Effects of hatching time on year-class strength in Norwegian spring-spawning herring (*Clupea harengus*)

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Effects of mean hatching date, post-hatching temperature, wintering temperature of adults, spawning stock size, and percentage of recruit spawners on larval survival in Norwegian spring-spawning herring (*Clupea harengus*) during the period 1987–2004 were analysed. In the final model, only hatching date proved to be significant. However, hatching date was itself negatively correlated with wintering temperature and positively correlated with the percentage of recruit spawners. This suggests indirect effects on larval survival, whereby low percentages of recruit spawners and high temperatures during gonad development lead to early spawning. Early hatching could be favourable for survival by allowing the larvae to drift away from areas where potential predators concentrate in spring, before predation pressure increases. Indirect support for this hypothesis was found in the activity of the purse-seine fishery for immature saithe (*Pollachius virens*) along the Norwegian coast. This fishery starts as soon as the saithe aggregate into large schools, which is presumed to reflect their feeding activity. The commercial catch data indicated that the saithe became active 2 months earlier in the area south of 67°N, than in areas to the north. Both field data and larval drift models confirmed that the majority of the early hatched larvae had passed across this border by that time of year.

Keywords: hatching time, herring, larval survival, post-hatch temperature, predation, recruit spawners, wintering temperature.

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Introduction

Mortality at the larval stage is often explained by the growth-rate hypothesis, which states that fast-growing individuals have a greater probability of survival than slow-growing individuals (Campana, 1996; Meekan and Fortier, 1996). In general, temperature is considered to be one of the most important environmental factors determining growth and survival of fish larvae (Houde, 1989; Morse, 1989). Correspondingly, Fiksen and Slotte (2002) suggested a correlation between the temperature of the Norwegian Coastal Current and the formation of good year classes in Norwegian spring-spawning (NSS) herring (*Clupea harengus*). However, studies on other species have indicated that early hatched larvae may experience lower predation pressure and have greater survival than larvae hatching later in the season, even if the early larvae experience lower temperatures and growth rates (Fortier and Quinonez-Velazquez, 1998; Lapolla and Buckley, 2005; Nishimura *et al.*, 2007). This explanation for recruitment variations may also apply to NSS herring. The hatching time in this stock is highly variable, which could be related to changes in stock structure, because recruit spawners spawn later in the season than repeat spawners (Slotte *et al.*, 2000). Variations in spawning time may also be linked to temperature fluctuations during wintering, because maturation rates may increase with increasing temperature (Hay, 1985).

NSS herring spawn on hard substrata (gravel, stones) on the central Norwegian continental shelf (to 250-m depth) between 58 and 69°N (Slotte, 2001). After hatching, most of the larvae drift northwards with the Norwegian Coastal Current towards the Barents Sea nursery areas, whereas a minority end up in fjords along the coast (Holst and Slotte, 1998). The route to the main nursery areas is long, and the larvae may experience a wide range of environmental conditions in terms of temperature and predation pressure along the way. Dragesund (1970) demonstrated that the proportion entering the fjords is inversely related to the total abundance of 0-group herring, and he suggested that strong year classes are formed in years with strong transport of larvae from the spawning grounds into the nursery areas in the Barents Sea.

The predation pressure might be expected to increase during spring because potential predators, such as herring (cannibalism), mackerel (*Scomber scombrus*), blue whiting (*Micromesistius poutassou*), and puffins (*Fratercula arctica*), are highly migratory and do not appear along the Norwegian coast until late spring. In addition, the less migratory saithe (*Pollachius virens*), which is also a main predator on herring larvae (Nedreaas, 1987), may be less active in early spring when temperatures are still low (Peck *et al.*, 2006). Hence, although fast transport and early hatching, both individually and in combination, may result in lower

growth rates, the benefits of low predation pressure may outweigh the potential disadvantage of slower growth.

Following this reasoning, our main objective was to test for possible confounding effects of hatching date, post-hatching temperature, wintering temperature, and percentage of recruit spawners on larval survival in NSS herring. To test for compensatory effects on survival (Hilborn and Walters, 1992), spawning-stock biomass (SSB) was also included in the analyses. An additional objective was to investigate whether early hatched larvae might experience a lower predation pressure by saithe.

Material and methods
Variables and statistical tests
The main dependent variable considered is the survival of NSS herring. Data on 0-group abundance (R_0) and SSB were taken from the last stock assessment available (ICES, 2007), and survival was estimated by R_0/SSB. Therefore, we assume that this ratio, as estimated from stock assessment, is a reliable measure of the actual survival rate. Data from the most recent (2005–2007) year classes have not been used in the analyses because the abundance of these cohorts cannot yet be reliably estimated by virtual population analysis.

Mean hatching date was estimated based on the larval data available yearly from 1987 on. From 1987 to 1991, mean hatching date was measured directly on the main spawning grounds outside Møre (Fossum and Moksness, 1993; Liang and Bjørke, 1997), where larvae were caught with 0.5 m² conical dipnets twice per week from mid-March to the end of April (Figure 1). Since 1991, hatching date has been estimated from the abundance of larvae recorded during surveys on the Norwegian shelf in March/April. The sampling area and techniques used are described in Fossum (1996). Larvae were staged according to Doyle (1977), and the number per substage (1a–1d and 2a–2c)
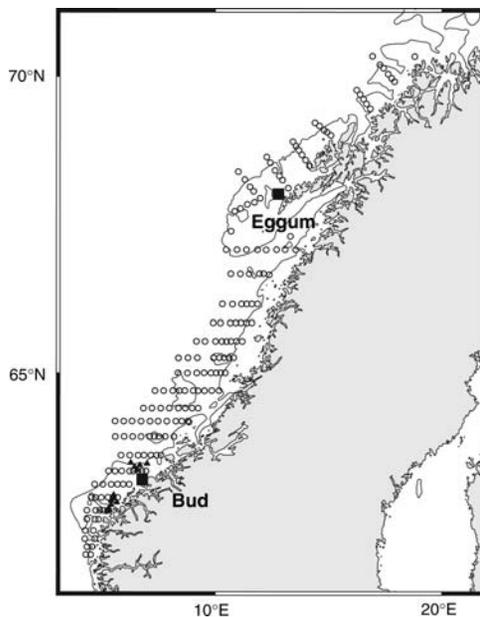

Figure 1. Map of the typical sampling grid for the herring larval survey along the Norwegian coast in April (open circles), the spawning grounds investigated in 1991 (filled triangles), and the monitoring stations at Bud and Eggum (filled squares). The 200 m isobaths are also shown.

for the first two stages was estimated. The duration from hatching to the end of the second stage is ∼30 d (Bjørke *et al.*, 1986). The numbers of larvae that should have hatched, according to the numbers found in the seven substages during each cruise, were back-calculated with a 10% daily mortality (Christensen, 1985), using the midpoint of the larval cruise as the starting point for the back-calculations. No consideration was given to the actual number by substage caught per day. The estimated day on which 50% of the sampled larval population should have hatched was used as a measure of the mean hatching date in the analyses.

The temperature experienced by newly hatched larvae was estimated as the mean temperature over the 0–50-m depth range at the Bud monitoring station (62°56′N 06°47′E, Figure 1; Aure and Østensen, 1993), located at the main spawning grounds off western Norway (Slotte, 2001). The post-hatching temperature was interpolated linearly between the measurements closest in time before and after the estimated mean hatching date. The choice of depth range (0–50 m) was based on vertical distribution data on larval NSS herring (Dragesund, 1970). In April, the water masses of the upper 50 m are normally well mixed.

The ambient wintering temperature of adults was estimated as the mean temperature over 0–200-m depth recorded during September–October at the monitoring station Eggum (68°22′N 13°38′E, Figure 1; Aure and Østensen, 1993), close to the wintering grounds of the adult population in northern Norway (Slotte, 2001). The depth interval is the typical depth range over which wintering NSS herring conduct diel vertical migrations between the upper layers, where they are found at night, and the deeper layers, which they occupy by day (Vabø *et al.*, 2002). The period September–October was chosen to represent ambient temperature during the early maturing phase, when the herring arrive in the wintering areas and gonad development increases rapidly (Slotte, 1999).

Percentages of recruit spawners were estimated as the percentage of herring (by numbers) in the spawning stock with a total length of <32 cm. The proportion of recruit spawners in NSS herring increases with body length over the interval 27–32 cm, after which all herring are repeat spawners (Slotte *et al.*, 2000; Oskarsson *et al.*, 2002; Kurita *et al.*, 2003). Hence, a length of 32 cm serves as an appropriate threshold between recruit spawners and repeat spawners. Support for this assumption can be found in Engelhard and Heino (2004), who demonstrated that length at 50% maturity was relatively stable at 29–30 cm from 1935 to 2000. The total numbers of spawning individuals (SSN) by year and age were calculated by adjusting total stock numbers for the proportions mature by year and age (ICES, 2006). To estimate the percentage of recruit spawners, SSN data were then assigned to 1 cm size classes based on observed length distributions by year and age at the spawning grounds (Institute of Marine Research database).

The effects of hatching date (HatchD), post-hatching temperature (HatchT), wintering temperature (WinterT), percentage of recruit spawners (Recpct), and SSB on larval survival were tested using pairwise linear correlations and the linear model

$$\log(\text{Survival}_y) = \alpha_0 + \alpha_1 \text{HatchD}_y + \alpha_2 \text{HatchT}_y + \alpha_3 \text{WinterT}_y$$
$$+ \alpha_4 \text{Recpct}_y + \alpha_5 \text{SSB}_y + \epsilon_y,$$

where y is the year and the errors ϵ are identical, independent, and normally distributed with zero mean and constant variance. This

fitting of the linear model with the logarithm of survival (Survival $= R_0/\text{SSB}$) as the dependent variable and SSB as the only independent variable is equivalent to fitting the Ricker function for the stock–recruitment relationship with multiplicative errors (Quinn and Deriso, 1999, p. 104). Furthermore, to analyse non-linear effects in the relationships, we used generalized additive models (GAM; Hastie and Tibshirani, 1990), in which each term in the linear model above is replaced by a non-linear function, e.g. $f(\text{HatchD}, k)$, where k is a parameter controlling the degree of smoothing. Each smoothing parameter is estimated using generalized cross-validation (Wood, 2006). To test for non-linear relationships, we applied an analysis of deviance, which allows models with and without non-linear terms to be compared, and the difference in respective residual deviances was tested using an F-test (Venables and Ripley, 1999). Finally, to select the best parsimonious model, we used stepwise selection in both directions (adding and removing terms as needed), based on Akaike's information criterion (AIC) and analysis of deviance (Venables and Ripley, 1999). All analyses were carried out using R (R Development Core Team, 2008) and including the R library *mgcv* for GAM analysis.

Overlap between larvae and saithe predators

During spring, immature saithe (mainly of ages 2–4) aggregate and form large schools around shallow reefs along the outermost part of the Norwegian coast. These schools feed actively on small crustaceans and fish (including herring larvae), passing in the Coastal Current, and are targeted by a coastal purse-seine fishery. The timing of the start of this fishery is assumed to be an indication that the saithe have started to aggregate and feed, because the vessels regularly monitor the fishing grounds. We used the cumulative weekly commercial catch data for 2001–2007 to investigate the peak in feeding activity of juvenile saithe in two latitudinal areas (62–67°N and >67°N). Data from the period before 2001 were not used because they were aggregated by month only. Logistic functions, based on linear regressions, with the logit fraction as the dependent variable and time as the independent variable were fitted to the data from each area (all years pooled), and the day on which 50% of the annual catch had been reached was used for comparing differences in the timing of predation pressure among areas.

To illustrate the potential magnitude of this predation pressure, the biomass of schooling juvenile saithe north of 62°N was roughly estimated by multiplying the estimated biomass-at-age (taken from ICES, 2007) with the estimated weight proportion of each age group taken by purse-seine (relative to the total catch in weight-at-age).

To investigate a potential relationship with the peak in saithe activity, the observed distribution, density, age, and size of herring larvae in May were analysed for the large 1991 and 1992 year classes. These larvae had been sampled on the Norwegian shelf using a modified Harstad trawl with an 8 mm mesh codend liner (Godø *et al.*, 1993). Trawling distance by station was 1.5 nautical miles. At some stations, larvae had been preserved in 80% buffered ethanol immediately after capture. In the laboratory, standard lengths of these larvae were measured, and both sagittal otoliths were extracted under a dissecting microscope. Larval age was estimated from counts of otolith increments (Methot, 1981), adding 10 d for yolk-sac stage development (Fossum and Moksness, 1993).

Because of uncertainty about the northern distribution limits of the larvae relative to the area sampled in May 1991 and 1992, a numerical circulation model (the Regional Ocean Modeling System: Rutgers Ocean Modeling Group, 2003; Shchepetkin and McWilliams, 2005) was used to simulate the transport of larvae. This free-surface, hydrostatic, primitive-equation ocean model is described in more detail by Vikebø *et al.* (2005). According to the estimated hatching curves (as deduced from the distribution in the April surveys of 1991 and 1992), particles were released as patches of 5000 individuals at depths of 5, 10, and 15 m. Particle movement was recorded until 15 May.

Results

During the period 1987–2004, interannual variations in larval survival, as well as in hatching date, post-hatching temperature, and wintering temperature, percentage of recruit spawners, and SSB were large (Figure 2). Pairwise, linear correlations (Figure 3) demonstrated that larval survival was highly negatively correlated with hatching date, indicating that early hatching was favourable. Survival was also positively correlated with wintering temperature
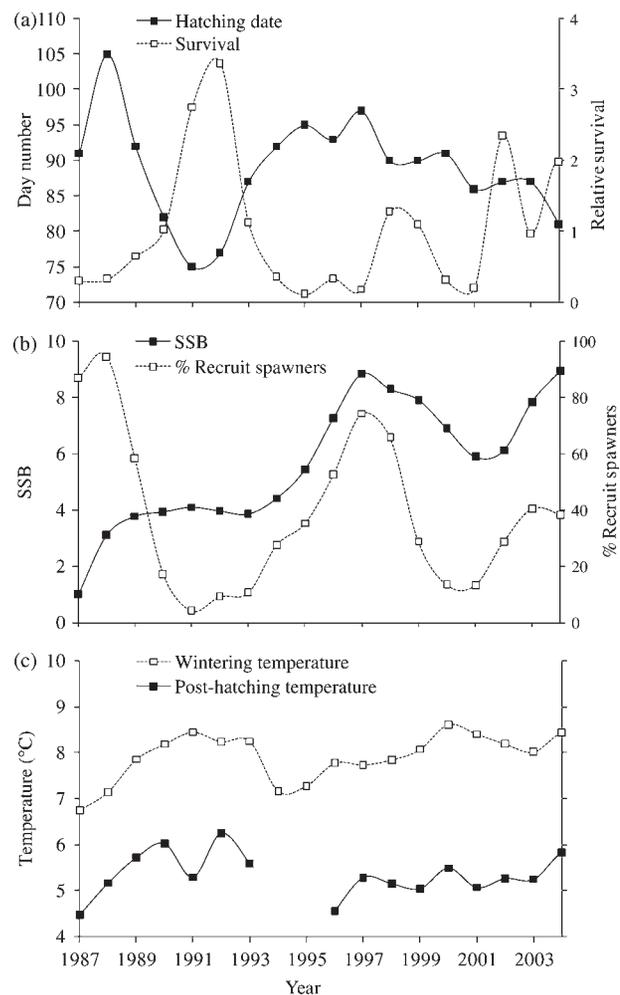
Figure 2. Interannual variations in (a) hatching date and survival of NSS herring, (b) corresponding SSB and percentage of recruit spawners, and (c) early wintering temperature (September–October) of the adults and larval post-hatching temperature, 1987–2004.
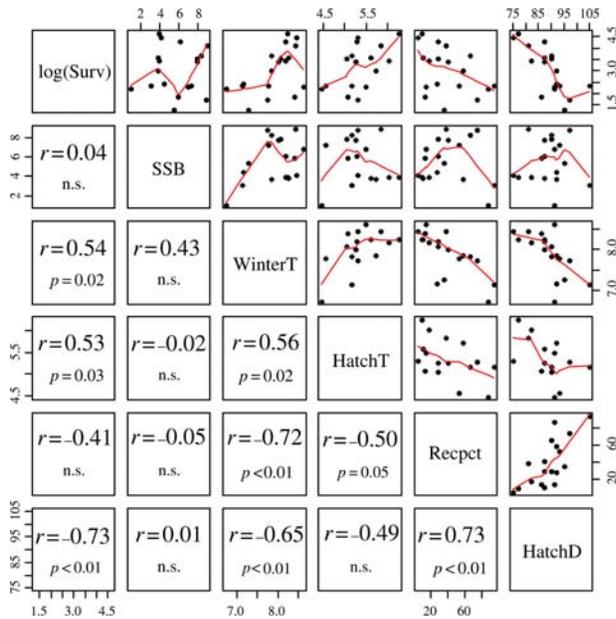
Figure 3. Pairwise scatterplots of log larval survival [log(Surv)], SSB, wintering temperature (WinterT), post-hatching temperature (HatchT), percentage of recruit spawners (Recpct), and hatching date (HatchD), together with a non-parametric smoother line to display the trend. The linear correlation coefficients and the corresponding *p*-values are given below the diagonal.

and post-hatching temperature, indicating the possible occurrence of confounding effects. On the other hand, SSB and percentage of recruit spawners had no significant influence on larval survival in these single-effect analyses.

To find the most appropriate model for larval survival, we first used GAM with and without non-linear terms to test for non-linearity. Although some factors were significantly non-linearly related to larval survival, the models including non-linear relationships did not provide a significantly better fit based on the *F*-test ($p = 0.14$ for the model including all covariates). Hence, we applied only linear models in the remaining analyses for log larval survival.

Values for post-hatching temperature were not available for 1994 and 1995, so models could not be compared for the entire time-series using this factor. Therefore, initial analyses were carried out to determine the most appropriate model using the reduced dataset (Table 1, log larval survival). The only significant term was hatching date. Using the full time-series, excluding post-hatching temperature, provided the same result. In the final model, using hatching date only, the slope was highly significant (adjusted $r^2 \approx 0.51$; $p < 0.001$).

The pairwise correlations (Figure 3) clearly demonstrated that hatching dates were earlier with increasing percentages of recruit spawners and later with falling wintering temperatures. Therefore, hatching date was analysed in the same manner as log survival, with wintering temperature and percentage of recruit spawners as the only covariates (Table 1, post-hatching date). In this case, wintering temperature was non-linearly related to hatching date, whereas the percentage of recruit spawners was linearly related to hatching date. However, the model selection based on the *F*-test suggested that variability in hatching date was most appropriately described using the percentage of recruit spawners

Table 1. Results for the (sequential) analysis of deviance for the models for log larval survival, and post-hatching date (see text): res d.f., residual degrees of freedom; res Dev, residual deviance; ΔF, sequential change in the *F*-statistic for change in log likelihood; *p*, corresponding *p*-values; AIC, Akaike's information criterion values.

Term	res d.f.	res Dev	ΔF	p	AIC
Log larval survival					
None	15	13.58	–	–	–
+ Hatching date	14	6.48	13.00	0.005	36.95
+ Post-hatching temperature	13	5.89	1.08	n.s.	37.42
+ Wintering temperature	12	5.71	0.33	n.s.	38.93
+ SSB	11	5.46	0.46	n.s.	40.22
+ Percentage of recruit spawners	10	5.46	0.01	n.s.	42.21
Post-hatching date					
None	17.00	873.1	–	–	–
+ Percentage of recruit spawners	16.00	412.4	25.03	<0.001	113.5
+ s(Wintering temperature)[a]	13.02	239.6	3.14	n.s.	109.6

[a]Wintering temperature enters the model as a non-linear function *s* and is estimated using the GAM.
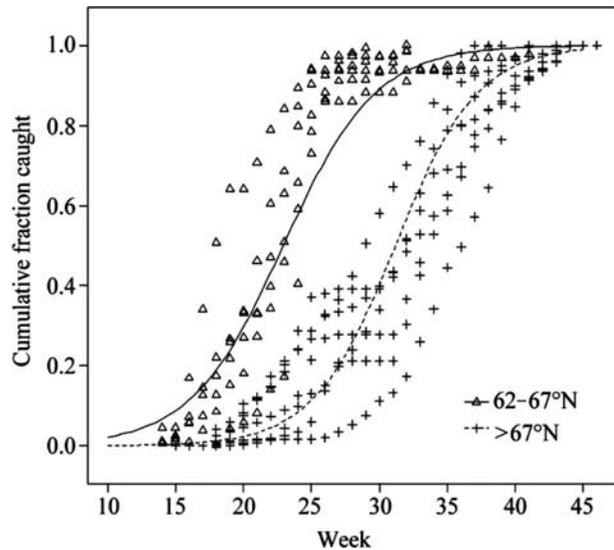

Figure 4. Relative cumulative catch of saithe taken by purse-seiners by week and year (2001–2007) in two areas along the Norwegian coast (between 62° and 67°, and north of 67°N). The lines are logistic curves fitted to the data from each area (all years pooled).

as the only independent variable, whereas in the selection based on AIC, both covariates should be included. In the final model, which included both terms, the slope for percentage of recruit spawners was highly significant (adjusted $r^2 \approx 0.64$; $p < 0.001$), whereas wintering temperature was not significant.

The average (2001–2007) development in the cumulative catch of juvenile saithe in the purse-seine fishery indicated a clear latitudinal trend (Figure 4). Between 62 and 67°N, the 50% catch was taken on average in week 23 (6 June). North of 67°N, the fishery reached 50% of the catch as late as week 32 (9 August) and did not level off before late September. The estimated biomass of

Table 2. Estimated biomass (B in kt) of saithe schooling in shallow waters along the Norwegian coast based on the assessment results and estimated catch-at-age from the purse-seine fishery.

Year	B
2001	299
2002	351
2003	299
2004	326
2005	403
2006	486

saithe schooling in shallow waters along the coast north of 62°N ranged from 299 to 486 kt (Table 2).

The May surveys in 1991 and 1992, in combination with the larval drift models for those years, indicated that the majority of the larvae had drifted beyond the 62–67°N area by the time the saithe became fully active there (Figure 5). The numerical circulation model suggested that, by mid-May, a substantial percentage of the larvae (12% in 1991 and 25% in 1992) may even have drifted to the north of 70°N, outside the surveyed area.

Larval age and size increased significantly ($p < 0.001$) with latitude in both surveys (Figure 6), confirming that, by that time of year, the early hatched larvae may have had a survival advantage relative to larvae hatched later in the year in respect of saithe predation.

Discussion

In exploring the effects of mean hatching date, post-hatching temperature, wintering temperature of adults, spawning stock size, and percentage of recruit spawners on larval survival in NSS herring, the statistical analyses demonstrated that, during the period 1987–2004, larval survival was best described by hatching date. The observed negative correlation between survival and hatching date indicates that it is advantageous for NSS herring to spawn early. The mechanism behind better survival in years with early hatching may be less overlap with predators during early spring (Fortier and Quinonez-Velazquez, 1998; Lapolla and Buckley, 2005; Nishimura et al., 2007). Survival of fish larvae is influenced by many factors, and predation is a complex factor that is poorly understood (Bailey and Houde, 1989; Fuiman, 1994). At the late larval stage, the predation pressure exerted by invertebrates generally decreases substantially, whereas the predation pressure exerted by fish increases (Fuiman and Gamble, 1989).

In using the cumulative catches of immature saithe (P. virens) as an indicator of spatial and temporal changes in predation pressure along the Norwegian coast, the underlying assumption is that catch rates reflect the feeding activity of the species. During winter, saithe are not available to the fishery because they are dispersed in deeper water and it is only in late spring that they form dense schools in their search for food. Data from the purse-seine fishery indicate that saithe become fully active 2 months earlier in the area 62–67°N compared with areas farther north. Tagging studies have not indicated extensive saithe migrations along the coast (Jakobsen and Olsen, 1987), so the difference in timing of the fishery is probably due to a later start in feeding activity farther north. Therefore, field data for the two, both large and early hatched, year classes (1991 and 1992) of NSS herring demonstrated that a large proportion of the larvae had drifted north of 67°N at a time when the availability of saithe in this area had reached a maximum. The drift models indicated that larvae may even have drifted out of the survey area, so the effect may well have been stronger than that suggested by the survey data. The age and size distributions also demonstrated a consistent northward trend towards older and bigger larvae. At any given time, the older and larger larvae may be less vulnerable to predation by invertebrates (Fuiman and Gamble, 1989) and out of reach of the fish predators, whereas the larvae that hatch late in the season run the risk of being preyed upon by both types of predator because they are still small and because their distribution overlaps with the saithe schools.

Herring larvae hatched late in the season may also be preyed upon by mackerel and blue whiting, which undertake long feeding migrations from their spawning grounds west of Ireland and enter the Norwegian Sea in June–July. In years of high recruitment, juvenile blue whiting may be present in large numbers along the coast throughout the year, and herring larvae have been found in their stomachs (Monstad, 2004). Their presence in the diet of mackerel has yet to be confirmed.

Perhaps an even greater threat to larval survival is cannibalism (Holst, 1992; Dalpadado et al., 2000; Prokopchuk and Sentyabov, 2006). Earlier studies have shown that juvenile NSS herring concentrate in the area off Lofoten and Vestrålen during summer for 1 and 2 years before maturing (Dragesund et al., 1980; Hamre, 1990). Consequently, large herring year classes are considered to have regulating effects on herring recruitment (Holst, 1992; Dalpadado et al., 2000) but, given the spatial and temporal characteristics described, the late-hatching larvae should be affected more than the early hatched larvae.

In addition seabirds such as puffins (F. arctica), may consume large numbers of herring larvae. In mid-April of every year, puffins arrive in northern Norway to breed, and the survival of their chicks is significantly related to the abundance of herring larvae (Sætre et al., 2002). Sætre et al. (2002) have shown that the year-class strength of NSS herring is determined before most of the larvae have drifted past the puffin colonies in July/August. Anker-Nilssen (1992) estimated that the puffins consume up to 54 000 t of 0-group herring in June–July, constituting a predation pressure of 5–15% by number for a strong year class (Barrett et al., 2002).

Although temperature often has a direct positive effect on recruitment through increased growth and greater survival rates (Leggett and Deblois, 1994), post-hatching temperature did not affect larval survival in our analysis. The delay in hatching date with falling wintering temperatures and its advance with increasing percentages of recruit spawners suggest that temperature conditions and stock structure may have indirect effects on larval survival, inducing early spawning in years with high temperature during wintering and delayed spawning in years with low wintering temperature and/or a large percentage of recruit spawners. However, we stress that the wintering NSS herring had an extremely narrow distribution in the fjords of northern Norway during the years investigated (Slotte, 2001), and this may explain the strong correlation between hatching time and temperature. In years when the herring are distributed over a wider area, with more variable temperatures, such a relationship might easily break down.

The relationship between hatching date and survival appeared to be less pronounced from year 2000 on (Figure 2). This may be related to the northward extension of the spawning activities from the 1980s (Røttingen, 1990) to the late 1990s (Slotte, 2001). The larvae originating from the northern spawning grounds face a much shorter drift route to the nursery areas in
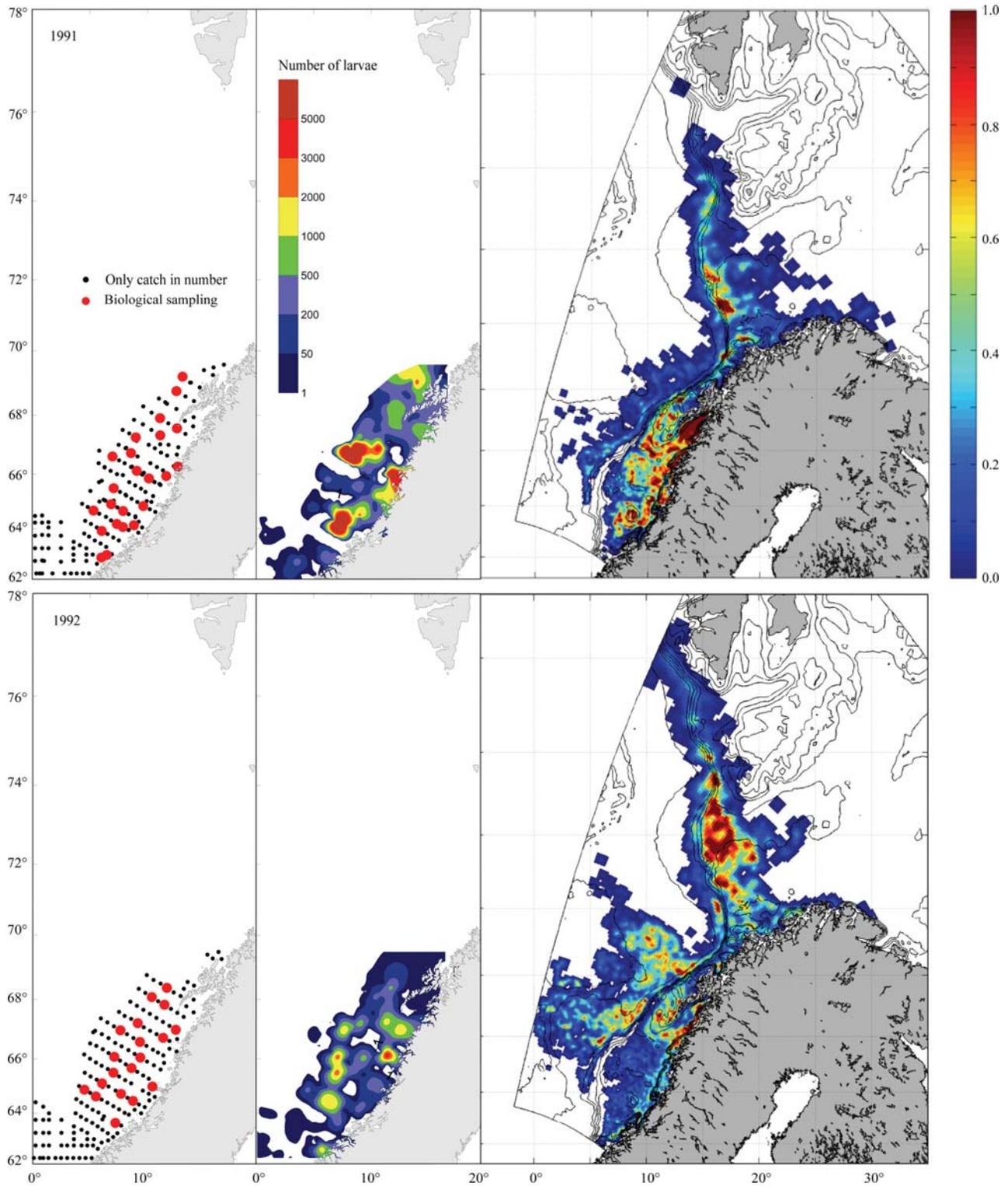
Figure 5. Stations sampled during the May survey (left), observed distribution of herring larvae in May (centre), and simulated distribution (right) on 15 May for 1991 (upper) and 1992 (lower).

the Barents Sea and, to follow our argument, the predation pressure during the drift period should be correspondingly lower.

We have focused on predation as the most important factor influencing year-class strength of NSS herring. However, bottom-up effects may also be important. Previous studies have

particularly addressed the match/mismatch hypothesis (Fossum and Moksness, 1993; Fossum, 1996), although those authors noted that, because of a lack of information, predation could not be discounted as a potentially important factor. Clearly, early spawning may have advantages that are more related to
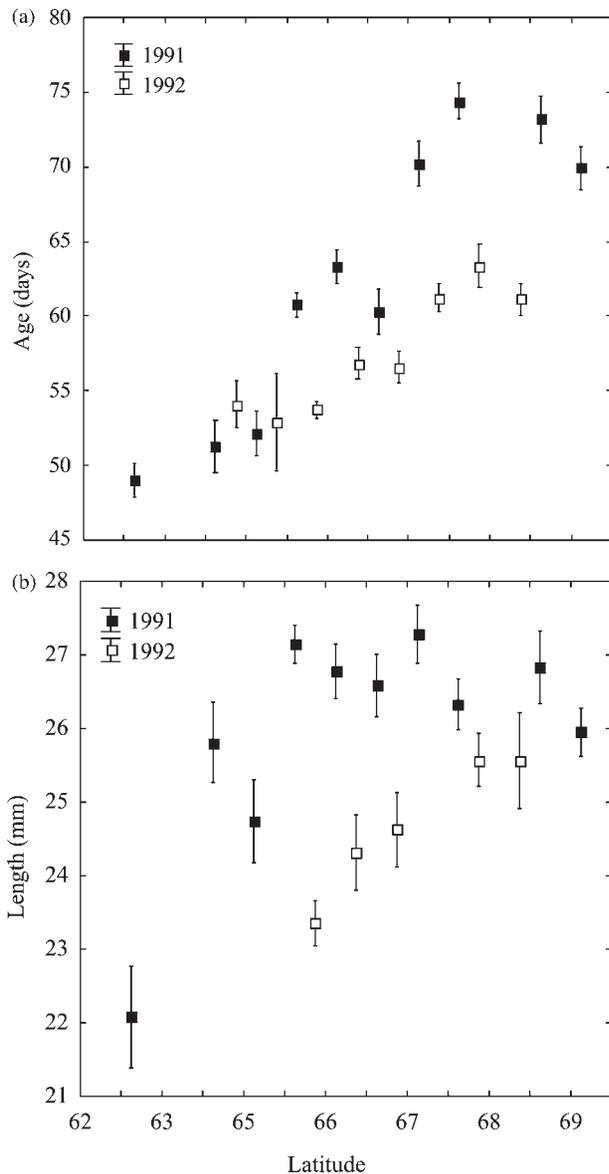
Figure 6. Geographic variation in (a) mean age, and (b) size, ± 95% confidence intervals of herring larvae sampled in May 1991 and 1992 (mean sampling dates: 16 and 11 May, respectively). In 1992, no data on length were available south of 66°N.

feeding success and growth than to predation pressure, but this remains a topic for further study. A low correlation between larval abundance and year-class strength measured later in life, as found in many fish populations (Bradford, 1992), has also been observed in NSS herring (Sætre *et al.*, 2002). This indicates that there are processes after first feeding which are critical for larval survival, and between-year variation in temporal and spatial overlap with predators while drifting along the Norwegian coast may well be a crucial factor.

Acknowledgements

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