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State-dependent spawning migration in Norwegian spring-spawning herring

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Norwegian spring-spawning herring *Clupea harengus* winter in fjords of northern Norway, whereas the subsequent spawning occurs at various locations along the coast with a main bulk off the south-western coast. The distance of the southward spawning migration tends to increase with the length and condition of the fish. The costs and benefits of the southward migration were modelled in terms of fitness (number of surviving offspring). The model assumes that larvae have increasing growth and survival rates further south as they pass through warmer water during the northward drift in the coastal current. In agreement with the observed spawning distribution, optimal spawning grounds were predicted off the south-western coast and farther south with increasing fish length and condition. The present study suggests that homing is not a successful strategy for these herring, and instead the selection of spawning grounds depends on individual internal state (length, condition), the cost of migration and the probability of larval survival.

Key words: herring; migration; spawning; larvae; temperature; fitness.

INTRODUCTION

Spawning migration in herring is a topic that has received much scientific attention, particularly with regard to homing and straying. Although tagging experiments on Pacific herring *Clupea harengus pallasi* Valenciennes (Hourston, 1982) and Atlantic herring *Clupea harengus* L. (Wheeler & Winters, 1984) have demonstrated high return rates to specific spawning grounds, there is disagreement about the actual nature of this behaviour. Three possible population concepts have been proposed to explain the homing strategy of herring: the discrete population, the dynamic balance population and the metapopulation. The discrete population concept subdivides the herring from different spawning grounds into discrete unit populations with independent life histories (Iles & Sinclair, 1982; Sinclair, 1988), which implies that each spawning ground is associated with a specific larval retention area, and that reproductive isolation is maintained by natal homing. Furthermore, this concept suggests that strays will not pass on their genes successfully. Thus, they are evolutionary losers. The dynamic balance population concept by Smith & Jamieson (1986) challenged the discrete population concept and considered the herring to consist of dynamic and relatively unstructured assemblages. They contended that herring populations

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may expand and contract their range in response to environmental and fishing pressures, which implies that there are no barriers to exchange between spawning grounds or spawning populations, and that straying or gene flow between populations are the rule rather than the exception and keep the populations in dynamic balance. McQuinn (1997) unified the discrete and dynamic balance population concepts and argued that Atlantic herring population structure and dynamics are best described within the metapopulation concept, in which the principal characteristics responsible for the structure, persistence and integrity of herring populations are of behavioural rather than genetic nature. He suggested that local herring populations, which are formed through straying from existing populations (colonization), 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. Consequently the tendency to disperse (stray) is strongest with the recruits, and diminishes with reinforcement of traditional migration and spawning patterns. Furthermore, dispersion is more prevalent in unstable populations, i.e. following a population collapse or a recruitment boom.

There is a lack of studies on the spawning dynamics of the Norwegian spring-spawning herring (NSS herring) in relation to the strategy of homing and the proposed population concepts. However, such a discussion is highly relevant, since this stock is also distributed over a wide range of spawning grounds and spawning areas. The present study hypothesises that homing, whether it is natal homing or simply return spawning, is neither a crucial nor a successful strategy in NSS herring, and that instead they should select spawning grounds based on individual state and prospects of larval survival. This contradictory hypothesis is evaluated by means of both empirical data and modelling.

EMPIRICAL DATA AND FORMATION OF THE HYPOTHESIS

GEOGRAPHICAL SPAWNING DISTRIBUTION

Within a population the environmental preferences favouring the survival of eggs and larvae may be specific, leading to spawning at specific locations (Haegele & Schweigert, 1985). In the case of NSS herring, particular banks and shelf areas with stony or rocky bottom and depths <250 m that are suitable for spawning (Runnstrøm, 1941*a*; Dragesund, 1970). Such areas are distributed over *c.* 1500 km along the Norwegian coast between 58 and 70° N. Traditionally the most important spawning grounds are, from north to south, Lofoten, Træna, Sklinnabanken, Haltenbanken, Frøyabanken, and south of Stad at Sogn, Karmøy, Egersund and Siragrunnen (Fig. 1). However, during the last century the relative importance of the different spawning grounds has varied considerably (Runnstrøm, 1941*a*, *b*; Devold, 1963, 1968; Dragesund, 1970; Dragesund *et al.*, 1980, 1997; Hamre, 1990; Røttingen, 1990; Slotte & Dommasnes, 1998, 1999; Slotte, 1999*a*).

In recent years, the NSS herring stock has recovered from near extinction in the late 1960s. Simultaneously, the stock has changed its feeding and wintering areas and hence migrations. The oceanic nursery, feeding and wintering areas were abandoned to the extent that the entire life cycle was spent in Norwegian coastal waters and fjords (Dragesund *et al.*, 1980; Hamre, 1990; Røttingen,

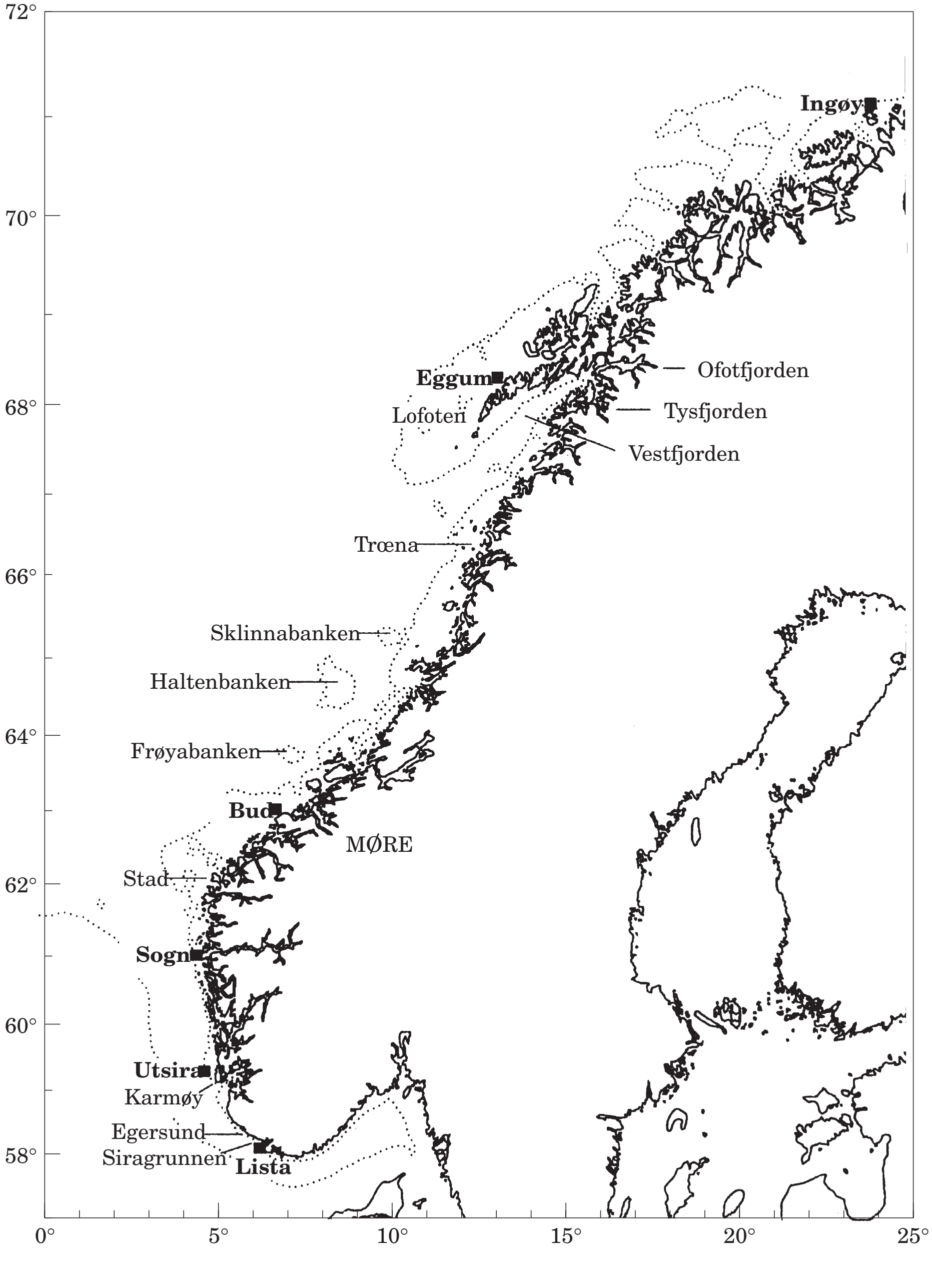

FIG. 1. Locations referred to in text and figures. ……, 200 m depth; ■, temperature stations.

1990). Since 1988 the wintering area of the NSS herring has been in Vestfjorden, Ofotfjorden and Tysfjorden, northern Norway. In addition, the feeding area has been extended westwards once again to the Norwegian sea in the 1990s (Dragesund *et al.*, 1997; Misund *et al.*, 1998). Correspondingly, the main spawning has taken place off Møre and to some extent northwards at Haltenbanken, Sklinnabanken, Træna and off Lofoten (Figs 2 and 5), whereas a

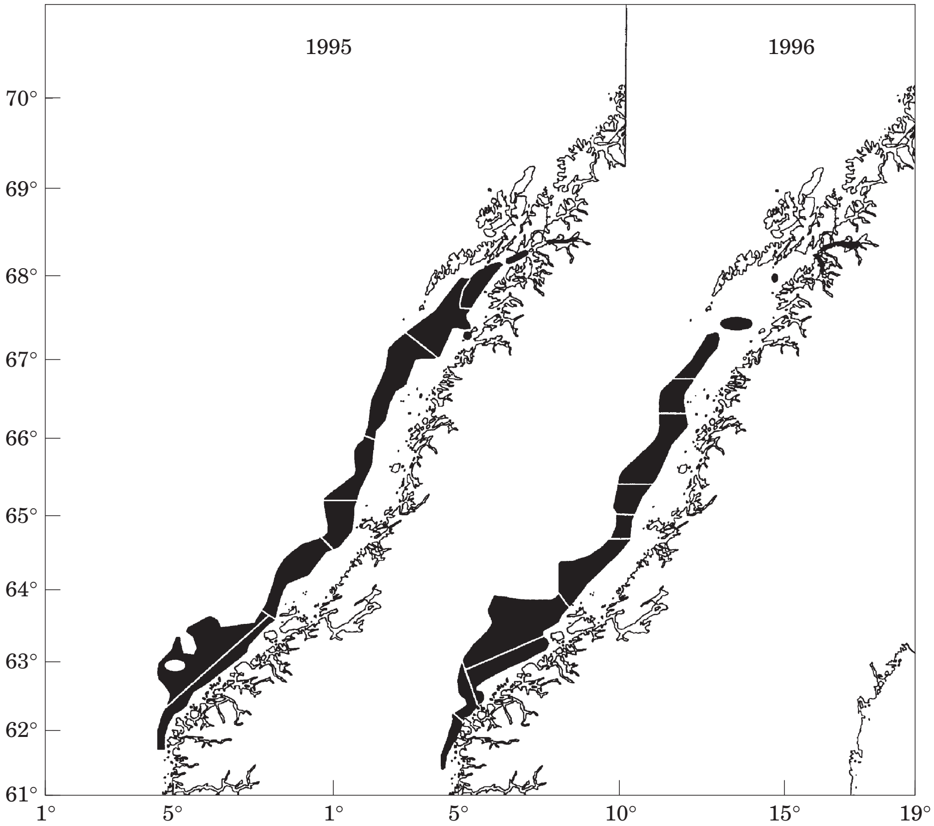

FIG. 2. Geographical distribution of NSS herring along the Norwegian coast during the pre-spawning periods 19 February–2 March 1995 and 17 February–6 March 1996. Adapted from Slotte (1999*a*). The abundance was estimated within sections, marked with white borderlines on the map, and corresponding values of relative abundance on a latitudinal scale is given in Fig. 5.

minor proportion (0–4%) of the spawning stock has utilized the traditionally important spawning grounds at Karmøy, Egersund and Siragrunnen (Røttingen, 1990; Johannessen *et al.*, 1995; Dragesund *et al.*, 1997; Slotte & Dommasnes, 1998, 1999; Slotte, 1999*a*)

COSTS OF SPAWNING MIGRATION

In general, NSS herring do not feed during the period from the arrival in the wintering area in September–October until the end of spawning in March–April (Slotte, 1999*b*). Instead the energy expended on maturation, swimming and maintenance metabolism is drawn from reserves stored during the summer feeding period. In 1995 and 1996 the total energy content in NSS herring was measured before (in Vestfjorden) and after (at Møre) the spawning migration (Fig. 3) and transformed into a length-specific swimming cost per km (Fig. 4) (Slotte, 1999*b*). These data demonstrated clearly that the southward spawning migration is highly energy demanding, and the relative energy loss (%) decreases with body length.

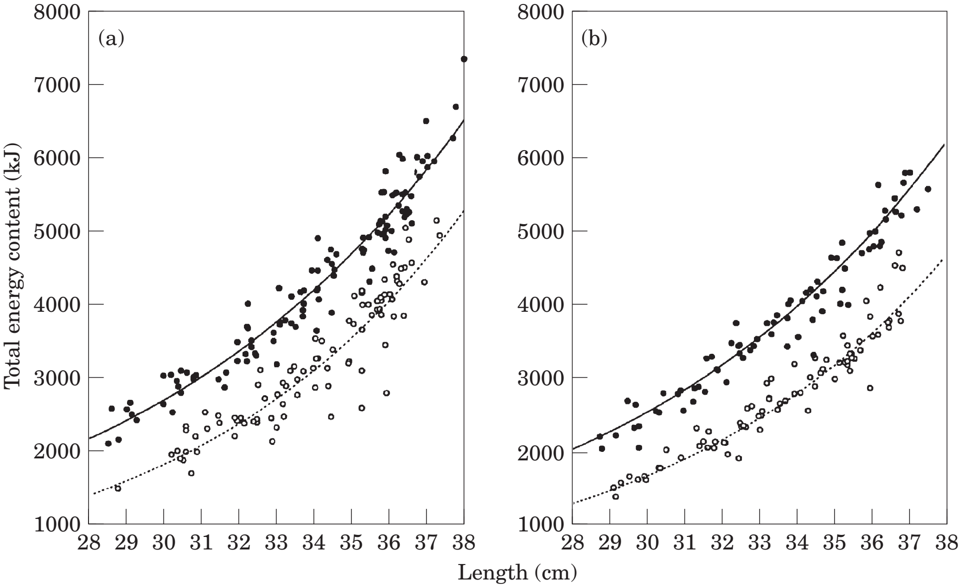

FIG. 3. The relation between body length and total energy content prior to (●) and after spawning migration (○) of NSS herring in (a) 1995 and (b) 1996. Data from Slotte (1999*b*). (a) $y=100{\cdot}012e^{0{\cdot}11x}$, $n=114$, $r^2=0{\cdot}95$, $P<0{\cdot}001$; $y=33{\cdot}834e^{0{\cdot}133x}$, $n=90$, $r^2=0{\cdot}86$, $P<0{\cdot}001$. (b) $y=88{\cdot}042e^{0{\cdot}112x}$, $n=76$, $r^2=0{\cdot}94$, $P<0{\cdot}001$; $y=34{\cdot}628e^{0{\cdot}129x}$, $n=76$, $r^2=0{\cdot}91$, $P<0{\cdot}001$.

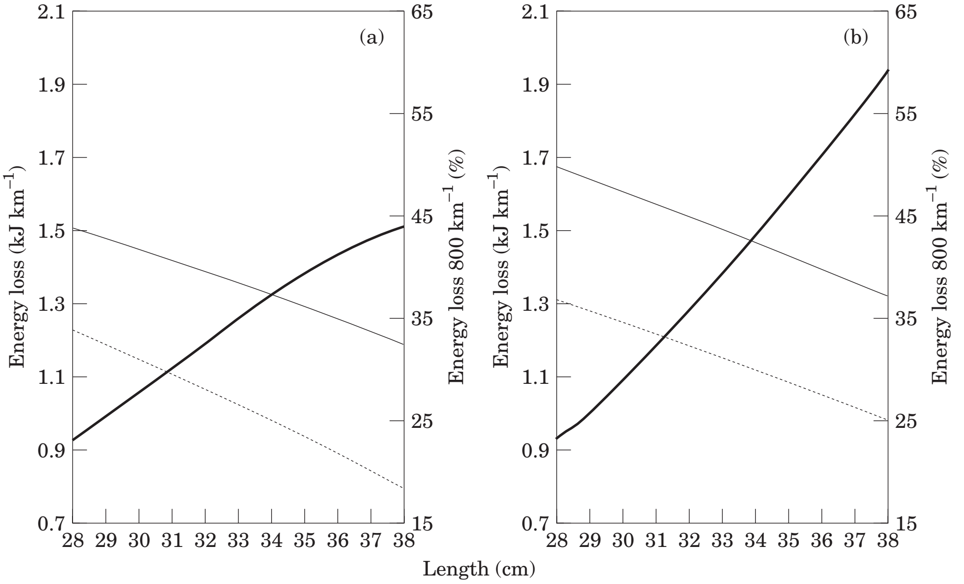

FIG. 4. Models of length-specific energy loss (kJ) per km (——), and length specific energy loss (%) prior to (– – – –) and after (——) spawning in NSS herring, during an 800-km migration distance from the wintering area Vestfjorden to the main spawning area off Møre in 1995 (a) and 1996 (b). Adapted from Slotte (1999*b*).

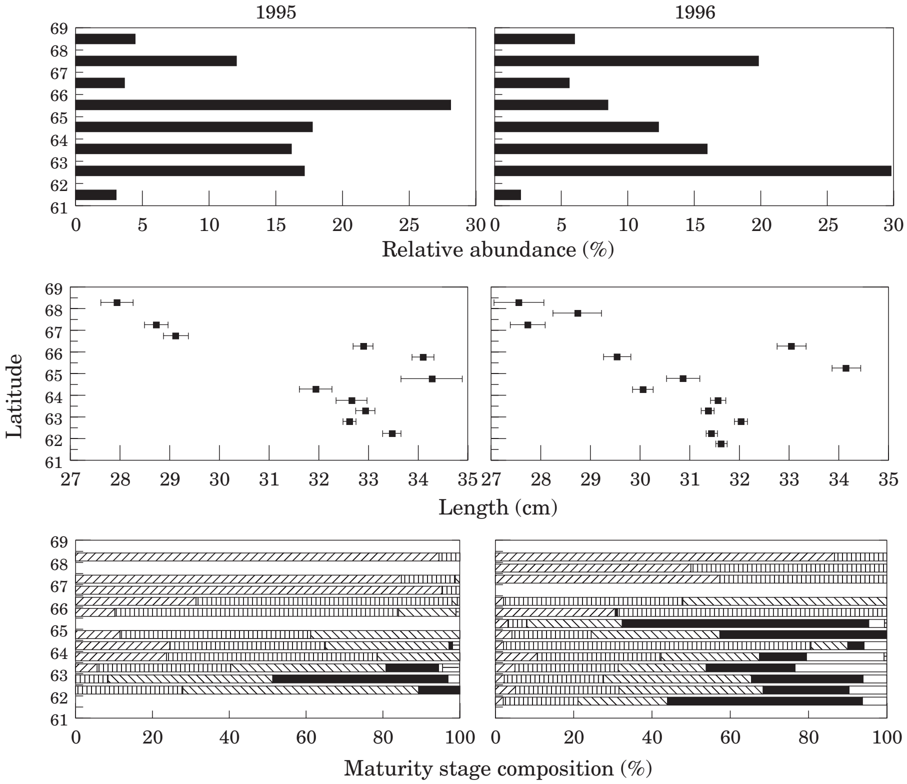

FIG. 5. Distribution of NSS herring on a latitudinal scale (within 60 nautical miles) relative to total abundance during the pre-spawning period 19 February–2 March 1995 and 17 February–6 March 1996 and corresponding data on body length (mean values ± S.E.) and maturity stage composition (within 30 nautical miles). Adapted from Slotte (1999*a*). Maturity stages: 3 (▨) and 4 (▥), developing; 5 (▧), fully mature; 6 (■), running; 7 (☐), spent; 8 (▤) resting.

MIGRATION IN RELATION TO INDIVIDUAL FISH SIZE AND CONDITION

There is an estimated difference in migration distance between the northernmost (Lofoten) and southernmost (Lista) spawning grounds of *c.* 1500 km. The energetic costs of migrating seem to influence the choice of spawning grounds, in that since 1995 the distance of the southward spawning migration is influenced by the length and condition of the fish (Slotte & Dommasnes, 1998, 1999; Slotte, 1999*a*). More specifically, both the mean body length in the overall spawning population (Fig. 5) and of given year classes (Fig. 6) increases southwards. Correspondingly, the condition factor of given year classes and 1-cm length groups increases southwards (Figs 6 and 7). In addition, gonad development and investment is influenced by the condition of the fish, so that the stage of maturity and gonad condition factor also increases southwards (Figs 5 and 6).

The relation between migration distance and gonad development and investment was investigated further in 1997 by Oskarsson (1998). He found that the oocyte diameter and fecundity increased southwards from 67 to 62° N along with an increase in condition, and correspondingly the level of atresia decreased. At

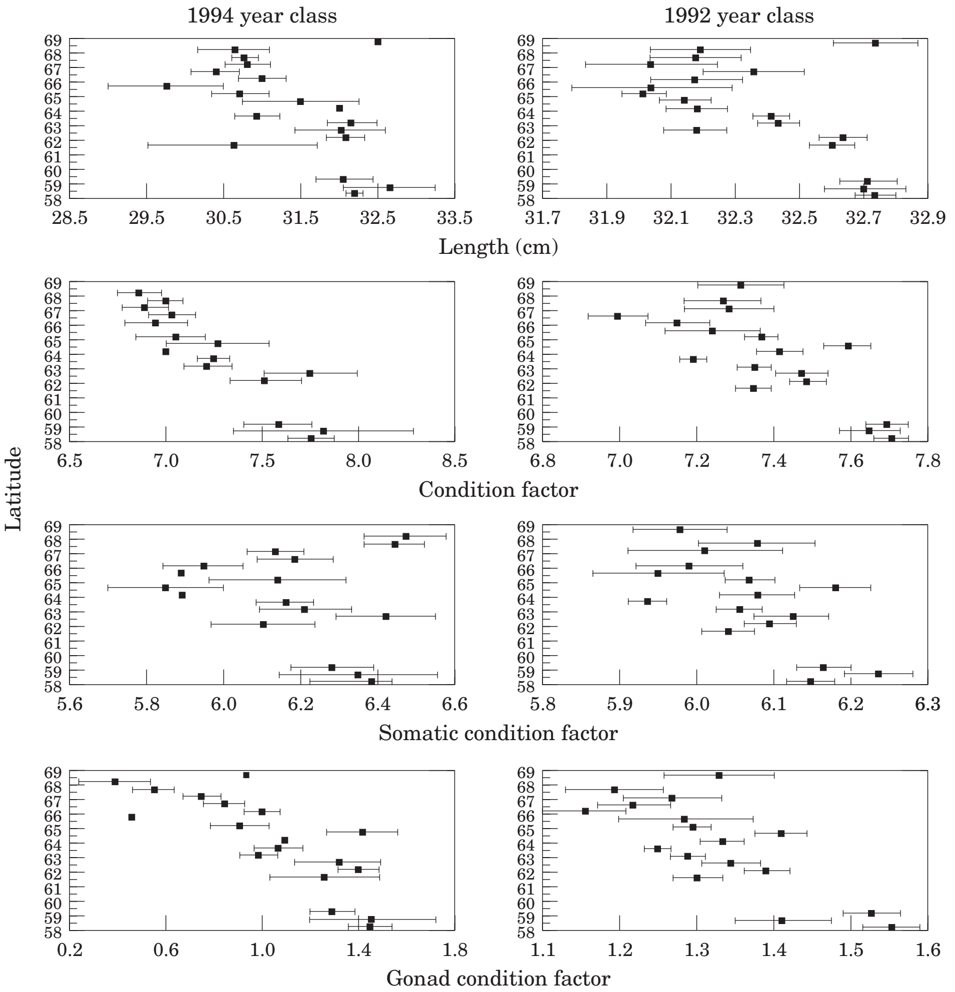

FIG. 6. Body length, condition factor (1000 $W L^{-3}$, where W is total weight in g and L is length in cm) somatic condition factor [1000($W-G$) L^{-3}, where G is gonad weight in g] and gonad condition factor (1000 $G L^{-3}$) of the 1992 and 1994 year class of NSS herring as recorded during an acoustic spawning survey in 15 February to 20 March 1999. (Mean values ± S.E.) Adapted from Slotte & Dommasnes (1999).

the main spawning area off Møre the level of atresia was close to zero, whereas some fish sampled close to the wintering area in Vestfjorden had up to 100% atresia.

These observations on the spawning migration of NSS herring in recent years contradict the hypothesis of homing. If homing (natal or return spawning) was of fundamental importance to this stock, then one should expect that individuals would select spawning grounds along the coast independent of body length or condition. Consequently, due to the high costs of migration, one should expect decreasing condition southwards. However, the opposite relationship suggests that the selection of spawning grounds is state dependent. It seems that larger individuals and/or individuals in better condition choose both to migrate a

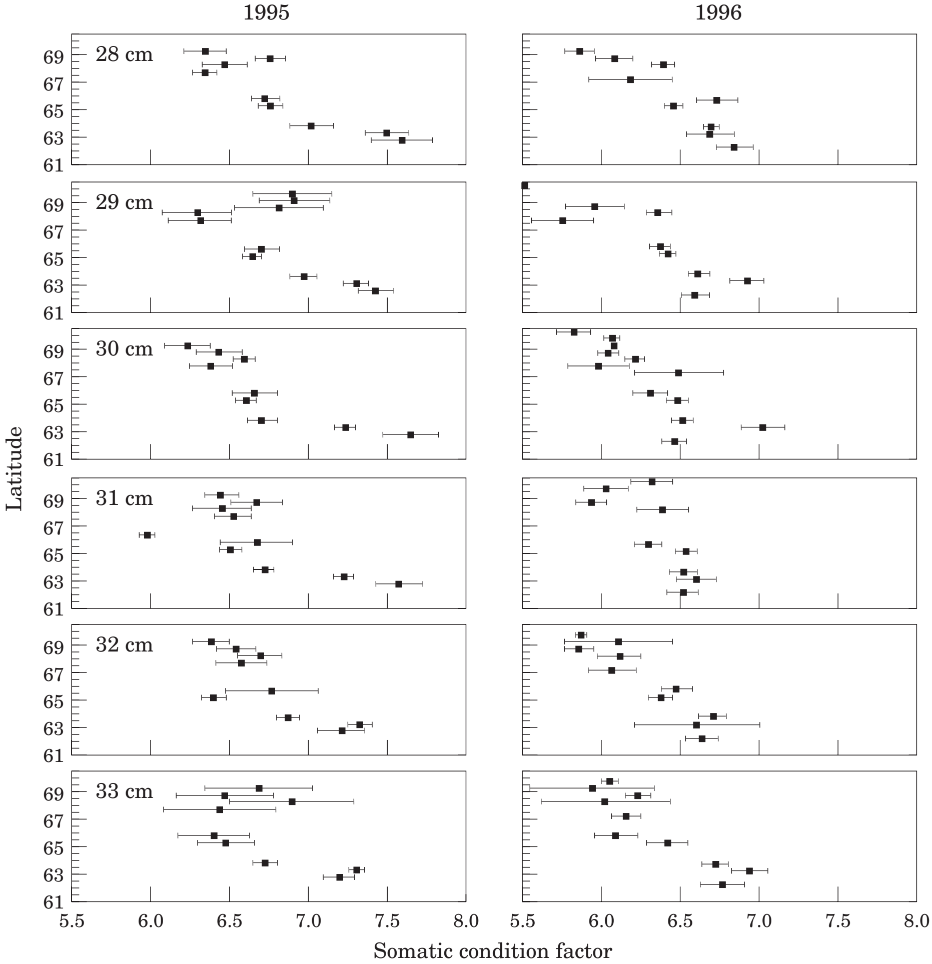

FIG. 7. Somatic condition factor in relation to latitude for 28–33-cm NSS herring during the latter part of the spawning period 11–30 March in 1995 and 1996. (Mean values ± S.E.) Adapted from Slotte (1999*a*).

greater distance southwards and invest more energy in gonads. Individuals in very weak condition may spawn close to the wintering area with reduced fecundity or even skip a season through total absorption of the eggs (atresia).

MIGRATION IN RELATION TO PROSPECTS OF PROGENY SURVIVAL

The observed size-dependent spatial distribution of spawning could be understood as a state-dependent trade-off between costs of migrating and benefits of spawning further south where the larvae may encounter warmer waters resulting in increased survival. The actual spawning occurs from late February until early April with a peak in early March (Slotte, 1998). The main bulk of larvae hatch during late March and early April after an incubation period of *c.* 3 weeks (Moksness, 1992; Moksness & Fossum, 1992; Fossum, 1996). The southward spawning migration follows the slope of the Norwegian continental shelf (Slotte 1999*a*), while the Norwegian coastal current runs in the opposite direction

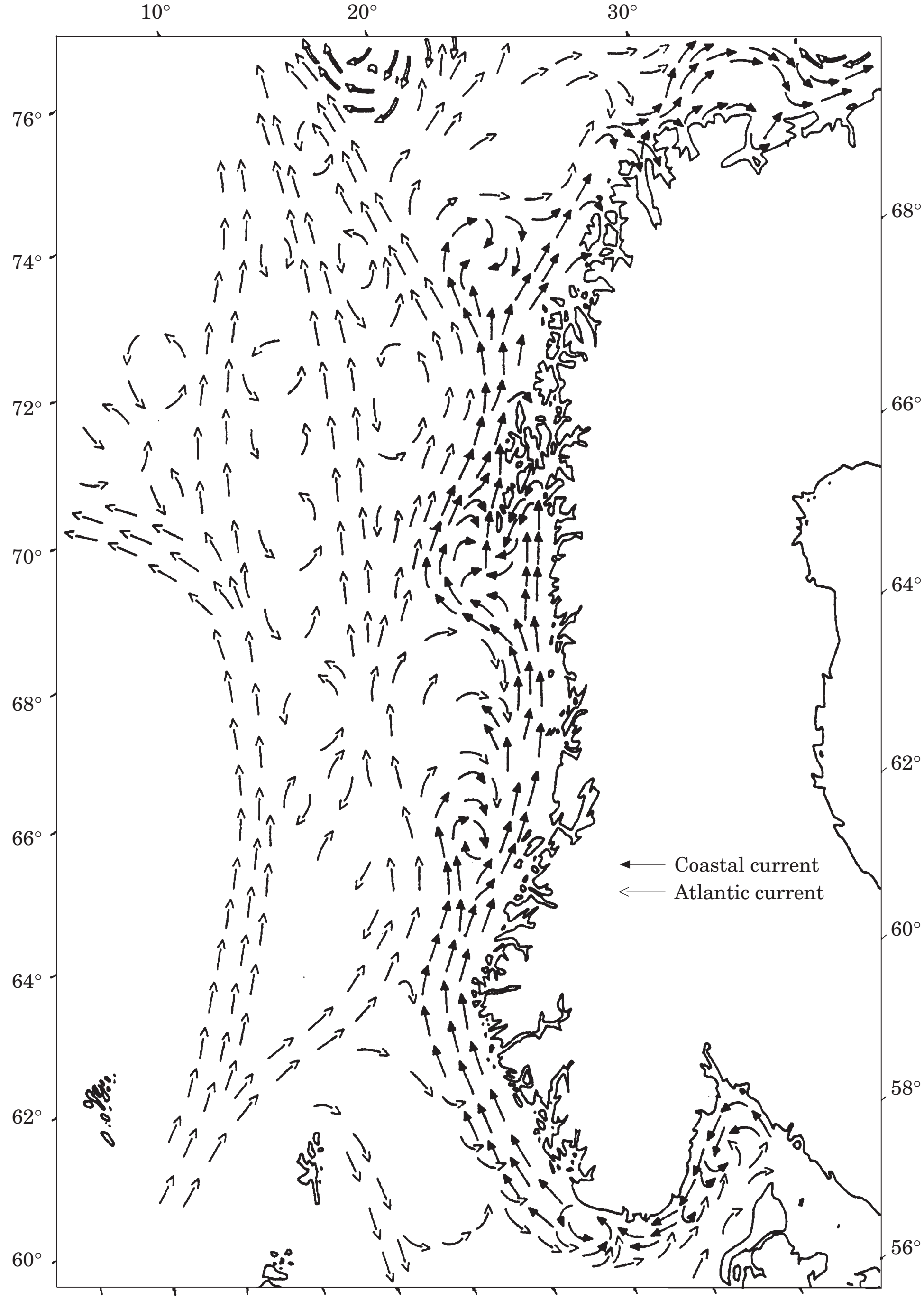

FIG. 8. Coastal currents and Atlantic currents along the Norwegian coast (adapted from Aure & Østensen, 1993).

(Fig. 8) at depths of up 150 m, at a maximum speed of 100 cm s^{-1} and at a mean speed of 15–40 cm s^{-1} (Aure & Østensen, 1993). Thus, in principle the present spawning migration of Norwegian spring spawning herring is analogous to upstream spawning migrations in anadromous fish, and the hatched larvae drift northwards along with the coastal current. Some larvae drift towards coastal nursery areas, whereas the majority ends up in the Barents Sea (Dragesund *et al.*, 1980; Holst & Slotte, 1998).

Temperature is often considered the most important environmental factor in determining growth and hence survival probabilities of fish larvae (Houde, 1989; Morse, 1989), although other environmental factors such as prey concentration, turbulence and light may also be important (Fiksen *et al.*, 1998). Correspondingly, there seems to be a correlation between the temperature of the Norwegian coastal current and the formation of good year classes in species like herring, cod *Gadus morhua* L. and haddock *Melanogrammus aeglefinus* L., having their first feeding, larval and juvenile drift in these water masses (Sætersdal & Loeng, 1987; Ellertsen *et al.*, 1990; Sundby, 1995). The temperature of coastal waters tends to increase southwards (Aure & Østensen, 1993), which suggests that southern spawning confers certain benefits in larval survival that could compensate for migration costs and/or reduced gonad production. In fact, Stenevik *et al.* (1996) found indications of higher growth rates in herring larvae hatched at southern grounds.

The importance of larval ecology in recruitment, life history and behaviour of fishes has been emphasized recently by a number of authors (Chambers & Trippel, 1997). As the larval period is crucial to recruitment of stocks and fitness of individuals, it is likely that much of the behaviour and life strategies of adult fishes are programmed to give larvae a good start in life (Dodson, 1997). 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. Similarly the present study emphasizes that functional understanding of spawning migrations in fish could be obtained by integration of larval ecology and constraints acting on adults. This is demonstrated by modelling of larval survival and individual fitness in relation to spawning on a latitudinal range.

MODEL AND PREDICTIONS

OVERVIEW OF THE MODEL

A simple model was developed of the costs and benefits of the spawning migration in NSS herring. The model assumed that the available energy could be traded off between metabolic and reproductive costs, which implied reduced fecundity given extensive migrations. The probability of survival until metamorphosis for an egg laid at each site was calculated by letting the larva drift with currents and grow as a function of the temperature to which it was exposed. With a size- or temperature-dependent mortality rate, the probability of surviving until metamorphosis was given by the time needed to reach this size. Finally, the optimum spawning site was that yielding the highest product of fecundity and offspring survival probability.

COSTS OF SPAWNING MIGRATION AND GONAD PRODUCTION

The length-dependent swimming costs per km from 1995 were used, as estimated by Slotte (1999*b*) (Figs 3 and 4). The difference in total energy content (kJ) between Vestfjorden in November 1994 (E_V $(l)=100{\cdot}012\,e^{0.11l}$) and Møre in February 1995 (E_M $(l)=33{\cdot}834\,e^{0{\cdot}133l}$) of herring at length l (cm), was transformed to costs per km c_l (kJ km^{-1}) with a distance migrated of 800 km; $c_l=(E_V\,(l)-E_M\,(l))\,800^{-1}$.

Some constraints on how much energy can be used on migration or reproduction were also included in the model. NSS herring are iteroparous and may live for more than 20 years and spawn up to 15 times, so they will not exhaust themselves completely during spawning activity. Therefore, migration costs and gonad production were constrained by a lower threshold of energy depletion from the winter level. It has been suggested that anadromous fish will not survive after spawning if <40% of the initial energy (before migration) remains (Glebe & Leggett, 1981*a*, *b*), or if the fat content is reduced below a limit of 2% (Jonsson *et al*., 1997). While anadromous fish often pass these limits and die, herring are much more conservative and have on the average *c*. 10% fat left after spawning (Slotte, 1999*b*). Thus, the lower threshold of energy left after spawning (q) was chosen to be higher than that of anadromous fish, so that $q=60\%$ of total energy content measured in Vestfjorden, in order to secure survival until next spawning. However, due to the uncertainty involved with the level of q, the sensitivity of this parameter was analysed.

Seventy-two possible spawning grounds were considered from Ingøy in the north to Lista in the south (Fig. 1), i.e. one site for every 25th km. The fecundity ($B_{l,d}$) of an l-cm herring spawning at site d (km from wintering area) will then be:

$$B_{l,d}=[(1-q)\,E_V\,(l)-c_l d]E_e^{-1} \tag{1}$$

where E_e is the energy content of one egg, which was estimated to 0·009 kJ from data on length specific fecundity (Oskarsson, 1998), length-specific gonad weight (Slotte, 1998) and egg energy density (kJ g^{-1}) (McGurk *et al*., 1980). The fecundities predicted by the model were in accordance with those observed by Oskarsson (1998).

Only a certain fraction of total body energy can be allocated to gonads. This implies that of the total energy content in a mature herring prior to migration E_V (l) some must remain after spawning qE_V (l), whereas the rest may be used to build gonads $E_eB_{l,d}$ or fuel migration c_ld:

$$E_V\,(l)=qE_V\,(l)+E_eB_{l,d}+c_ld, \tag{2}$$

where $q>0{\cdot}6$ and $E_eB_{l,d}\leq$ the maximal energy allowed in gonads, $G_{max}\,(l)$ (Fig. 9). The function $G_{max}\,(l)$ was set to the same as mean length specific gonad weight of fully mature females off Møre in 1995: $G_{max}\,(l)=3387{\cdot}8-322{\cdot}82l+10{\cdot}106l^2-0{\cdot}1023l^3$, $n=568$, $r^2=0{\cdot}73$, $P<0{\cdot}001$ (Slotte, 1998). We also tested the sensitivity of this parameter. 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 $E_eB_{l,d}$. This implies that an increase in $G_{max}\,(l)$ or q would reduce the possible migration distance prior to reduction of fecundity (Fig. 10).

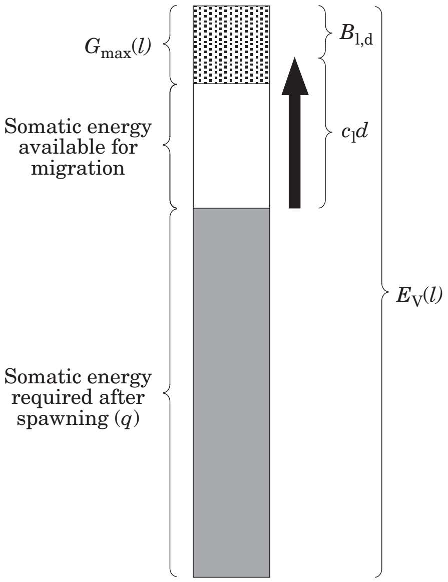

FIG. 9. A schematic overview of how the energy content $E_{\mathrm{V}}(l)$ of a herring in its wintering habitat (Vestfjorden) is allocated to different alternatives. Some energy is required to survive after spawning (q), while the rest may be allocated to the spawning migration $c_1 d$ or fecundity $B_{\mathrm{l,d}}$. There is a length dependent limit to how much energy that can be invested in gonads $G_{\max}(l)$.

LARVAL DRIFT, GROWTH AND SURVIVAL

To find the benefit of spawning at the different sites, a separate module was needed to calculate the fate of larvae hatched at the various sites. This was accomplished by exposing larvae to average temperatures as they drift northwards along the coast, and letting them grow as a function of the temperature-trajectory they experience. The probability of survival until a given size (35 mm) is then a function of hatching site.

Along the Norwegian coast, the water temperature has been measured continuously at fixed depths and locations from the 1930s to the present (Aure & Østensen, 1993). A basic drift depth at 10 m was used in the model. At this depth the average temperature (T) is higher farther south, particularly during summer (Fig. 11). The costs in terms of reduced fecundity may be outweighed by enhanced larval survival in warmer waters. To analyse this possibility, data were used on larval growth $g(T)$ (mm day^{-1}) of Norwegian spring spawning herring at five different temperatures (T=4, 6, 8, 10 and 12° C) (Folkvord, Department of Fisheries and Marine Biology, University of Bergen, Bergen, Norway, unpublished data). These data fitted the following logistic equation:

$$g(T)=0{\cdot}419(1+20{\cdot}6e^{-0{\cdot}57T})^{-1},\ n=5,\ r^2=0{\cdot}96,\ P<0{\cdot}001, \tag{3}$$

and this equation was used to calculate daily growth as a function of the temperature-trajectory of the larvae. The larvae were reared under high food concentrations in the experiments (Folkvord, personal communication). The present model ran with individual herring larvae from hatching until metamorphosis (35 mm). Age at metamorphosis was then a function of time and site at

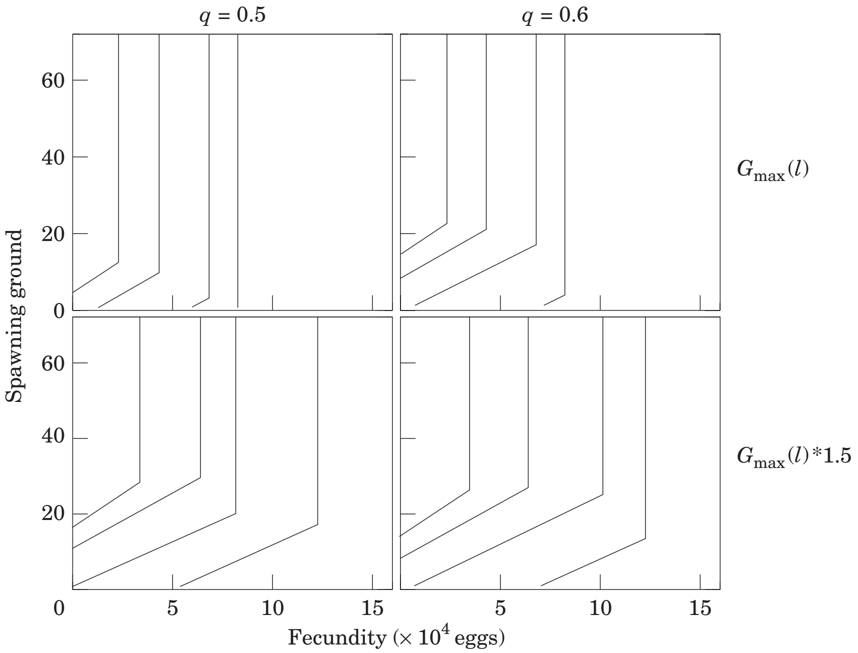

FIG. 10. The fecundity of 29-, 32-, 35- and 38-cm herring (larger herring more fecund) migrating from Vestfjorden to spawning sites along the coast, given different values of q and $G_{\max}$ (l).

hatching and the drift route northwards in the coastal current, and length was updated each day:

$$L_{t+1} = L_t + g\,(T_{d,t}) \tag{4}$$

where L_t is larval length in mm at day t, and $g\,(T_{d,t})$ is the increase in length from the temperature at site d at day t. If $L_t > 35$ mm, the cumulated survival probability is assessed (see below).

Some possible drift routes, given spawning off Møre, are superimposed on Fig. 11, and the differences in larval stage duration and temperature history can be read from the trajectories in Fig. 12. The temperature trajectories from some hatching sites along the coast, with equal drift, are given in Fig. 13. The Norwegian coastal current has an average velocity of 15–40 cm s^{-1} (Aure & Østensen, 1993), and 15 cm s^{-1} was used as a baseline (12·5 km day^{-1}), but simulations were made with higher or lower drift velocities also.

Mortality rates are high in fish larvae, and even marginal reductions in these will have large effects on fitness. However, the mortality is also variable and notoriously difficult to measure. Therefore, the focus was on the potential consequences of different levels and functional relations of mortality. Two formulations of mortality rates of fish larvae μ (day^{-1}) were used: one related to temperature (T);

$$\mu_H = 0{\cdot}0256 + 0{\cdot}0123T,\ n = 22,\ r^2 = 0{\cdot}41 \text{ (Houde, 1989)} \tag{5}$$

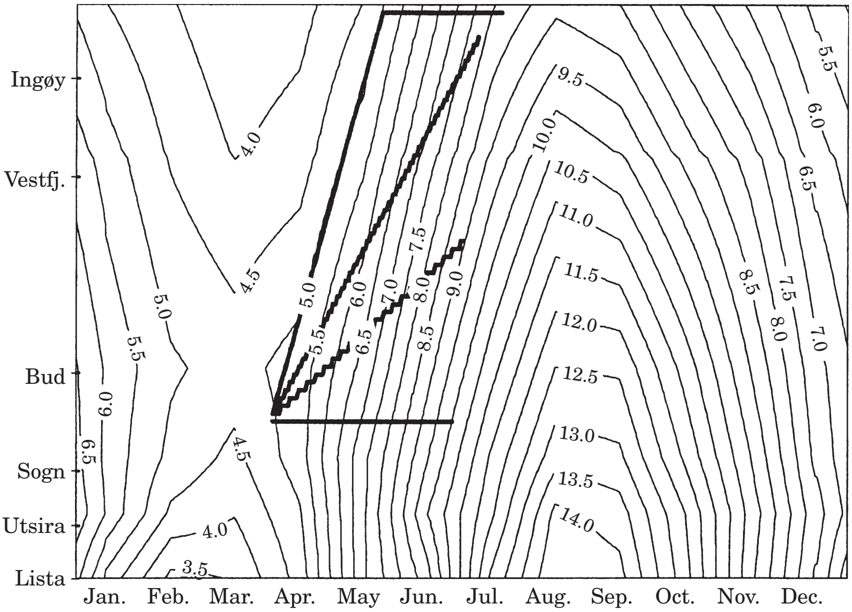

FIG. 11. Temporal and spatial distribution of temperature along the Norwegian coast at 10 m depth (see Fig. 1 for stations). Possible drift routes and the corresponding larval stage duration, given hatching off Møre and four different drift speeds: 25 top, 12·5, 6 and 0 (bottom) km day^{-1}.

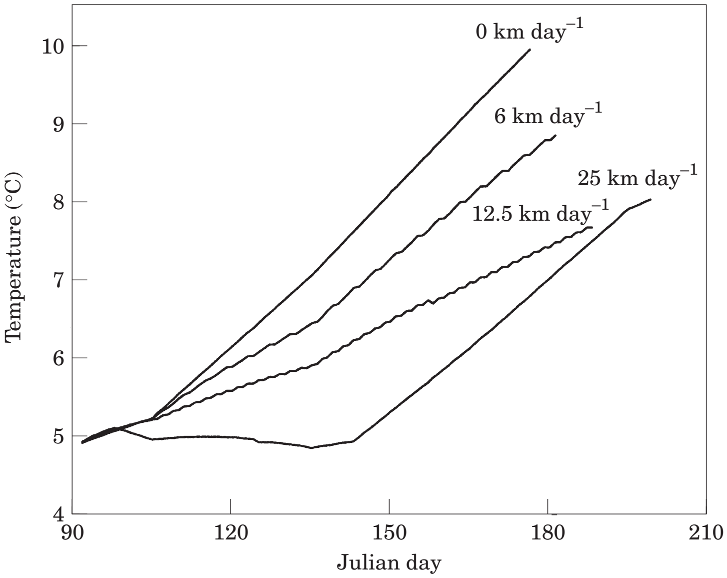

FIG. 12. Temperature trajectories at 10 m depth and the corresponding larval stage duration, given hatching off Møre and four different drift speeds: 25, 12·5, 6 and 0 km day^{-1}.

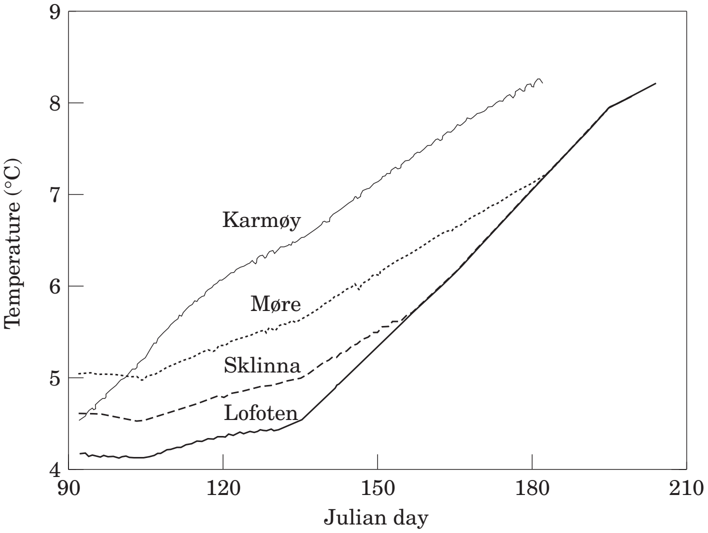

FIG. 13. Temperature trajectories at 10 m depth and the corresponding larval stage duration and hatching at four different locations given basic drift speed at 12·5 km day^{-1}.

whereas the other was related to larval size;

$$\mu_M = 2{\cdot}2W^{-0{\cdot}85}\,10^{-4},\ n=74,\ r=0{\cdot}58\ \text{(McGurk, 1986)}, \tag{6}$$

where W is larval weight in g dry weight. Dry weights were obtained from length L (mm) by $W=0{\cdot}001e^{-5{\cdot}28+0{\cdot}275L}$ (Folkvord, unpublished data). The probability of surviving until metamorphosis $P_{\mathrm{Sd,t}}$ for a larvae is:

$$P_{\mathrm{Sd,t}} = \prod_{0,A} \exp(-\mu), \tag{7}$$

where A is the number of days to metamorphosis, i.e. the time required to reach 35 mm for a larva drifting in the coastal current at 12·5 km day^{-1} (from equation 4), spawned at site d at time t. The predicted probability of larval survival increased with the delay in hatching from 1–15 April, when temperatures increased (Fig. 14). The survival was highest when the temperature-dependent mortality was utilized. However, the size-dependent mortality resulted in a steeper gradient over the latitudinal range, indicating a stronger correlation with the shifts in temperature. There was a tendency towards increasing survival at hatching locations further south.

Then the larval module was run with two mortality rates and three different larval drift speeds (Fig. 15). When the drift speed was reduced 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 moved northwards, which is an expected response.

The swimming costs and larval growth in the presence of abundant food are likely to be represented reasonably well in the model. Probably the timing of spawning is tuned to match the peak of plankton blooms (Sinclair & Tremblay, 1984; Cushing, 1990), and the model assumes that there are no limits in food

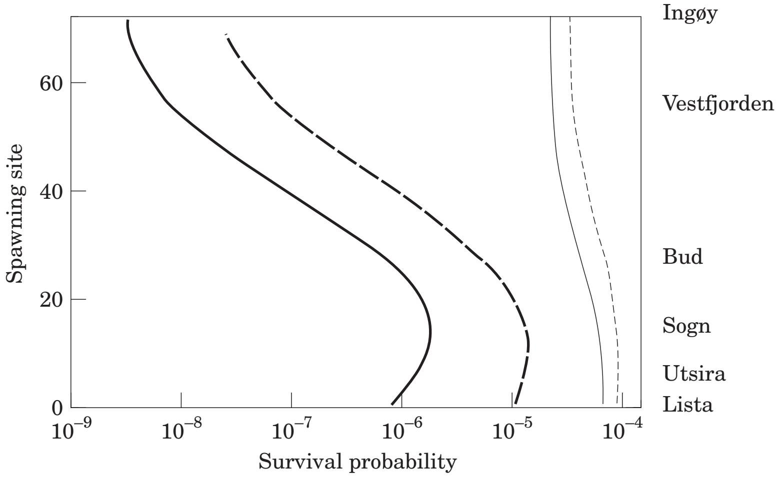

FIG. 14. Survival probabilities of herring larvae related to hatching location for two different hatching times (solid lines, 1 April; dashed lines, 15 April) and two different mortality functions: temperature-dependent (thin lines, from Houde, 1989) and size-dependent (thick lines, from McGurk, 1986).

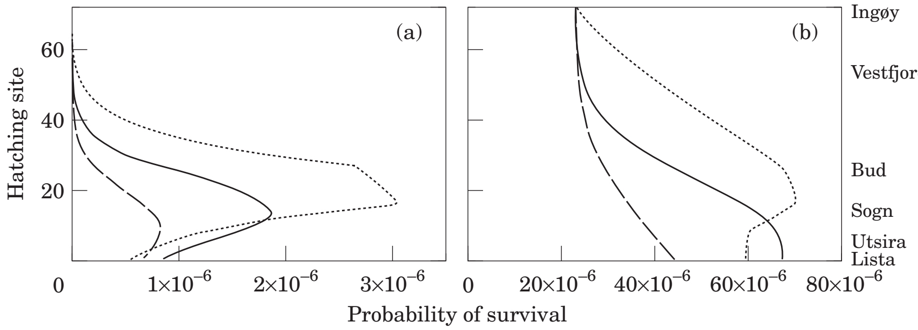

FIG. 15. Survival probabilities of larvae related to hatching site, given hatching at 1 April, three different drift speeds (· · · , no drift; ——, 12·5 km day^{-1}, – – –, 25 km day^{-1}) and two different mortality functions: (a) McGurk (1986) and (b) Houde (1989).

concentrations during the larval stage. However, the food level probably varies both on a temporal and latitudinal scale, but no quantitative studies were found on this element of larval growth.

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 thereby will increase the number of progeny surviving the larval period. The fitness $\varphi_{l,d,t}$ of a herring of length l, spawning at site d at day t will be the number off eggs laid at d, $B_{\mathrm{l,d}}$, times the integrated probability of larval survival $P_{\mathrm{Sd,t}}$:

$$\varphi_{l,d,t}=B_{\mathrm{l,d}}Ps_{\mathrm{d,t}} \tag{8}$$

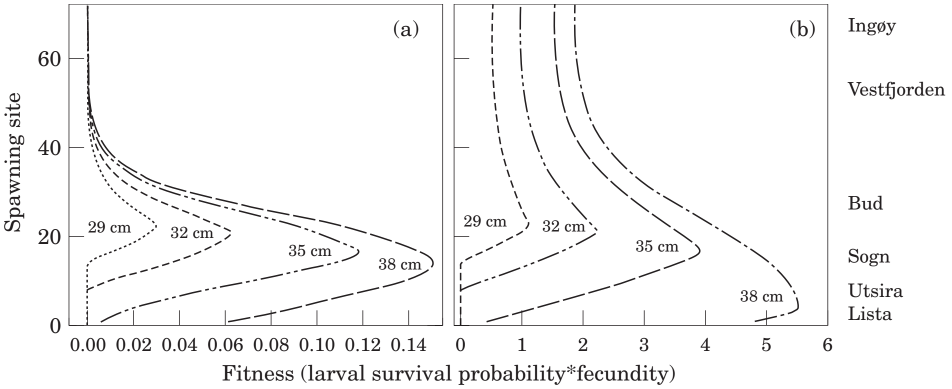

FIG. 16. Fitness of herring related to selected spawning ground and body length, given hatching at 1 April, drift speed at 12·5 km day^{-1} and two different larval mortality functions: (a) size dependent, from McGurk (1986) and (b) temperature dependent, from Houde (1989).

TABLE I. A summary of predicted optimal spawning sites numbered from 1 at Lista (south) to 72 at Ingøy (with 25 km between each site), by individual fish size

Fish length	Sensitivity analyses (simulation number)					
	1	2	3	4	5	6
29 cm	22	23	24	14	23	22
32 cm	21	21	22	14	21	20
35 cm	16	17	20	14	17	16
38 cm	14	4	17	14	16	9

1, Baseline version [i.e. size-dependent mortality as in Fig. 16(a)]; 2, temperature-dependent mortality as in Fig. 16(b); 3, baseline version with no limitation on gonads (all migration have costs in terms of reduced fecundity); 4, baseline version with minimum energy left after spawning $(q)=0{\cdot}5$; 5, baseline version with no larval drift; 6, baseline version with fast drift (25 km day^{-1}).

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 as the costs of migration are size dependent. The optimal spawning location for different sizes of herring was predicted for the two mortality assumptions, basic larval drift and hatching at 1 April (Fig. 16). 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. 10). 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.

The optimal spawning grounds for different size groups were predicted through various simulations (Table I). Simulations 1 and 2 were similar to those given in the previous paragraph (Fig. 16). The optimal spawning site is very

TABLE II. Effects of variations in initial condition (in Vestfjorden) on optimal spawning site and fecundity

Gonad limitation	Fish length (cm)	Initial condition	Optimal spawning site	Fecundity	Fitness reduction with homing (%)
G_{max}	32	× 1·25	14	43 050	21·0
		× 1	21	43 050	—
		× 0·75	27	26 480	60·9
G_{max}	38	× 1·25	14	82 130	0
		× 1	14	82 130	—
		× 0·75	20	80 490	18·4
No limits on gonads	32	× 1·25	19	74 000	3·25
		× 1	22	46 800	—
		× 0·75	27	26 480	41·6
No limits on gonads	38	× 1·25	15	204 300	1·14
		× 1	17	140 200	—
		× 0·75	20	80 490	5·14

The effects were tested for herring at 32 and 38 cm and with use of both G_{max} and no limitations on gonads. The fitness cost of homing was found by assuming that herring migrate to a fixed habitat (optimal habitat with average condition) to spawn, independently of condition. The difference is in terms of surviving offspring at metamorphosis for one spawning season.

similar for both mortality assumptions, except for the more southerly spawning of the largest fish when mortality increase with temperature (simulation 2 in Table I). Simulation 3 was run with no limits on gonads, and this shifted the optimal spawning ground slightly to the north. Reducing the minimum level of energy required after spawning from 60 to 50% will allow all size groups to reach the spawning site providing maximum survival probabilities of the larva with no loss of fecundity (simulation 4, Table I). Changing the average drift speed of the larvae did not affect the optimal site greatly, moving it only slightly northward with no drift and southward at fast drift (simulations 5 and 6, Table I).

Finally, the effect was analysed of variations in condition on optimal spawning site and fecundity (Table II). This was done by changing the value of $E_V(l)$ in equation 2 within each length category. The results demonstrated that it was optimal for herring with increasing condition to migrate farther south and to increase fecundity at the same time. This prediction was even stronger if the limitation on gonad energy was omitted. It was also demonstrated that a homing strategy would result in major reductions in fitness, if variations in condition were not taken into account.

DISCUSSION

The present study has demonstrated that spawning migration in NSS herring could be influenced by a state-dependent trade-off between costs of migrating and benefits accruing to larvae of spawning farther south. Consequently, it contradicts the widely accepted hypothesis of homing in herring. The southward spawning migration along the Norwegian coast involves significant energetic costs similar to upstream migrations in anadromous fish (Glebe & Leggett, 1981*a*, *b*; Crawford *et al*., 1986; Lambert & Dodson, 1990*a*; Jonsson *et al*., 1997). From the assumptions of the model, it seems reasonable that benefits in larval survival may outweigh the metabolic costs of migration. Anadromous fish are suggested to undertake freshwater migrations in order to protect their progeny from predators that are more abundant in the more productive marine environment (Thorpe, 1994). However, the benefits of migration in NSS herring are more likely related to the growth environments of their offspring rather than the potential presence of predators. The model suggests that an increase in the ambient temperature of larvae and a corresponding increase in growth and survival was sufficient to justify the costs of herring migrating towards southern spawning grounds. If growth is temperature dependent, the survival probability of larvae may differ by two orders of magnitude between the best and the worst spawning ground. Fecundity diminishes linearly after surplus somatic energy is used, but this is of minor importance compared with the potential change in larval survival. Consequently, the model suggests that the main reason for the spawning migration in NSS herring is to maximize larval survival.

Stock recruitment has been correlated with temperature in both Atlantic herring and Pacific herring (Anthony & Fogarty, 1985; Stocker *et al*., 1985; Winters *et al*., 1986; Winters & Wheeler, 1987) but this may also be a result of temperature influence on life history stages before and after the larval stage. For instance, the hatching success of herring eggs is also suggested to be temperature dependent (Blaxter & Hempel, 1963; Hempel & Hempel, 1968; Taylor, 1971; Alderdice & Hourston, 1985). Nevertheless, the incubation period was not included in the model since the eggs are laid at various depths, i.e. various temperatures (Aure & Østensen, 1993), both within and between spawning grounds. Warmer water farther south will probably also increase the survival from metamorphosis until the stage of first maturation. It has even been suggested that temperature-related effects are more important in the late larval to early juvenile phase than in the early larval period, due to the high predation rate in these stages (Sissenwine *et al*., 1984; Anthony & Fogarty, 1985). In this regard there is an increasing probability southwards that larvae of NSS herring will drift into coastal areas and fjords (Dragesund, 1970) and hence stay at higher temperatures through the juvenile stage.

Density-dependent mortality was not accounted for in the present analysis but this is probably an additional factor in the selection of spawning grounds: migrating southwards from the wintering area to spawn could decrease the density-dependent mortality of the progeny. Development and survival of eggs are correlated inversely with egg density in herring (Galkina, 1971; Taylor, 1971; Hourston & Rosenthal, 1981), and reduced density may also reduce competition for food among larvae (Kiørboe *et al*., 1988). Consequently, herring recruitment may decrease with increasing fish densities (Anthony & Fogarty, 1985; Stocker *et al*., 1985; Winters *et al*., 1986; Winters & Wheeler, 1987), which may explain the relationship between stock level and spatial distribution of NSS herring; i.e. when the stock increases, the feeding areas and spawning areas are extended (Devold, 1963; Dragesund *et al*., 1980, 1997; Hamre, 1990; Røttingen, 1990; Slotte & Dommasnes, 1998, 1999; Slotte 1999*a*). However, to include density-dependence in the model would require a game-theoretic approach, since the actions of others influence the optimal spawning site. The ideal free distribution concept may be the appropriate framework for modelling density-dependent migratory strategies (Giske *et al*., 1998).

It is not by coincidence that a major part of the NSS herring stock migrates towards the shelf area off Møre to spawn. Here an influx of warmer Atlantic waters mixes with the colder waters of the coastal current, and in general the temperature at spawning depth does decrease northwards and southwards from *c*. 62° N (Aure & Østensen, 1993; Slotte & Dommasnes, 1998, 1999). This was recognised also by the present model, which predicted optimal spawning grounds off Møre given increased larval retention. On the other hand, the model predicted optimal spawning sites south of Møre when the baseline 12·5 km day^{-1} was applied. The Møre shelf area is comparatively larger than the southern grounds and favourable bottom substrata (stony and rocky bottom) prevail (Runnstrøm, 1941*a*), which emphasises the potential of this area to receive a larger spawning biomass without decreasing hatching success due to density-dependent egg mortality. In fact, low competition for optimal spawning substrata off Møre, may explain why the fraction at the traditional grounds farther south at Karmøy, Egersund and Siragrunnen has been comparatively insignificant since it reappeared in 1989 after an absence of 30 years (Johannessen *et al*., 1995; Slotte & Dommasnes, 1998, 1999; Slotte, 1998). The increase in abundance in these areas from <20 000 t in 1989–1996 to 200 000 t in 1997 (own unpublished data) with the recruitment of the strong 1991 and 1992 year classes, supports this hypothesis.

An important assumption of the model was that fish might allocate available energy to migration or reproduction in order to maximize lifetime reproduction. Trade-off decisions between metabolic costs and reproduction are quite common in fish. Bradford (1993*a*, *b*) found that the relative allocation of storage energy to reproduction and metabolism differed with spawning season in herring; the spring spawning herring (long non-feeding maturation period) allocated proportionally more storage energy to routine and active metabolism than autumn spawners (brief maturation period with feeding). Allocation of energy to reproductive products also varies with different migration related costs in anadromous fish (Glebe & Leggett, 1981*a*, *b*; Crawford *et al*., 1986; Lambert & Dodson, 1990*a*, *b*). Support for the hypothesis of a trade-off between migration costs and reproductive output is found in the South American characin *Procilodus mariae* Eigenmann, in which 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).

In agreement with the observed spawning distribution, optimal spawning grounds were predicted off the south-western coast and farther south with increasing fish length and condition. One may expect that similar-sized herring should decrease in fecundity with migration distance southwards, analogous to the results of Saldana & Venables (1983). In fact, most studies indicate that longer migrations are paid for by reduced fecundity (Dodson, 1997). However, this trend is not found in NSS herring. Instead the empirical data indicate that herring in good condition invest more energy into both migration and gonads, and the present model also predicted that this in fact is an optimal use of energy.

The present results demonstrates clearly that homing, whether it is natal homing or simply return spawning, is neither a crucial nor a successful strategy in NSS herring. The model predicted that homing regardless of condition, would result in major fitness reductions. It is likely that the strategies of NSS herring differ from those of other herring stocks in which homing apparently is more important (Hourston, 1982; Iles & Sinclair, 1982; Wheeler & Winters, 1984; Sinclair, 1988; McQuinn, 1997). No other herring stocks cover such extensive distances between spawning grounds, nursery areas and feeding grounds as the NSS herring, which suggests that their strategies are tightly connected to migrations. In fact, the overall impression is that the geographical spawning distribution of NSS herring is highly dynamic and involves a considerable degree of straying between spawning grounds (Runnstrøm, 1941*a*, *b*; Devold, 1963, 1968; Dragesund, 1970; Dragesund *et al*., 1980, 1997; Hamre, 1990; Røttingen, 1990; Slotte & Dommasnes, 1998, 1999; Slotte, 1999*a*). In addition, there is a lack of data to support the suggestion that herring occurring at different spawning grounds along the coast belong to populations with their own integrity that persist in time. The larvae that hatch along the Norwegian coast may drift to a variety of nurseries in coastal areas, fjords and in the Barents Sea (Dragesund, 1970), but later in life they mix with other conspecifics and spawn at selected grounds along the coast regardless of the nursery area of origin (Holst & Slotte, 1998). It is also likely that herring select the spawning grounds regardless of where they were born, as there is no evidence for imprinting and natal homing. Instead, the strong dynamics demonstrated in this stock indicate that a possible tendency towards returning to spawn at specific spawning grounds could be more of an assurance to find a spawning location with suitable environmental conditions with respect to bottom substratum and temperature. This implies that all spawning contributes to the same gene pool regardless of the selected spawning ground, whereas the spawning success with respect to fitness may differ with the selected spawning ground as suggested by the present model.

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