PAPER V

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

THE SPAWNING MIGRATION OF NORWEGIAN SPRING SPAWNING HERRING (*CLUPEA HARENGUS* L.): A STATE-DEPENDENT TRADE OFF?

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ABSTRACT

The spawning migration of Norwegian spring spawning herring originates from the wintering area in Vestfjorden, northern Norway. The herring may choose between spawning grounds spaced out southwards along the coast from Lofoten (next to Vestfjorden) in the north to Siragrunnen in the south, a range of approximately 1500 km. The migration is 'upstream' against the coastal current, and larvae drift northwards to nursery areas along the coast and in the Barent Sea. The spawning herring is observed to distribute according to size, larger fish and fish in better condition migrate farther south.

In this paper we explore the hypothesis that spawning distribution of Norwegian spring spawning herring could be understood as a trade-off between the costs of migrating and benefits of spawning farther south, where the hatched larvae encounter warmer water leading to higher survival. We present a simple model quantifying fitness related to the distance of the spawning migration and individual size of the herring. The model predicts that the optimal spawning ground is found farther south with increasing individual fish size, and that higher mortality rates make southern spawning more profitable. In addition, increased larval retention enhances larval survival and shifts optimal spawning grounds to the north.

Key words: Herring, migration, spawning, temperature, larvae, survival, fitness.

INTRODUCTION

In recent years the Norwegian spring spawning herring stock has recovered due to the strong 1983 year class. Since this year class matured in 1988 the spawning stock biomass increased to about 5 million tons in 1995, and the strong 1991 and 1992 year classes increased the spawning stock further to about 9 million tons in 1996 (Anon., 1997). Since 1988 the stock has utilised a fjord system (Vestfjorden, Tysfjorden and Ofotfjorden) in northern Norway as wintering area during September-January (see Fig. 1). The spawning migration has started in mid January and spawning has taken place in March-April mainly on the shelf area off Møre and to some extent northwards, particularly at sites like Frøyabanken, Haltenbanken, Sklinnabanken, Træna and Lofoten (Slotte, 1998). Only a minor part of the stock has migrated past Stadt to the traditional important spawning grounds at Karmøy, Egersund and Siragrunnen (Johannessen et al., 1995; Røttingen and Slotte, 1998). The southward

spawning migration follows the slope of the Norwegian continental shelf (Slotte, 1998), while the Norwegian coastal current runs the opposite direction (Fig. 2) at depths down to 150 m, at a maximum speed of 100 cm · sec^{-1} and at a mean speed of 15-40 cm · sec^{-1} (Aure and Østensen, 1993). Thus, the spawning migration of Norwegian spring spawning herring is 'upstream' analogous to spawning migration as in anadromous fish, and hatched larvae will drift with the coastal current to nursery areas along the coast and in the Barent Sea.
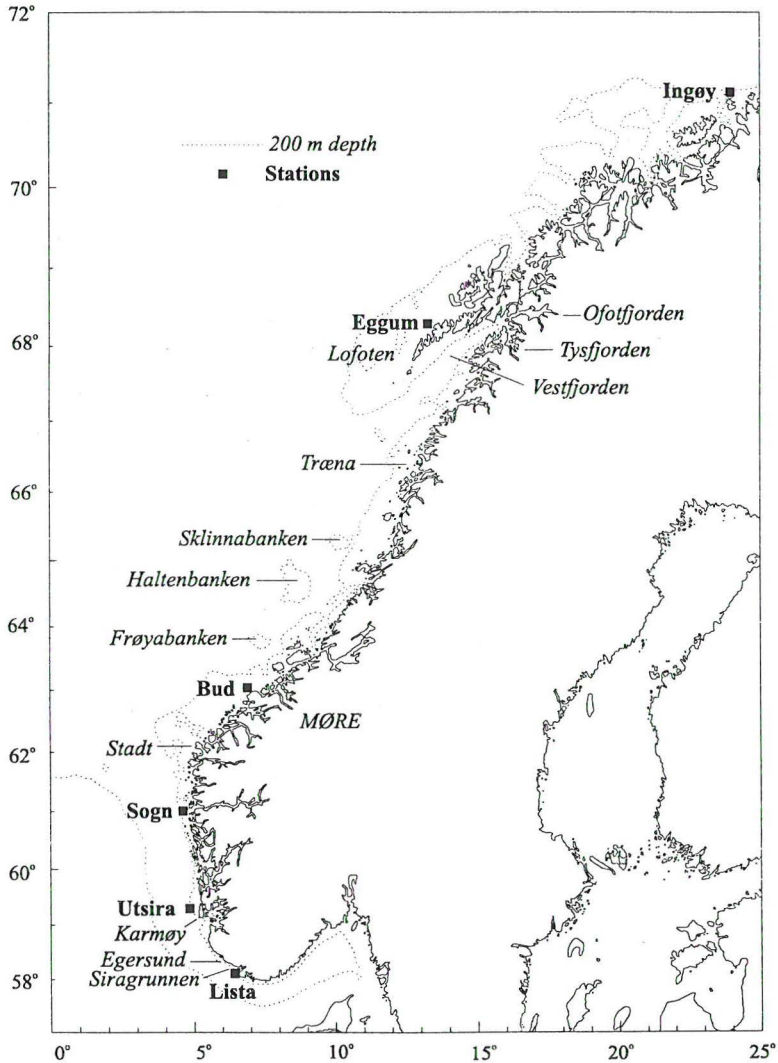

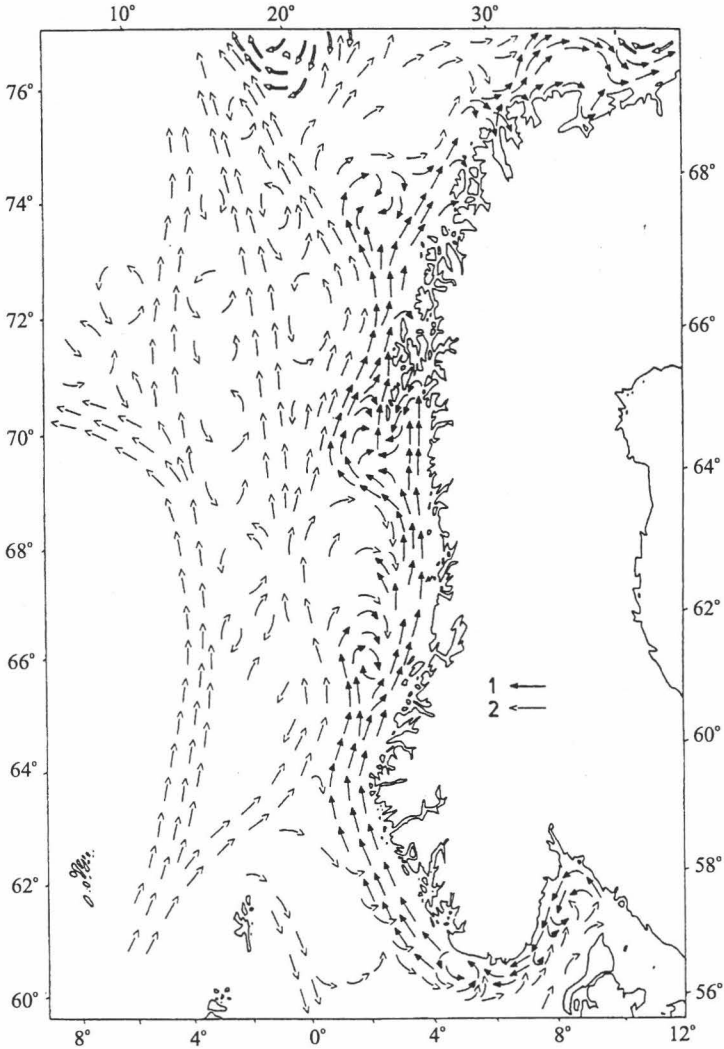Fig.1. Locations referred to in text and figures. Temperature stations are outlined.

Fig. 2. Coastal currents (1) and Atlantic currents (2) along the Norwegian coast (from Aure and Østensen, 1993).

The herring does not feed during the period from the arrival in the wintering area in September-October until the end of spawning in March-April (Slotte, in press). The energy expended on maturation, swimming and metabolism is taken from reserves stored during the feeding period in summer. There is an estimated difference in migration distance between the northernmost (Lofoten) and southernmost (Siragrunnen) spawning grounds of approximately 1500 km, given that migration follows the continental slope (Slotte, 1998). Field studies have shown that the herring suffer a great energy loss during spawning migration, and that the energy expenditure decreases with increasing fish

size (Slotte, in press). This also seems to influence the spawning migration of the stock. The herring arrives at spawning areas in decreasing order of length and body condition, and in addition the length and body condition at the spawning grounds increases with the migration distance from the wintering area (Slotte and Johannessen, 1997; Slotte, 1998).

We hypothesise that the spawning distribution could be understood as a state dependent trade-off between costs of migrating and benefits of spawning further south. We connect the benefits of southern spawning to higher temperatures (Aure & Østensen, 1993), which is known to increase larval growth (Houde 1989; Morse 1989). Houde (1989) found that rising temperature resulted in increased mortality rates and growth rates of fish larvae, and consequently decreased larval stage duration. The highest variability in stage duration was observed at low temperature (similar to Norwegian waters). He concluded that small changes in growth rate could induce large changes in stage duration when temperature is low. This may affect the recruitment process significantly since the larval mortality is strongly size dependent (McGurk, 1986).

The main purpose of this study is to test our hypothesis about state-dependent trade off during spawning migration. This is done by presenting a simple model quantifying the costs and benefits in terms of fitness related to the distance of the spawning migration and individual size of the herring. An additional purpose is to test for differences in larval survival and fitness between two larval mortality rates, one connected to temperature (Houde, 1989) and another to larval size (McGurk, 1986), and with different larval drift speeds along with the coastal current.

MODEL

SWIMMING COSTS AND STRUCTURE OF ADULT HERRING

The model was spatially resolute into 72 possible spawning grounds from Ingøy in the north to Lista in the south (Fig. 1), i. e. one location for every 25th km. The cost of spawning migration was estimated taken from data on energy content in Vestfjorden prior to the spawning migration (November 1994) and off Møre after the spawning migration (February 1995) (Slotte, in press). The energy content $E(l)$ (kJ) for herring of length l (cm) in the wintering area was found to be $E_v = 100.012 \cdot e^{0.11l}$ (n = 114, r^2 = 0.95, p < 0,001), and after the spawning migration to Møre it was $E_m = 33.834 \cdot e^{0.133l}$ (n = 90, r^2 = 0.86, p < 0,001). The difference between each length group was transformed to a cost per km $c(l)$ (kJ $\cdot$ km^{-1}), with distance migrated = 800 km, $c(l) = (E_v(l) - E_m(l)) \cdot 800^{-1}$. The migration costs were clearly size dependent; the relative costs were lower for larger herring, though absolute costs were higher.

Norwegian spring spawning herring is highly iteroparous and may live for more than 20 years and spawn up to 15 times. It will not exhaust itself completely during spawning activity, therefore we constrained migration costs and gonad production by a lower threshold of energy depletion from the winter level. It has been suggested that anadromous fish will not survive after spawning if more than 60 % of the initial energy (before migration) is utilised (Glebe and Leggett, 1981 b), or if fat content is reduced below a limit of 2% (Jonsson et al., 1997). While anadromous fish often pass these limits and die, the herring is much more conservative and have on the average around 10 % fat left after spawning (Slotte, in press). Thus, the lower threshold of energy (q) was chosen to be 20 % higher than that of anadromous fish, $q = 60\%$ of total energy content (including gonads) measured in Vestfjorden, in order to secure survival until next spawning.

The fecundity of an l cm long herring spawning at site d [km from wintering area] will then be

$$B(l,d) = \frac{(1-q)E_v(l) - c(l)d}{e} \qquad (1)$$

where e is the energy content of one egg. The energy content of an egg was estimated from data on fecundity, gonad weight (g) and egg energy density (kJ · g^{-1}). Fecundity data from Vestfjorden December 1996 (data from Oskarsson, 1998) was related to length as follows: $B(l) = 1.316 \cdot e^{0.112l} \cdot 1000$ (n = 76, r^2 = 0.80, p < 0,001). Gonad weight (W_g) prior to spawning of Møre in February 1995 was related to length as follows: $W_g(l) = 0.805 \cdot e^{0.13l}$ (n = 562, r^2 = 0.66, p < 0,001) (data from Slotte 1998). Given an energy density of 8 kJ · g^{-1} egg (McGurk et al., 1980), the energy of an egg was related to length as follows: $e(l) = W_g(l) \cdot B(l)^{-1} \cdot 8$. The egg energy increased from 0.0081 kJ to 0.0097 kJ for 28 cm and 38 cm fish respectively. Survival of herring larvae is known to increase with egg size (Blaxter and Hempel, 1963). This relation was not included in the model, and instead we chose to use a basic egg energy of 0.009kJ.

Physiological constraints limit the maximum load of gonads in each individual. Maximal energy in gonads related to length was estimated by adding 50% to the mean gonad energy, $G_{max}(l) = W_g(l) \cdot 8 \cdot 1.5$; an approach which agreed with the observed maximum values. This implies that of the total energy content in a mature herring some must remain after spawning $qE_v(l)$, and the rest may be used to build gonads (up to $G_{max}(l)$) or to migration $c(l)d$:

$$E_v(l) = qE_v(l) + eB(l,d) + c(l)d, \quad \begin{cases} q \geq 0.6 \\ eB(l,d) \leq G_{max}(l) \end{cases}. \qquad (2)$$

If the energy spent in migration exceeds $(1-q)E_v(l) - G_{max}(l)$, further migration will be possible only at the expense of reproduction $eB(l,d)$ (Fig. 3). Evidently, the cost of migrating from Vestfjorden to

the coast of western Norway depends heavily on length of the fish. The predicted numbers of eggs are within a reasonable range.
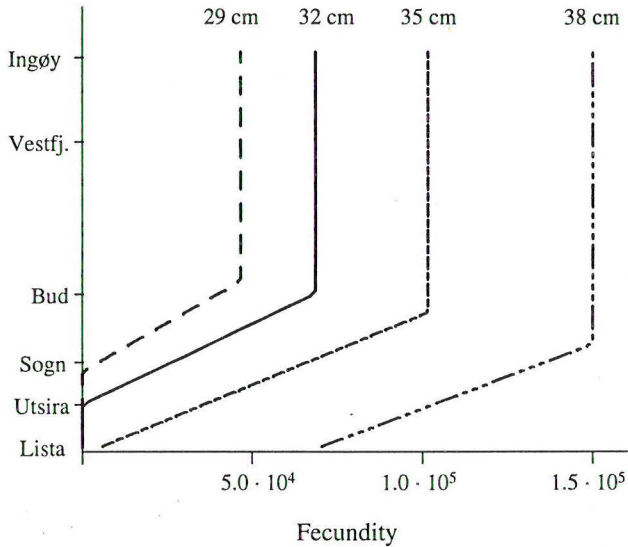

Fig. 3. Potential fecundity related to individual fish size and migration distance. The migration starts in Vestfjorden, and will proceed at the expense of fecundity after a certain distance.

LARVAL DRIFT, GROWTH AND SURVIVAL

Temperature is often considered the most important environmental factor in determining growth and mortality rates of fish larvae (Houde, 1989; Morse, 1989). Along the Norwegian coast, temperature has been measured continuously at fixed locations for decades (Aure & Østensen, 1993). We used a basic drift depth at 10 m in our model. At this depth the temperature is higher further south, particularly during summer (Fig. 4), and this difference may be a candidate to explain the efforts made by herring during migration (Slotte in press), i. e. the costs in terms of fecundity may be outweighed by enhanced larval survival in warmer waters. To analyse this possibility, we used data on larval growth g [d^{-1}] of Norwegian spring spawning herring at 5 different temperatures (4, 6, 8, 10 and 12°C) (Folkvord, Departement of Fisheries and Marine Biology, University of Bergen, Bergen, Norway, unpublished data) These data fitted to the logistic equation

$$g = \frac{0.419}{1 + 20.6e^{-0.57T}}, \qquad n=5, r^2=0.96, p < 0.001 \qquad (3)$$
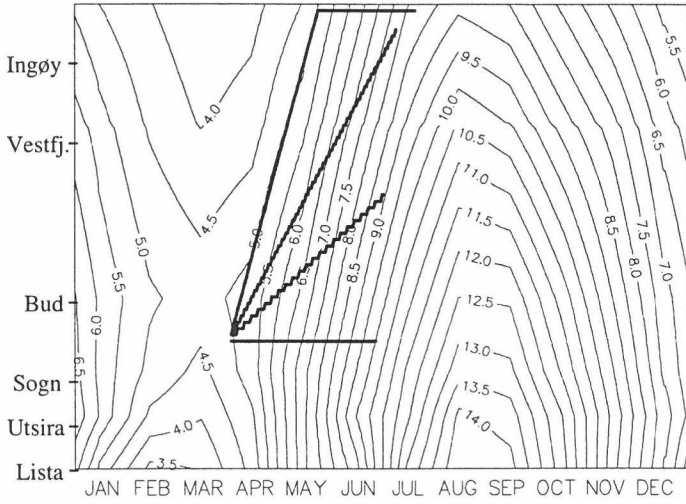
Fig. 4. Temporal and spatial distribution of temperature along the Norwegian coast at 10 m depth (see Fig. 1 for stations). Possible drift routes, given spawning off Møre, are given for 4 different drift speeds: 25 (top), 12.5, 6 and 0 (bottom) km · day⁻¹.

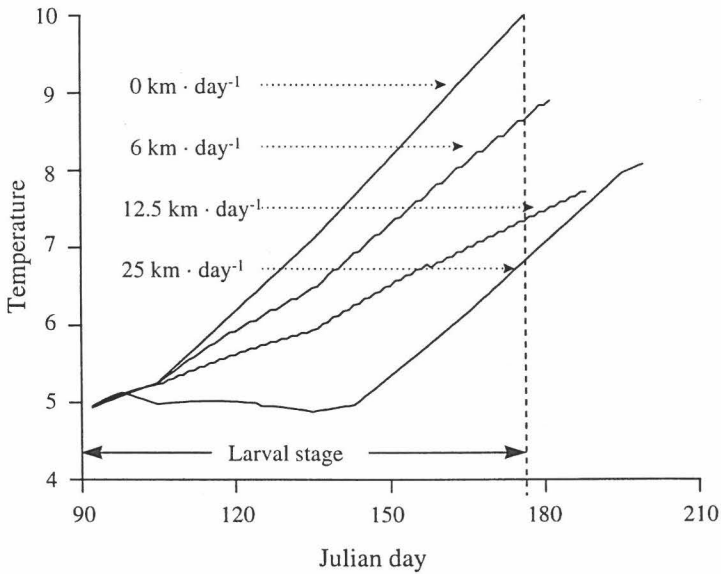Fig. 5. Temperature trajectories at 10 m depth (spawning off Møre) for four different drift speeds; 25, 12.5, 6 and 0 km · day⁻¹).

The larvae were reared under high food concentrations in the experiments (Folkvord, personal communication). In the present model, herring were initiated at hatching and traced until metamorphosis (3.5 cm). Age at metamorphosis is then a function of time and site at hatching and the drift route northwards in the coastal current. Some possible drift routes, given spawning off Møre, are imposed in Fig. 4, and the differences in larval stage duration and temperature history can be read from the trajectories in Fig.5. The temperature trajectories from different hatching sites along the coast, given equal drift, are given in Fig. 6. The Norwegian coastal current has an average velocity of 15-40 cm · sec^{-1} (Aure & Østensen, 1993), and as our basic drift value we used 30 cm · sec^{-1} (25 km · day^{-1}).
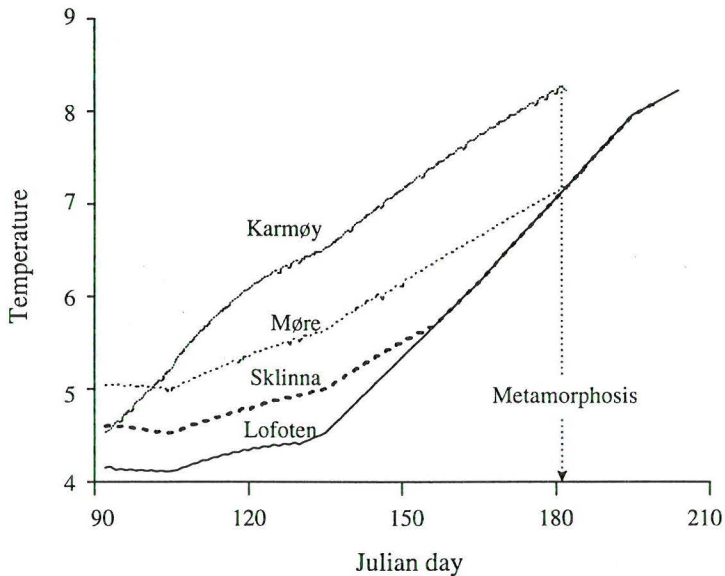

Fig. 6. Temperature trajectories at 10 m depth, given a drift speed of 12.5 km · day^{-1}, for larvae hatched at four different spawning grounds.

The major focus of our analysis is on the potential benefit of southern spawning. Mortality rates are high in fish larvae, and even marginal reductions in these will have large effects on fitness. However, mortality is variable and notoriously difficult to measure. We used two formulations of mortality of fish larvae μ [d^{-1}], one related to environmental temperature

$$\mu_H = 0.0256 + 0.0123T, \qquad\qquad n = 22, r^2 = 0.41 \qquad\qquad (4)$$

from Houde (1989), and one related to larval size

$$\mu_M = 2.2 \cdot 10^{-4} W^{-0.85}, \qquad\qquad n = 74, r = 0.58 \tag{5}$$

from McGurk (1986), where W is larval weight in g dry weight. Dry weights were obtained from length L [mm] by $W = 0.001 \cdot e^{-5.28 + 0.275L}$ (Folkvord, unpublished data). The probability of surviving to after metamorphosis $Ps(d, t)$ for a larvae can now be found from

$$Ps(d,t) = \prod_{0,A} \exp(-\mu) \tag{6}$$

where A is the number of days to metamorphosis, i. e. the time required to reach 3.5 cm for a larvae drifting in the coastal current, spawned at site d at time t.

FITNESS

The trade-off situation for a mature female herring is now evident; by migrating further south and 'upstream' the susceptible larval period will be reduced and such increase the number of progeny surviving larval period. The fitness $\Phi(l,d,t)$ of a herring of length l, spawning at site d at time t will be the number off eggs laid at d, $B(l,d)$, times the integrated probability of larval survival $Ps(d,t)$:

$$\Phi(l,d,t) = B(l,d)Ps(d,t). \tag{7}$$

From evolutionary principles, the selected spawning ground d^* should be the one providing highest fitness, and may not be the same for different size classes when costs of migration differs.

   The model assumes that there are no limits in food concentrations during the larval stage. The timing of spawning is probably tuned in to match the peak of plankton blooms (Cushing, 1975; Sinclair and Tremblay, 1984), so we limit simulations to this period of the year (April-June). However, we acknowledge that the food level may vary both on a temporal and latitudinal scale, but we have not been able to find quantitative studies on this element of larval growth.

RESULTS

Firstly, the model was run with a basic drift speed of 25 km · day (mean coastal current speed), two hatching times and in addition two mortality rates; one related to temperature and another to larval size (Fig. 7). The predicted probability of larval survival increased with the delay in hatching from 1-

15 April, when temperatures increased. The survival was highest when the temperature related mortality was utilised. However, size dependent mortality resulted in a higher variation on a latitudinal range, indicating a stronger correlation with the shifts in temperature. There was a main tendency towards an increasing survival at hatching locations southwards from Vestfjorden.
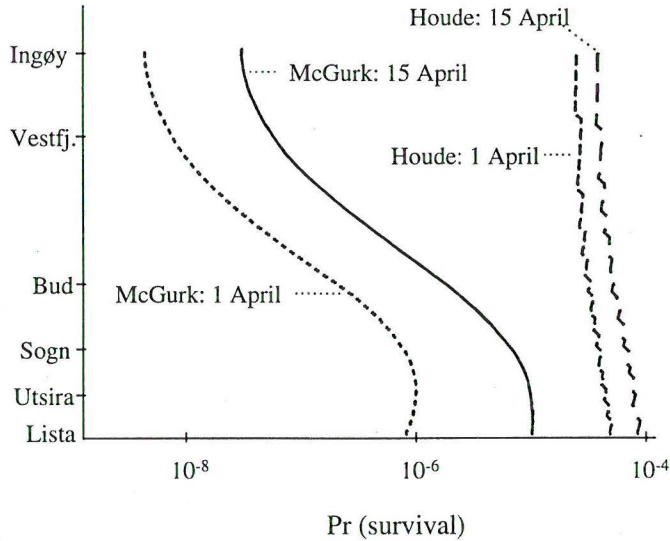

Fig. 7. Survival of larvae related to hatching time and place given a drift speed at 25 km · day⁻¹ and with two different mortality functions; temperature- dependent (Houde 1989) and size-dependent (McGurk 1986).

Secondly, the model was run with hatching time at 1 April, two mortality rates and three different larval drift speeds (Fig. 8 a, b). When the drift speed was lowered the predicted larval survival increased, i.e. the larva stayed for a longer period at higher temperatures. At the same time the optimal hatching location was moved northwards, i.e. energy was reallocated from migration to fecundity.

Thirdly, the optimal spawning location in terms of fitness of different sizes of herring was predicted using both mortality rates, basic larval drift and hatching day at 1 April (Fig. 9 a, b). As the fish size increased, the predicted optimal spawning ground was found farther south, i.e. larger fish can swim a longer distance before using potential egg energy (see also Fig. 3). Optimal spawning grounds were predicted farther south when the size dependent mortality rate was used. Given a size dependent mortality, the predicted fitness north of Møre was very low for all fish sizes, while the fitness was quite stable north of Møre when temperature dependent mortality was utilised.
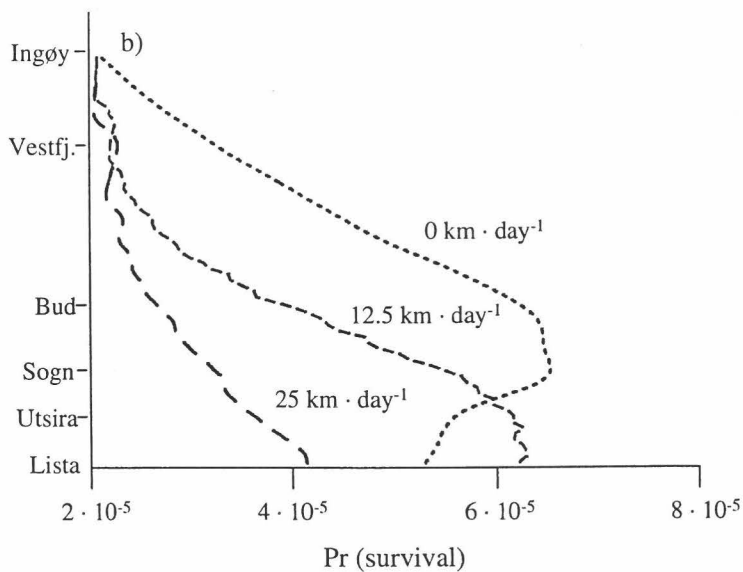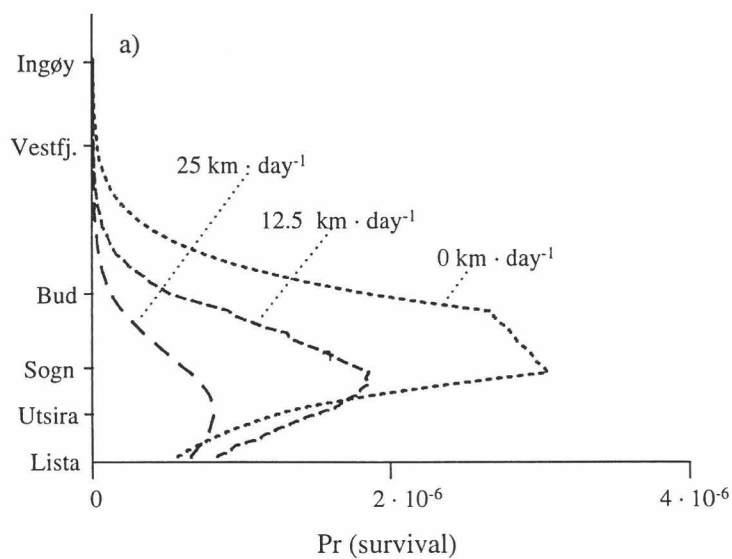
Fig. 8. Survival of larvae (hatched at 1 April) related to hatching site, given three different drift speeds and two different mortality functions: a) McGurk (1986) and b) Houde (1989).
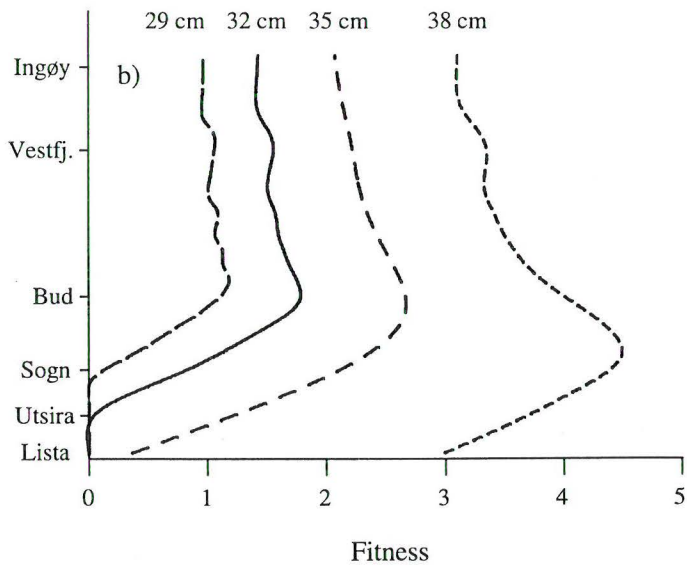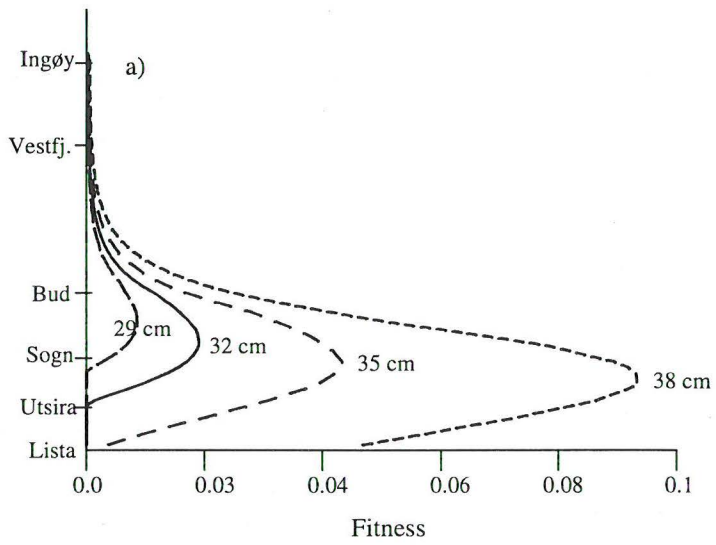
Fig. 9. Fitness of herring related to spawning ground and individual fish size given a larval drift speed at 25 km · day⁻¹ and two different mortality functions: a) McGurk (1986) and b) Houde (1989).

At last the optimal spawning grounds for different size groups was summarised through various simulations (Fig. 10). Simulation 1 and 2 were similar to the results given in the previous paragraph (Fig. 9 a, b). Simulation 3 and 4 were run with a spatially homogeneous low and high mortality and a basic larval drift. A shift from low to high mortality resulted in a shift of optimal spawning ground southwards, which illustrated the importance of increasing the growth and decreasing the larval stage duration under such conditions. Simulation 5 and 6 illustrated the same results as in Fig. 8 a, i.e. the optimal spawning ground was shifted northwards when the larval drift, and hence mortality, was decreased.
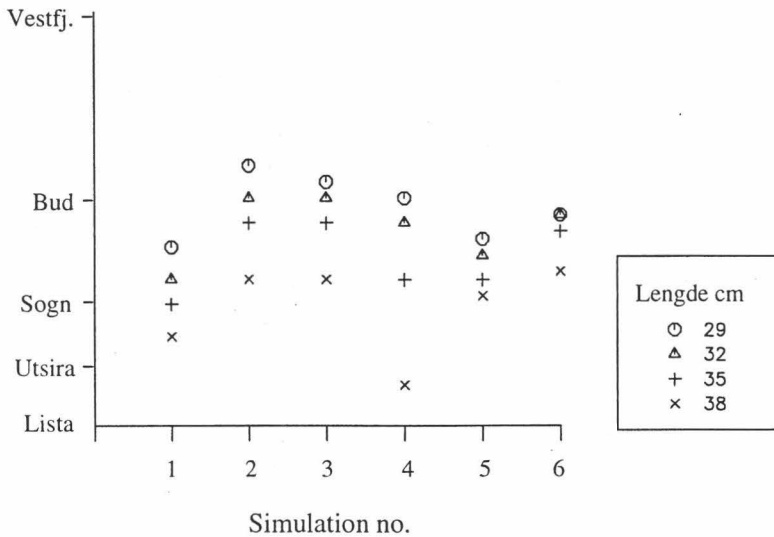
Fig. 10. A summary of simulations of optimal spawning ground by individual fish size (hatching time is 1. April): basic drift (25 km · day^{-1}) and mortality from McGurk (1986) (1) and Houde (1989) (2); basic drift and spatially uniform low (T = 5 °C) (3) and high (T = 10 °C) (4) mortality from Houde; McGurk's mortality and drift speed at 12.5 km/day (5) and 0 km · day^{-1} (6).

DISCUSSION

THE MODEL

We have quantified the costs and benefits of the spawning migration of herring along the Norwegian coast by use of a set of empirical relationships. The most uncertain part of the analysis is the spatial and temporal distribution of larval mortality risk, while swimming costs and larval growth (in the presence of abundant food) are likely to be reasonably well represented in the model. Therefore we

focused on the potential consequences of different levels and functional relations of mortality in terms of fitness (i.e. spawning success), survival probability and optimal spawning ground.

The predicted spawning grounds overlapped the main spawning areas, suggesting that the model may catch essential elements of the trade off decisions in herring migration behaviour. The modelled herring were strongly constrained by empirically derived functions (migration costs, larval growth and survival, options of energy allocation), and these dictated the predictions from the model. To our knowledge, this is the first time the adaptive value of the spawning migration has been described quantitatively. If the assumptions in the model were correct, then the latitudinal differences in temperature will be sufficient to defend the costs of migrating to the southern spawning grounds. The model supported our hypothesis that the migration is a case of state dependent trade off between costs of migrating and benefits of spawning farther south. Larger fish, or fish in good condition, have more energy that can be utilised for migration purposes, and should therefore choose spawning grounds farther south, where the larval growth and consequently larval survival is higher.

Our analysis resembled the model by Ware (1975), where he predicted optimal egg-size of fishes under various mortality- or incubation schedules. His general conclusion was that we should expect larger eggs under longer incubation conditions or higher mortality rates. This is supported in numbers of studies concluding by that herring do regulate the egg size or fecundity according to wintering temperatures (Hempel and Blaxter, 1967; Tanasichuk and Ware, 1987; Tanasichuk et al., 1993; Winters et al., 1993). Similarly, our model predicted that herring should swim farther south under higher rates of mortality, i.e. to lay fewer eggs with increased probabilities of survival. This also affected the spawning strategies under different assumptions of drift. Increased larval retention resulted in higher growth rate and survival, and consequently shifted optimal spawning northwards.

OTHER BENEFITS OF SPAWNING FARTHER SOUTH

We connected the benefit of spawning farther south to increased survival caused by higher temperatures during the larval stage. Support for the hypothesis that herring recruitment is positively correlated with temperature is found both in Atlantic and Pacific herring (Anthony and Fogarty, 1985; Stocker et al., 1985; Winters et al., 1986; Winters and Wheeler, 1987). However, temperature may also influence earlier and later life history stages than the larval stage. The hatching success of herring eggs are suggested to be temperature dependent (Blaxter and Hempel, 1963; Hempel and Hempel, 1968; Taylor, 1971; Alderdice and Hourston, 1985). The incubation period was not included in the model, because the eggs are laid at various depths, i.e. various temperatures (Aure and Østensen, 1993), both within and between spawning grounds. Warmer water will probably also increase the survival from metamorphosis until the stage of first maturation. 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 in these stages (Anthony and Fogarty, 1985; Sissenwine et

al., 1984). In case of the Norwegian spring spawners there is an increasing probability southward that larvae will drift into coastal areas and fjords (Dragesund, 1970), i.e. larva will stay at higher temperatures through the juvenile stage. Herring originating from coastal nursery areas grow faster than individuals in the Barents Sea, and as a result they recruit to the spawning stock 1-2 years earlier (Lea, 1929 a and b; Ottestad, 1934; Runnstrøm, 1936; Holst, 1996).

The salinity may also influence herring egg and larval survival (Taylor, 1971; Alderdice and Hourston, 1985). However, the latitudinal variations in salinity along the Norwegian coast are small (Aure and Østensen, 1993), and probably do not have significant influence on the recruitment.

Another benefit of undertaking a longer migration, could be a decreased density dependent mortality of larvae. The idea would be to migrate a farther distance southwards to avoid competition of suitable spawning substrates with other conspecifics with less migration potential. Recruitment has been related to stock density in herring by several authors (Anthony and Fogarty, 1985; Stocker et al., 1985; Winters et al. 1986; Winters and Wheeler 1987). Development and survival of eggs are inversely correlated with egg density in herring (Taylor, 1971; Galkina, 1971; Hourston and Rosental, 1981). Reduced density may also reduce competition for food among larvae (Kiørboe et al., 1988).

A number of studies have emphasised the importance of dispersal in a population under high spatial and temporal environmental variability (Gadgil, 1970; Roff, 1975; Kuno, 1981; Levin et al., 1984; Levin and Cohen, 1991; Cohen, 1993). A selection towards state-dependent spawning migration would be of advantage for the stock, since this will result in more dispersed spawning products. By spreading the spawning products from north to south, the Norwegian spring spawning herring overcomes the variations in environmental conditions and increases the overall recruitment to the stock (Dragesund, 1970). Similarly the individual fitness of herring could increase by migrating a longer distance southwards, which will increase the dispersal of larvae. Larvae hatched off Karmøy will be spread to nursery areas (in shore areas and fjords) all along the coast and in the Barents Sea, whereas larva hatched off Lofoten only have fjords in northern Norway and the Barents Sea as nursery areas. The really large year classes are produced in the Barents Sea, while the nursery areas along the coast function as a buffer; i.e. individuals originating from these areas predominate in years with low recruitment (Holst and Slotte, in press). Thus, in order to secure long term fitness, the herring should choose the southern grounds.

LIFE HISTORY CONSEQUENCES OF MIGRATION

One of our model predictions was that larger fish, and fish in better condition, should choose to migrate a longer distance to the spawning grounds to maximise fitness. This is in agreement with other studies on migration and life history consequences in marine, freshwater and anadromous fish. Marine migratory species are relatively larger, mature later and at a larger size and grow faster than stationary species (Roff, 1988). Larger individuals within marine species are known to undertake

longer feeding migrations than smaller ones (Nøttestad et al., Institute of Marine Research, Bergen, Norway, unpublished data). Age of maturity in Atlantic salmon (*Salmo salar*) is found to increase with the length of the rivers whose water the salmon spawns, which is believed to be an adaptive response to the migration costs (Schaffer and Elson, 1975; Schaffer, 1979). Migratory Arctic charr (*Salvelinus alpinus*) mature at older ages, have higher fecundity and greater longevity than stationary charr (Tallman and Saurette, 1996). Glebe and Leggett (1981 a and b) found an inverse correlation between the proportion of total energy reserves used for migration and the proportion of fish that are repeat spawners in American shad (*Alosa sapidissima*). They found that semelparous shad use 70-80% of their total energy reserves during a spawning run, while iteroparous shad use only 40-60%. A similar pattern was also found in other anadromous species (several salmon and shad stocks), in which semelparous fish use more than 70 % of their energy reserves, while iteroparous fish use less than 60 %. Semelparous fish also swim at a rate close to maximum sustainable speed, thereby reducing the duration of the migration to a minimum, whereas iteroparous fish swim at rates near optimum, and thus reduce the energy costs of the migration. There is also a positive correlation between body size and river harshness in Atlantic salmon (Schaffer and Elson, 1975) and in American shad (Glebe and Leggett, 1981 b). Larger shad also use less energy than smaller individuals during the spawning migration (Glebe and Leggett, 1981 a and b), similar to Norwegian spring spawning herring. Another similarity is found in the American smelt (*Osmerus mordax*), where the largest individuals travel the furthest distance upstream in the Miramichi River to spawn (McKenzie, 1964). 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 and Venables, 1983). This suggests that migration confer important benefits in survival that compensate for the lower investment in eggs.

'TRADE-OFF' VERSUS 'HOMING'

We have treated the spawning migration of Norwegian spring spawning herring as a life history strategy, where the herring must trade off energy used for migration (fecundity) and survival of larvae. However, this hypothesis is in conflict with the concept of 'homing', which infers that individual fish return year after year to the same spawning grounds as they spawned for the first time, regardless whether they were born there (Wheeler and Winters, 1984). Hourston (1982) found a degree of homing between 66% and 96% for 18 of 22 management units in Pacific herring (*Clupea harengus pallasi*) after analysis of tag recovery data from 1937-67. This is supported by a study of Wheeler and Winters (1984). Based on tag recovery data from a tagging program carried out in Atlantic herring (*Clupea harengus*) off Newfoundland in the 1970s, they found and average homing rate of 81%. In the period 1975-86 there were two distinct components of Norwegian spring spawning

herring, with two separated wintering areas, one in the Lofoten and Vestfjorden area another in fjords at Møre (Holst, 1991). Holst (1991) found that the herring wintering at Møre tended to spawn south of 63°N, whereas the herring wintering in the north tended to spawn north of 63°N. The data on the degree of homing to the specific spawning grounds of these two components were not very clear, but he suggested a homing rate of approximately 90%. Although data in both Pacific and Atlantic herring have indicated a high homing rate to specific spawning grounds, such a conclusion is difficult to draw in Norwegian spring spawning herring given the present migration pattern. The amount of tag recovery data from the 1990s is very high, but not sufficiently accurate to study homing rate in the stock. Tagging is normally conducted in spent herring in April (maturity stage 7). This may very well be herring conducting feeding migrations along the coast, and therefore spawning may have occurred in other locations than that of capture and tagging. For instance, in 1990 4296 herring were tagged and released off Karmøy, and only 42 hours later 37 of these tagged herring were caught on their way northwards along the coast about 60 nautical miles away from the location of tagging (Røttingen and Røttingen, 1991). In 1989 Norwegian spring spawning herring, dominated by 6 year olds (1983 year class), were found off Karmøy for the first time in 30 years. This is unlikely to be due to homing because this herring had spawned once or twice off Møre before spawning off Karmøy (Johannessen et al. 1995). We suggest that young and small herring will tend to spawn closer to the wintering area in the first years, whereas the spawning may occur farther south in preceding years, when the fish is larger. We furthermore suggest that individuals may undertake shorter spawning migrations in years when the condition is low due to low feeding success during summer. We do not neglect the hypothesis of homing, but suggest that a potential tendency towards homing in this stock is clearly limited by the state of the fish, i.e. an individual do not home to a particular spawning ground if this decreases the chance of survival until next spawning, or more specific decreases it's future fitness.

Tagging experiments by Jakobsson (1970) and studies by Holst (1996) support our hypothesis that Norwegian spring spawners may shift spawning grounds according to their size and condition. Jakobsson's results can be summarised in three points: 1) during the period 1963-1968 in excess of 90 % of the herring spawning off the Faeroes were Norwegian spring spawners, 2) individuals spawning one year (1960, 1963, 1964, 1965, 1966) off western Norway spawned off the Faeroes one or several years later (1967) and 3) the herring spawning off the Faeroes during 1965-1968 were mainly contributed by the recruitment of the strong 1959 year class. Growth studies by Holst (1996) show that there was a considerable decrease in body weight at length in herring during the period 1960 - 1968, especially among the smaller herring, which coincided with a decrease in sea temperatures. The herring spawning off the Faeroes migrated about half the distance from the wintering grounds east of Iceland compared with the herring which spawned off the Norwegian coast. Considering the results of Jakobson (1970) and Holst (1996), the spawning of herring off the Faeroes could have been induced by the energetic state, thus improving the probability to survive until next spawning.

CONCLUSIONS

The importance of larval ecology in recruitment, life history and behaviour of fishes has recently been emphasised by a number of authors (Chambers & Trippel, 1997). As the larval period is crucial to recruitment of stocks and fitness of individuals, it is to be expected that much of the behaviour and life strategies of adult fishes are programmed to give larvae a good start in life. Houde (1989) concluded that differences in spawning strategies of marine fishes may have evolved as a consequence of the different constraints on larval growth and survival from high and low latitudes. Wiener and Tuljaourkar (1994) concluded that environmental variation favours the evolution of migration. Similarly, Leggett (1985) concluded that migrations greatly reduced the impact of environmental variance on reproductive success, when strongly coupled with reliable environmental signals. We are convinced that functional understanding of spawning migrations in fish will be found by integration of larval ecology and constraints acting on adults.

ACKNOWLEDGEMENT

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