Orientation behavior and swimming speed of Atlantic herring larvae (*Clupea harengus*) *in situ* and in laboratory exposures to rotated artificial magnetic fields

Alessandro Cresci[a,b,*,1], Bridie J.M. Allan[c,b,1], Steven D. Shema[d], Anne Berit Skiftesvik[b], Howard I. Browman[b]

[a] *Department of Ocean Sciences, Rosenstiel School of Marine & Atmospheric Science, 4600 Rickenbacker Causeway, FL 33149-1098, USA*
[b] *Institute of Marine Research, Austevoll Research Station, Sauganeset 16, N-5392 Storebø, Norway*
[c] *Department of Marine Science, University of Otago, Dunedin 9016, New Zealand*
[d] *Grótti ehf., Grundarstíg 4, 101, Reykjavík, Iceland*

ABSTRACT

The dispersal of fish larvae during the early life stages plays an important role in recruitment. Together with oceanographic processes, larval orientation and swimming behavior significantly influences dispersal. However, currently there is no information of larval behavior *in situ* for most subpolar species. The Atlantic herring (*Clupea harengus*) is an ecologically and commercially important component of the North Atlantic ecosystem. This species has sustained a large fishery for over a century, and its stocks have experienced both dramatic collapse and recovery. The Atlantic herring is highly migratory, making it challenging for researchers to determine with certainty the structure and discreteness of different herring stocks. In this context, studying the behavior of herring larvae at sea is crucial for a deeper understanding of their dispersal. However, to date information on the orientation behavior and swimming abilities of herring larvae *in situ* is missing. In this study, we coupled *in situ* observations and laboratory experiments to investigate whether herring larvae display orientation when swimming *in situ*, and which mechanisms/cues they could use. We video recorded the orientation behavior of 208 herring larvae between 14 and 28 days post hatch (DPH) in the coastal Norwegian North Sea while they drifted in transparent behavioral chambers. We also tested the orientation of 136 larvae in a magnetic laboratory, in which they were deprived of any external cue and where we could modify the direction of the magnetic field. We report evidence that herring larvae have a significant preferred orientation direction to the southeast, which does not change between 14 and 28 DPH. Moreover, our results suggest that sunlight plays a key role as larvae had a highly significant orientation towards the sun during sunny weather, but they lost this ability, and exhibited lower precision in their orientation, under an overcast sky. We did not find evidence of magnetic compass orientation, indicating that the orientation direction of herring larvae is not magnetic, at least at this life history stage. Larvae swam at an average speed of 0.36–0.40 cm/s and reached maximum speeds of 3–3.36 cm/s. These results demonstrate that 14–28 DPH herring larvae are capable of orienting *in situ*. Possible implications of this orientation behavior for larval transport in Norwegian waters are also explored.

1. Introduction

The dispersal of the early life stages of fish plays an important role in recruitment (Hjort, 1914; Rothschild, 2000). Larval swimming and orientation abilities are among the factors determining whether the dispersal of fish larvae leads to recruitment (Hjort, 1914; Houde, 2016). If fish larvae drift to nursery areas where there is enough food and predation is low their chances of survival increase. Orientation, coupled with active swimming, can significantly influence dispersal (Faillettaz et al., 2018; Fiksen et al., 2007; Swearer et al., 2019), particularly when

guided by environmental cues to orient *in situ* (Faillettaz et al., 2015; Irisson et al., 2015; Leis et al., 2003, Leis et al., 1996; Paris et al., 2013; Rossi et al., 2019). Thus, in order to understand and predict dispersal of fish larvae, data on their orientation and swimming, *in situ*, are needed. While many studies describe such behavior for tropical and Mediterranean larvae, with the exception of one study on a gadoid (Cresci et al., 2019b) there is no such information on high latitude fish larvae.

Atlantic herring (*Clupea harengus*) is an ecologically and commercially important component of the North Atlantic ecosystem (Daan et al., 1990) that is characterized by complex population connectivity and highly variable recruitment, with an apparent disconnect between spawning stock size (early larval abundance) and subsequent recruitment to the adult population (Geffen, 2009; Toresen et al., 2019; Zimmermann et al., 2018). Pelagic species such as herring are considered to have open populations with high levels of genetic mixing (Ruzzante et al., 2006). For such species, larval dispersal plays a key role in determining populations genetic structure (White et al., 2010). In the case of herring, it is currently unclear what the characteristics and limitations of dispersal are during the early-life stages (Deschepper et al., 2019).

Dispersal of fish larvae depends on oceanographic processes that occur at various temporal and spatial scales (*meso* to large) (Adams and Flierl, 2010; Leis et al., 2013; Sinclair and Iles, 1985). For herring, numerical simulations revealed that larval dispersal is affected by abiotic factors such as persistent oceanographic features like the Norwegian coastal current (NCC) (Skagseth et al., 2015; Zimmermann et al., 2019). Variability in thermal regimes, light and turbulence can also contribute to variation in survival (Kiørboe et al., 1988), growth (Husebø et al., 2007) and abundance (Maravelias and Reid, 1997) of herring larvae, with consequences for subsequent recruitment success (Toresen and Østvedt, 2000). However, while contemporary modelling approaches can provide important insights into the mechanisms underlying dispersal of herring, in most cases they are missing an important component –horizontal orientation and swimming. This is due to a lack of empirical observations of these behaviors, particularly *in situ*. Specifically, whether herring larvae drift passively with the current or perform active, oriented swimming *in situ* is unknown.

Here, we conducted experiments that combined *in situ* observations and laboratory experiments to quantify the orientation and swimming abilities of Atlantic herring larvae from the Norwegian spring spawning (NSSH) stock. We tested the null hypothesis that herring larvae (14–28 post hatch,DPH) orient randomly when swimming *in situ*. We used a well-established method involving a drifting transparent behavioral arena (Drifting *In Situ* Chamber (DISC), (Paris et al., 2008)) that is designed to observe the swimming and orientation behavior of the early life stages of marine organisms *in situ* (Cresci et al., 2019c, Cresci et al., 2017; Faillettaz et al., 2015; Irisson et al., 2015; Kough et al., 2014; Paris et al., 2013; Rossi et al., 2019). We observed the orientation of herring larvae in the Norwegian North Sea, around the Austevoll archipelago, after releasing the DISC from a boat 1–2 km away from the coast. We also conducted experiments on herring larvae in a magnetic laboratory (MagLab), in which the direction of the magnetic field can be manipulated through the use of electric coils. The MagLab is specifically designed for the study of magnetic orientation of marine organisms (Cresci et al., 2019c, Cresci et al., 2017; Durif et al., 2013). We tested the hypothesis that herring larvae display a significant orientation direction using the magnetic field only as orientation cue, *versus* the null hypothesis of random orientation when only the magnetic field is available as a cue. We used observations from the DISC to measure swimming speed and to assess whether 14–28 DPH herring larvae display a preferred orientation direction. Since herring undertake light-dependent vertical movements, disperse from spawning to nursery areas as larvae, and perform long distance migrations as adults, we also assessed whether solar (visual) cues and the earth's magnetic field are involved in guiding their orientation.

2. Methods

2.1. Larval rearing and collection

Ripe adult herring from the Norwegian spring spawning (NSSH) stock were collected by net at Åskoy, Bergen, Norway on May 4th, 2017 and used as the brood stock in this study. Fish were transported to the Bergen High Technology Centre at the University of Bergen where ripe males and females were strip spawned. Eggs from 2 females were stripped onto 12 glass plates in each of four separate seawater filled trays with a water depth of 3 cm. The gonads from 3 ripe males were removed and the sperm was extracted. Sperm was activated and diluted with seawater before being added to the respective trays which created a total of 4 parental crosses. Egg plates were incubated with the milt from 3 males at 10 °C and 19 ppt for 30 min after which the plates were placed in 8 °C and 35 ppt. This process yielded high fertilization success (50–80%) on the glass plates. After several minutes, each glass plate was transferred into a temperature-controlled room for incubation. Incubation tanks were supplied with filtered seawater at 8 °C and at a rate of 2.51 l min $^{-1}$. Eggs were transferred to Austevoll Research Station on 8th May 2017 in 5 l buckets filled with filtered seawater. Eggs were incubated at 8 °C for the remainder of the incubation period. Incubation tanks were supplied with filtered seawater at a rate of 1.6 l min $^{-1}$. Eggs plates were examined daily for mortality and dead eggs were noted and removed. During the experiment, eggs were counted, and developmental stage was assessed on a degree day [(˚d = temperature (˚C) x time (d)] schedule. The egg hatch date was estimated using degree days, which meant that the fish were due to hatch on the 18th of May. Two days after hatching, on 20th May, larvae were transferred to each of six 50 l green fiberglass rearing tanks and were fed a diet of lipid enriched rotifers, 3 times daily at a concentration of 2000 l $^{-1}$. Algal paste was added to tank water to improve the contrast of the rotifers and improve feeding success.

On the day of trials, larvae were placed into 120 mL cups, with two larvae per cup, at least 12 h prior to be deployed *in situ*. The cups were then immersed in a 12 °C water bath to acclimate the larvae to the local seawater temperature at 4 m depth in the deployment area.

2.2. Experimental device and deployments in situ

To collect data on the swimming and orientation behavior at sea, we video recorded the swimming behavior of herring larvae while swimming in a transparent drifting circular arena (DISC, Drifting *In Situ* Chamber, Paris et al., 2013, Paris et al., 2008). We used larvae that were 14–28 days post hatch (DPH) for the tests *in situ* (Fig. 1B, Table S1). The developmental state of the larvae was monitored using a stereomicroscope throughout the experiment. All tests were conducted between the 1st and the 15th of June 2017 in the coastal areas of a Norwegian fjord (Bjørnafjorden, Northeast of Austevoll, 60.09 N, 5.28 E), at a distance of 1–2 km from the shore.

The DISC is a drifting behavioral circular arena, with an acrylic structure and a semi-open transparent circular chamber 20 cm wide and 15 cm deep. The lower part of the DISC is attached to a drogue, which allows the whole system to drift with the current. The DISC is equipped with a GOPRO camera, three analog compasses and a custom Arduino digital compass. When the DISC is placed in the water, it drifts at a depth of *ca.* 4 m. For each deployment, we held the DISC semi-submerged along the side of the boat and placed two herring larvae in the arena. Afterwards, the DISC was released and left to drift for 15 min. The GOPRO camera placed underneath the chamber recorded the behavior of the larvae for the duration of the deployments. However, when processing the videos we considered the first 5 min of each deployment as a habituation period and analyzed the swimming behavior of the individual larvae during the last 10 min (Cresci et al., 2017; Paris et al., 2013). All of the videos were processed using the DISCR tracking procedure, utilizing R and a graphical user interface provided by
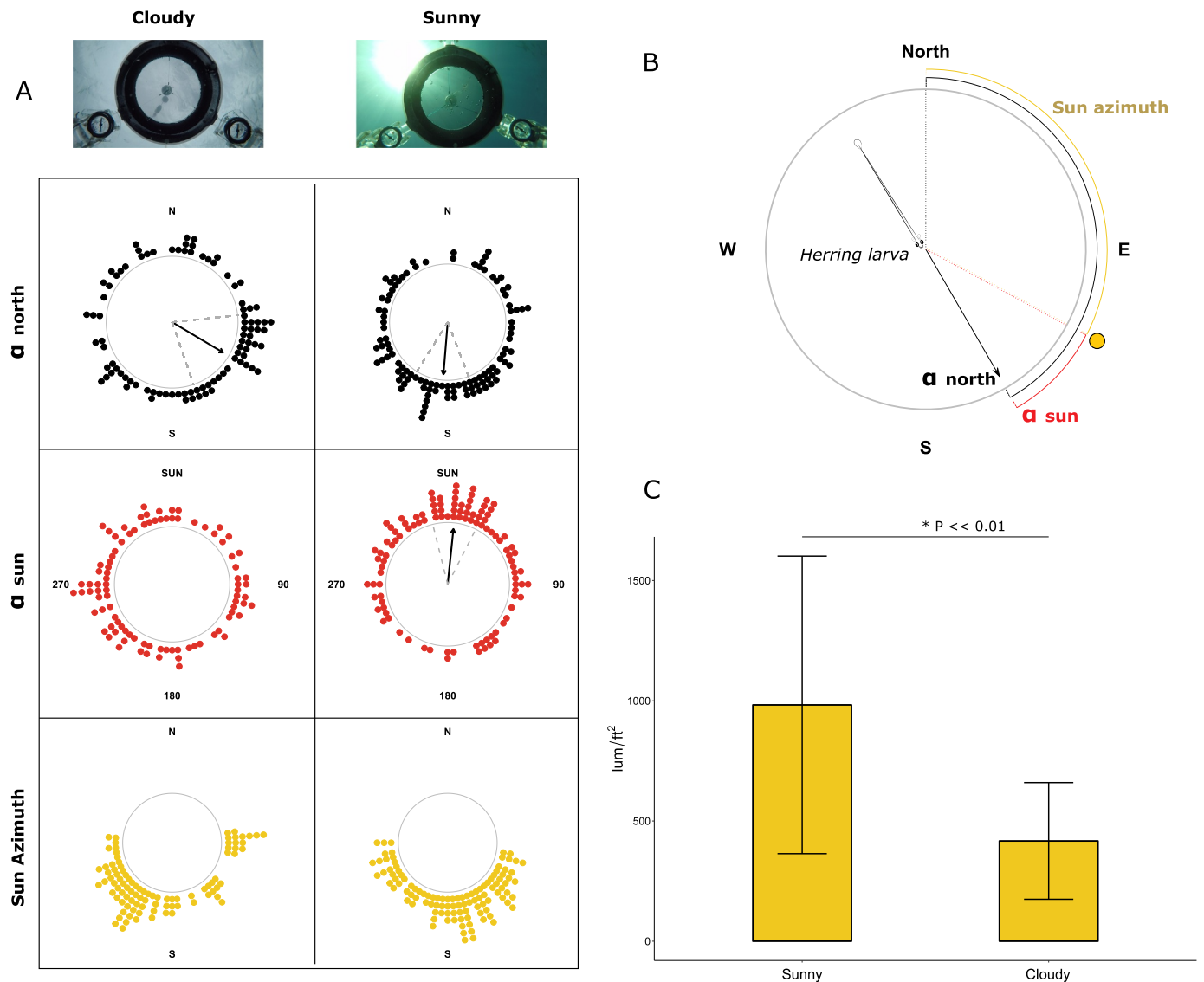
Orientation *in situ*
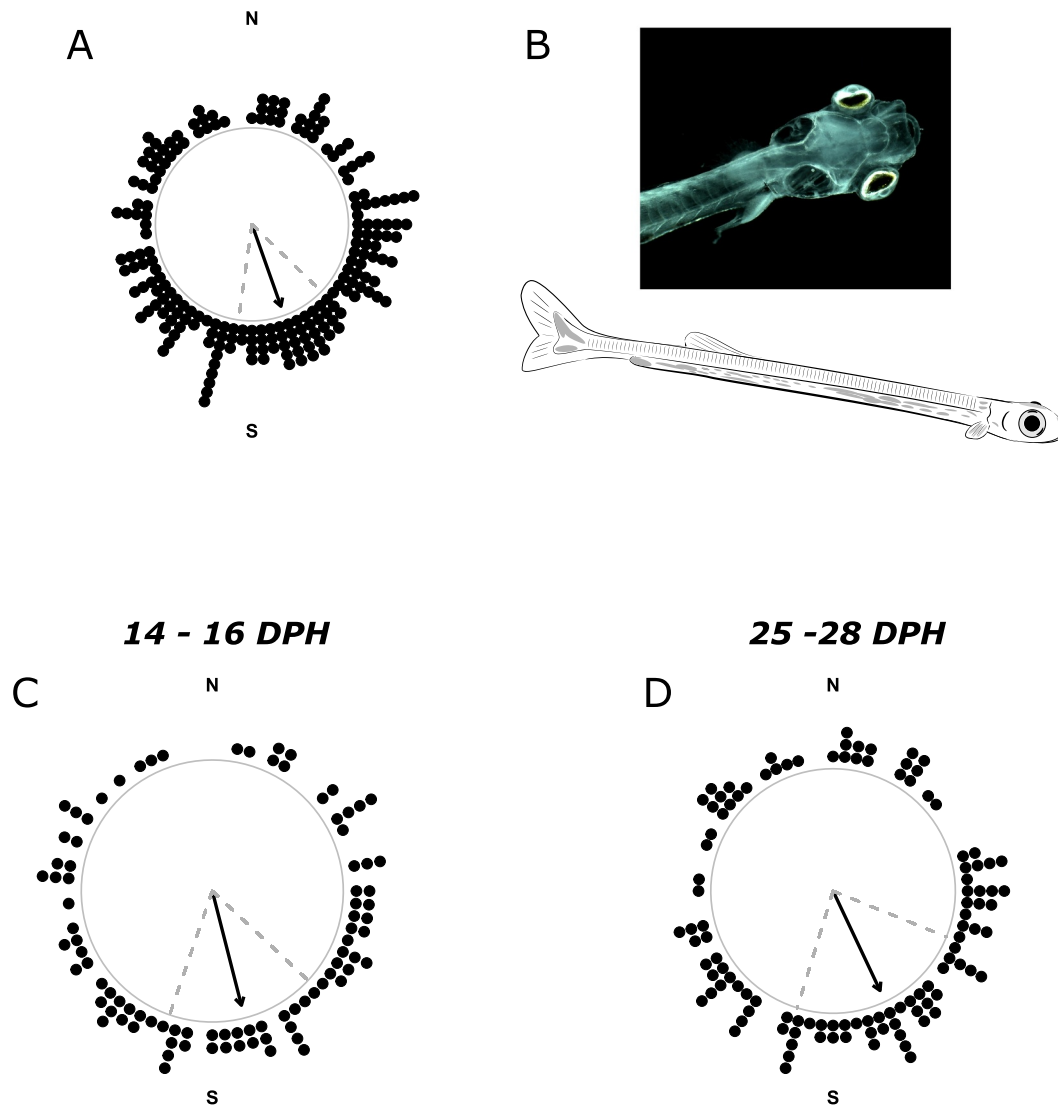
Fig. 1. Orientation of herring (*Clupea harengus*) larvae *in situ*. The orientation is presented with respect to the magnetic North (N) and South (S). Each black point corresponds to the mean bearing of one herring larva *in situ* (averaged over 600 data points from the video tracks, Fig. S1). These figures display the mean bearings of the larvae that showed an individual preferred orientation. The black arrow points towards the mean angle of all the individual bearings Dashed grey lines are the 95% confidence intervals around the mean. A. Mean orientation direction of all the herring larvae that displayed a significant orientation *in situ* ($N = 203$, mean bearing = 160°). B. Picture of a herring larva and artwork showing the general morphology of the larvae used in this study. C. Mean orientation of larvae 14–16 DPH ($N = 91$, mean bearing = 166°). D. Mean orientation of larvae 25–28 DPH ($N = 112$, mean bearing = 155°). Data displayed in C and D are subsets of the data in A. Artwork and photo by Alessandro Cresci.

ImageJ software (Irisson et al., 2009, 2015). The code utilized is available at the web page, Drifting *In Situ* Chamber User Software in R (https://github.com/jiho/discr) written by Jean-Olivier Irisson at the Université Pierre et Marie Curie UPMC, released under the GNU General Public License v3.0.

For this analysis, we tracked the position of each fish, every second, for a 10-min period in each deployment (600 data points per each larva). A detailed diagram showing all of the steps in the analysis is provided in Fig. S1. Each data point corresponds to a specific bearing (the position of the fish in degrees with respect to the center of the arena, Fig. S1.2). Afterwards, we corrected the bearings with respect to the magnetic North using the DISC's digital compass. If the frequency distribution of the 600 bearings was significantly different from random (Rayleigh's $P < .05$, Fig. S1.3), we considered it as evidence of orientation and used the mean individual bearing as the orientation direction of the larva (Fig. S1.3). The null hypothesis of the Rayleigh test

is uniformity of the distribution of the bearings. If the hypothesis of uniformity is rejected, we report the mean angle (mean), test statistic (z), concentration parameter (r) and a p value for significance (Batschelet, 1981; Jammalamadaka and SenGupta, 2001). The alternative hypothesis is a unimodal or a Von Mises distribution (which is narrower than the unimodal) with a mean angle, representing the mean direction of the larva. This test is particularly recommended for sample sizes > 30 (Batschelet, 1981) (here it is 600 per fish for the within-individual analysis, and > 30 for the analysis on each experimental group). For the Rayleigh test, the distribution of the test statistic under uniformity is a chi-square with two degrees of freedom.

The next step in the analysis consisted of investigating whether the larvae of each experimental group (larvae *in situ* and larvae in the MagLab) were swimming towards a common direction (*i.e.* displayed common orientation behavior, Fig. S1.4). To explore that, we performed the Rayleigh's test of uniformity using all of the mean individual

Fig. 2. Influence of the sun on the orientation of herring (*Clupea harengus*) larvae *in situ*. A. Data on the orientation direction and the azimuth of the sun. α_{north} is the orientation direction with respect to the magnetic north. Each black point corresponds to the mean bearing of one herring larva *in situ* (averaged over 600 data points from the video tracks, Fig. S1). These figures display the mean bearings of the larvae that showed an individual preferred orientation, and are the same as those displayed in Fig. 1 but split according to the visibility of the sun: sunny ($N = 109$), overcast ($N = 94$). The black arrow points towards the mean angle of all the individual bearings Dashed grey lines are the 95% confidence intervals around the mean. α_{sun} is the angle between the mean orientation of each herring (α_{north}) and the azimuth of the sun during the test (Sun Azimuth, third row). When there is significant orientation (Rayleigh's $p < .05$) towards the direction of the sun, this is represented by an arrow pointing towards the top of the plot in α_{sun} (sun = 0° in α_{sun}). B. Diagram of all the three circular variables considered in A: α_{north}, α_{sun}, Sun Azimuth. C. Light intensity (lumen/ft^2) during the tests *in situ* during sunny or overcast weather. * ANOVA p value from comparison of the light intensity between the 2 different weather conditions.

bearings of all of the larvae from each of the experimental groups as data points. When the Rayleigh's P was < 0.05, we considered the group to be displaying a common orientation and considered the mean as the overall common direction of the group (Irisson et al., 2009).

The orientation direction relative to the sun azimuth was calculated considering the angle between the orientation of the larva (α_{north}, Fig. 2B) and the azimuth of the sun during the test (Sun azimuth, Fig. 2B) = α_{sun} (Fig. 2B). Significance of the orientation with respect to the direction of the sun (which for α_{sun} is 0°) was assessed using the same statistical method shown in Fig. S1.4. Sun azimuth data were obtained from www.timeanddate.com/sun (Copyright © Time and Date AS 1995–2019. All rights reserved). Forecast conditions (sunny/overcast) were assessed visually during the tests and from analysis of the GOPRO images. Weather conditions were considered "sunny" when it was possible to assess the direction of the sun by human eye. The sky

was considered "overcast" when we were not able to determine the direction of the sun because of the cloud cover. This selection criterion was applied as we wanted to investigate whether the direction of the sun was playing a role in the orientation direction of the larvae. Light intensity during sunny and overcast weather conditions was recorded using HOBO light sensors, which confirmed that the light intensity was significantly lower under overcast sky compared to sunny sky (Fig. 2C).

Length (total length) of the larvae observed during the deployments was estimated from the videos using ImageJ 1.51 J8. The diameter of the chamber was used as a size reference. The length of the larvae was measured when larvae were at the bottom of the chamber with the body positioned in a straight line.

The swimming speed of herring larvae was estimated from the video tracks by dividing the distance that the animal swam in the chamber by time observed (1 s), for the 10 min observation period (Cresci et al.,

Table 1
Average and maximum speed of herring larvae (*Clupea harengus*) *in situ* by age group. A Mann-Whitney test was used to compare age groups.

Age (DPH)	Average speed (cm/s)	Maximum speed (cm/s)
14–16	0.36 ± 0.19	3.00 ± 1.42
25–28	0.40 ± 0.17	3.36 ± 1.70
M.W. test	N.S. (w = 5302; p = .6215)	N.S. (w = 4353, p = .18)

N.S. (Non-Significant) = $p > .05$. Data are displayed as mean ± SD.

2019b). The average of all the calculated speeds was considered as the average speed of one larva. The swimming speed values reported in Table 1 correspond to the average of the individual speeds for each experimental group (the two age groups). The highest speed that one larva displayed between frames, during the 10 min observation period, was considered as the maximum speed of that individual. The maximum speeds reported in Table 1 correspond to the average of all the individual maximum speeds for each experimental group.

2.3. Experiments in the magnetic laboratory

The experiments in the MagLab followed the same protocol as described in Cresci et al. (2017). We tested the hypothesis that herring larvae display a significant orientation direction when only the magnetic field is available as an orientation cue (*versus* the null hypothesis of random orientation direction). The MagLab is designed to study the magnetic orientation of aquatic animals. It is equipped with a triaxial electric coil system (Fig. S2A), with a design described by (Merritt et al., 1983), and connected to a power supply (max. 3 A). At the center of the coils, there is a black circular tank made of fiberglass (diameter, 1.40 m; height, 0.90 m; see Fig. S2A) and filled with seawater, which is pumped from the sea 300 m away. The building (see fig. S2B; S2C) is constructed of nonmagnetic material and is far from any source of magnetic interference (163 m from the nearest electrical disturbance and 365 m from the closest building; Fig. S2C).

For the tests in the MagLab, we used the DISC as a behavioral chamber, submerged in the circular dark tank (see Fig. S2A). The chamber was of the same size as the one used for the tests *in situ*. Light intensity in the tank was low and constant (around 0 lum/ft^2 from HOBO light sensor on the bottom plate of the DISC frame). The DISC was equipped with an analog compass attached to the acrylic poles of the DISC frame and placed below the circular arena. This positioning eliminates the possibility that the compass would be a visual reference for the larvae.

The laboratory is equipped with two nested electric coil systems. One was used to cancel out the horizontal component of the ambient field. With the second coil system, we were able to generate a magnetic field with the same total intensity as the ambient field (48.8 to 50 μT) and to reorient the magnetic north. The intensity and inclination inside the coil were set to match the ambient field (48.8 to 50 μT and 73°, with a deviation of < 1°).

For these tests, we used larvae ranging between 22 and 30 DPH. Tests were conducted from the 9th to the 17th of June 2017 (Table S2). Each larva was observed for 15 min, with the first 5 min considered as an acclimation period (as for the tests *in situ*) (Cresci et al., 2017; Paris et al., 2013), under one of the four simulated magnetic field conditions, with the magnetic north reoriented to the Earth's east, south, west, or north (see Fig. S3). Each larva experienced only one of these 4 magnetic conditions. Using this approach, we eliminated any nonmagnetic bias that could have influenced the orientation response of the animals. Moreover, the MagLab is designed to cancel out all the possible external cues that animals could use for orientation except for the magnetic field, as the animals are not exposed to water flows, odor plumes, sunlight or any celestial cues. All tests were conducted during daytime under artificial light.

The orientation of the larvae was determined through the analysis of the GOPRO images using the same process described in the previous section (see also Fig. S1). However, the magnetic north had a different orientation in the laboratory during each test, and the position of the larva was corrected with respect to the magnetic north in the MagLlab (Fig. S3, red North = 0°) using the digital compass.

3. Results

3.1. Compass orientation and swimming speed in situ

When drifting in the DISC *in situ*, the proportion of herring larvae displaying significant orientation at the individual level (Rayleigh test of uniformity applied to the track of each larva, Fig. S1.3) was 98% - 203 larvae of the 208 tested *in situ* had a preferred bearing (Rayleigh's $p < .05$; Fig. S1.3). The herring larvae that oriented had a highly significant common orientation direction (Fig. S1.4) towards the southeast ($N = 203$; mean angle = 160°, z = 9.82, $r = 0.22$, $p = .00005$; Fig. 1A). This common orientation direction did not change between the 2 age groups observed in this study: 14–16 DPH larvae oriented to the southeast ($N = 91$; mean angle = 166°, z = 6.15, $r = 0.26$, $p = .002$; Fig. 1B), as did 25–28 DPH larvae ($N = 112$; mean angle = 155°, z = 4.04, $r = 0.19$, $p = .02$; Fig. 1C). Younger larvae ($N = 91$; 14–16 DPH) displayed significantly more precise orientation (median of individual r values = 0.46) compared to older larvae ($N = 112$; 25–28 DPH; median of individual r values = 0.34) (Mann-Whitney test, w = 6406, $P = .002$). Mean orientation direction, significance of the orientation, and Rayleigh's r values for each larva are presented in Table S1.

Larvae of the older group were longer (total length 14–16 DPH larvae = 10.7 [9.05–11.05] mm; 25–28 DPH larvae = 12.7 [10.7–15.9] mm (median [minimum-maximum]); Mann-Whitney test, w = 28.5, P = .002).

The average swimming speed of the larvae was 0.37 ± 0.18 cm/s; there was no significant effect of age on swimming speed (Table 1) nor of larval length on swimming speed (linear model: F = 0.001, $R^2_{adj} = -0.005$, $P = .97$).

3.2. Orientation and external cues: role of the sun

We calculated the angle between the orientation direction of each larva ($α_{north}$, Fig. 2B) and the direction of the sun azimuth during each DISC deployment (Sun azimuth, Fig. 2B) = $α_{sun}$ (Fig. 2B). Under a sunny sky, larval orientation towards the azimuth of the sun was highly significant ($N = 109$; mean $α_{sun}$ = 6°, z = 14.92, $r = 0.37$, $p = .000002$; Fig. 2A). In trials conducted during sunny conditions, the average direction of the sun azimuth was south (sun azimuth, Fig. 2A), with herring larvae significantly orienting towards the south (N = 109; mean $α_{north}$ = 184°, z = 9.17, $r = 0.29$, $p = .0001$; Fig. 2A). However, during overcast conditions (the azimuth of the sun was not visible to the human eye), there was no significant orientation with respect to the sun (Fig. 2A) and, although the sun azimuth was primarily southwest, larvae oriented ($α_{north}$) to the southeast ($N = 94$; mean $α_{north}$ = 121°, z = 4.55 $r = 0.22$, $p = .01$; Fig. 2A). Moreover, larvae swimming under sunny sky displayed significantly higher precision of orientation (N = 109; sunny sky; median of individual r values = 0.44) compared to larvae swimming under overcast sky (N = 94; overcast sky; median of individual r values = 0.38) (Mann-Whitney test, w = 4128, $p = .02$). During overcast weather, the light intensity was significantly lower compared to sunny weather based on HOBO data from the DISC (less than half; ANOVA: Df = 1, F = 51.1, P < < 0.01, Fig. 2C).

3.3. Orientation and external cues: role of the earth magnetic field

The proportion of orienting larvae in the MagLab was the same as *in situ* (98%). In the lab, 133 of the 136 larvae tested displayed significant
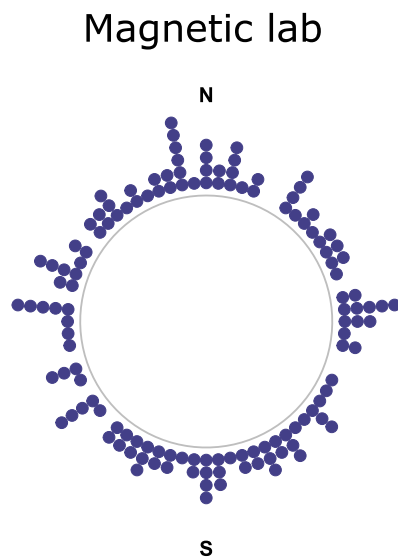
Magnetic lab

Fig. 3. Magnetic orientation of herring (*Clupea harengus*) larvae in the magnetic lab. Each blue data point is the mean bearing of one haddock larva in the magnetic laboratory (*N* = 133). During the experiments, the magnetic north in the laboratory was rotated for each larva (*i.e.* the magnetic north in the lab had a different direction for each of the blue data points). The orientation of each larva was corrected to the artificially rotated magnetic north in the laboratory (red magnetic north in fig. S3). Herring did not display significant magnetic orientation (Rayleigh's *p* > .05). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

orientation. However, we did not find evidence of magnetic orientation - the 133 larvae exhibited random orientation relative to the rotated magnetic north (Rayleigh's *P* > .05, Fig. 3). Mean orientation direction, significance of the orientation, and Rayleigh's r values for each larva are presented in Table S2.

4. Discussion

4.1. Swimming and orientation behavior in herring and implications for dispersal and retention

Herring larvae displayed directional, oriented swimming *in situ*. This ability has been observed in the larvae and post larvae of multiple genera of fish, including Pomacentridae, Sparidae, Apogonidae, Anguillidae and Gadoids (Bottesch et al., 2016; Cresci et al., 2019c, Cresci et al., 2017; Faillettaz et al., 2015; Irisson et al., 2015; Kough et al., 2014; Leis, 2010; Paris et al., 2013; Rossi et al., 2019). Simulations performed using biophysical coupled models suggest that, at subarctic latitudes, vertical and horizontal movement behavior of larvae significantly affects dispersal, especially in proximity of boundary currents (Fiksen et al., 2007; Vikebø et al., 2007). For Atlantic herring (*Clupea harengus*), there is little empirical data describing their swimming and orientation behavior *in situ*, which is needed to improve modelled predictions of their dispersal. The results presented here provide evidence that 14–28 DPH herring larvae perform oriented horizontal swimming and maintain the same orientation direction throughout this ontogenetic period.

In the northeast Atlantic, herring are regarded as comprising two main groups: the Atlantic-Scandinavian winter-spring spawning stocks, which migrate off the continental shelf, and another group spread around the whole west coast of Norway (Norwegian Spring spawning herring), from the Lofoten Islands to the Skagerrak area (Haegele and Schweigert, 1985). In the North Sea, herring spawning grounds are spread along the eastern Scottish and British coasts, and along the southwestern coast of Norway and Sweden (Haegele and Schweigert, 1985). However, although these two herring populations have been

considered separate stocks in the past, genetic data from microsatellite analysis suggests that the North Sea herring might belong to a single unit-stock (Mariani et al., 2005).

In the area of the North Sea and along the Norwegian coast, adult herring perform two major migrations: a spawning migration from the northern feeding areas in the Norwegian Sea towards the spawning areas to the south-southeast (Møre, Haltenbanken and Røst), and a feeding migration in the opposite direction (northwest) from the spawning areas to the feeding grounds around Iceland ("migrating herring") (Dragesund et al., 1980). The herring larvae tested *in situ* in this study consistently oriented towards the southeast (Fig. 1). Furthermore, their orientation direction was more strongly southward when the sun was available as a cue for orientation. Several minor spawning areas are located along the coast of south-western Norway and the Baltic Sea; these local herring stocks are referred to as "coastal spawners" and do not migrate as extensively as, for example, the more northern stocks ("migratory herring") outside the North Sea (Haegele and Schweigert, 1985). As the herring larvae used in this study came from a local stock (collected in Askøy), it is possible that the orientation direction that they displayed is a retention mechanism of local "coastal spawners" (Haegele and Schweigert, 1985; Rossi et al., 2019). If this is the case, the orientation to the southwest would delay/contrast northward drift with the Norwegian Coastal Current (NCC) (Mork, 1981). Conversely, it is possible that, for larvae of "migratory herring", orientation towards the SE would help them move between retention areas and transport areas within the NCC. The NCC has two main drift routes that carry herring larvae along the Norwegian shelf, one main inner route along the coast and a secondary route following the shelf break (Sætre, 1999). Between these routes, there are stable eddies, which represent retention areas and spawning sites for migrating herring (Sætre, 1999). Orientation to the SE would increase the chances of leaving the retention eddies and entering the main inner drift route closer to the coast (which has the fastest transport velocity) to start the feeding migration.

The precision of the orientation (r values) of herring larvae was relatively low (median r was 0.46 for 14–16 DPH larvae and 0.34 for 25–28 DPH larvae) when compared to that reported in studies on orientation in the larvae of tropical reef fish (Leis et al., 2015, Leis et al., 2014). Observations of the orientation behaviour of fish larvae *in situ* using the DISC report less precise directionality than those made using the 'following methodology' (Leis et al., 2014), which is based on observations of freely-swimming larvae followed by a diver (Leis et al., 1996). However, comparisons between the methods using larvae from the same origin, at the same developmental stage, and tested in the same area at the same time are necessary to better understand the effect of the methodologies on the quantification of larval directionality. The lower r values observed for herring larvae could be related to the limited space that they have to swim in the DISC chamber. However, these results might also reflect the tendency of herring larvae to explore their environment: they swam around the edges of the DISC chamber continuously and did not hold their position as other species, like gadoids, do (Cresci et al., 2019c). This continuous exploratory swimming would produce a less precise estimate of orientation, as has been reported in studies on anguillids using the DISC (Cresci et al., 2019b, Cresci et al., 2017).

Herring larvae 14–28 DPH displayed oriented swimming *in situ*. The degree to which this behavior influences dispersal in larvae of this size remains an open question. Herring larvae would not be able to swim faster than the ambient current in which they are drifting and, therefore, passive transport is likely the dominant factor in their dispersal. Nonetheless, there are several reasons why the oriented swimming reported in this study could still influence their dispersal ecology. The herring larvae swimming in the DISC *in situ* (at 12–13.5C°, Fig. S4) displayed an average speed of 0.37 ± 0.18 cm/s and a maximum speed of 3.41 ± 2.33 cm/s (mean ± SD). These speeds are consistent with those reported for herring larvae 1–2 cm long observed in the

laboratory: 0.5–6 cm/s at temperatures of 8–14C° (Batty, 1984). The maximum swimming speed recorded in this study represents the maximum speed of the larvae when swimming in the DISC and can be considered a proxy for acceleration. The average speed in the DISC can be considered as an estimate of routine speed, which is the spontaneous speed of undisturbed larvae over a period of time that varies depending on the study (usually several minutes) (Leis, 2006). The routine speeds measured in the DISC underestimate true *in situ* swimming speeds (Paris et al., 2013). That is because the routine speed is sensitive to the size of the chamber in which the observations are made: the smaller the chamber the greater the speed measured underestimates the speed *in situ* (Fuiman et al., 1999; von Westernhagen and Rosenthal, 1979). Pacific herring larvae (*Clupea harengus pallasi*) of the same size of the Atlantic herring larvae observed in this study swam on average four times faster than those tested in this study when observed *in situ* without the constraint of a chamber (von Westernhagen and Rosenthal, 1979). The same study reports that Pacific herring larvae reared in the laboratory swam three times faster, and wild-caught larvae swam four times faster, than those in the DISC when observed under laboratory conditions, but with a chamber of 35 cm-diameter (15 cm larger than the DISC) (von Westernhagen and Rosenthal, 1979). Thus, in general, the literature indicates that routine speed measured in small chambers underestimate real speeds by 400% or more, suggesting that herring larvae could have much higher routine speeds in the wild than that observed in the DISC chamber.

Considering both the length of the larvae and the water temperatures at this latitude, the herring larvae used in this study have low Reynolds numbers (Re = 35–270; Fig. S6) and, therefore, swim in a viscous regime. These values are lower than 300, which marks the transition from a viscous to a more intermediate (inertial) hydrodynamic environment (Leis, 2006; Moyano et al., 2016). However, because herring larvae can have higher routine speeds than those displayed in the DISC, they can actually operate at across wide range of (higher) Reynolds numbers, and this range increases rapidly when the larvae are just a few mm longer than those observe in this study (Fig. S6). Herring larvae that are 15 mm-long enter an intermediate hydrodynamic environment when they are swimming at speeds of 2.5–3.0 cm/s (Moyano et al., 2016). This indicates that the oriented swimming observed in this study could have some impact on dispersal at the sizes observed and that this would quickly become more prominent when the larvae are just a few mm longer.

Fish larvae can perform significant movements relative to the parcel of water that they occupy even when swimming in a viscous regime. Fish larval morphology is adapted to compensate for the high drag of a viscous environment by increased thrust (Voesenek et al., 2018). Specifically, fish larvae such as herring are long and thin, possessing a fin-fold that extends along most of the body, and they move using an anguilliform swimming style (Batty, 1984) with a large region along the body that curves substantially and produces thrust (Voesenek et al., 2018). Furthermore, closely related Pacific herring larvae move continuously and undertake around 26 bursts/min (von Westernhagen and Rosenthal, 1979), thereby often moving towards the viscous-intermediate transition regime. This argues for the possibility that they may influence their dispersal by oriented swimming even at small sizes.

When swimming *in situ*, fish larvae would clearly be able to influence their drifting trajectory when their swimming speed is higher than the mean current speed ("effective swimming") (Leis and Stobutzki, 1997; Leis, 2006); the degree to which they can influence their trajectory is dependent on their endurance (something that has been measured for the larvae of only a very few species). However, in order to affect dispersal, swimming speed does not have to be greater than the surrounding current velocity (Fiksen et al., 2007; Fisher, 2005; Pepin and Helbig, 1997). This is especially true when the direction of larvae is orthogonal to the current speed (Leis, 2006). If larvae swim orthogonal to the current - something that swimming in a preferred direction might help them achieve - they can significantly influence the direction of

their dispersal even if the current is faster than they can swim. Models showed that simulated dispersal of cod larvae was strongly affected by horizontal swimming speeds of 1–3 cm/s, which is lower than speed of the current in that case study (Pepin and Helbig, 1997). Atlantic herring hatching off the coast of Norway would become entrained in the Norwegian Coastal Currrent (NCC) in which the average transport speeds of the main (inner) drift route ranges between 10 and 16 cm/s at 64–68°N (Sætre, 1999), which is faster than the swimming speed of herring larvae. However, the NCC flows mostly to the northeast, and swimming to the southeast (the orientation behaviour observed in this study) could affect dispersal in proximity of NCC boundaries and at boundaries of oceanographic structures because the orientation direction is close to being orthogonal to the NCC. For example, swimming to the SE at the speeds observed in this study could affect the fate of herring larvae at the boundaries of NCC eddies, where they can be retained for a period of 10–50 days (Sætre, 1999).

Whether herring larvae can actively influence their dispersal at this size is still unknown and the scenarios discussed above need to be explored in future work using biophysical coupled models.

4.2. Orientation cues

Some fish species use the magnetic field of the Earth as an orientation cue during the early life stages. This was reported in tropical fish larvae (Bottesch et al., 2016; O'connor and Muheim, 2017) and, at subarctic latitudes, in glass eels (Cresci et al., 2019a, Cresci et al., 2017) and in larvae of Atlantic haddock (Cresci et al., 2019c). In this study, the orientation direction of 14–28 DPH herring larvae was not related to the magnetic field. Herring larvae may lack this orientation ability. However, it is also a possible that they develop it later in life, something that we will assess in future work.

Orientation *in situ* was significantly correlated with the direction of the sun, suggesting that the mechanism involved is visual. Furthermore, herring larvae displayed significantly higher precision of orientation at the individual level when the sky was clear. This is consistent with earlier studies reporting that tropical fish larvae such as *C. atripectoralis* are strongly directional under sunny conditions, but the ability to orient is reduced when the sky is overcast (Leis et al., 2014; Leis and Carson-Ewart, 2003). Additionally, the larvae of coral reef and Mediterranean species of fish display better orientation when the altitude of the sun is lower (Faillettaz et al., 2015; Leis et al., 2014), implying that the sun is used by these larvae as an orientation cue.

In this study, herring significantly oriented straight towards the direction of the sun when the sun azimuth was visible to the human eye (Fig. 2A). However, under overcast conditions, larvae oriented towards the southeast. This orientation direction could be related to the e-vector of polarized light (Waterman, 1988). Orientation to polarized light is widespread in aquatic animals and it has been observed in many species of marine invertebrates (Chiou et al., 2008; Cronin, 1986; Lerner and Browman, 2016; Shashar and Cronin, 1996). This ability has also been reported in several species of fish, such as rainbow trout (*Oncorhynchus mykiss*) (Hawryshyn et al., 1990), damselfish (*Chromis viridis*) (Mussi et al., 2005), sockeye salmon (Dill, 1971), and herring (Waterman, 1988).

Herring larvae have well developed eyes from early in ontogeny and feed on small zooplankton, which they locate visually (Blaxter, 1968). Herring larvae display a preferred orientation direction with respect to the e-vector of polarized light, specifically at 45° and 90° to the e-vector (Waterman, 1988). The underwater polarized light field has been measured *in situ* in shallow clear tropical water (Cronin and Shashar, 2001) and in the Gulf of Eilat (Red Sea) (Lerner et al., 2011). These studies show that the axis of the e-vector varies between 45 and 90° from the axis of the sun azimuth (Cronin and Shashar, 2001). Thus, it is possible that the orientation response of herring larvae observed *in situ* depended on both the e-vector of polarized light and sun azimuth-related orientation. The polarized light field is still present under overcast

sky (Brines and Gould, 1982), and this might explain why in these conditions the larvae oriented to the southeast even though the sun azimuth was primarily southwest (around 90° from the axis of the sun azimuth). In future research we will assess the orientation of herring larvae to polarized light.

4.3. Limitations of the study

In this study, we assessed orientation and swimming speeds of 14–28 DPH herring larvae. Future studies should investigate a larger range of sizes and developmental stages targeting, for example, how metamorphosis and further growth affects swimming and orientation, including whether larger herring develop a magnetic sense and orient to the Earth's magnetic field. Finally, future work should investigate whether herring larvae belonging to different stocks and locations display different orientation behavior, as this is relevant to understand the dispersal and mixing (or lack thereof) of different stocks.

Funding

Ethics statement

The Austevoll Research station has a permit to operate as a Research Animal facility for fish (all developmental stages), under code 93 from the national Institutional Animal Care and Use Committee (IACUC); NARA. We did not require specific approval for these experiments because they are non-intrusive behavioral observations. After the trials, larvae were sacrificed using humane endpoint sanctioned for fish.

Author contributions

A.C. designed the study; collected, analyzed, and interpreted the data; and wrote the paper. B.J.M.A. designed the study; collected the data; interpreted the data; wrote the paper. S.S. collected and analyzed the data. A.B.S. designed the study, interpreted the data, and wrote the paper. H.I.B. designed the study, interpreted the data, wrote the paper, and funded the research.

Declaration of Competing Interest

The authors declare that they have no competing interests.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2020.151358.

References

Adams, D.K., Flierl, G.R., 2010. Modeled interactions of mesoscale eddies with the east Pacific rise: implications for larval dispersal. Oceanogr. Res. Paper. https://doi.org/10.1016/j.dsr.2010.06.009.

Batschelet, E., 1981. Circular Statistics in Biology. Academic Press, London.

Batty, R.S., 1984. Development of swimming movements and musculature of larval herring (clupea harengus). J. Exp. Biol. 110, 217–229.

Blaxter, J.H.S., 1968. Visual thresholds and spectral sensitivity of herring larvae. J. Exp. Biol. 48, 39–53.

Bottesch, M., Gerlach, G., Halbach, M., Bally, A., Kingsford, M.J., Mouritsen, H., 2016. A magnetic compass that might help coral reef fish larvae return to their natal reef. Curr. Biol. 26, R1266–R1267. https://doi.org/10.1016/j.cub.2016.10.051.

Brines, M.L., Gould, J.L., 1982. Skylight polarization patterns and animal orientation. J. Exp. Biol. 96.

Chiou, T.-H., Kleinlogel, S., Cronin, T., Caldwell, R., Loeffler, B., Siddiqi, A., Goldizen, A., Marshall, J., 2008. Circular polarization vision in a stomatopod crustacean. Curr. Biol. 18, 429–434. https://doi.org/10.1016/J.CUB.2008.02.066.

Cresci, A., Durif, C.M., Paris, C.B., Thompson, C.R.S., Shema, S., Skiftesvik, A.B., Browman, H.I., 2019b. The relationship between the moon cycle and the orientation of glass eels (*Anguilla anguilla*) at sea. R. Soc. Open Sci. 6, 190812. https://doi.org/10.1098/rsos.190812.

Cresci, A., Paris, C.B., Durif, C.M.F., Shema, S., Bjelland, R.M., Skiftesvik, A.B., Browman, H.I., 2017. Glass eels (*Anguilla anguilla*) have a magnetic compass linked to the tidal cycle. Sci. Adv. 3, 1–9. https://doi.org/10.1126/sciadv.1602007.

Cresci, A., Durif, C.M., Paris, C.B., Shema, S.D., Skiftesvik, A.B., Browman, H.I., 2019a. Glass eels (*Anguilla anguilla*) imprint the magnetic direction of tidal currents from their juvenile estuaries. Commun. Biol. 2, 366. https://doi.org/10.1038/s42003-019-0619-8.

Cresci, A., Paris, C.B., Foretich, M.A., Durif, C.M., Shema, S.D., O'Brien, C.E., Vikebø, F.B., Skiftesvik, A.B., Browman, H.I., 2019c. Atlantic haddock (*Melanogrammus aeglefinus*) larvae have a magnetic compass that guides their orientation. iScience 19, 1173–1178. https://doi.org/10.1016/j.isci.2019.09.001.

Cronin, T.W., 1986. Photoreception in marine invertebrates. Am. Zool. 26, 403–415. https://doi.org/10.1093/icb/26.2.403.

Cronin, T.W., Shashar, N., 2001. The linearly polarized light field in clear, tropical marine waters: spatial and temporal variation of light intensity, degree of polarization and e-vector angle. J. Exp. Biol. 204.

Daan, N., Bromley, P.J., Hislop, J.R.G., Nielsen, N.A., 1990. Ecology of North Sea fish. Neth. J. Sea Res. 26, 343–386. https://doi.org/10.1016/0077-7579(90)90096-Y.

Deschepper, I., Lyons, K., Lyashevska, O., Brophy, D., 2019. Bio-physical models reveal the role of tides, wind and larval behaviour in early transport and retention of Atlantic herring (*Clupea harengus* L.) in the Celtic sea. Can. J. Fish. Aquat. Sci. https://doi.org/10.1139/cjfas-2018-0491. cjfas-2018-0491.

Dill, P.A., 1971. Perception of polarized light by yearling sockeye salmon (*oncorhynchus nerka*). J. Fish. Res. Board Can. 28, 1319–1322. https://doi.org/10.1139/f71-199.

Dragesund, O., Hamre, J., Ulltang, Ø., 1980. Biology and population dynamics of the norwegian spring-spawning herring. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 177, 43–71.

Durif, C.M.F., Browman, H.I., Phillips, J.B., Skiftesvik, A.B., Vøllestad, L.A., Stockhausen, H.H., 2013. Magnetic compass orientation in the European eel. PLoS One 8, 1–7. https://doi.org/10.1371/journal.pone.0059212.

Faillettaz, R., Blandin, A., Paris, C.B., Koubbi, P., Irisson, J.-O., 2015. Sun-Compass Orientation in Mediterranean Fish Larvae. https://doi.org/10.1371/journal.pone.0135213.

Faillettaz, R., Durand, E., Paris, C.B., Koubbi, P., Irisson, J.O., 2018. Swimming speeds of Mediterranean settlement-stage fish larvae nuance Hjort's aberrant drift hypothesis. Limnol. Oceanogr. 63, 509–523. https://doi.org/10.1002/lno.10643.

Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F., Huse, G., 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. Mar. Ecol. Prog. Ser. 347, 195–205. https://doi.org/10.3354/meps06978.

Fisher, R., 2005. Swimming speeds of larval coral reef fishes: impacts on self-recruitment and dispersal. Mar. Ecol. Prog. Ser. 285, 223–232. https://doi.org/10.3354/meps285223.

Fuiman, L.A., Smith, M.E., Malley, V.N., 1999. Ontogeny of routine swimming speed and startle responses in red drum, with a comparison of responses to acoustic and visual stimuli. J. Fish Biol. 55, 215–226. https://doi.org/10.1111/j.1095-8649.1999.tb01057.x.

Geffen, A.J., 2009. Advances in herring biology: from simple to complex, coping with plasticity and adaptability. ICES J. Mar. Sci. 66, 1688–1695. https://doi.org/10.1093/icesjms/fsp028.

Haegele, C.W., Schweigert, J.F., 1985. Distribution and characteristics of herring spawning grounds and description of spawning behavior. Can. J. Fish. Aquat. Sci. 42, s39–s55. https://doi.org/10.1139/f85-261.

Hawryshyn, C., Arnold, M., Bowering, E., Cole, R., 1990. Spatial orientation of rainbow trout to plane-polarized light: the ontogeny of E-vector discrimination and spectral sensitivity characteristics. J. Comp. Physiol. A. 166, 565–574. https://doi.org/10.1007/BF00192027.

Hjort, J., 1914. Fluctuations in the Great Fisheries of Northern Europe Viewed in the Light of Biological Research.

Houde, E.D., 2016. Recruitment variability. In: Fish Reproductive Biology : Implications For Assessment And Management. John Wiley & Sons, ltd, pp. 98–187.

Husebø, Å., Slotte, A., Stenevik, E.K., 2007. Growth of juvenile Norwegian spring-spawning herring in relation to latitudinal and interannual differences in temperature and fish density in their coastal and fjord nursery areas. ICES J. Mar. Sci. 64,

1161–1172. https://doi.org/10.1093/icesjms/fsm081.

Irisson, J.-O., Guigand, C., Paris, C.B., 2009. Detection and quantification of marine larvae orientation in the pelagic environment. Limnol. Oceanogr. Methods 7, 664–672. https://doi.org/10.4319/lom.2009.7.664.

Irisson, J.O., Paris, C.B., Leis, J.M., Yerman, M.N., 2015. With a little help from my friends: group orientation by larvae of a coral reef fish. PLoS One 10, 1–14. https://doi.org/10.1371/journal.pone.0144060.

Jammalamadaka, S.R., SenGupta, A., 2001. Topics in circular statistics. Series on multivariate analysis. world scientific. https://doi.org/10.1142/4031.

Kiørboe, T., Munk, P., Richardson, K., Christensen, V., Paulsen, H., 1988. Plankton dynamics and larval herring growth, drift and survival in a frontal area. Mar. Ecol. Prog. Ser. 44, 205–219.

Kough, A., Paris, C., Staaterman, E., 2014. In situ swimming and orientation behavior of spiny lobster (*Panulirus argus*) postlarvae. Mar. Ecol. Prog. Ser. 504, 207–219. https://doi.org/10.3354/meps10748.

Leis, J.M., 2006. Are larvae of Demersal fishes plankton or nekton? Adv. Mar. Biol. 57–141. https://doi.org/10.1016/S0065-2881(06)51002-8.

Leis, J.M., 2010. Ontogeny of behaviour in larvae of marine demersal fishes. Ichthyol. Res. 57, 325–342. https://doi.org/10.1007/s10228-010-0177-z.

Leis, J., Carson-Ewart, B., 2003. Orientation of pelagic larvae of coral-reef fishes in the ocean. Mar. Ecol. Prog. Ser. 252, 239–253. https://doi.org/10.3354/meps252239.

Leis, J.M., Stobutzki, I.C., 1997. Swimming performance of late pelagic larvae of coral-reef fishes: in situand laboratory-based measurements. In: Proceedings of the 5th Indo-Pacific Fish Conference, Nouméa. SociétéFrançaise d'Ichtyologie & Institut de Recherche pour le Développement, Paris at: Noumea, New Caledonia, pp. 575–858.

Leis, J.M., Sweatman, H.P.A., Reader, S.E., 1996. What the pelagic stages of coral reef fishes are doing out in blue water: daytime field observations of larval behavioural capabilities. Mar. Freshw. Res. 401–411. https://doi.org/10.1071/MF9960401. CSIRO.

Leis, J.M., Carson-Ewart, B.M., Hay, A.C., Cato, D.H., 2003. Coral-reef sounds enable nocturnal navigation by some reef-fish larvae in some places and at some times. J. Fish Biol. 63, 724–737. https://doi.org/10.1046/j.1095-8649.2003.00182.x.

Leis, J.M., Caselle, J.E., Bradbury, I.R., Kristiansen, T., Llopiz, J.K., Miller, M.J., O'Connor, M.I., Paris, C.B., Shanks, A.L., Sogard, S.M., Swearer, S.E., Treml, E.A., Vetter, R.D., Warner, R.R., 2013. Does fish larval dispersal differ between high and low latitudes? Proc. R. Soc. B Biol. Sci. https://doi.org/10.1098/rspb.2013.0327.

Leis, J., Paris, C., Irisson, J., Yerman, M., Siebeck, U., 2014. Orientation of fish larvae in situ is consistent among locations, years and methods, but varies with time of day. Mar. Ecol. Prog. Ser. 505, 193–208. https://doi.org/10.3354/meps10792.

Leis, J., Siebeck, U., Hay, A., Paris, C., Chateau, O., Wantiez, L., 2015. In situ orientation of fish larvae can vary among regions. Mar. Ecol. Prog. Ser. 537, 191–203. https://doi.org/10.3354/meps11446.

Lerner, A., Browman, H.I., 2016. The copepod Calanus spp. (Calanidae) is repelled by polarized light. Sci. Rep. 6, 35891. https://doi.org/10.1038/srep35891.

Lerner, A., Sabbah, S., Erlick, C., Shashar, N., 2011. Navigation by light polarization in clear and turbid waters. Trans. R. Soc. B. 366, 671–679. https://doi.org/10.1098/rstb.2010.0189.

Maravelias, C., Reid, D., 1997. Identifying the effects of oceanographic features and zooplankton on prespawning herring abundance using generalized additive models. Mar. Ecol. Prog. Ser. 147, 1–9. https://doi.org/10.3354/meps147001.

Mariani, S., Hutchinson, W., Hatfield, E., Ruzzante, D., Simmonds, E., Dahlgren, T., Andre, C., Brigham, J., Torstensen, E., Carvalho, G., 2005. North Sea herring population structure revealed by microsatellite analysis. Mar. Ecol. Prog. Ser. 303, 245–257. https://doi.org/10.3354/meps303245.

Merritt, R., Purcell, C., Stroink, G., 1983. Uniform magnetic field produced by three, four, and fivesquare coils. Rev. Sci. Instrum. 54, 879–882.

Mork, M., 1981. Circulation phenomena and frontal dynamics of the Norwegian coastal current. Philos. Trans. R. Soc. A Math. Phys. Eng. Sci. 302, 635–647. https://doi.org/10.1098/rsta.1981.0188.

Moyano, M., Illing, B., Peschutter, P., Huebert, K.B., Peck, M.A., 2016. Thermal impacts on the growth, development and ontogeny of critical swimming speed in Atlantic herring larvae. Comp. Biochem. Physiol. - Part A Mol. Integr. Physiol. 197, 23–34. https://doi.org/10.1016/j.cbpa.2016.02.020.

Mussi, M., Haimberger, T.J., Hawryshyn, C.W., 2005. Behavioural discrimination of polarized light in the damselfish chromis viridis (family pomacentridae). J. Exp. Biol.

208, 3037–3046. https://doi.org/10.1242/jeb.01750.

O'connor, J., Muheim, R., 2017. Pre-Settlement Coral-Reef Fish Larvae Respond to Magnetic Field Changes during the Day. https://doi.org/10.1242/jeb.159491.

Paris, C.B., Guigand, C.M., Irisson, J., Fisher, R., 2008. Orientation with no frame of reference (OWNFOR): a novel system to observe and quantify orientation in reef fish larvae. Carribbean Connect. Implic. Mar. Prot. Area Manag. NOAA Natl. Mar. Sanctuary Progr. 52–62. https://doi.org/10.1046/j.1467-2960.2001.00053.x.

Paris, C.B., Atema, J., Irisson, J.O., Kingsford, M., Gerlach, G., Guigand, C.M., 2013. Reef odor: a wake up call for navigation in reef fish larvae. PLoS One 8, 1–8. https://doi.org/10.1371/journal.pone.0072808.

Pepin, P., Helbig, J.A., 1997. Distribution and drift of Atlantic cod (*gadus morhua*) eggs and larvae on the Northeast Newfoundland shelf. Can. J. Fish. Aquat. Sci. 54, 670–685. https://doi.org/10.1139/f96-317.

Rossi, A., Irisson, J.-O., Levaray, M., Pasqualini, V., Agostini, S., 2019. Orientation of Mediterranean fish larvae varies with location. Mar. Biol. 166, 100. https://doi.org/10.1007/s00227-019-3548-7.

Rothschild, B.J.R., 2000. "'Fish stocks and recruitment'": the past thirty years. ICES J. Mar. Sci. 57, 191–201. https://doi.org/10.1006/jmsc.2000.0645.

Ruzzante, D.E., Mariani, S., Bekkevold, D., André, C., Mosegaard, H., Clausen, L.A.W., Dahlgren, T.G., Hutchinson, W.F., Hatfield, E.M.C., Torstensen, E., Brigham, J., Simmonds, E.J., Laikre, L., Larsson, L.C., Stet, R.J.M., Ryman, N., Carvalho, G.R., 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. Proc. R. Soc. B Biol. Sci. 273, 1459–1464. https://doi.org/10.1098/rspb.2005.3463.

Sætre, R., 1999. Features of the central Norwegian shelf circulation. Cont. Shelf Res. 19, 1809–1831. https://doi.org/10.1016/S0278-4343(99)00041-2.

Shashar, N., Cronin, T.W., 1996. Polarization contrast vision in octopus. J. Exp. Biol. 199, 999–1004.

Sinclair, M., Iles, T.D., 1985. Atlantic herring (*clupea harengus*) distributions in the Gulf of Maine – Scotian shelf area in relation to oceanographic features. Can. J. Fish. Aquat. Sci. 42, 880–887. https://doi.org/10.1139/f85-112.

Skagseth, Ø., Slotte, A., Stenevik, E.K., Nash, R.D.M., 2015. Characteristics of the Norwegian coastal current during years with high recruitment of Norwegian spring spawning herring (*Clupea harengus* L.). PLoS One 10, e0144117. https://doi.org/10.1371/journal.pone.0144117.

Swearer, S.E., Treml, E.A., Shima, J.S., 2019. A review of biophysical models of marine larval dispersal. In: Hawkins, S.J., Allcock, A.L., Bates, A.E., Firth, L.B., Smith, I.P., Swearer, S.E., Todd, P.A. (Eds.), Oceanography and Marine Biology. Taylor & Francis.

Toresen, R., Østvedt, O.J., 2000. Variation in abundance of Norwegian spring-spawning herring (clupea harengus, clupeidae) throughout the 20th century and the influence of climatic fluctuations. Fish Fish. 1, 231–256. https://doi.org/10.1111/j.1467-2979.2000.00022.x.

Toresen, R., Skjoldal, H.R., Vikebø, F., Martinussen, M.B., 2019. Sudden change in long-term ocean climate fluctuations corresponds with ecosystem alterations and reduced recruitment in Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae). Fish Fish 20 https://doi.org/10.1111/faf.12369. faf.12369.

Vikebø, F., Jørgensen, C., Kristiansen, T., Fiksen, Ø., 2007. Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. Mar. Ecol. Prog. Ser. 347, 207–219. https://doi.org/10.3354/meps06979.

Voesenek, C.J., Muijres, F.T., Van Leeuwen, J.L., 2018. Biomechanics of swimming in developing larval fish. J. Exp. Biol. https://doi.org/10.1242/jeb.149583.

Waterman, T.H., 1988. In: Blizard, M.A. (Ed.), Polarization Of Marine Light Fields And Animal Orientation. International Society for Optics and Photonics, pp. 431. https://doi.org/10.1117/12.945752.

von Westernhagen, H., Rosenthal, H., 1979. Laboratory and in-situ studies on larval development and swimming performance of Pacific herring clupea harengus pallasi. Helgoländer Meeresun. 32, 539–549. https://doi.org/10.1007/BF02277993.

White, C., Selkoe, K.A., Watson, J., Siegel, D.A., Zacherl, D.C., Toonen, R.J., 2010. Ocean currents help explain population genetic structure. Proc. Royal Soc. B: Biol. Sci. 1685–1694. https://doi.org/10.1098/rspb.2009.2214.

Zimmermann, F., Ricard, D., Heino, M., 2018. Density regulation in northeast Atlantic fish populations: density dependence is stronger in recruitment than in somatic growth. J. Anim. Ecol. 87, 672–681. https://doi.org/10.1111/1365-2656.12800.

Zimmermann, F., Claireaux, M., Enberg, K., 2019. Common trends in recruitment dynamics of north-east Atlantic fish stocks and their links to environment, ecology and management. Fish Fish. 20, 518–536. https://doi.org/10.1111/faf.12360.