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The effect of temperature gradients and stomach fullness on the vertical distribution of larval herring in experimental columns

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ABSTRACT

Larval vertical distribution can be a result of various interacting extrinsic and intrinsic factors. Here, we explore potential interactions between thermal stratification and stomach fullness in the behavioural response of larval Atlantic herring (*Clupea harengus*). We use a factorial design based on an experimental columns system to observe larval herring at four different ages (17, 31, 38 and 45 days post hatch [dph]), in isothermal and stratified water and with two prior feeding conditions (fed and unfed). Light was applied above or below the columns to attract the larvae. While the light direction was alternated, the larvae were observed in the columns. Older larvae were more likely to be observed in the lower part of the column, and all larvae were more likely to be observed in the lower part of the column when there was no thermocline and light was directed from above. However, when light was directed from below, there was no such effect. Prior feeding conditions had no effect on the distribution. We discuss our results in light of field observations of vertical migration.

1. Introduction

The issue of vertical behaviour in fish larvae has attracted much scientific interest due to its implications for distribution and mortality. Vertical distribution is related to swim bladder inflation dynamics (Govoni and Hoss, 2001), predator avoidance and prey search activity (Brewer and Kleppel, 1986; Fiksen et al., 2007). It is driven by species-specific and ontogeny-dependent sensitivity to light, temperature (Munk et al., 1989; Wurtsbaugh and Neverman, 1988), prey concentrations and types (Gallego, 1994; Munk et al., 1989) and turbulence (Franks, 2001).

The vertical behaviour of many clupeid fish in all developmental stages has been studied extensively (Graham and Sampson, 1982; Haslob et al., 2009; Olivar et al., 2001; Parada et al., 2008; Stephenson and Power, 1988). Ambiguous results with regard to diel vertical migration in herring (Grainger, 1980; Heath et al., 1991; Potter and Lough, 1980; Wood, 1971) have raised speculation that vertical migration is more dynamic than estimated from purely light-induced vertical behaviour. Phototaxis in larval herring was described by Woodhead and Woodhead (1955), and there is no doubt that larval herring behaviour is strongly affected by light. This has led to several field studies that have tried to link the isolumen (i.e., preferred depth according to light attenuation) with vertical behaviour of larval herring, with variable results (Haslob et al., 2009; Munk et al., 1989; Wood, 1971). Batty (1987) showed that larval herring exhibit different behaviour in different light conditions, moving up and down in darkness while swimming horizontally in light, a behaviour mechanism that could explain light-induced vertical distribution. However, responses to light are ontogenetically dependent. Recent field studies show that individuals <10 mm tend to stay at the surface during the day and distribute homogeneously at night, whereas individuals >16 mm migrate or sink down to deeper layers at night (Haslob et al., 2009). Although this pattern is well-known in non-stratified waters (Munk et al., 1989; Wood, 1971), the existence of thermoclines or pycnoclines alters the above patterns (Clay et al., 2004; Olla et al., 1985).

Temperature has a large effect on larval growth in various species including herring (Buckley et al., 1999; Pepin, 1991). Fast growth can be potentially beneficial because faster-growing individuals develop more rapidly and thus have a higher probability of surviving until recruitment (Houde, 1989). Therefore, we expect larval fish to maximise ambient temperature through temperature-dependent behaviour. Batty (1994) used experimental columns to demonstrate that larval Atlantic herring choose the warmer side of a thermocline in darkness. However, it has also been postulated that lower ambient temperature is used for decreasing metabolic rates during starvation after an initial burst of activity searching for food (Sogard and Olla, 1996; Wurtsbaugh and Neverman, 1988). Furthermore, work with gadoids has shown that juvenile fish can alter their temperature-dependent behaviour according to feeding conditions (Sogard and Olla, 1996).

Despite more than a century of studying herring biology (Geffen, 2009), little work has been done to disentangle the behavioural

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strategies of larval herring by combining several extrinsic (e.g. temperature) and/or intrinsic (e.g. stomach fullness) factors. Knowing the relative importance of factors driving larval fish behaviour through ontogeny is of great importance to understanding the functional link between environmental conditions and survival of larval fish (Beaugrand et al., 2003; Fiksen et al., 2007). Several modelling exercises have recently included state-dependent (state meaning physiological condition) behavioural strategies in individual based-models (IBM) (Kristiansen et al., 2007, 2009). Here, we test the hypothesis that response to a thermocline depends on internal state, defined here as stomach fullness, and age. To test this, we observed fed and unfed larval herring at four different larval ages in experimental temperature gradients.

2. Materials and methods

2.1. Larval rearing

Eggs used in this experiment came from mature herring caught in gill nets on 29 February 2008 in Lindåspollane, north of Bergen, Norway. They were transported on ice to the High Technology Center in Bergen, where 6 females (mean TL = 32.1 ± 1.8 (S.D.) cm) and 3 males (mean TL = 32.5 ± 0.9 cm) were stripped. Eggs were fertilised by stripping the female herring onto a glass plate submerged in seawater and then stripping male herring and letting them fertilise eggs for 15 min at approximately 6 °C. Eggs were spread in a single layer on the plates. The plates were placed in a flow-through system, where they were incubated for approximately 120 degree-days. Fertilisation rate was estimated by taking pictures of random parts of the plates and counting fertilised and unfertilised eggs. The temperature remained stable (5.7 ± 0.23 °C) throughout the incubation period. Mean fertilisation rate was 89.3% per female. As hatching time approached, the embryos were observed daily, and at initiation of hatching, the plates from individual females were placed in separate buckets. When 50% of eggs had hatched (estimated through sampling of the bucket) equal amounts of herring larvae from each bucket were introduced into three green 500 l tanks with a stocking density of 6 larvae l^{-1}. The larval fish were reared for 45 days at approximately 6 °C and maintained under a controlled photoperiod simulating natural light conditions. They were fed wild zooplankton collected using a Hydrotech© filter, which concentrated zooplankton from fjord water pumped from 8 m depth and enabled the provision of progressively larger size fractions of zooplankton. Nominal prey density was kept at 2000 prey l^{-1}, which was counted and added daily around noon.

To assess the quality of the larval cohort used in this experiment, a group of 30 larval fish was randomly sampled weekly for standard length (SL, mm, precision = 0.1 mm, ImageJ v. 1.41) and weight measurements (μg of dry weight (DW, precision 1 μg) after 24 h at 60 °C in a Thermax © oven). No significant differences were found (ANOVA, $p > 0.05$ in all cases) among replicated tanks. Non-feeding small tanks (n = 3) with 100 larval herring each were kept in darkness to assess larval quality and did not show any signs of pre-yolk absorption mortality.

2.2. Experimental columns

The basic design of the experimental columns used for measuring vertical behaviour has been described in detail in Vollset et al. (2009). In short, the columns consisted of 2.2 m long transparent plastic bags that were hung from a metal frame and submerged into large aquariums (60 × 60 × 100 cm) that function as water baths (Fig. 1). The bags were filled up half way (115 cm) to create a water column of uniform shape with a diameter of approximately 15 cm. The thermocline was at a level of 55 cm. No oxygenation was provided due to i) the low concentrations of larvae within the bags, ii) the short experimental time, iii) the need to maintain stable thermoclines and iv) the low temperatures.

There were three modifications to the original design described by Vollset et al. (2009). First, the individual light sources used below each column had a higher intensity (Fig. 2). Second, temperature in each column was logged every other second (using a Tempscan system, Comark) to avoid the unwanted temperature difference in the isothermal controls. Third, a black curtain was used as background to the columns to facilitate the observation of the poorly pigmented clupeid larvae because transparent larvae appear white against a black background in diffuse light. An inert green dye (Baker Green, 0.22 ml l^{-1}) was also added to the water column to create a sharper light gradient (K = 1.39) and diffuse light conditions, which have been proven beneficial in fish rearing (Naas et al., 1996). The green dye stayed in solution throughout the experiment, and during preliminary trials, no adverse behaviour was observed in 24 larvae kept in a 10× concentration of the dye for 48 h.

2.3. Experimental setup

Larval fish were observed at 17, 31, 38 and 45 days post hatch (dph). For each sampling day, the experimental treatments were split into i) column stratification (mild thermocline (T) and isothermal column (IS)) and ii) feeding (fed (F) and unfed (UF)). Thermal regime consisted of isothermal control columns (IS = 8 °C) and thermocline

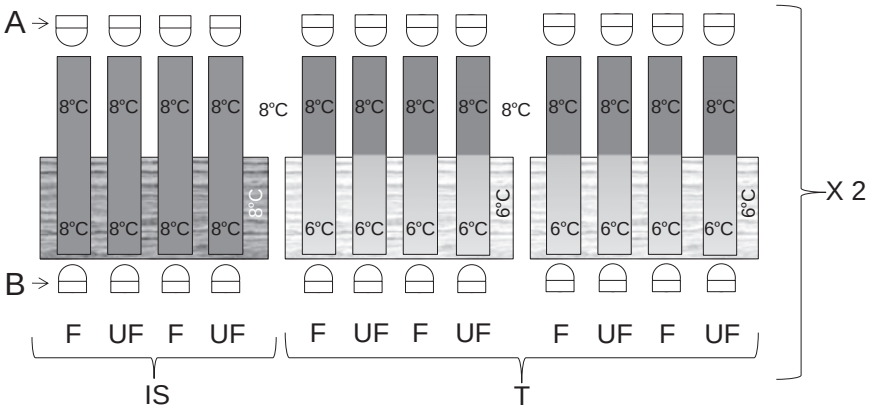

Fig. 1. Schematic view of the experimental column sampling design used for each day of the experiment (17, 31, 38, 45). The thermal regime is depicted by Isothermal (IS) and thermocline (T) columns. The feeding treatments were fed (F) and unfed (UF). Lights were lit from above (A) or from below (B) at different times (see text). Twenty larvae were introduced at each column from the top, and the whole process was run twice each day of measurement.

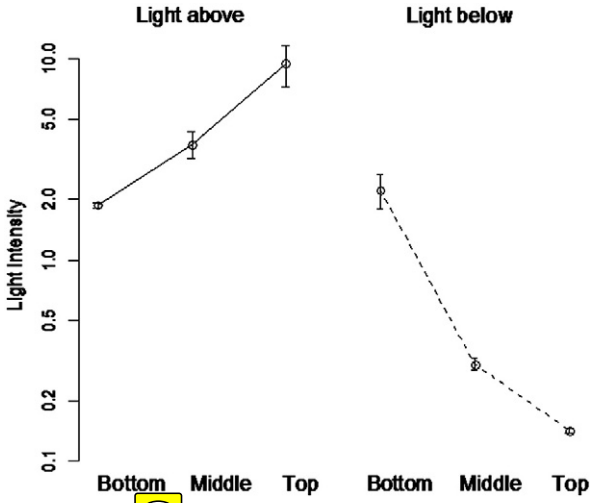

Fig. 2. Light intensity (lux) in the two different light settings, light from above (A), and light from below (B), measured at the bottom, middle and top of the column. Error bars represent ±2 standard error.

columns (T = 8 °C above vs. 6 °C below, dT of 2 °C taking place in a smooth fashion but with its strongest gradient within 20 cm from the water-air interface; Vollset et al., 2009). Feeding regimes were set 16 h prior to each experiment by starving (UF) or feeding *ad libitum* (F) fish that had been sub-sampled from the rearing tanks and placed in 40 l aquaria. Visual inspection confirmed that dead larvae generally had food in their guts. Each feeding regime was replicated 8 times in T and 4 times in IS (Fig. 1). Half of the replicates were started at 10:00 and the second half at 17:00, within the natural light period. No larvae were used in the columns more than once. At the initiation of each experiment, 20 larvae were introduced into each column from above (i.e., 240 larvae in the morning replicate). Light was directed from above first. After 60 minutes, it was switched to be directed from below, and then switched back to the original settings after 130 min. Larval distributions were assessed visually after 30, 70, 100, 140 and 170 min (Fig. 1). At each time, individual positions within the column were recorded using a dictaphone, resulting in 2400 individual positions for each larval age analysed. The column was pursed at the mid position after 200 min (as explained in Vollset et al., 2009), and the larvae picked out, counted and frozen for later DW determination.

2.4. Statistical analysis

To test for the effects of feeding (F, UF), thermocline (IS, T) and age (17, 31, 38 and 45) on the number of larvae in the lower part of the column, we applied a generalised linear model (GLM) with a binomial distribution. A Quasi-GLM error structure was applied because the ratio between residual deviance and degrees of freedom was >1.4 (i.e., over dispersion), and an F-test was used for significance testing (Wood, 2006). We used the number of larvae in the lower part of the column rather than the number distributed throughout the entire column because our interest was in the crossing of larvae into the lower part and because it was difficult to observe the larvae in the upper part. Two analyses were done: one from the period when light was directed from below (after 100 min), and one during the period when light was directed from above (after 170). Based on the short length of the column and the swimming speed of the larvae, they should have had sufficient time to acclimatise and respond to the new light settings at these times. All predictor variables were factorial. Model selection was done by fitting all model combinations including all two and three way interactions, performing stepwise removal of non-significant explanatory variables on the basis of the p-value and then comparing the new model on the basis of the F-distribution. Because analyses were done on repeated datasets two times, a simple Bonferroni-correction was made by dividing the threshold p-value by the number of analyses (α: p/2 = 0.025).

3. Results

The average DW for different ages was 189 µg (17 dph), 532 µg (31), 1041 µg (38 dph) and 2225 µg (45 dph). Larval distributions could be modified in the Thermocline treatment by manipulating the light direction, attracting individuals to the deeper parts of the columns and back to the shallower parts to promote contact with cooler layers (Fig. 3). The stepwise model selection showed that, at 100 min (light from below), only age explained the larval distribution. (GLM, ANOVA, $F_{3,91} = 34.83$, $p < 0.025$). Older larvae were more likely to be in the lower part of the water column than younger larvae (Figs. 3 and 4). The estimated likelihood of being in the upper part of the column was 78, 67, 52 and 45% at 100 min for 17, 31, 38 and 45 dph, respectively.

At 170 min (light from above), the stepwise model selection showed that both age and the presence of a thermocline explained the number of larvae in the lower part of the columns. Although older larvae appeared more frequently in the lower part of the column (GLM, ANOVA, $F_{3,92} = 5.01$, $p < 0.025$), these differences were due to the large contrast between the youngest age class and the rest (Fig. 5). The estimated likelihood of being in the upper part was 88, 79, 78 and 78% for 17, 31, 38 and 45 dph, respectively (Fig. 3). There was a significantly lower probability that larvae were found in the lower column when thermocline was present (GLM, ANOVA, $F_{1,91} = 9.03$, $p < 0.025$). There was no significant effect of prior feeding conditions at either 100 min or 170 min.

4. Discussion

Our results suggest that recent feeding history does not significantly affect vertical behaviour with regard to light and thermal stratification in larvae younger than 46 dph. The effect of light and temperature has been shown to be extremely important for herring distribution (Batty, 1987; Blaxter, 1973; Heath et al., 1991; Munk et al., 1989; Utne-Palm and Stiansen, 2002), although many authors have found contradictory evidence in the field (Grainger, 1980; Heath et al., 1991; Potter and Lough, 1980; Wood, 1971), possibly owing to the interplay of larval size, turbulence and prey fields (Heath et al., 1991). In this experiment, light direction was effectively used to attract larvae to the thermocline and resulted in most larvae crossing the thermocline. Our light intensity values, from approximately 0.1 to 10 lux, are within the range that provokes herring larval ascension during periods of dusk and dawn in the field (e.g., Munk et al., 1989). The herring larvae followed the light direction, behaving as expected with regard to this modulating factor but at rates dependent on other factors, like ontogeny. The well-known pattern of intermittent vertical swimming and sinking that occurs both in the presence of dim light (Woodhead and Woodhead, 1955) and in darkness (Batty, 1994) was observed and can partly explain the observed distributions in our experiment.

4.1. Ontogeny and vertical distribution

There was a clear ontogenetic effect on the distribution of larval herring: older larvae had deeper distributions. Field evidence exists for small-scale, size-related vertical migrations in larval herring (Haslob et al., 2009). These authors showed that smaller larvae were more bound to the surface. Our results agree with these patterns and can be partially explained by increased sinking rates and searching behaviour in older larvae (Batty, 1987; Gallego, 1994). The surface-bound distribution of younger larvae (17 dph) might be due to mechanisms involving surface tension (Batty, 1987) and the

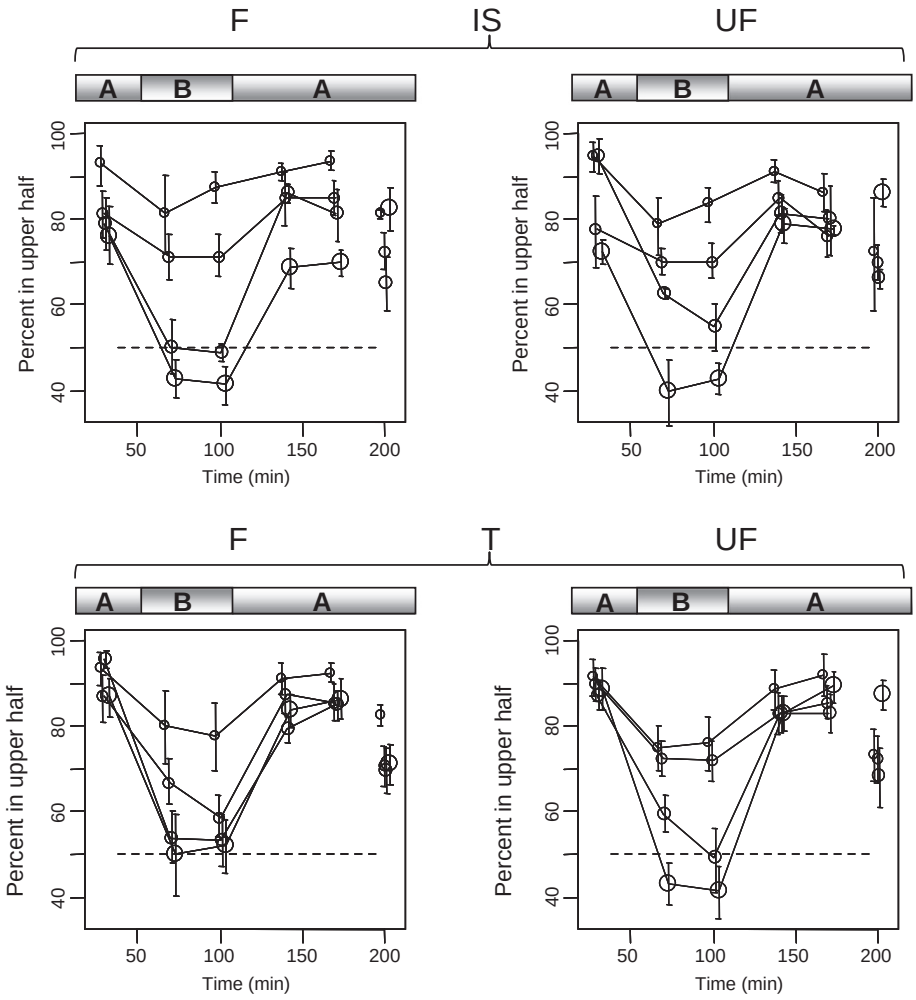

Fig. 3. Percentage larvae (± standard error) in the upper half of the column under isothermal and thermocline conditions for the fed and unfed treatments. Increased size of circles indicates consecutively older larvae (17–45 dph). Horizontal bars indicate the light regime through time (A, lights from above; B, lights from below). Circles at 200 min are recovered larvae after bag pursing (methods in Vollset et al., 2009).

high frequency of burst swimming. The accumulation of herring at the edges of rearing tanks is widely observed and is progressively reduced throughout ontogeny (Batty, 1987). However, when light was directed from below, older larvae accumulated at the bottom, which can be explained by a combination of buoyancy and behavioural response to the reversed light settings.

The comparisons of ontogenetic response to light are radically different from that of other species under quasi-identical experimental conditions, such as larval cod (Vollset, pers. comm.). In contrast to larval herring's increasing attraction to light with age, as they grow, larval cod choose deeper depths, which are characterised by lower illumination levels. Interpreting the different light responses of larval fish species is far from trivial. Factors like trade-offs between rapid growth and high cannibalism, or even differences in retinal pigment composition, might help in explaining the single-factorial differences among species. Herring larvae were much more difficult to observe than cod larvae for the same age due to the low pigmentation. This result might imply that herring would be able to feed at higher light levels with equal risk of predation mortality compared to cod, which would confer a competitive advantage for herring.

4.2. Temperature-dependent behaviour

Herring larvae displayed a strong phototactic reaction to a light source directed from below, causing a large proportion of them to cross the thermocline (Figs. 3 and 4). Although no significant thermocline effect was found, Fig. 4 suggests a higher larval concentration around the thermocline that was not observed at the equivalent level in the isothermal columns. However, our statistical test did not enable rigorous testing of distribution properties. Directing the lights from above (the 'natural' position) resulted in significantly more larvae occupying the thermocline level compared to the isothermal columns (Fig. 5). It is likely that these larvae experienced the low temperature in the T treatment because of the previous light direction. Several authors have shown that fish larvae usually respond to thermoclines by selecting the warmer side (Batty, 1994; Clay et al., 2004; Olla et al., 1985; Olla and Davis, 1990). Experimental work on Atlantic herring has been performed in darkness to avoid the light-temperature interaction (Batty, 1994), but this only partially reproduces the herring behaviour in a diel cycle. Reasons to explain a preference for the higher temperature side of a thermocline are numerous. Selecting warmer waters when light is available may result in a higher energy expenditure but also higher predatory success (Paul, 1983). Pacific herring larvae are known to respond to thin layers of temperature even more strongly than to prey patchiness, choosing the warmer layers close to the thermocline (Clay et al., 2004). Prey of larval herring can also potentially respond to thermoclines, creating a correlation between thermocline and prey. This correlation could explain the benefit of responding to a thermocline as an indirect effect of prey encounters. Escape reactions

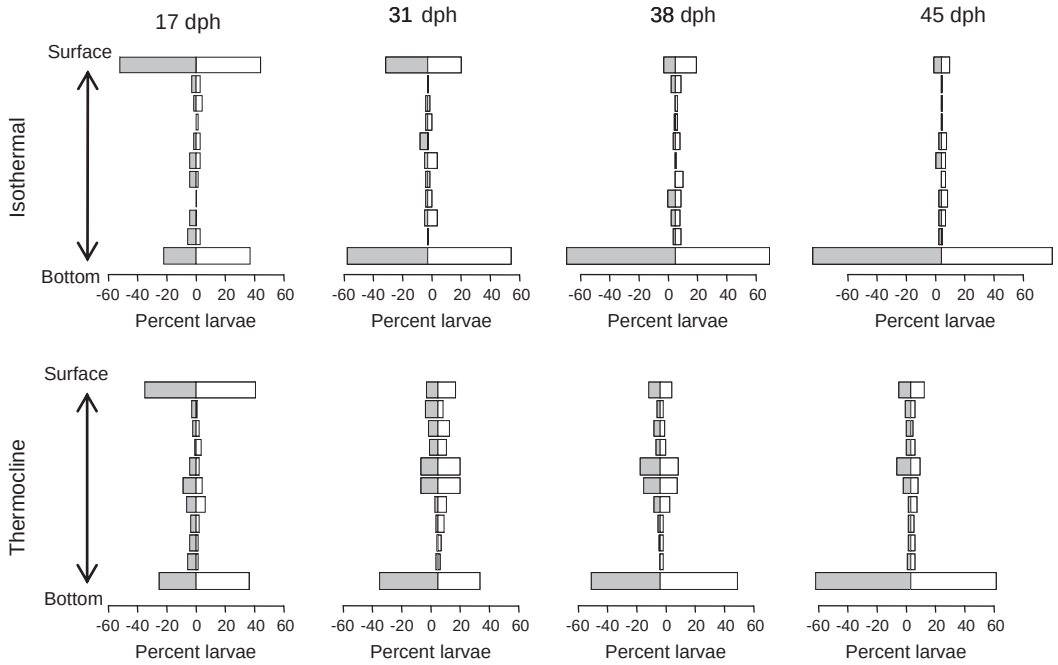

Fig. 4. Vertical histograms of the mean distribution of herring larvae in experimental columns between 70 and 100 min (light shining from below), for fed (grey bars) and unfed (white bars) larvae. Histograms are in 10 cm bins with a height of total 115 cm for 17, 31, 38 and 45 dph (left to right) and isothermal (upper panel) and thermocline columns (lower panel). The choice of 70 and 100 min was to provide two measurement times separated within this light setting (see also Fig. 3).

of herring are also faster in warmer temperatures (Batty and Blaxter, 1992) and, added to the high transparency of larval herring, may result in a situation where feeding and growth are traded off against a relatively low predation mortality cost.

In the wild, evidence is more difficult to assess because of various potential interactions. Field data indicate that weak thermoclines do not affect vertical distributions of larval herring (Seliverstov, 1974), but that in thermally stratified waters, herring choose the mixed layer (Heath et al., 1988). A purely physiological response of both increased upward swimming activity combined with higher sinking rates in warmer waters might explain the aggregation close to the thermocline. In this respect, our 2 °C thermocline is comparable to the 1 °C thermocline associated with larval herring vertical distribution in the field (Munk et al., 1989). In the case of a mixed water column, response to light might only be modulated by larval size and prey patchiness, thus maximising conditions for successful prey detection and capture (Haslob et al., 2009; Munk et al., 1989), or physical forcing like turbulence, which might severely affect both vertical

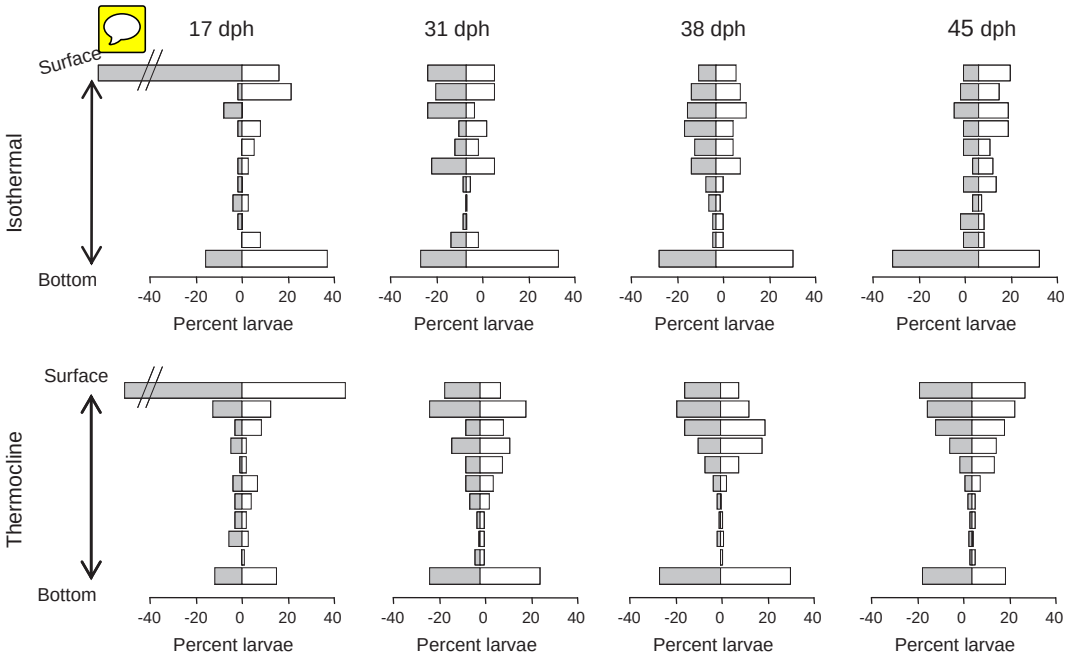

Fig. 5. Vertical histograms of the mean distribution of herring larvae in experimental columns between 140 and 170 min (light shining from above after a period of light shining from below) for fed (grey bars) and unfed (white bars) larvae. Histograms are in 10 cm bins with a total height of 115 cm for 17, 31, 38 and 45 dph (left to right) and isothermal (upper panel) and thermocline columns (lower panel). The choice of 140 and 170 min was to provide two measurement times separated within this light setting (see also Fig. 3).

distribution and encounter rates (Rothchild and Osborn, 1988). The lack of apparent behaviour other than phototaxis in our IS columns would partially support this.

One characteristic of the observed distributions that is difficult to explain is the relatively large percentage of bottom-bound larvae (20–40%) when the light was directed from above. The exposure to a non-natural shift in light combined with an "edge effect" could be involved in these patterns. Statistical analyses and Fig. 5, when compared with Fig. 4, suggest that larvae that had crossed the thermocline tended to come back to the warmer side of it. With regard to the causes of different larval distributions between the IS and T columns (excluding the edges), we observed an active cold water avoidance behaviour, in accordance with previous works (Batty, 1994).

4.3. Stomach fullness

Growth is affected by enhanced metabolic processes in warmer waters (Wurtsbaugh and Neverman, 1988). However, increased metabolism can only be beneficial as long as there is sufficient prey to sustain growth (Brett, 1972). Larval herring behaviour is influenced by extrinsic food-related factors including chemical cues and prey presence, which generates higher searching activity within the prey patches, even in darkness (Batty, 1987; Dempsey, 1978; Gallego, 1994). Nevertheless, experimental evidence shows that prey presence may be less important than other factors, like temperature discontinuities, for depth selection (Clay et al., 2004). In the absence of real prey or chemical cues, we might expect behavioural differences according to internal state. Moderately starved individuals might choose to lower their metabolic rates by selecting colder water or they might choose to increase their searching behaviour to locate food, which might in turn increase their vertical excursions. We were interested in these possible responses and their interaction with thermal gradients. The feeding treatments' lack of significant effect on the vertical distribution might be due to the strong effect of light and temperature on the distribution. As noted by Clark and Levy (1988), a single factor theoretical framework to explain vertical distribution is often flawed because of several interactive individual trade-offs.

Our experimental setup was capable of showing a feeding-dependent response in cod (Vollset et al., in prep). The only way of observing such behaviour in herring would have been to film in total darkness (Batty, 1994), but that would have defeated the purpose of studying this behaviour under the conditions in which feeding takes place (under light). Larval herring are highly plastic in their physiology, behaviour and meristics (Geffen, 2009) and are particularly suited to withstand starvation events (Johannessen et al., 2000), which may explain the lack of sensitivity to state (gut fullness) when compared to other species, like cod.

4.4. Potential bias

According to Whittingham et al. (2006), a potential bias in the parameters or type I error may occur using stepwise model selection procedures. However, this is particularly a problem in certain cases. For example, when i) variance components are not manipulated by the researcher (observational data) and/or when ii) the number of factors is large and the variables are correlated or iii) when no-alternative models are accounted for. However, we used a controlled experimental scheme with few factors and evaluated all possible model combinations. With regards to the probability of increasing the type I error using the current statistical approach, we have clearly demonstrated that this is not the case because the only significant factors explaining the distribution are known drivers of vertical distribution (age, thermocline strength).

The possible explanations for "edge effects" were addressed in previous sections. The magnitude of these edge effects changed with ontogeny, was similar between F and UF treatments, and has been observed in similar setups (e.g., Batty, 1987). We believe that those effects do not, within a given age, invalidate the statistical differences found among treatments. Another potential source of bias is that changes in depth were due to buoyancy changes. Sclafani et al. (1993, 1997) showed experimentally that larval cod decreased their density with starvation, affecting their distribution. Here, herring displayed a high behavioural activity in all treatments, which suggests that buoyancy was not a main driver of the vertical larval distribution.

The system of plastic bags used herein is adequate for pigmented larvae (Vollset et al., 2009) and was modified using a black background to enhance the detection of herring larvae. It is unlikely that this background modification interfered with the factors tested, as these factors (at least external stimuli) elicited a very strong response in herring larvae. A putative bias could be assigned to the visual counting of larvae after observation of the columns at regular intervals. This might have introduced errors due to lack of larval detection or double-counting of larvae. However, the comparison of bag pursing and observational data offered a high degree of concordance which increases confidence in our measurements (Fig. 3).

Using daylight conditions, we showed that the vertical behaviour of 17 to 45 dph herring larvae is sensitive to the presence of thermoclines. A strong ontogenetic effect in vertical behaviour was found, corroborating field studies. A feeding regime of starvation for 16 h did not elicit a significant response in vertical behaviour. Future directions for laboratory research include testing longer periods of starvation and how this interacts with prey and predator fields on larval depth selection.

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