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REGULAR PAPER

Development stage distribution as a proxy for feeding success and growth for first feeding Norwegian spring spawning herring larvae

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Abstract

The estimation of growth rates in young herring larvae (*Clupea harengus*) in the field can be difficult because the primary increments in the otoliths may not be discernible or formed at a daily level. Likewise, the estimation of mortality rates of fish larvae in the field is very difficult to achieve, especially in a rigorous quantitative manner. In this study, the authors suggest the use of a stage-based proxy of feeding success, growth and potential survival or mortality risk of field-caught larvae. The stage-based proxy is derived based on observations from previous laboratory studies where larvae successfully completing start-feeding on external food sources will advance through the early development stages, whereas those that do not (unsuccessful larvae) remain and accumulate in the development stage preceding first feeding. The relative occurrence of larvae in the early development stages is therefore expected to reflect feeding conditions of the larvae, with higher ratios of unsuccessful larvae indicative of poor feeding success and higher mortality risk. Using field data on Norwegian spring spawning herring, the authors document that the relative occurrence of larvae in the late non-feeding stage is significantly higher at lower average zooplankton concentrations, in line with the predictions of the authors that this novel approach of using a stage-based proxy could be a useful indication of feeding success, growth and mortality in the field. Further, there was a significant interaction effect with ambient temperature, with the ratio being higher at low zooplankton concentrations at higher temperatures. This study also suggests that these findings are not population specific as the same accumulation of non-feeding larvae in the late non-feeding stage was observed in laboratory-reared larvae of both autumn and spring spawning herring populations.

KEYWORDS

growth, larvae, mortality, Norwegian spring spawning herring, proxy for start feeding

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1 | INTRODUCTION

Growth rate during the larval stage has been suggested to influence mortality and thereby recruitment dynamics of fish through the "growth-mortality" hypothesis (Anderson, 1988). Larval stage duration is highly variable and has been shown to be size dependent rather than age dependent (*e.g.*, Francis, 1994). Based on this, one of the functional mechanisms that compose the "growth-mortality" hypothesis is the "stage-duration" mechanism which postulates elevated survival for fast-developing larvae (Chambers & Leggett, 1987; Hare & Cowen, 1997; Houde, 1987; Takasuka *et al*., 2004). Larval growth rate has been shown to be mainly influenced by food availability and temperature (Folkvord *et al*., 2000; Folkvord *et al*., 2009b; Kiørboe & Munk, 1986), and variability in these factors could therefore indirectly influence the accumulated mortality of fish larvae by altering larval stage duration (Francis, 1994).

Atlantic herring (*Clupea harengus*) is a key species in the northeast Atlantic both ecologically and commercially. It has a complex population structure and although low levels of genetic differentiation have been found, there is considerable variability in life-history traits such as spawning time and spawning areas (Pampoulie *et al*., 2015). The two largest herring populations, North Sea autumn spawners (NSAS) and Norwegian spring spawning herring (NSSH), are important populations in the North Sea and Norwegian Sea ecosystems, respectively.

Herring larvae are able to survive extended periods of low prey concentrations and low growth rates (Folkvord *et al*., 2009a; Geffen, 2009; Kiørboe & Munk, 1986; McGurk, 1984). Therefore, the effects of reduced food availability and/or low temperatures on mortality could be expected to be primarily indirect through higher accumulated mortality caused by increased duration of the larval stage, for this species. It is challenging to measure mortality in the field (Gallego *et al*., 2012), and estimates of larval growth based on methods such as otolith microstructure analyses, RNA/DNA analyses and fatty acid analyses (*e.g.*, Folkvord *et al*., 1996) are often time consuming and expensive. It is particularly challenging to obtain reliable estimates of growth for first feeding larvae where otolith microstructure based on daily increments cannot always reliably be used (Fox *et al*., 2003).

An alternative approach to the study of larval mortality could be to investigate variability in larval stage duration. If accumulated mortality is related to the duration of the larval stage as postulated by the stage-duration mechanism, and stage duration is related to feeding conditions and temperature, then estimates of larval stage duration could serve as a proxy for growth and mortality. It has been shown in laboratory experiments that in herring, the duration of stage 1d, which is the stage where larvae become developmentally ready for exogenous feeding (Øiestad, 1983), is clearly linked to prey availability. Slow-growing larvae will remain in this stage for extended periods (Folkvord *et al*., 2009a). In particular, non-feeding early larvae will eventually end up in stage 1d, representing herring larvae with no remaining yolk (Øiestad, 1983), and not progress into the next stage (2a), which is characterized by identifiable dorsal-fin anlagen (Doyle, 1977). The transition from stage 1d to 2a thus represents a food-dependent bottleneck where larvae will "accumulate" in stage 1d during poor feeding conditions, whereas more larvae will pass to stage 2a during good feeding conditions (Figure 1).

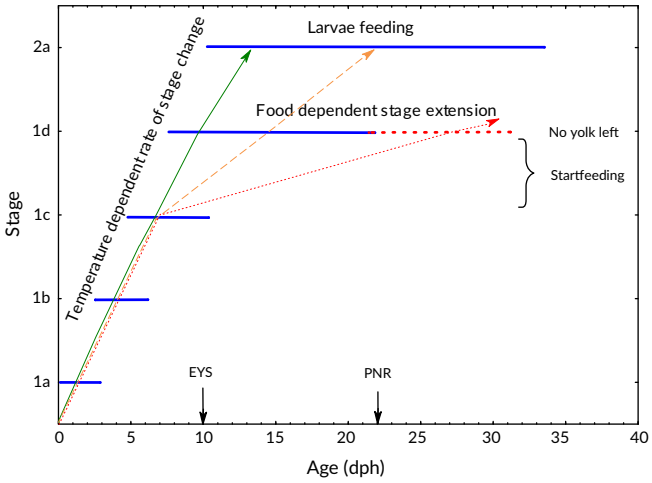

FIGURE 1 Conceptual figure illustrating developmental trajectories of three hypothetical larvae with good (solid arrow line), intermediate (dashed arrow line) and poor feeding conditions (starving, dotted arrow line). Age range of larval developmental stages as defined by Doyle (1977) and Øiestad (1983) is shown as horizontal thick lines. Start feeding is indicated from stage 1c (Doyle, 1977). Note the increased range of larval ages at stage 1d (when no yolk remains are present, Øiestad, 1983) as a consequence of reduced food intake. EYS and PNR indicate age of "end of yolk sac" and "point of no return", respectively

Therefore, we used the relative occurrence of stages 1d and 2a (proportion of 1d) as an indirect measure of larval growth and stage duration. Data on NSAS and NSSH from laboratory experiments and from a 22 year field sampling programme on the main spawning grounds for NSSH along the Norwegian west coast are used to investigate interannual variability in the proportion of 1d larvae. Further, the variability in occurrence is linked to feeding conditions and ambient sea temperature. The assumption that the duration of stage 1d can be related to feeding success was tested using laboratory data where both age and stage of the larvae were known. From the field, it was hypothesized that larvae with unsuccessful first feeding will accumulate in stage 1d and not progress to the following stage, and thus result in a higher proportion of 1d larvae relative to stage 2a larvae.

2 | MATERIALS AND METHODS

2.1 | Laboratory studies

The data from seven laboratory experiments with herring larvae were compiled to obtain stage durations and growth of larvae from different populations and environmental regimes (Table 1). Both spring and autumn spawned larvae are reported here to investigate the utility of

TABLE 1 Laboratory studies used for analysis of stage-dependent age and growth

					Average age-at-stage[a] (dph)		DLI (mm day^{-1})
Study	Spawning season	Stock	Temp (°C)	Ration	Stage 1 d	Stage 2a	Overall
1	Spring	NSSH	5	High	13.4		0.18
1	Spring	NSSH	8	High	11.0	21.6	0.22
1	Spring	NSSH	11	High	9.7	17.3	0.28
2	Spring	NSSH	4	High	19.5	29.3	0.15
2	Spring	NSSH	12	High		9.0	0.36
3	Spring	NSSH	8	High	11.0	13.9	0.30
3	Spring	NSSH	8	Low	14.8	24.1	0.10
4	Spring	NSSH	6	High	14.0	19.3	0.22
4	Spring	NSSH	6	Low	18.1	29.0	0.10
4	Spring	NSSH	10	High	7.3	12.3	0.40
4	Spring	NSSH	10	Low	7.8	24.5	0.05
5	Autumn	Buchan	10	High	7.4	14.8	0.29
5	Autumn	Buchan	10	Low	15.6	37.6	0.14
5	Autumn	Buchan[b]	10	High	7.0	14.7	0.33
5	Autumn	Buchan[b]	10	Low	15.4	28.0	0.17
6	Autumn	Buchan	10	High	9.3	15.9	0.31
6	Autumn	Buchan	10	Low	9.6	18.4	0.21
7	Autumn	Local Askøy	8	High	10.2	20.6	0.25
7	Autumn	Local Askøy	8	Low	21.6	31.5	0.06
7	Autumn	Local Askøy[c]	12	High	7.3	13.7	0.31
7	Autumn	Local Askøy[c]	12	Low	17.5	29.9	0.08

Note: Studies: (1) Suneetha *et al*., 1999, (2) Folkvord *et al*., 2004, (3) Folkvord *et al*., 2000, (4) Folkvord *et al*., 2009a, (5) Folkvord *et al*., 2009b, (6) Fox *et al*., 2003, (7) Johannessen *et al*., 2000. dph: days post hatch; DLI: daily length increment; NSSH: Norwegian spring spawning herring; Buchan: east of Scotland, North Sea Autumn spawning herring; Local Askøy: inshore west coast of Norway.

[a]Stage according to Doyle (1977) and Øiestad (1983).

[b]Spring light regime.

[c]Additional unpubl. data.

the results for herring in general rather than simply for autumn or spring spawners or being stock specific. Common for all the experiments were that known aged larvae were staged and length measured live before further processing (Folkvord *et al*., 2009b). Sampling of fed larval groups typically was carried out systematically on a weekly basis with *c*. 20 larvae sampled per tank. Average age of larvae at different stages was estimated from these samples, as was average growth in length if not available from source publications (see Table 1, Supporting Information S1 and references therein). Temperatures in the experiments ranged from 4 to 12°C, and the constant level feeding conditions ranged from *ad libitum* prey (wild-caught zooplankton) concentrations (typically 2000 prey per litre), to *c*. 50-fold lower concentrations in the low prey concentration groups (Table 1). These divergent environmental conditions resulted in larval groups of widely different growth and developmental rates. In total, over 8000 larvae were length measured and staged during these experiments, and larvae from a sub-set of stages are used in the following analyses. The stages were determined according to Doyle (1977) with the addition of a 1d stage, representing a larva with no remaining yolk, but without dorsal-fin anlagen (Øiestad, 1983).

2.2 | Ethical statement

All laboratory experiments reported in this study were carried out before 1999, and the care and use of experimental animals complied with Norwegian animal welfare regulations, guidelines and policies as approved by the Norwegian Animal Research Authority (NARA) at that time.

2.3 | Field sampling

Field data (1994–2016) were obtained from the NSSH larvae survey (March/April) time series at Institute of Marine Research (IMR), Norway. NSSH spawning grounds are distributed widely along the Norwegian west coast, and newly hatched larvae therefore experience variable environments. It is also known that first-time spawners often use other spawning grounds (farther north) than repeat spawners (Slotte, 1999, 2001). To reduce spatial effects (including maternal effects), the authors only included larvae sampled at the main spawning grounds off the Møre coast (62°N to 63°30 N) which

TABLE 2 Summary of the field samples (1994–2016) from the Møre area (west coast of Norway) used in the present study

Date	Year	Stations	Number of measured larvae	Average standard length (mm) in stage 1d
11–13 April	1994	10	99	10.6
10–15 April	1995	14	481	10.6
21–23 April	1996	14	545	10.3
12–18 April	1997	22	626	10.6
15–19 April	1998	15	755	10.5
19–21 April	1999	12	325	10.9
21–23 April	2000	13	623	10.9
8–9 April	2001	9	381	10.7
10–12 April	2004	6	285	10.7
30–31 March	2005	11	543	10.6
26–28 March	2006	12	531	10.6
29–31 March	2007	11	409	10.4
15–17 April	2008	11	502	10.4
12–14 April	2009	10	456	11.2
8–10 April	2010	14	620	9.9
4–7 April	2011	10	393	10.2
29–31 March	2012	11	514	10.8
3–5 April	2013	12	511	11.9
1–3 April	2014	10	370	11.4
10–12 April	2015	12	254	11.4
3–5 April	2016	9	174	10.4

is well defined spatially and where the fraction of first-time spawners are generally low (Slotte, 1999, 2001). Because of a lack of standardization of plankton sampling during the early period, only the period from 1994 to 2016 was included in the analyses (Table 2), although the survey extends back to the 1970s.

In the survey, herring larvae were collected using a Gulf III plankton sampler (Gehringer, 1952) during daytime and a T-80 (80 cm diameter ring net with a 375 μm mesh net) hauled vertically from maximum 150 m during night-time. The Gulf III is a high-speed sampler (towing speed five knots) that often damages the larvae, resulting in poor quality and sometimes difficult to classify to development stage, whereas larvae sampled with the T-80 (which is hauled slowly to the surface) are generally of good quality. To secure good-quality data on development stage, only data from the T-80 samples are included in the analysis here. On each sampling station, a maximum of 50 larvae were length measured (to the nearest millimetre below) immediately after collection and staged according to Doyle (1977) and Øiestad (1983). In total, over 140,000 larvae were sampled on the Møre grounds with the T-80 in the years 1994–2016, of which 9397 larvae were length measured and staged. Because the age of the field-caught herring larvae could not be estimated directly, an index of stage duration was made. The proportion of 1d larvae was defined as number of 1d larvae divided by sum of 1d and 2a larvae and used as an index of stage duration in stage 1d.

Zooplankton was collected in vertical hauls using a WP II net (Fraser, 1968) with a 180 μm mesh net. Samples included were taken from a maximum depth of 200 m. The zooplankton sample was divided using a Motoda splitting device (Motoda, 1959). Half of the zooplankton sample was stored in seawater buffered 4% formalin for the later identification of species. The other half was passed through 2000, 1000 and 180 μm mesh sieves and dried on pre-weighed aluminium trays at 70°C for 24 h (at sea) to give >2000 μm, 1000–2000 μm and 180–1000 μm size fractions. The trays were weighed to ±0.001 g on a Mettler precision balance back in the laboratory. The weight of the dried zooplankton fraction was converted to milligrams per square metre (mg m^{-2}), and the samples from the smallest size fraction (180–1000 μm) were used here to calculate an annual average biomass index from the Møre area (62°N to 63°30 N) as an index of potential food availability for the herring larvae. The reason for using average values and not including spatial resolution in the zooplankton data was that zooplankton was only sampled on every third larvae station, and therefore not all larvae stations could be coupled to a plankton station.

Temperature data were collected with a Seabird CTD (SBE 911) from close to the bottom to the surface. Average temperature in the upper 100 m was used in the analyses.

2.4 | Statistical analysis

Linear regressions of length *vs*. days post hatch (dph) were used to estimate group-specific daily length growth (increment, DLI) from the different laboratory experiments (Supporting Information S1). Factorial general linear models (GLMs) were then used for the laboratory-derived data to test for effects of growth (DLI) and seasonal origin (autumn *vs*. spring) on average size-at-stage and age-at-stage. Models with non-significant second-order interactions were replaced by more parsimonious additive models. Additional analyses were carried out by adding temperature as a covariate to the models resulting from above (Supporting Information S2). All GLM analyses and graphs were produced using Statistica v.13 software.

The effect of zooplankton abundance and temperature on the proportion of 1d larvae in the field was tested using the glmer function in the lme4 package in R (Bates *et al*., 2015), with larvae being a 1d stage (or not) was treated as a binomial response variable. This was carried out by weighting the number of 1d larvae at any given station against the total number of stage 1d and 2a larvae and using logit as link function. The authors used log (zooplankton index) and average station temperature as covariates, and station within year, and year as random factor. Thus, the fixed part model formulation for the additive model was as follows:

$$\mathrm{Log}[(p(X)/(1-p(X)] = \beta 0 + \beta 1X + \beta 2X$$

where p(X) represents the proportion 1d larvae, β0 the intercept of the model, β1 the parameter for the zooplankton index and β2 for the average temperature the given year. The inclusion of significant covariates and interactions was determined by model comparison using AIC criteria (Zuur *et al.*, 2009). Further details on statistical model output can be found in Supporting Information S2. In general, effects were considered significant at a level of 0.05.

3 | RESULTS

3.1 | Laboratory data

3.1.1 | Effects of growth on age-at-stage

The average age of larvae at a given stage was higher in groups with lower growth rates (GLM tests, $P < 0.001$, Figure 2, Supporting Information S2, one outlier removed based on residual analysis), but the authors found no significant differences in age-at-stage as a function of growth between larvae of spring and autumn spawners (GLM tests, $P > 0.08$, Figure 2, Supporting Information S2). There was no consistent effect of temperature on the average age-at-stage (GLM tests, $P > 0.19$, Supporting Information S2). The development from yolk-sac stages to stage 1d depended on ambient temperature (Figure 3), resulting in initially lower ages-at-stage at higher temperatures, and thus probably contributed somewhat to the variability in average age-at-stage. The estimated range in average ages of larvae growing at 0.05 and 0.4 mm day^{-1} was *c.* 14 days in stage 1d larvae and 22 days in stage 2a larvae (Figure 2). Unfed larvae and larvae that did not successfully initiate feeding ceased developing beyond stage 1d (own observations), and slower-growing larvae from low food level groups also tended to stay at the 1d stage to an older age (Figure 2a).

3.2 | Field data

The proportion of 1d larvae which is suggested as a proxy for first feeding success was negatively related to zooplankton biomass (lme4, mixed-effects, $P < 0.02$), indicating accumulation of larvae in stage 1d. This would lead to a delayed transition for the larvae through the bottleneck to stage 2a and hence longer duration of stage 1d in years with relatively lower food availability. The relationship between the

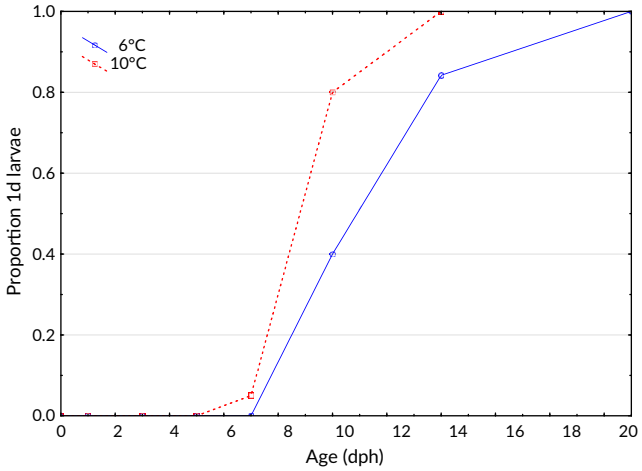

FIGURE 3 Proportion of unfed laboratory-reared herring larvae that have entered stage 1d *vs.* age (days post hatch). Data from Norwegian spring spawning herring larvae reared at 6 and 10°C (case study 4; Table 1). 6°C and 10°C

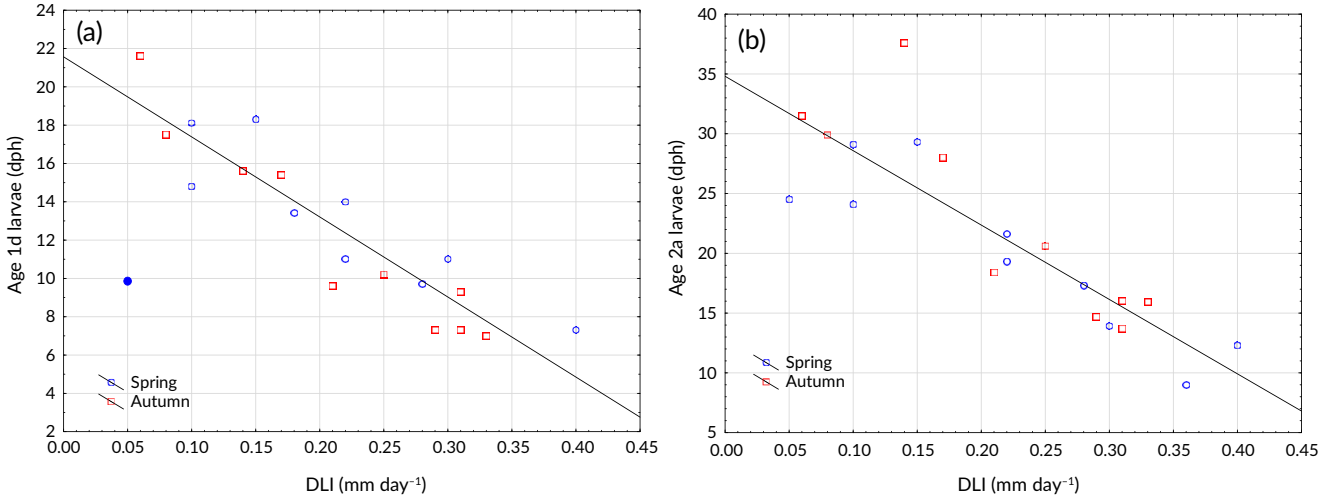

FIGURE 2 Linear regressions of average age of herring larvae (days post hatch, dph) and length growth (DLI, mm day^{-1}) of spring and autumn spawners at stages 1d (top, Age 1d = 21.6–41.8 * DLI, $P < <0.001$, $r^2 = 0.834$, $n = 20$) spring and autumn, and 2a (bottom, Age 2a = 34.8–62.2 * DLI, $P < <0.001$, $r^2 = 0.744$, $n = 21$) spring and autumn. One marked outlier is not included in the linear regression estimate. DLI: daily length increment

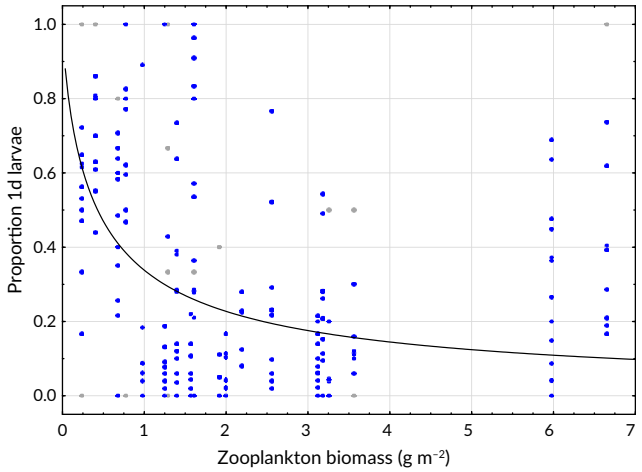

FIGURE 4 Relationship between the proportion of herring larvae in stage 1d (number of 1d larvae divided by the sum of 1d and 2a larvae) and zooplankton biomass (dry weight, 180–1000 μm) for 1994–2016 in the Møre area, west coast of Norway. Fitted line represents relationship at average temperature. Grey points represent stations with five or less 1d and 2a larvae in total

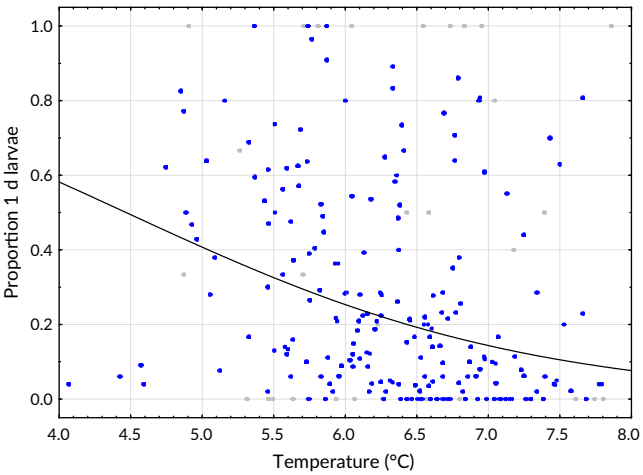

FIGURE 5 Relationship between the proportion of herring larvae in stage 1d (number of 1d larvae divided by the sum of 1d and 2a larvae) and temperature (average, 100–0 m depth) for 1994–2016 in the Møre area, west coast of Norway. Fitted line represents relationship at average zooplankton biomass. Grey points represent stations with five or less 1d and 2a larvae in total

proportion of 1d larvae and zooplankton biomass was non-linear but indicated that the effect of feeding conditions on stage duration was mainly present at relatively low levels of zooplankton abundance (Figure 4). Temperature was also highly significant when added as a factor (Figure 5), with lower proportions of 1d larvae found at higher temperatures (lme4, mixed-effects, $P < 0.001$). Nonetheless, the better model was obtained by including a zooplankton × temperature interaction term (lme4, mixed-effects, $P < 0.001$, Supporting Information 2), where the highest proportion of 1d larvae at low zooplankton concentrations and a more rapid decrease in ratios with increasing zooplankton concentrations occurred at higher ambient temperatures.

4 | DISCUSSION

The proportion of 1d larvae at the main spawning grounds (Møre) for NSSH was significantly negatively related to zooplankton abundance. The trend was especially noticeable at lower food concentrations (<1 g m^{-2}), and this is expected as a fixed nominal reduction in food concentration will represent an increasing proportional loss towards lower concentrations. Developmental stage 1d represents early larvae without yolk, needing to initiate exogenous feeding to continue developing, whereas in the subsequent stage 2a larvae have already been feeding. This finding indicates that the larvae accumulated in the 1d stage when feeding conditions were poor, narrowing the bottleneck of transition to stage 2a. This will likely result in a longer overall duration at this pre-metamorphoses stage during such conditions. Within the framework of the stage-duration mechanism (Chambers & Leggett, 1987; Hare & Cowen, 1997; Houde, 1987; Takasuka *et al*., 2004), the authors suggest that poorer feeding condition resulted in longer stage duration and higher accumulated mortality as suggested by Shepherd and Cushing (1980). The proportion of 1d herring larvae could therefore be a useful proxy of larvae feeding success, growth and possibly mortality in the absence of alternative reliable indicators in the field. The laboratory experiments yielded similar accumulation in stage 1d for both NSSH and North Sea autumn spawning herring larvae. This indicates that there are no major differences in first feeding capabilities and development related to population origin (Folkvord *et al*., 2009b; Johannessen *et al*., 2000). It would be interesting to see similar field studies being undertaken on other herring populations as well as other fish species.

The results from the field were consistent with the results from laboratory experiments, which showed that the average age of 1d larvae was significantly higher in all groups with low growth rates, and that the larvae developed very slowly or may even have ceased developing beyond stage 1d when feeding conditions were exceedingly poor. In addition, the finding that the effect of food concentration on stage transition was especially noticeable at lower food concentrations is concurrent with the previous findings, which have shown that above a certain threshold of food concentrations the larval feeding rate is not compromised and growth is not limited, both in the laboratory (Kiørboe & Munk, 1986; Munk & Kiørboe, 1985) and in the field (Robert *et al*., 2009).

Temperature had a similar effect on the proportion of 1d larvae and by including a zooplankton × temperature interaction term, model performance improved. Because temperature is expected to have an overall effect on stage distribution with increasing temperature resulting in shorter duration of all development stages (Doyle, 1977; Peck *et al*., 2012), it is less intuitive that temperature should have a direct effect on the proportion of 1d larvae. Dodson *et al*. (2019)

found a greater positive relationship between abundance of yolk-sac larvae and preflexion larvae for western Baltic spring spawning herring at low range of temperatures indicating higher mortality during the transition at higher temperatures. Nonetheless, the temperature range in Dodson *et al*. (2019) was much larger (5–20°C) than in the present study (4–8°C). The analyses presented here showed that the effect of zooplankton on the relative stage occurrence is only significant when temperature is above a certain level (>6°C). This is in line with the findings by Suneetha *et al*. (1999) which documented higher responsiveness of herring larvae growth to low food conditions, at higher temperatures.

The surveys were only snapshots and did not follow cohorts of larvae over time. Therefore, accumulation of larvae in stage 1d could not be investigated directly, and the relative occurrence of stages 1d and 2a was used instead. Although the goal has been for the survey timing to be consistent between years, there is variability in timing of sampling at the Møre stations in the time series. The earliest start date was 26 March, whereas the latest was 21 April (Table 2). NSSH spawns over a large area along the Norwegian coast, and although the drift is mainly northward, there are important retention areas such as the Møre spawning ground where larvae reside for days to weeks (Sætre *et al*., 2002). In addition, it has been shown that mean hatching date of herring larvae may vary by up to 30 days (Husebø *et al*., 2009). This could confound the results because variability of stage distribution in the survey will be influenced by timing issues related to when the survey was undertaken relative to the mean hatching date.

Even though the mesh size of the zooplankton sampling gear was too big to quantitatively sample the main feeding organisms of the larvae (such as copepods eggs and nauplii; Last, 1989), the zooplankton abundance estimated in the survey could be regarded as an index of the quantity of food available for the larvae because this time of the year is the main reproductive period of copepods such as *Calanus finmarchicus* (Niehoff & Hirche, 2000; Tande *et al*., 2000).

In this study, the authors show that enumerating the proportion of herring larvae in the developmental stage 1d *vs*. stage 2a could be a useful proxy for feeding success and growth, without having to interpret otolith primary increments. The proportions provide indications of the mortality rates that will be encountered by the larvae and is especially responsive at relatively high ambient temperatures. To undertake this type of study requires that the development stages of larvae are recorded in addition to other standard measures. The authors suggest that this extra effort will be worthwhile given the possibility of obtaining a stage-based mortality proxy.

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AUTHOR CONTRIBUTIONS

E.K.S. and A.F. conceived the hypothesis and organized the data. A.F. carried out the analyses. All authors contributed to writing the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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