFECTS OF FISH LENGTH AND CONDITION ON SPAWNING TIME

Paper II demonstrated that the maturity level and spawning time in 1994-97 were influenced by the body length of the herring. The maturity level was measured applying an index given as gonad weight on the day of collection in percentage of expected gonad weight at full maturity for a given fish length (I_G). At any given time during the wintering period and spawning season I_G tended to increase with body lengths in the range 27-31 cm, whereas insignificant differences in I_G were found between body lengths in the range 32-37 cm (Fig. 8). This length specific relationship was observed both in males and females, although the males were at a higher maturity level in the wintering area in accordance with other studies on Pacific herring (HAY 1985; WARE & TANASICHUK 1989) and Atlantic herring (BLAXTER & HOLLIDAY 1963; MCQUINN 1989; RAJASILTA 1992; BRADFORD 1993a). The fact that the relation between fish length and I_G was maintained in the spawning stock throughout the wintering and spawning season, implies that the delayed spawning time in the smallest fish was most likely induced by delayed onset of maturation rather than a slower maturation rate.

Mean length at maturity has been estimated to 30.9 cm for the period 1946-62 (ØSTVEDT 1964) and 30.0 cm for the year classes 1973-78 (TORESEN 1986). In addition, data on length at age indicate a growth at 1-2 cm from the age of first spawning (age 4 or age 5 years) until next spawning (TORESEN 1990). It is therefore likely that herring equal to or larger than 32 cm mainly consist of repeat spawners, whereas the proportion of recruit spawners increases with decreasing lengths in herring smaller than 32.0 cm. Thus, the observed relationship between maturity level and fish length, could be explained by the difference in maturity level between recruit spawners and repeat spawners. However, in order to get a more realistic picture of the relation between herring length and maturity level, one should be able do differentiate between recruit spawners and repeat spawners within all length groups. Then one could have tested whether the maturity level increases with fish length within the recruit spawners and repeat spawners. Such a differentiation between recruit spawners and repeat spawners is possible from analyses of growth checks in the herring scale, but this would require a large amount of work and is therefore considered as project in a more future perspective.

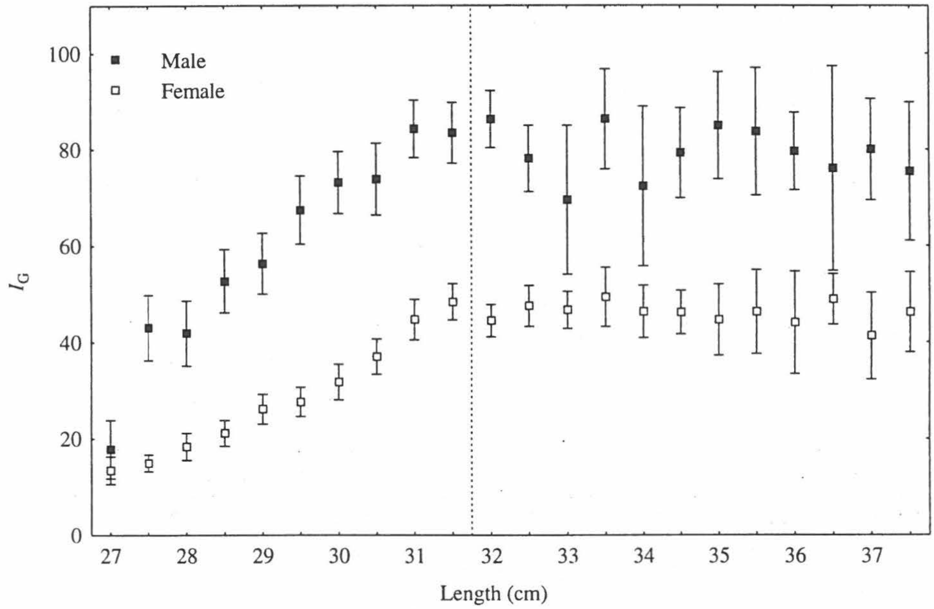

Fig. 8. The relation between body length and maturity level (I_G) in male (n = 815) and female (n =895) herring from the wintering area in December 1996. Mean values ± 95 % confidence limits (n ≥ 3). The length groups to the right of the dotted line is assumed to be repeat spawners. Adapted from **Paper II**.

The results of **Paper II** imply that the stock in general will spawn in two distinct waves, represented by the repeat spawners (first wave) and recruit spawners (second wave), which is supported by previous studies on Norwegian spring spawning herring (RUNNSTRØM 1941a, b; DRAGESUND 1970a). In addition, a corresponding detailed histological study on oocyte growth of Norwegian spring spawning herring in relation to body length (OSKARSSON 1998), also showed similar results. On the other hand the conclusions of **Paper II** differ in some important aspects from the conclusions reached by LAMBERT (1987) on Norwegian spring spawning herring, by LAMBERT & MESSIEH (1989) on Atlantic herring from Canadian waters and by WARE & TANASICHUK (1989, 1990) on Pacific herring from Canadian waters. These authors conclude that herring spawn in a decreasing order of size throughout the entire size spectrum, due to a size dependent maturation rate rather than delayed onset of maturation (WARE & TANASICHUK 1989), which could cause several spawning waves as reflected by the number of age modes or length modes in the reproductive stock (LAMBERT 1987; LAMBERT &

MESSIEH 1989). However, although **Paper II** contrasts with similar studies in herring populations, the differences may not necessarily be due to actual differences between populations. The differences could be influenced by different sampling and methodology. The other mentioned studies were mainly based on data from the spawning season, whereas **Paper II** was mainly based on data from the wintering population within the Vestfjorden system, only supplemented with data from the main spawning area during the spawning season. In addition, the measure of maturity level differed between **Paper II** and the other mentioned studies. The subjective maturity scale (ANON. 1962), based upon macroscopic inspection of the gonad, was used by LAMBERT (1987) and by LAMBERT & MESSIEH (1989), whereas WARE & TANASICHUK (1989, 1990) used a size independent measure of maturity, which is the difference between the observed gonadosomatic index (GSI) and the GSI at full maturity for a given body weight. The subjective maturity scale does not give precise values of herring maturity level, except in spawning (running) and spent herring. Increasing GSI values may be the results of both increasing gonad weights and decreasing somatic weights. In addition, the body weight may change substantially during the maturation cycle, and it may describe both the body length and condition at the same time. Consequently another, and perhaps more robust index was used in **Paper II**; I_G. **Paper II** does not challenge the studies stating that herring may spawn in more than two waves. However, the age or length distribution within a population may not necessarily always form the basis for such spawning waves.

It is possible that spawning waves may occur on the basis of differences in the individual condition. **Paper II** demonstrated an increase in maturity level (I_G) with the condition or energy level of the herring (Fig. 9), which is supported by other studies on captive herring (HAY & al. 1988; Ma & al. 1998) and wild herring (ANEER 1985; HENDERSON & ALMATAR 1989; RAJASILTA 1992). RAJASILTA (1992) found that fish with high muscular fat reserves had reached maturity stage 3 already in December and would become early spawners, whereas those with low fat content were supposed to spawn significantly later. Correspondingly, lower energetic status may also be the reason for delayed spawning in the recruits compared to the repeat spawners. **Paper I** demonstrated a length-dependent storage energy capacity and energy depletion, which suggest that the smaller fish is particularly vulnerable for variations in the energetic status. Fat content is also found to be lower in immature herring compared with mature conspecifics and increase with body length within immature herring (LEIM 1958; HODDER & al. 1973). Apparently there is a difference between the onset of maturation in repeat spawners and recruit spawners. Depending on an individual's state determined by its body length and condition, the immature herring will either spawn or not, whereas adult herring normally spawns every year for the rest of its lifetime, although there may be extremes where all the oocytes are atretic and absorbed (OSKARSSON 1998). Thus, it seems likely that the low energy capacity, high relative costs of spawning migration in the recruit spawners, could result in delayed onset of maturation compared with the mature stock.

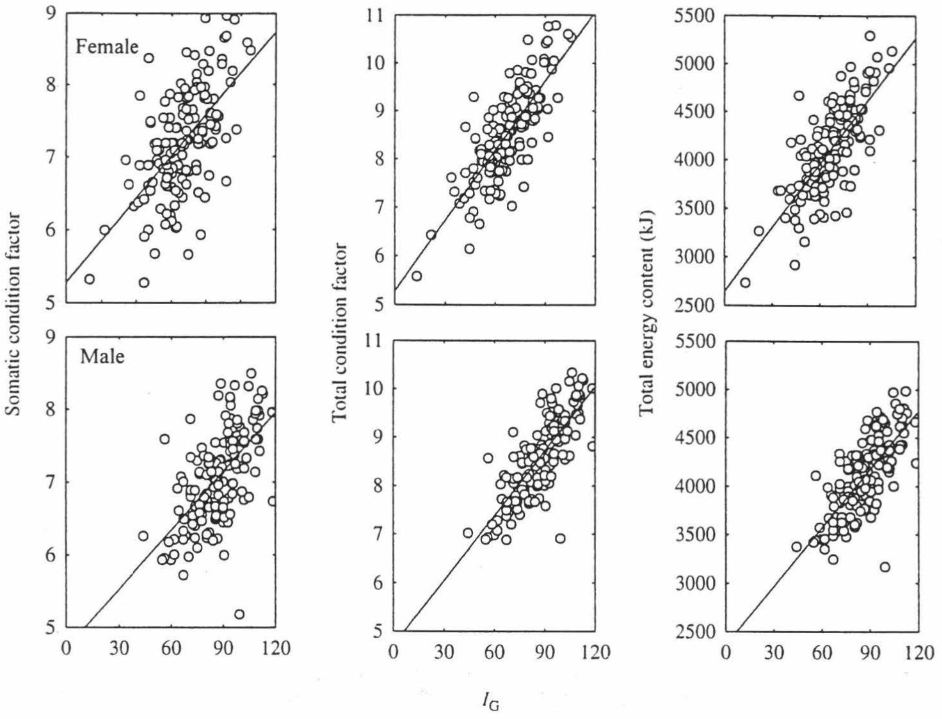

Fig. 9. Maturity level (I_G) in 35 cm herring from the wintering area in January 1995 in relation to somatic condition factor ((total weight-gonad weight) · L^{-3} · 1000), total condition factor (total weight · L^{-3} · 1000) and total energy content ($p < 0.001$). Adapted from **Paper II**.

EFFECTS OF JUVENILE NURSERY ON GEOGRAPHIC SPAWNING DISTRIBUTION

Paper III demonstrated the geographical, temporal and age-dependent recruitment patterns of the coastal and the Barents Sea components of most year classes from 1930 to 1989. The relative importance of each component in the year classes varied with the fluctuating stock size observed during the period studied. In periods with a low spawning stock hardly any recruitment appeared from the Barents Sea juvenile areas, while at high stock levels the Barents Sea component totally dominated the spawning stock (Fig. 10). The asynchronous maturation of the two components caused a recruitment pattern characterised by a high proportion of the coastal component at low ages and an increasing proportion of the Barents Sea component at older ages. The hypothesis proposing that the juvenile area is a factor determining the geographic spawning distribution of fully recruited components was not supported by the data. The only pronounced latitudinal gradient of the component composition at the studied spawning grounds was observed during the recruitment period (ages 3 to 6) between the northernmost area (area 06) and the more southern areas (areas 07, 28 and

08, see Fig. 3). Both components recruited along the entire spawning range studied, and once fully recruited, no latitudinal gradient in the spawning stock component composition was observed.

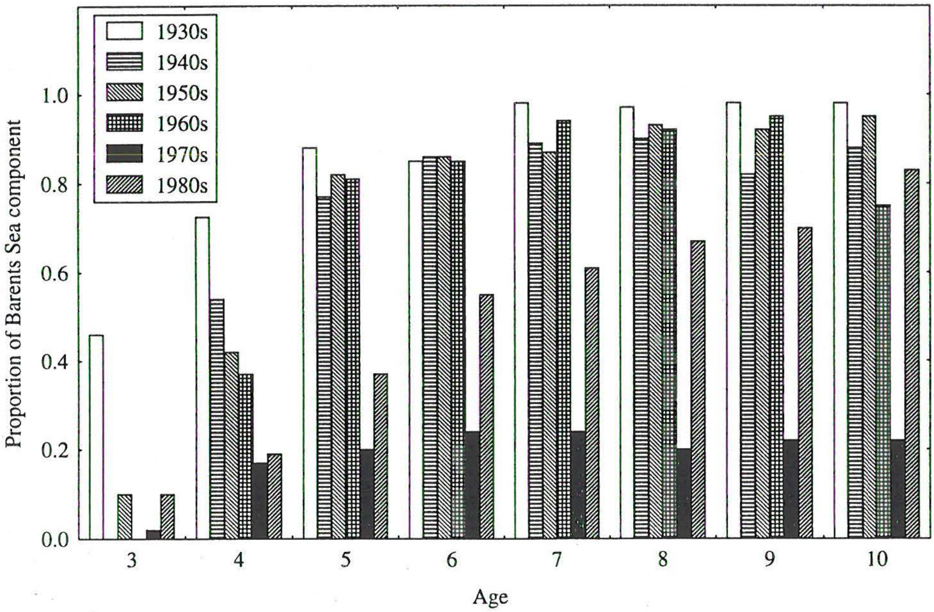

Figure 10. Estimated mean proportion of the Barents Sea component by age and blocks of 10 year classes. Adapted from **Paper III**.

Paper III has demonstrated the association of the Barents Sea component with high catch levels in the fisheries. On the other hand, these results have also demonstrated the importance of the coastal component as a buffer at low stock levels and a major contributor to new recruitment in such periods. The strong 1983 year class, which was predominated by close to 100 % of the Barents Sea component, was a product of several rather weak year classes born in the 1970s, which were predominated with about 80 % of the coastal component. Due to the higher temperature and growth rates in juvenile herring from coastal areas compared with the Barents Sea (DRAGESUND 1970a), it is likely that also the mortality rates are lower at the coast. In fact it has been suggested that temperature related effects are more important in the late larval - early juvenile phase than in the early larval period, due to the high predation rate at these stages (ANTHONY & FOGARTY 1985, SISSENWINE & al. 1984). DRAGESUND (1970a) emphasised that the proportion of herring larvae accumulating in coastal areas and fjords, will increase as the spawning occurs farther south. Thus, with respect to larval retention and higher growth rate in coastal areas, spawning farther south would be beneficial. This is important with regard to the hypotheses evaluated in **Paper V** and **Paper VI**. Consequently, it is also of importance for the management of this stock to provide adequate recruitment both to the Barents Sea nursery and other potential nurseries along the coast. This goal can best be achieved by first securing a spawning stock which is sufficiently large to produce a large Barents Sea component, and second, allowing for a maximum geographic extent of the spawning area, especially southwards. This second goal will in some cases imply the closing or reduced fishing effort in marginal spawning grounds. Such regulations are included in the present management regime. The fraction spawning south of 61°N has been protected since it arrived in these areas in 1989 for the first time in 30 years (RØTTINGEN & SLOTTE 1998).

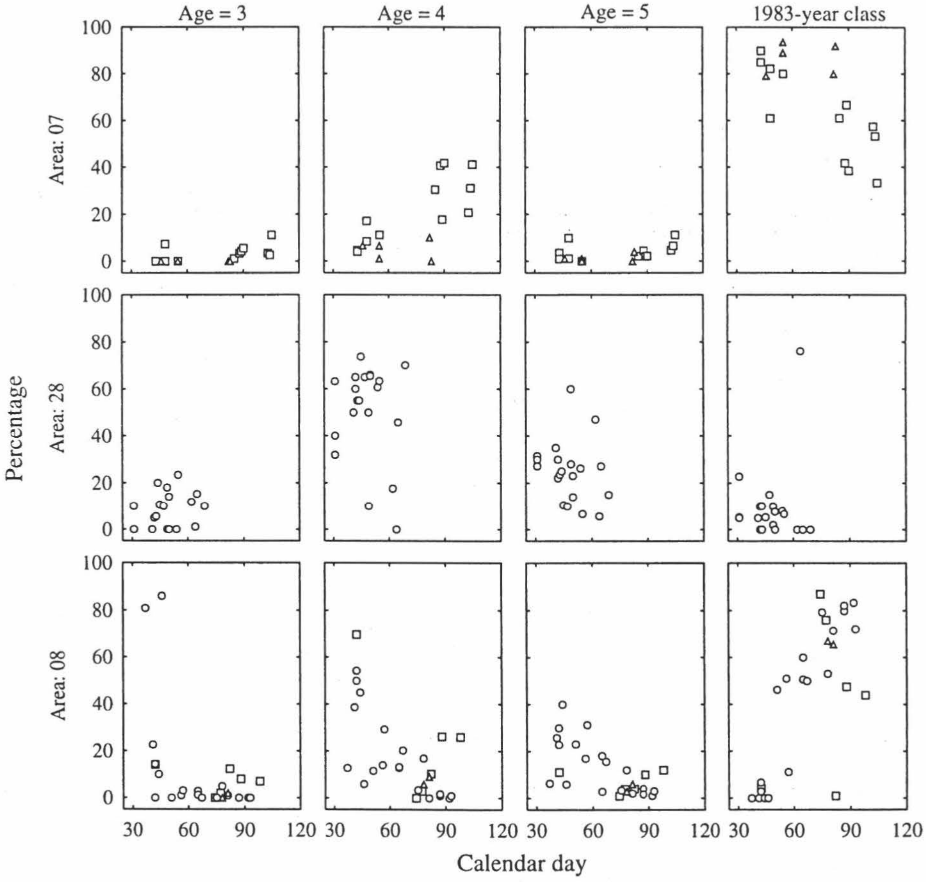

Fig. 11. Comparison of temporal variation in age composition between spawning areas in 1992. The percentage of young spawners of age 3-5 years is compared with the percentage of the abundant 1983 year class. Symbol definitions: circles = gill net samples, squares = purse seine samples and triangles = trawl samples. Adapted from **Paper IV**.

CHARACTERISTICS OF HERRING AT THE SOUTHERN SPAWNING GROUNDS

Paper IV demonstrated that the Norwegian spring spawning herring arrived at the southernmost spawning grounds (south of 61°N) in two distinct groups (Fig. 11). The first and apparently less abundant group arrived already in late January off the Hordaland and Rogaland districts. This group comprised mainly recruit spawners (age 3-5 years) originating from coastal nurseries, in accordance with the asynchronous recruitment pattern of the coastal and Barent Sea component (**Paper III**). This was probably herring that had left the coast the year before to feed and winter in more southern areas than the rest of the stock, probably in the northern North Sea. Such a hypothesis is supported by studies of LEA (1928) and HARALDSVIK (1968). The major group did not arrive until around 20 February and comprised mainly older repeat spawners. This group did hardly appear at the coast off Hordaland, and occurred mainly at the more traditional spawning grounds at Karmøy, Egersund and Siragrunnen, in particular.

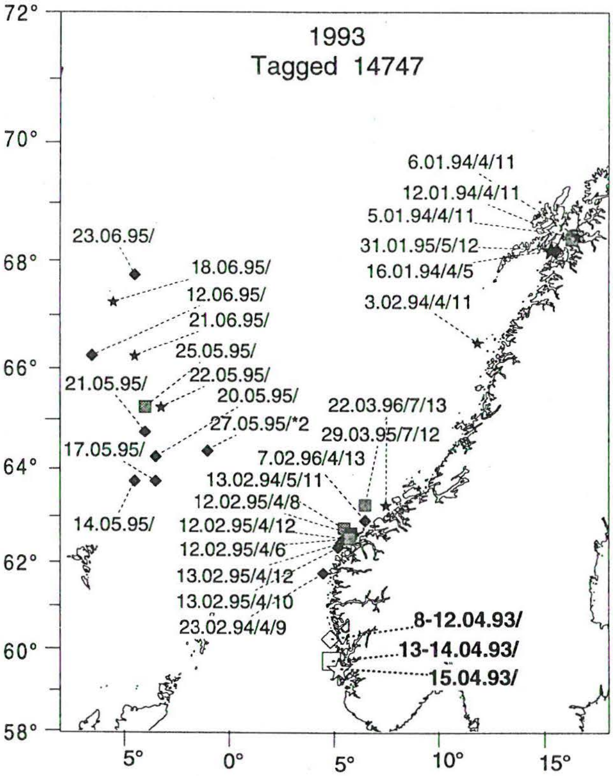

Fig. 12. Results from tagging experiments at southern spawning grounds in 1993. Each tagging position and the tags recovered from that release is marked with different symbols. Open symbols denote the position and date of release, whereas hatched symbols denote position and date/maturity stage/age (*2 denotes two individuals). Total number of herring tagged was 14747. Adapted from **Paper IV**.

Spent herring were tagged annually at the southern grounds in 1990-93, and during 1990-96 tags were recovered from feeding herring in the Norwegian Sea, from wintering herring in the Vestfjord system, and from herring on southward migration along the coast, particularly off Møre (Fig. 12). The fishery at the southern grounds was closed during 1990-96, and only 5 tags were recovered at these grounds, of which three were found to belong to local fjord herring populations. Herring tagged at age 5 years or younger were recovered both on northward migration from the southern grounds, in the Vestfjord system and off Møre. Thus, the tagging experiments indicate that the major group of older repeat spawners at the southernmost grounds were dissenters from the main spawning stock, feeding in the Norwegian Sea, wintering in the Vestfjord system and spawning off the Møre district. In addition, they indicate that the young recruit spawners followed the older spawners and adapted a similar migration pattern in subsequent years.

Despite different arrival dates, recruits and repeat spawners were at similar maturity levels and appeared to spawn simultaneously. This observation is in contrast with the observed relationship between fish length and maturity level as observed in the wintering area in 1995-97 (**Paper II**). However, also in 1995-96 less distinct differences in maturity level were found between the small and larger sized herring off Møre. This was probably related to the fact that recruits that migrated towards Møre and farther south were in better condition than recruits spawning farther north (**Paper VI**). Better condition could have improved the maturation abilities (**Paper II**), and consequently resulted in a more synchronised spawning with the adults. Also the spawning period commenced simultaneously along the coast, but it was prolonged at the southern grounds compared to Møre. This was probably due to the fact that the herring migrating a longer distance, past Møre towards the southern grounds, had to hold at a mature stage for a longer period. Such a delay in spawning may have positive influence on egg and larval survival due to increased temperatures (**Paper V**), although holding of mature ovaries also may have negative influence on egg quality and result in decreased survival of the progeny (HAY 1986).

Analyses of meristic characters (vertebral and gillraker count) gave no indications that the herring at the southern grounds belonged to a particular sub-population with its own integrity compared to the herring spawning off Møre. Negligible and non-significant differences in meristic characters were found between herring wintering in Vestfjorden and herring at the spawning grounds off Møre and farther south. However, herring at age 3-4 years had lower gillraker count than herring of the same age groups in Vestfjorden. This was probably due to differential nursery conditions (**Paper III**), as the gillraker count may be subject to environmental modifications due to variations in available food (ANDRAU 1969, LINDSEY 1981).

MODELLING THE OPTIMAL SPAWNING MIGRATION

In **Paper V** a model was constructed as an attempt to quantify the fitness related to the distance of the spawning migration and individual size of the herring. The model was based on the following: 1) the migration route between Vestfjorden and the southernmost grounds as indicated in **Paper IV** and Fig. 6; 2) the length specific migration costs estimated in **Paper I**; 3) data on temperatures along the coast at 10 m depth (AURE & ØSTENSEN 1993); 4) functions of larval growth of Norwegian spring spawning herring in relation to temperature (Folkvord, Departement of Fisheries and Marine Biology, University of Bergen, Norway, unpublished data); and 5) functions of larval mortality related to temperature (HOUDE 1989) and larval size (MCGURK 1986).

In the present model, herring were initiated at hatching and traced until metamorphosis (3.5 cm). Age at metamorphosis was a function of time and site at hatching and the drift route northwards in the coastal current. The model predicted an increasing probability of larval survival at hatching locations southwards from the wintering area, due to increasing temperatures during the larval stage (Fig. 13). The predicted probability of larval survival increased with the delay in time of hatching from 1. - 15. April, when temperatures were increasing. Larval survival was predicted to increase if the drift speed northwards along with the coastal current decreased, i.e. the larvae remained for a longer period at higher temperatures. Also the optimal hatching location moved northwards with decreasing drift speed.

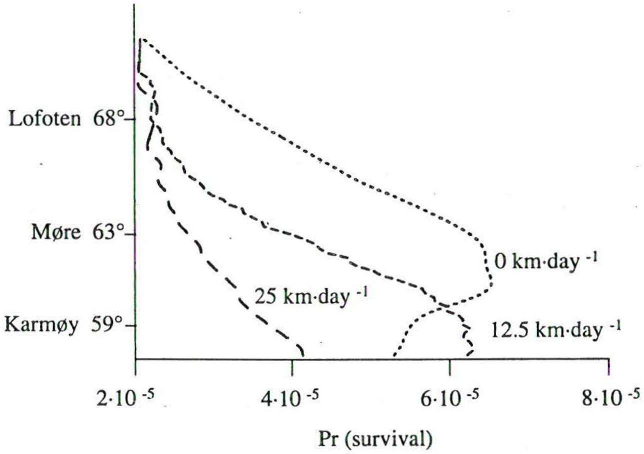

Fig. 13. Survival of larvae (hatched at 1. April) related to hatching site, given three different drift speeds and mortality function from HOUDE (1989). Adapted from **Paper V**.

However, although the larval survival may increase southwards, it is not necessarily as optimal to spawn in the respective areas. The costs of migration should be taken into account. Thus, the model assumed that the herring had a limited amount of energy to utilise on migration and fecundity. In order to secure survival until next spawning, the herring should not exceed a lower threshold of energy at 60 % of total energy content (including gonads) in Vestfjorden prior to spawning migration. The model also assumed that the herring fecundity could not exceed an estimated maximum number, whereas it could be reduced in order to migrate for a longer distance. In other words, the herring may trade off energy between fecundity and migration, based on differential larval survival probabilities along the coast.

When the costs and benefits of migration was taken into account, the model predicted that the optimal spawning ground was found farther south with increasing individual fish size (Fig. 14). Also higher larval mortality rates coastal wide made southern spawning more profitable, and increased larval retention enhanced larval survival and shifted optimal spawning grounds northwards. The potential migration distance prior to the need for a reduction of maximum fecundity increased with fish length. The potential migration distance using all available energy from eggs, increased also with body length. For example, the model predicted that an average herring at 29 cm would exceed the lower energy threshold before arriving at Karmøy. However, it must be emphasised that this is the average herring, and within all length groups the body weight, condition, or energy content are normally distributed. Thus, the herring at the right hand side of such a normal distribution, would have higher migration potential than those at the left hand side.

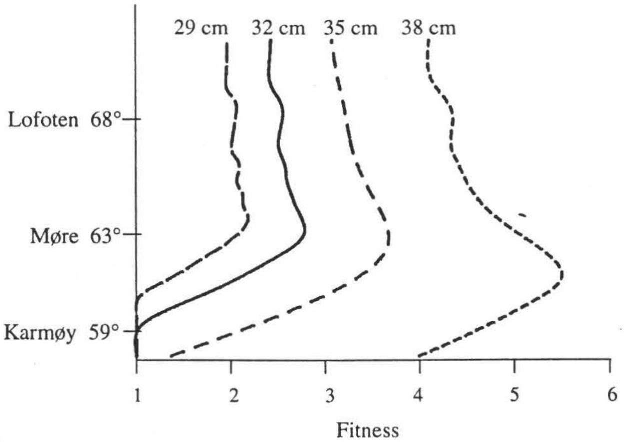

Fig. 14. Fitness of herring related to spawning ground, individual fish size and mortality function from HOUDE (1989). Hatching at 1. April, and basic drift speed 25 km·day^{-1}. Adapted from **Paper V**.

The model related the benefits of migration to temperature related mortality of the larvae, but there are at least three possible additional benefits of spawning farther south. First, as mentioned above, spawning farther south will increase the probability of drifting into coastal nurseries, which may enhance the survival. Second, by spawning farther south the larvae may also be dispersed to a wider range of environments along the coast and in the Barents Sea through differential retention and drift routes of the coastal current. Thus, by spreading the larvae from nursery areas in the south towards north, the progeny may overcome some variations in environmental conditions, which may ultimately increase the overall survival. A number of studies have emphasised advantages of dispersal of progeny in populations under high spatial and temporal environmental variability (GADGIL 1970; ROFF 1975; KUNO 1981; LEVIN & al. 1984; LEVIN & COHEN 1991; COHEN 1993). Third, when migrating southwards the large herring and herring in good condition could avoid competition from herring with less migration potential, and thus reduce density dependent mortality of eggs (TAYLOR 1971, GALKINA 1971, HOURSTON & ROSENTAL 1981). Reduced density may also reduce competition for food among larvae (KIØRBOE & al. 1988).

EVIDENCE FOR STATE-DEPENDENT MIGRATIONS IN HERRING

The predictions of the model in **Paper V** were supported by field data. **Paper VI** demonstrated that during the spawning seasons in 1995 and 1996 the herring were distributed mainly between Sogn and Lofoten (61°-70°N), with the shelf area off Møre (62°-64°N) being most important. Both the fish length and condition increased southwards, but the condition appeared to be the most important variable influencing the migration distance (Fig. 15). Corresponding with the southward increase in

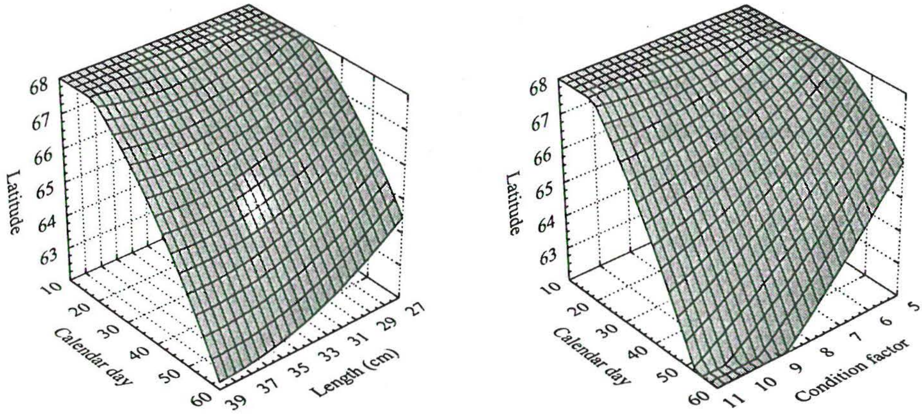

Fig. 15. Models of the spawning migration of Norwegian spring spawning herring related to body length and condition factor during January through February 1995. Taken from **Paper VI**.

body length and condition, the maturity level also increased (Fig. 16). Thus, the delay in maturation was probably reflected by lower body length and lower body condition of the fish (**Paper II**). This suggests that the small herring and herring in bad condition trades off energy both for migration and for gonad production, to enhance survival in successive years. Other studies have also demonstrated that the metabolic costs of pre-spawning activities may influence allocation of energy for gonad development. It has been demonstrated experimentally in captive herring (MA & al 1998) and cod (KJESBU & al 1991) and in wild herring (OSKARSSON 1998), that the fish may reduce the fecundity by absorbing oocytes (atresia) and instead invest the energy in remaining oocytes or use it for other needs. In fact OSKARSSON (1998) found that herring in low condition to the north of Møre in March 1997 had high levels of atresia including figures of up to 100 % atresia, which implies that herring may skip spawning a particular season and instead absorb all eggs and use the energy for metabolic purposes. Analogous to these studies are the findings by HOLST (1996a) on prevalence of *Ichthyophonus hoferi* in this stock. He found that the infected individuals lagged behind in the wintering area when the healthy fish migrated towards the spawning grounds.

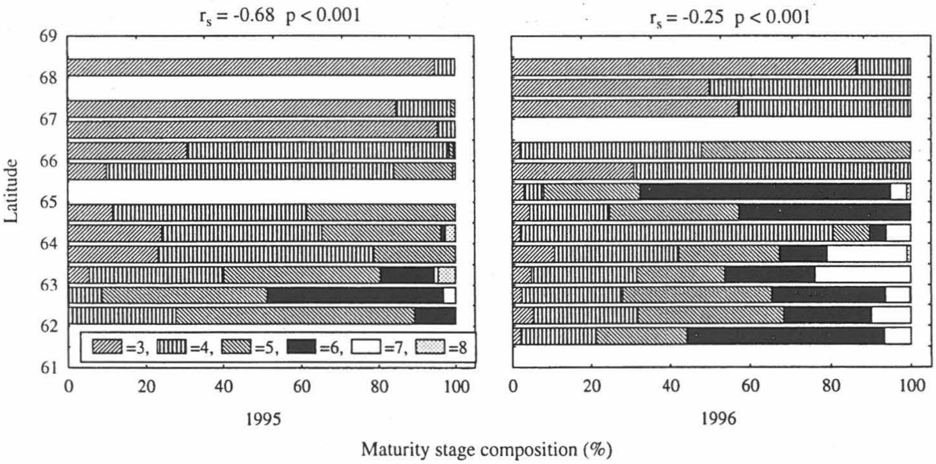

Fig. 16. Maturity stage composition (3-4 = maturing, 5 = ripe, 6 = spawning, 7 = spent and 8 = recovering) in Norwegian spring spawning herring on a latitudinal scale (within 30 nautical miles) during the pre-spawning period 19 February - 2 March 1995 and 17 February - 6 March 1996. Results are given of Spearman correlation (r_s, p) between latitude and maturity stage. Cases with n < 10 were excluded. Adapted from **Paper VI**.

The state-dependent spawning migration proposed by the model in **Paper V** and indicated by the field study in **Paper VI**, was supported by recent data on Norwegian spring spawning herring from 1997 and 1998. In 1997 the spawning stock biomass increased from 5 million tonnes to approximately 10 million tonnes due to the recruitment of the strong 1991 and 1992 year classes (ANON. 1998). This year bad weather prevented IMR from adequate surveying of the spawning areas north of Møre, but the grounds at Karmøy, Egersund and Siragrunnen were allotted extra attention. This year a total of 215.000 tonnes were recorded at the southernmost grounds (SLOTTE & DOMMASNES 1997), which was the highest estimate since the herring showed up in these areas in 1989 for the first time since 1959. This may have been a result of increased fish densities, i.e. increased competition for spawning substrates. As the population increased a more distinct extension of the spawning area was observed northwards from Møre, too. In 1998 the spawning stock was surveyed adequately at all spawning grounds between 70°N and 58°N. This year 63 % of the spawning stock utilised the spawning grounds to the north of Møre (north of 64°N) (SLOTTE & DOMMASNES 1998), and the abundance estimate at the southern grounds was only 77.000 tonnes. During the wintering and spawning season in 1997-98 individual condition and gonad investment were recorded at the lowest level since the stock recovered (Fig. 17), and consequently some herring could have reduced the migration distance this year.

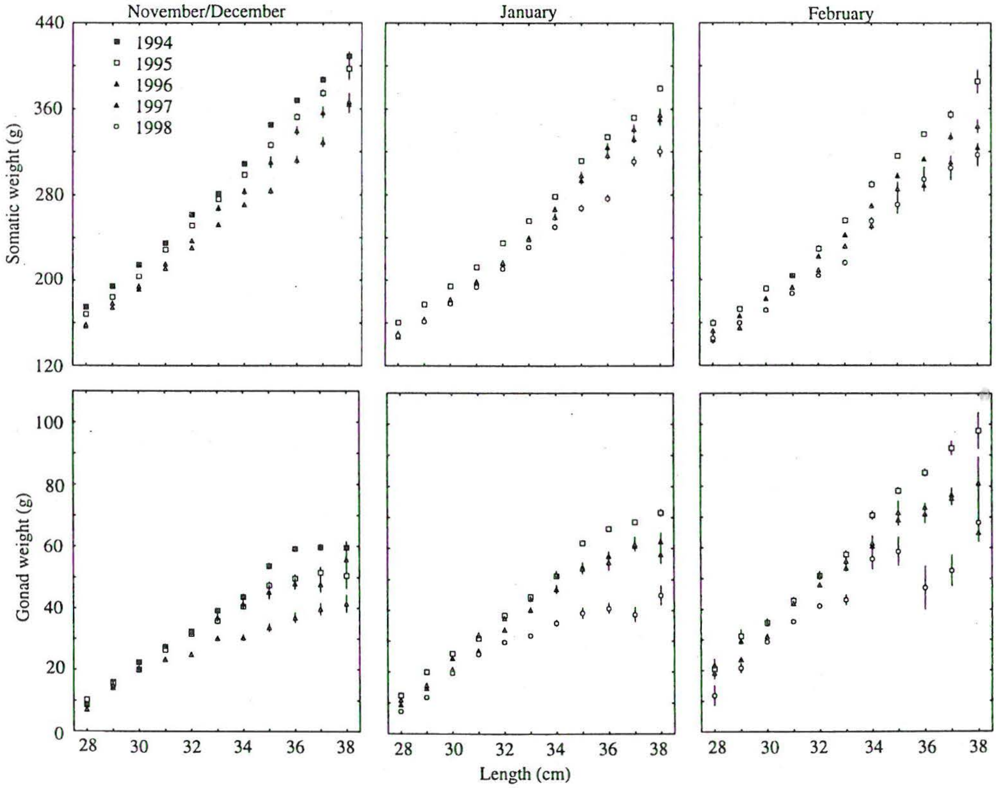

Fig. 17. Annual mean length specific somatic weights and gonad weights by month (Vestfjorden in November/December pooled and January; Møre in February) of Norwegian spring spawning herring during 1994-98. Mean values per date ± SE are given. (own unpublished data).

Furthermore, data from 1997-98 on the relationship between migration distance and the state of the herring were in accordance with the data from 1995-96. In 1997 the biological data demonstrated that the body length, age and condition increased southwards from Træna to the southernmost grounds of Karmøy, Egersund and Siragrunnen (SLOTTE & DOMMASNES 1997). In fact this year the herring in best condition were recorded at Egersund. In 1998 spawning herring were sampled from 69°N to 58°N, and the strong 1991 and 1992 year classes predominated at all latitudes. The proportion of the 1991 year class was estimated to increase northwards, indicating that the fish size decreased southwards (SLOTTE & DOMMASNES 1998). However, a closer look at these data revealed that in both the 1991 and 1992 year classes, the mean length increased southwards, and also the overall mean length tended to increase southwards (own unpublished data). The somatic condition of the herring were equal along the coast in 1998 (SLOTTE & DOMMASNES 1998). However, given the high costs of migration (**Paper I**), the initial condition in the wintering area in Vestfjorden January 1998 was probably higher in herring undertaking long migrations (Siragrunnen) compared to the herring undertaking short migrations (Lofoten). Thus, with regard to the present data and the data from 1997-98, one may hypothesise that the individuals heading for spawning grounds in the southernmost areas belong to an elite group of the spawning stock.

Support for state-dependent migrations is also found in studies of school behaviour and integrity. Size segregation of fish in shoals is apparently a common phenomenon (PITCHER & PARRISH 1993), and hydrodynamics may provide advantages for herring in a school when swimming close to conspecifics of similar size (PITCHER & al. 1985). This suggests that in the wintering area prior to spawning migration the herring could form schools according to fish size and condition rather than according to where the different conspecifics spawned in previous years. Thus, theoretically schools of herring migrating southwards from Vestfjorden could contain specimens which had spawned at wide range of spawning grounds from Lofoten to Siragrunnen in previous years. During the spawning migration the herring may split and form new schools, or aggregate in larger shoals or layer of different densities (SLOTTE 1998). However, it seems unlikely that such splitting of schools or aggregating behaviour would occur progressively as the herring reach the respective spawning grounds, to which they are supposed to home. It seems more likely that members of schools or aggregations of herring will maintain their position and follow the same direction as the others, unless they are prevented by reduced energy storage. This is the concept of learning or copying that is further discussed below.

The opportunities of Norwegian spring spawning herring to spawn within the vicinity of the wintering area are numerous given the present migration pattern compared to periods prior to the stock decline, when the herring were wintering to the east of Iceland. One may therefore question how individuals approached similar problems with migration constraints during previous periods. Data exist on individual condition and tagging experiments indicating similar behaviour also during the period with oceanic wintering. Coinciding with decreasing body condition (length specific weight) in the stock in the 1960s (HOLST 1996b), in excess of 90 % of the herring spawning off the Faeroes were estimated to be Norwegian spring spawners, mainly contributed by the recruitment of the strong 1959 year class (JAKOBSSON 1970). In addition, individuals spawning one year (1960, 1963, 1964, 1965, 1966) off western Norway spawned off the Faeroes one or several years later (1967). It must also be emphasised that the herring stopped visiting the southernmost grounds (south of 61°N) in 1960. With regard to the above mentioned studies, it seems possible that the herring in poor condition migrating towards Norway to spawn from the oceanic wintering area east of Iceland, instead stopped at the Faroes due to migration constraints. In fact, this reduced the migration distance by approximately 700 km. Similarly, the herring arriving within the vicinity of Møre after migration from Iceland, reduced the migration distance by up to 500 km by spawning off Møre compared to at the southernmost grounds.

The fact that also the feeding migration of Norwegian spring spawning herring is less extensive in smaller individuals (ANON. 1995, 1996; NØTTESTAD et al., IMR, unpublished), strengthens the general importance of fish size in the migrations of this stock. The state-dependent spawning migrations is furthermore supported by other studies on energy trade off between reproduction and metabolic purposes in animals. BRADFORD (1993b) found that the relative allocation of storage energy to reproduction and metabolism differed with spawning season in herring. The spring spawning herring with a long maturation period, allocated proportionally more storage energy to routine and active metabolism than did autumn spawners with a brief maturation period. Allocation of energy to reproductive products varies also with different migration related costs between anadromous populations of American shad (GLEBE & LEGETT 1981a, b), cisco (*Coregonus artedi*) and lake whitefish (*C. clupeaformis*) (LAMBERT & DODSON 1990), alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) (CRAWFORD & al. 1986). Further support for the hypothesis of trade off between migration costs and reproductive output is found in the South American characin, *Prochilodus mariae*. Females that remain resident in a lagoon devote five times as much energy to egg production as do females that undertake up-river migration (SALDANA & VENABLES 1983). This suggests that migration confer important benefits in survival that compensate for the lower investment in eggs. BULL & al. (1996) found that foraging of juvenile Atlantic salmon, which became anorexic and gradually depleted their energy reserves during the winter, depended not on current energy state, but on projected energy state at the end of the winter. Their model predicted that the juvenile salmon would have a greater foraging effort when their lipids where higher if the fish were anticipating future energy requirements. Thus, by appropriate regulation of the energy reserves, the fish were able to maximise over-winter survival, a key component of their life history. Birds are particularly migratory animals, which depend heavily on energetic resources, and consequently they also have to trade off energy in order to maximise expected lifetime reproduction (CLARK & HARVELL 1992; MCNAMARA

& HOUSTON 1992; CLARK & EKMAN 1995). Also zooplankton may have state-dependent trade offs with respect to diel vertical migrations (FIKSEN 1997).

It is not by coincidence that a major part of the Norwegian spring spawning herring chooses to spawn at the shelf area off Møre. This area has temperatures, bottom topography and currents, which are suggested to be profitable for the recruitment in this stock (SÆTRE & al. 1998). Influx of warmer Atlantic waters mix with the colder waters of the coastal current, and the herring will experience the highest spawning temperatures in this area, i.e. the temperature at spawning depth decreases northwards and southwards from approximately 62°N (AURE & ØSTENSEN 1993; SLOTTE & DOMMASNES 1998; SÆTRE & al. 1998). Thus, with respect to hatching success of herring eggs being related to temperature (BLAXTER & HEMPEL 1963; HEMPEL & HEMPEL 1968; TAYLOR 1971; ALDERDICE & HOURSTON 1985), the Møre shelf area is a profitable area. On the other hand areas to the south of 62°N may be more optimal with respect to larval survival (**Paper V**). Also the availability of suitable spawning substrates may favour the shelf area off Møre for spawning. During the period 1931-37 RUNNSTRØM (1941b) performed investigations on the composition of bottom substrates and the associated occurrence of herring eggs at the southern spawning grounds and off Møre. Based on a total of 2232 grab stations he found that the herring preferred to spawn at stony or rocky bottoms, but eggs were also deposited on algae, gravel and coarse shell sand. Fine sand seemed to be less favourable as spawning bottom, whereas muddy bottoms were entirely avoided. Eggs deposited on the latter mentioned bottom types will soon be covered by fine particles preventing important gas exchanges and ultimately result in high mortality. Runnstrøm demonstrated that the preferred hard bottoms were more prevailing at the Møre shelf area, than at the southern grounds. In addition the shelf area off Møre is comparatively much larger than at the southern grounds, which emphasise the potential of this area to receive a major spawning biomass without decreasing hatching success due to density dependent egg mortality (TAYLOR 1971, GALKINA 1971, HOURSTON & ROSENTAL 1981). Thus, low competition for optimal spawning substrates at the shelf off Møre, may have prevented a larger proportion of the stock from migrating further southwards towards the traditional grounds of Karmøy, Egersund and Siragrunnen.

STATE-DEPENDENT MIGRATIONS IN RELATION TO POPULATION CONCEPTS

The results of this thesis are particularly relevant with respect to the recent discussion about stock discreteness in herring. Herring along the Pacific (HOURSTON 1982) and Atlantic (WHEELER & WINTERS 1984) coasts of the North-American continent have high return rates to specific spawning grounds, although there is no clear evidence for natal homing as in anadromous fish (HARDEN JONES 1968, NORTHCOTE 1984; THORPE 1988). Based on observed geographical spawning distributions and data on return rates at spawning grounds, three possible population concepts have been proposed to describe the population dynamics of herring: the discrete population (ILES & SINCLAIR 1982, SINCLAIR 1988) the dynamic balance population (SMITH & JAMIESON 1986) and the metapopulation (MCQUINN 1997).

The discrete population concept subdivides herring from different spawning grounds into discrete population units with independent life histories (ILES & SINCLAIR 1982; SINCLAIR 1988). This concept implies that each spawning ground is associated with a specific larval retention area, and that reproductive isolation is maintained by natal homing. SINCLAIR (1988) proposed that larval retention will result in a number of survivors (members) within a population which will exceed the number of losses (vagrants), the member/vagrant hypothesis. This hypothesis implies that straying herring will not successfully pass on their genes. Thus, in a sense they are evolutionary 'losers'. On the other hand the dynamic balance population concept by SMITH & JAMIESON (1986) disputed the discrete population concept based on the lack of evidence for genetic differences between herring at different spawning grounds. Instead SMITH & JAMIESON (1986) considered the herring to consist of dynamic and relatively unstructured assemblages. They contended that herring populations may expand and contract their range in response to environmental and fishing pressures. This concept implies that there are no barriers to exchange between spawning grounds or spawning populations. It implies that straying or gene flow between populations are the rule rather the exception, and keep the populations in dynamic balance. Stock discreteness and the member/vagrant hypothesis was subject for discussion at a workshop during the International herring symposium in Anchorage, Alaska, 1990. It was apparent from the discussion at this workshop (ANON. 1991) and from a review article (STEPHENSON 1991), that there were disagreements about the stock discreteness in herring and the validity of the member/vagrant hypothesis. Except for a study by STEPHENSON & KORNFIELD (1990) evidence for the discrete population concept was lacking. The main uncertainty was related to the degree and mechanisms of natal homing and separation between neighbouring groups. The Pacific herring off British Colombia consist of several stocks, of which each is connected to a number of spawning sites within a particular area (HAY & KRONLUND 1987), and studies on larval distribution have indicated mixing within areas but not between areas (HAY & MCCARTER 1991, 1997). However, HAY & MCCARTER (1997) emphasised that these stocks mix during summer feeding migrations, and that larval imprinting could explain the observed geographical spawning distribution without demonstrating genetic differentiation. Thus, with exception of the genetic aspect, their data supported the larval retention hypothesis (ILES & SINCLAIR 1982; SINCLAIR 1988).

MCQUINN (1997) concluded that neither the discrete population concept nor the dynamic population concept adequately explains all data associated with herring population structure and dynamics. He found that the weakness in the dynamic balance population concept lies in the lack of an explanation for the temporal persistence and integrity of populations. Therefore he unified the discrete and dynamic balance population concepts and argued that Atlantic herring population structure and dynamics are best described by the metapopulation concept. He forwarded an 'adoptedmigrant' hypothesis, in which the principal characteristics responsible for the structure, persistence and integrity of a population are of behavioural rather than genetic nature. The hypothesis proposes that local herring populations, which are formed through straying from existing populations (colonisation), are perpetuated in geographic space through the social transmission of migration and homing patterns from adults to the recruiting juveniles in the year preceding first spawning. This implies that learning of spatial structures and not imprinting is important with respect to homing. The recruiting herring must learn from older, more experienced repeat spawners how to find the respective feeding, wintering and spawning grounds of the population. Thus, the hypothesis predicts that the tendency to disperse (stray) is stronger within the recruits, and diminishes with reinforcement of traditional migration and spawning patterns. Furthermore, it predicts that dispersion is more prevalent in unstable populations, i.e. following a population collapse or a recruitment boom.

Which of the existing population concept fits best with the dynamics of Norwegian spring spawning herring? The above mentioned studies of the herring stock discreteness are mainly related to Pacific herring and Atlantic herring along the Canadian coasts. There is a lack of discussion on the spawning dynamics of the Norwegian spring spawning herring in relation to the suggested population concepts. However, such a discussion is highly relevant, since this stock also distributes at a wide range of spawning grounds and spawning areas. The discrete population concept does not fit well with the observed spawning dynamics of this stock, since retention area or nursery area have negligible influence on the spawning distribution of adult fish (**Paper III**), and since the implication that strays will not successfully pass on their genes, is contrary to that indicated above (**Paper V** and **Paper VI**). Also the dynamics of Norwegian spring spawning herring differ from the dynamics of a metapopulation with respect to the importance of homing contra straying. In this respect McQuinn's concern about the persistence and integrity of local spawning populations, is not considered important. The present results indicate that a possible selection towards persistence and integrity of sub-populations of Norwegian spring spawning herring at different spawning grounds is overruled by the aim towards increasing the individual fitness. Thus, the dynamic balance population concept by SMITH & JAMIESON (1986) fits better to this stock than the metapopulation concept. The strong dynamics demonstrated in this stock indicate that homing to specific spawning grounds could be more of an assurance to find a spawning location with suitable environmental conditions with respect to bottom substrate and temperature, rather than an assurance to maintain population integrity. This implies that all spawning contributes to the same gene pool regardless of the selected spawning ground (**Paper V**), as long as it is within the vicinity of the coastal current allowing for distribution into coastal and Barents Sea nursery areas (**Paper III**), whereas the spawning success with respect to fitness may differ with the selected spawning ground (**Paper V** and **Paper VI**).

STATE-DEPENDENT MIGRATIONS IN RELATION TO LEARNING

Paper V and **Paper VI** and previous studies on the dynamics of this stock (DEVOLD 1963; DEVOLD 1968; JAKOBSSON 1968; DRAGESUND 1970a; DRAGESUND & al. 1980; DRAGESUND & al. 1997; HAMRE 1990; RØTTINGEN 1990, 1992) are in agreement with MCQUINN (1997) with respect to the importance of learning rather than imprinting to establish migration patterns, and that straying to new areas increases in unstable populations and in recruits compared to repeat spawners. In the context of homing to suitable spawning grounds, feeding grounds or wintering grounds, or in the context of exploring new spawning grounds, feeding grounds or wintering grounds, the learning associated with migration may have at least two different aspects, which both contribute to the strong dynamics of the stock.

First, in the absence of older repeat spawners to show their way the recruiting herring may deviate from a particular migration pattern, as also suggested by MCQUINN (1997). This may explain the migration behaviour observed in 1963, when a group of recruits mainly belonging to the strong 1959 year class commenced spawning at Lofoten, and feeding and wintering in the open sea to the north of Lofoten (DEVOLD 1968; JAKOBSSON 1968). They could have been herring leaving the Barents Sea nursery area without finding older 'teachers' showing them the migration route. This migration pattern was, however, only maintained until the summer in 1966, when the unit joined the main part of the stock wintering to the east of Iceland and spawning off Møre. In addition, data from the stock decline period emphasise the importance of learning to establish migration patterns. Two different components of immature herring survived the heavy exploitation in the 1960's, one in the Barents Sea and one at the west coast of Norway (DRAGESUND & al. 1980; HAMRE 1990; HOLST 1991). Both components spawned for the first time in 1973; the northern component spawned off Lofoten and the southern component spawned off Møre. In the following years the two components developed as separate units with different spawning grounds, feeding areas and wintering areas. The northern component spawned from northern Møre to Lofoten, whereas the southern component spawned at southern Møre earlier in the season. Both components fed off the coast, but the northern component distributed farther north and wintered in the Vestfjorden area, whereas the southern component wintered in fjords at Møre. It must be emphasised that the examples of high homing rates to particular spawning grounds in Norwegian spring spawning herring (DRAGESUND & al. 1980; HAMRE 1990; HOLST 1991), are obtained from tagging experiments on these two components. The low abundance and different migration patterns of the components probably reduced the mixing of shoals, and thus prevented the herring from learning 'new' migration routes. Local fjord herring stocks mixed to some extent with the two components in the wintering areas (HAMRE 1990). Thus, it is possible that the Norwegian spring spawners were guided by these local herring to their wintering areas. However, when the stock size increased, with the recruitment of the strong 1983 year class, the separation between the two different components disappeared. Wintering was established within the

Vestfjorden area, whereas during the spawning season the stock was distributed all over the Møre shelf area and northwards at Haltenbanken and Sklinnabanken (HAMRE 1990; RØTTINGEN 1990).

A second aspect of learning in relation to migration is that recruits, small herring or herring in bad condition, might be unable to follow their 'teachers' of larger size and in better condition. This is likely with respect to the size dependent migration speed in fish (BLAXTER 1969; WARE 1975, 1978), size segregation of fish in shoals (PITCHER & PARRISH 1993), hydrodynamic advantages of swimming close to neighbours of similar size (PITCHER & al. 1985), and the size dependent energetic costs of migration (**Paper I**). Instead these individuals with less migration potential may stop at suitable spawning grounds closer to the starting point of the migration (the wintering area), in accordance with **Paper V** and **Paper VI**. Analogously, larger fish and fish in good condition may be attracted to similarly disposed conspecifics, and thus be guided to another spawning ground than the previous one.

SUMMARY AND CONCLUSIONS

The results of the present thesis indicate that spawning migration in Norwegian spring spawning herring may be influenced by the following aspects of population structure: the size of the population, the age and length composition, the composition with respect to nursery area of origin, and composition with respect to body condition (amount of energy reserves).

Energy storage seemed to be of great importance both with respect to gonad development and migrations during the non-feeding wintering and spawning season. The spawning migration was particularly energy demanding compared to the stationary wintering period. The relative energy expenditure decreased with fish length, and in addition the larger fish had higher storage energy capacity. This apparently influenced the reproductive investment and migration distance of the herring.

At any time during the maturation period the maturity level increased with fish length up to approximately 32 cm, after which it stabilised. This suggests that in Norwegian spring spawning herring the recruits spawn with a delay compared to the repeat spawners, whereas there are no length dependent spawning time within the repeat spawners. Consequently there will mainly be two distinct spawning waves related to the length composition of this stock. This is contrary to other investigations, which have indicated that both Pacific herring (WARE & TANASICHUK 1989, 1990). and Atlantic herring (LAMBERT 1987; LAMBERT & MESSIEH 1989) spawn in a decreasing order of size throughout the entire size spectrum, resulting in up to four spawning waves. However, the present thesis demonstrates that spawning may be delayed with decreasing fish condition, which suggests that spawning waves also could be formed based on differences in individual energetic state.

Herring migrated from wintering grounds in the Vestfjord system (68°N), northern Norway, towards spawning grounds along the coast from Lofoten (70°N) to Lista (58°N), a range of approximately 1500 km. A migration model quantified the fitness related to the distance of the spawning migration, southwards or northwards from the wintering area, and individual size of the herring. The larvae hatched farther south were predicted to drift through higher temperatures, and thus have higher survival probabilities. Taking these benefits of migration and the corresponding costs of migration into account, the optimal spawning grounds were predicted within the vicinity of Møre or farther to the south, and they were predicted farther to the south with increasing fish size. The model was supported by the field data, in which the distance migrated to spawn increased with fish size and condition.

Tagging experiments on Pacific herring (HOURSTON 1982) and Atlantic herring (WHEELER & WINTERS 1984) have demonstrated high return rates to specific spawning grounds. This has led to a general consensus that the herring maintains population integrity and persistence by repeatedly returning to spawn (i.e. home) with high precision at specific spawning grounds (MCQUINN 1997). Due to this homing tendency Pacific herring along the coast of Canada and USA are managed as units within each spawning area (TRUMBLE & HUMPHREYS 1985, HAY & KRONLUND 1987; HAY & MCCARTER 1997), and it has been proposed that also Atlantic herring should be managed in a similar way (DOUBLEDAY 1985; SINCLAIR & al. 1985). However, although Norwegian spring spawning herring utilise a wide variety of spawning grounds along the Norwegian coast, such a management strategy has not been considered appropriate in this stock, and the conclusions of the present study indicate that this is unlikely a successful option. It was clearly demonstrated that this stock distributes at all spawning grounds regardless of nursery area of origin, which contrasts with the idea that spawning grounds are associated with specific larval retention areas, and that reproductive isolation is maintained by natal homing (SINCLAIR 1988). In fact, the demonstrated dynamics of spawning migration in Norwegian spring spawning herring, indicate that the precision of homing to particular spawning grounds, whether it is natal homing or simply repeat spawning, will not be a crucial factor in the life history strategy of this stock. However, this stock may have some tendency towards homing as an assurance to find suitable spawning grounds.

Apparently the Norwegian spring spawning herring are quite different from those stocks of the north-west Atlantic and north-east Pacific. It is to a larger extent a migratory stock. Consequently it may also have other strategies, which could include more extensive mixing and straying between spawning grounds as influenced by learning, migration constraints and the aim towards increased fitness. Such strategies will evidently prevent the establishment of persistent sub-populations with their own integrity within each spawning ground.

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