Journal of Experimental Marine Biology and Ecology 404 (2011) 26–32

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

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

I.A. Catalán [a,*], K.W. Vollset [b], B. Morales-Nin [a], A. Folkvord [b]

[a] Department of Ecology and Marine Resources, Mediterranean Institute for Advanced Studies (IMEDEA-CSIC/UIB), C/ Miquel Marques 21, CP 07190, Esporles, Balearic Islands, Spain
[b] Department of Biology, University of Bergen, N-5020 Bergen, Norway

ARTICLE INFO

Article history:
Received 15 July 2010
Received in revised form 3 May 2011
Accepted 9 May 2011
Available online 2 June 2011

Keywords:
Thermoregulatory behaviour
Phototaxis
Feeding history
Larval fish
Vertical migration
Clupea harengus

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

* Corresponding author. Tel.: +34 971611402.
E-mail address: ignacio@imedea.uib-csic.es (I.A. Catalán).

0022-0981/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2011.05.005

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

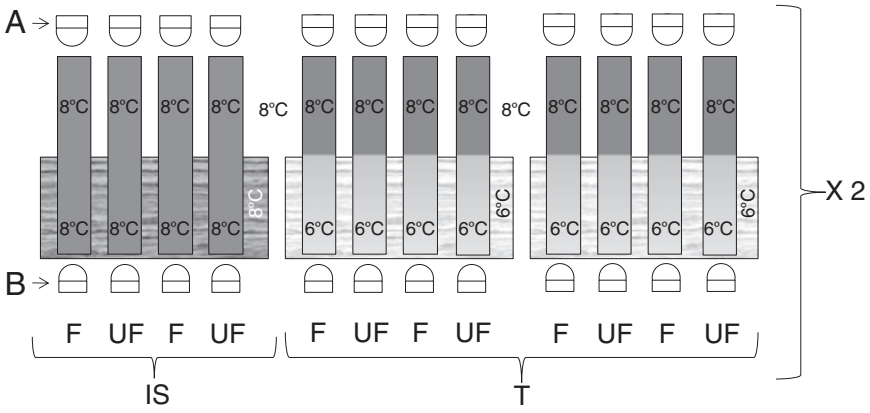

Fig. 1. Schematic view of the experimental column sampling design used for each day of the experiment (17, 31, 38, 45). The thermal regime is depicted by Isothermal (IS) and thermocline (T) columns. The feeding treatments were fed (F) and unfed (UF). Lights were lit from above (A) or from below (B) at 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.