

Size dependency in the migrations and distribution of Norwegian spring spawning herring

By Aril Slotte

The size at first spawning is comparatively larger in Norwegian spring spawning herring (*Clupea harengus* L.) than in other herring stocks in the Atlantic and Pacific oceans. This is probably an adaptation to a life with long seasonal migrations between wintering-, spawning- and feeding grounds. The present paper presents empirical data and model results suggesting that also historic long-term shifts and annual variations in migrations and distribution pattern may be attributed to size dependency.

Keywords: herring, migration, spawning, distribution, size dependency.

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INTRODUCTION

Within herring populations the environmental preferences favouring the survival of eggs and larvae may be specific, leading to spawning at specific locations and times (Haegele and Schweigert 1985). In the case of Norwegian spring spawning herring (*Clupea harengus* L.) (NSS herring) it is in particular banks and shelf areas with stony or rocky bottom and depths less than 250 m that are utilised for spawning (Runnstrøm 1941b, Dragesund 1970a). Such areas are distributed at range of approximately 1500 km along the Norwegian coast between 58°N and 70°N. Traditionally the most important spawning grounds are found from north to south at Lofoten, Træna, Sklinnabanken, Haltenbanken, Frøyabanken, and along the districts of Møre, Sogn, and Rogaland. In recent years the NSS herring stock has recovered from a nearly distinct state in the late 1960s. Simultaneously the stock has changed its feeding and wintering areas and hence the migration routes to the spawning grounds. Prior to the stock decline the herring spent the summer feeding season in the Norwegian Sea, whereas the wintering occurred to the east of Iceland (Fig. 1) The herring had to cross the open waters of the Norwegian Sea before entering the Norwegian west coast to find the spawning grounds. After the stock decline oceanic feeding- and wintering areas were abandoned, and instead the herring spent the entire year in Norwegian coastal waters and fjords (Fig. 2) (Dragesund et al. 1980, Hamre 1990, Røttingen 1990). When the large 1983-year class recruited in 1988, wintering commenced in Vestfjorden, Tysfjorden and Ofotfjorden (Vestfjorden system), northern Norway (Fig. 3), and for the first time in 30 years they started to utilize the southernmost spawning grounds. Furthermore, after the recruitment of the large 1991- and 1992-year classes the feeding area was once again extended far westwards into the Norwegian Sea (Dragesund et al. 1997, Misund et al. 1998). At present NSS herring (*Clupea harengus* L.) spend the feeding season April-August covering large areas of the Norwegian Sea, but in September they gather as a rather homogenous mass in the Vestfjorden system (Fig. 4). When the spawning migration begins in mid January they split up again heading for spawning grounds located with different migration distances, from Lofoten in the north to Lista in the south.

The present paper is review of empirical data and model predictions suggesting that the historic long-term shifts and also annual variations in migrations and distribution pattern may be attributed to size. This is also discussed in relation to established population concepts.

EMPIRICAL DATA

Feeding migration

After the stock recovered and distributed into the Norwegian Sea an international several nations have carried out acoustical surveys in this area during May every year. Data from trawl samples taken during these surveys indicate that the size of the fish tends to increase westwards from the coast, i.e. the largest fish migrate the longest distance to feed (Fig. 6).

Spawning time

SLOTTE & AL (1999) demonstrated that the maturity level and spawning time of NSS herring 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. 7). 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 to 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.

The results of SLOTTE & AL (1999) 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 & AL 2002), also showed similar results. On the other hand the conclusions of Slotte (1999a) 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 SLOTTE & AL (1999) 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 SLOTTE & AL (1999) 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 SLOTTE & AL (1999) 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 SLOTTE & AL. (1999); I_G . SLOTTE & AL (1999) 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. SLOTTE & AL (1999) 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. Slotte (1999b) 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 & AL.2002). 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.

Selection of spawning grounds

SLOTTE (1999b) 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, SLOTTE (1999b) 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.

The main result of SLOTTE (1999b) 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. 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 ($\text{kJ} \cdot \text{km}^{-1}$) 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 (Fig. 8). These results clearly demonstrate the benefits of being large and/or in good condition with respect to the spawning migration in this stock.

SLOTTE (1999a) demonstrated that fish length and condition in 1996 and 1996 increased southwards, but the condition appeared to be the most important variable influencing the migration distance. Corresponding with the southward increase in body length and condition, the maturity level also increased. Thus, the delay in maturation was probably reflected by lower body length and lower body condition of the fish (Slotte et al 1999). 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 et al. 2002), 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 et al (2002) 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.

The size-dependent spawning migration indicated by the field study in Slotte (1999a), was supported by 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 Siragrunden 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 and consequently some herring could have reduced the migration distance this year.

Furthermore, data from 1997-2000 (SLOTTE & DOMMASNES 1997, 1998, 1999, 2000) 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 Siragrunden (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 (SLOTTE 1999b), 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.

In Slotte (2000) the migration distance from the wintering grounds to the spawning grounds was calculated as a midpoint weighted by acoustic abundance for each year class over the entire period 1994-2000. These data indicate very clearly that a year class migrate a longer distance to spawn as it grows to be older, whereas it may reduce the distance in periods with low condition (Fig. 9).

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 Faeroes 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 (Fig. 6) (ANON. 1995, 1996, 1997), 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 & LEGGETT 1981a, b), cisco (*Coregonus artedii*) 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 were 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 (SLOTTE AND FIKSEN 2000). 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 & ROSENAL 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.

MODEL PREDICTIONS

In SLOTTE & FIKSEN (2000) 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 Slotte (1999a) and Fig. 6; 2) the length specific migration costs estimated in SLOTTE (1999B); 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. 10). 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.

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 (Fig. 11). 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. 12). 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. This was also demonstrated by the model by sensitivity analysis with condition as varying factor.

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 & ROSENAL 1981). Reduced density may also reduce competition for food among larvae (KIØRBOE & al. 1988).

SIZE-DEPENDENT MIGRATIONS IN RELATION TO POPULATION CONCEPTS

The results presented 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 & KORNFELD (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 Columbia 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 'adopted-migrant' 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? Slotte (2001) demonstrates the neither the discrete nor the metapopulation concept fits well with the observed dynamics. 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 (HOLST & SLOTTE 1998), and since the implication that strays will not successfully pass on their genes, is contrary to that indicated above (SLOTTE 1999A, SLOTTE & FIKSEN 2000). 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 (SLOTTE & FIKSEN 2000), as long as it is within the vicinity of the coastal current allowing for distribution into coastal and Barents Sea nursery areas (HOLST & SLOTTE 1998), whereas the spawning success with respect to fitness may differ with the selected spawning ground (SLOTTE 1999A, SLOTTE & FIKSEN 2000).

SIZE-DEPENDENT MIGRATIONS IN RELATION TO LEARNING

SLOTTE (1999a), SLOTTE (2001), SLOTTE & FIKSEN (2000) 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 (Fig. 1), 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 (Fig. 2). 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 (SLOTTE 1999b). 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 SLOTTE (1999)a and SLOTTE & FIKSEN (2000). 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.

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FIGURES

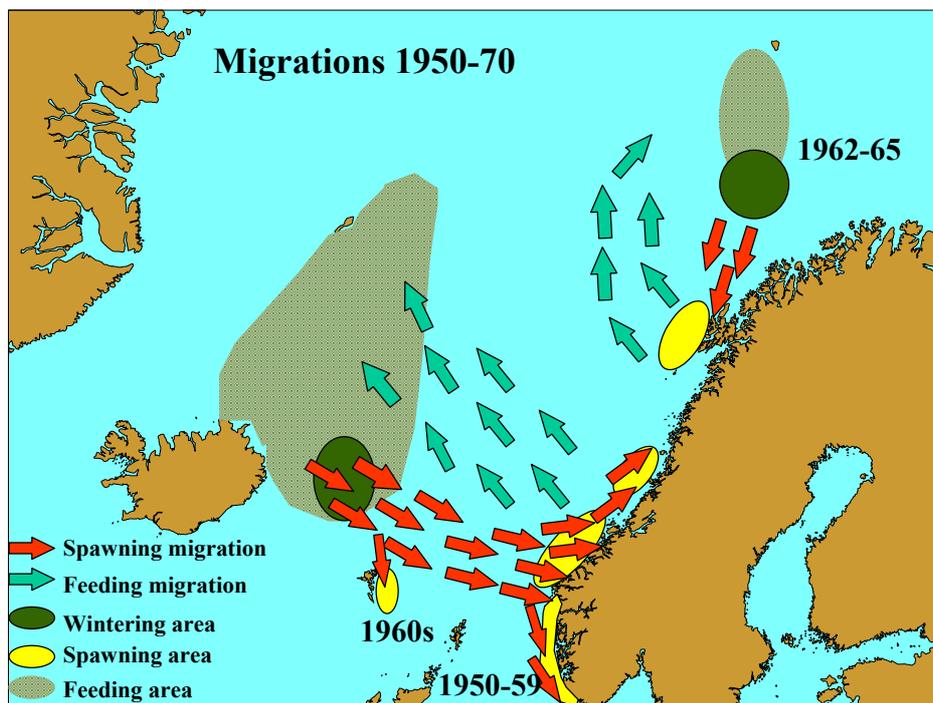


Figure 1. Seasonal migrations of NSS herring prior to the stock collapse in the late 1960s.

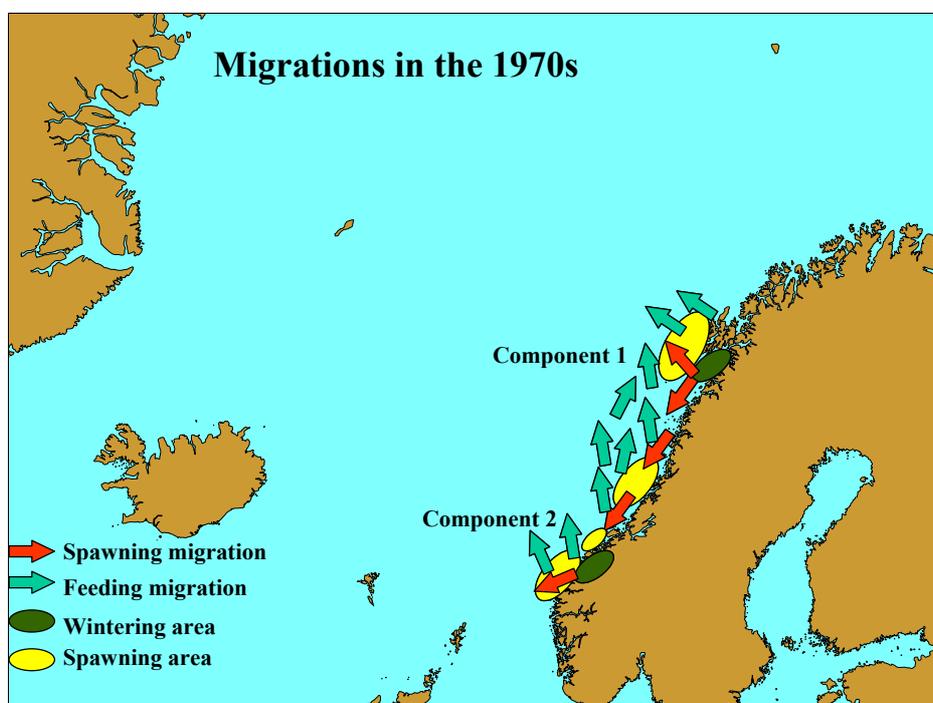


Figure 2. Seasonal migrations of NSS herring after the stock collapse in the late 1960s.

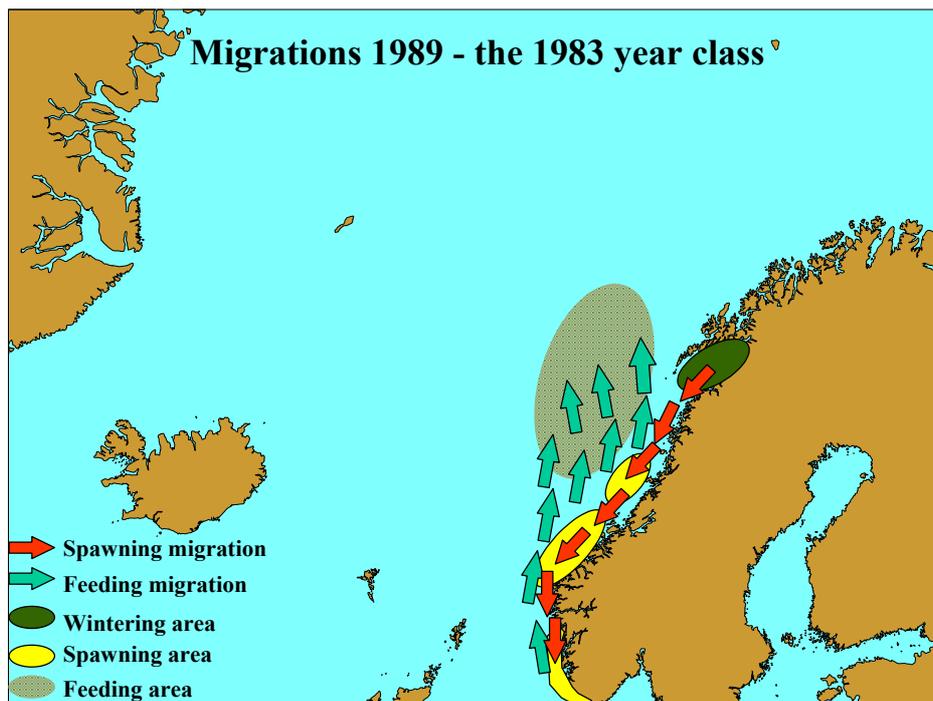


Figure 3. Seasonal migrations of NSS herring in 1989; the strong 1983 year class.

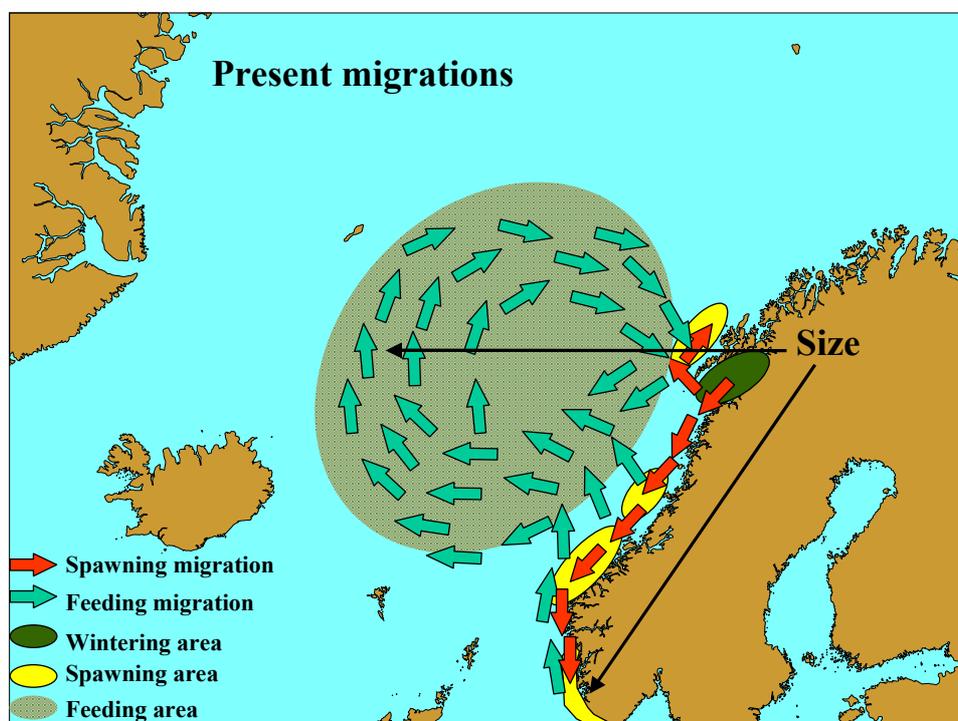


Figure 4. Present seasonal migrations of NSS herring; both feeding- and spawning migration is dependent on the size of the fish.

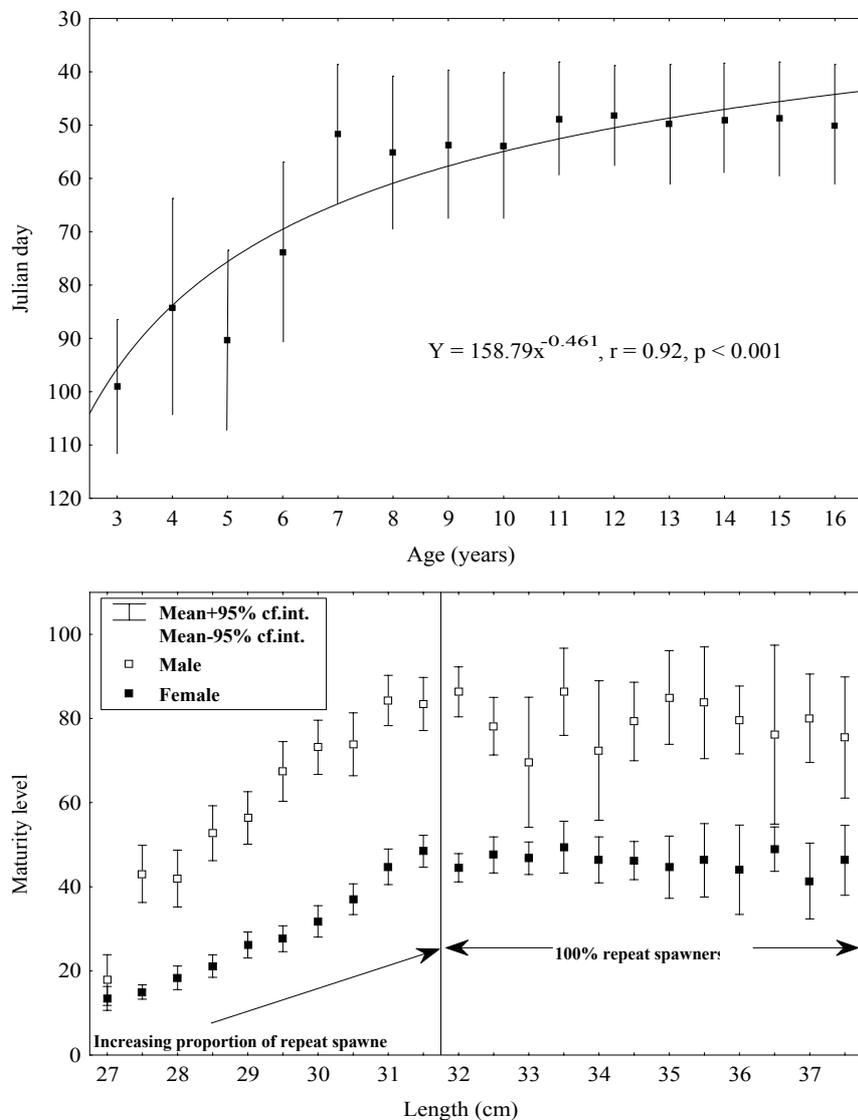


Figure 7. The relation between weighted mean date (\pm SD) for peak of maturity stage 6 (spawning) and age for Norwegian spring spawning herring in 1934. Adapted from Lambert (1987), who did the calculations based on data from Runnström (1941a). Bottom: The relation between body length and maturity level (I_G) in male ($n = 815$) and female ($n = 895$) herring from the wintering area in December 1996. Mean values \pm 95 % confidence limits ($n \geq 3$). The length groups to the right of the dotted line are assumed to be repeat spawners. Adapted from Slotte et al. 2000.

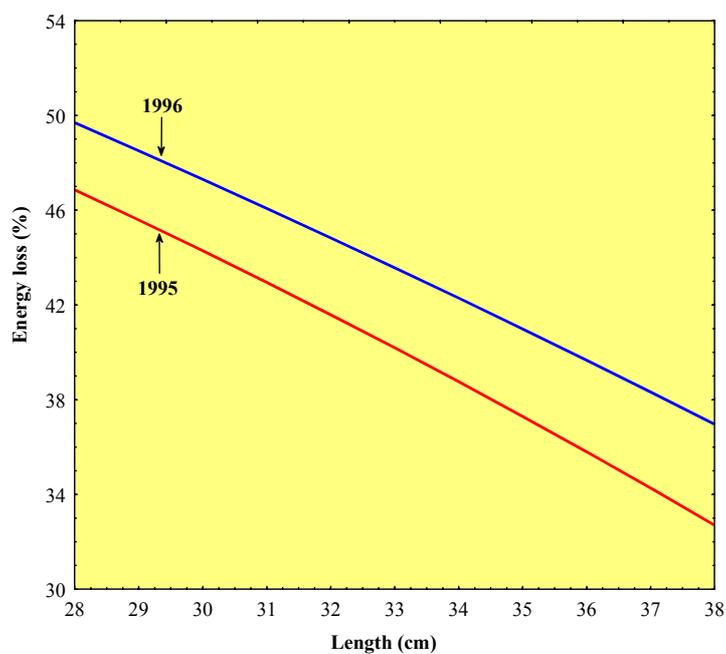


Figure 8. Energy loss (%) in relation to body length of NSS herring during 800 km migration from wintering Vestfjorden (northern Norway) to the main spawning grounds off western Norway. Examples from 1995 and 1996. The condition was in a decreasing trend from 1995-1998, which caused a higher energy loss than in 1996 than in 1995. Adapted from Slotte 1999b.

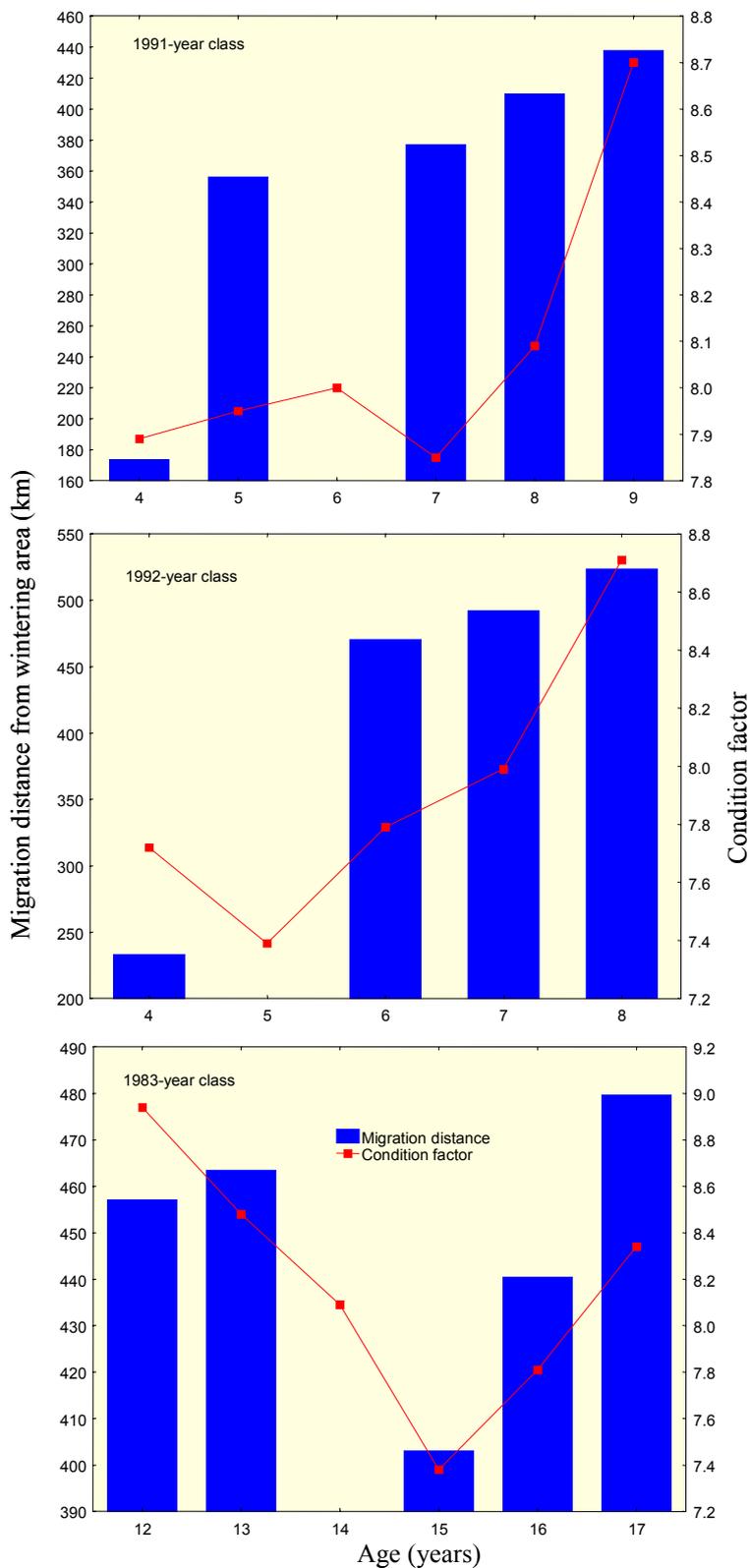


Figure 9. Migration distance (weighted by acoustic abundance) of NSS herring southwards from wintering grounds in Vestfjorden to spawning grounds along the coast in relation to age and condition of the fish. Examples from year classes recruiting to the stock (1991 and 1992-year classes and old herring (1983-year class). Adapted from Slotte (2001).

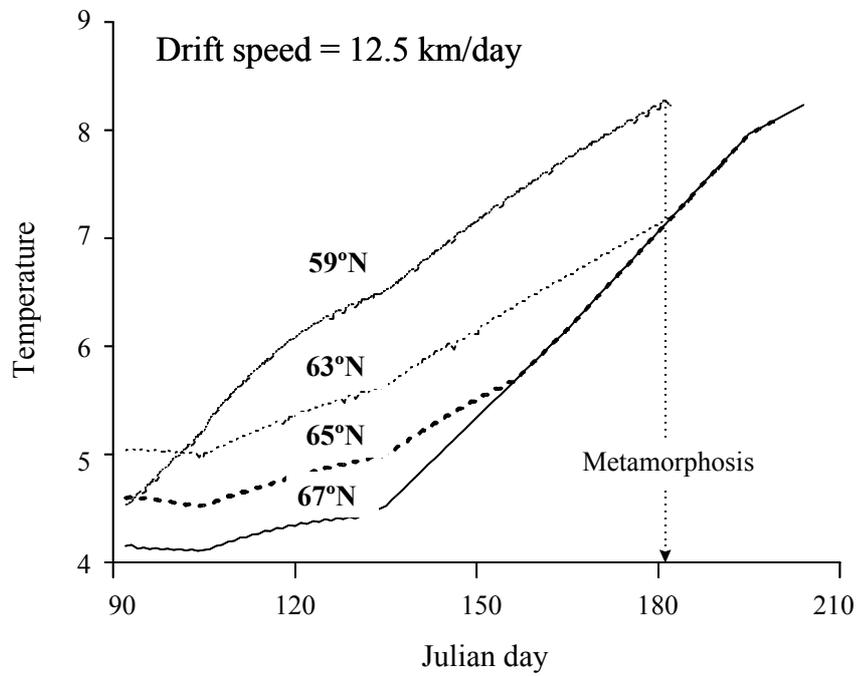


Figure 10. Temperature trajectories at 10 m depth and the corresponding larval stage duration given hatching at different locations and average drift speed. Adapted from the model by Slotte and Fiksen (2000).

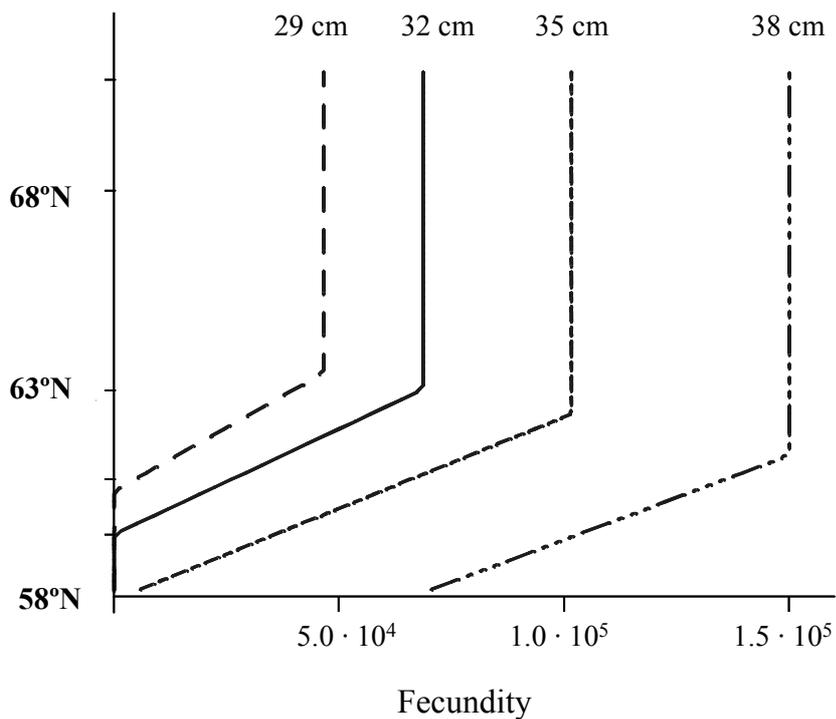


Figure 11. Fecundity of herring related to length and migration distance. Estimated for herring in average condition. Fecundity is reduced when the energy for migration is emptied Adapted from the model by Slotte and Fiksen (2000).

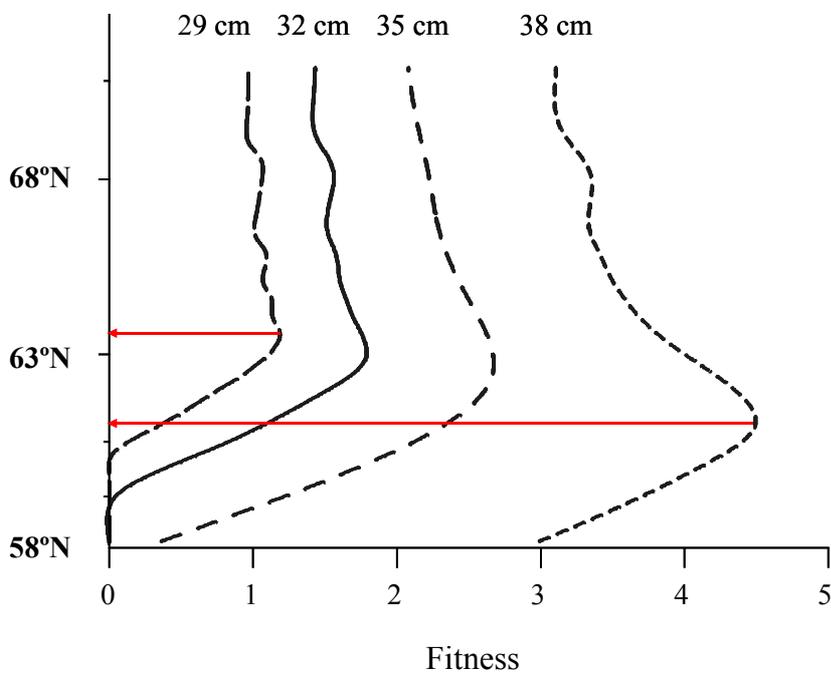


Figure 12. Location of the optimal spawning ground by length of herring in average condition. Migration starts at 68°N. Adapted from the model by Slotte and Fiksen (2000).