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SHORT COMMUNICATION

Juvenile Atlantic herring (*Clupea harengus*) use a time-compensated sun compass for orientation

Lisa Spiecker[1,*,‡], Malien Laurien[1,*], Wiebke Dammann[1], Andrea Franke[2,3], Catriona Clemmesen[4] and Gabriele Gerlach[1,2]

ABSTRACT

Atlantic herring (*Clupea harengus*), an ecologically and economically important species in the northern hemisphere, shows pronounced seasonal migratory behaviour. To follow distinctive migration patterns over hundreds of kilometers between feeding, overwintering and spawning grounds, they are probably guided by orientation mechanisms. We tested whether juvenile spring-spawning Atlantic herring, caught in the western Baltic, use a sun compass for orientation just before they start leaving their hatching area. Fish were randomly divided into two groups, one of them clock-shifted 6 h backwards, to investigate whether they shift their orientation direction accordingly. Individual fish were placed in a circular bowl and their orientation was tested multiple times with the sun as a sole visual orientational cue. Our results show for the first time that juvenile Atlantic herring use a time-compensated sun compass during their migration. Their swimming direction was impaired, but still present, even when the sky was very cloudy, indicating additional orientation capabilities.

KEY WORDS: Atlantic herring, Migration, Sun compass orientation, Orientation behaviour

INTRODUCTION

The Atlantic herring (*Clupea harengus* Linnaeus 1758), an ecologically and economically important species in the northern hemisphere, exhibits complex seasonal migration behaviour. In the western Baltic Sea, adult herring migrate hundreds of kilometers between the Sound (overwintering grounds), coastal areas of the western Baltic Sea (spawning grounds) and Kattegat, Skagerrak and eastern North Sea (summer feeding grounds) (see Fig. 1; Aro, 1989, Clausen et al., 2015, Miethe et al., 2014). Goal-oriented migration over mid-range distances is a difficult task and requires the right cues for orientation and navigation. Fish can use a range of sensory cues for orientation: sound (e.g. Radford et al., 2011), olfaction (e.g. Gerlach et al., 2007), Earth's magnetic field (e.g. Bottesch et al., 2016, Cresci et al., 2017) or celestial cues, such as the sun (e.g. Loyacano et al., 1977, Mouritsen et al., 2013, Quinn, 1980).

[1]Institute of Biology and Environmental Science, Carl von Ossietzky University Oldenburg, 26111 Oldenburg, Germany. [2]Helmholtz Institute for Functional Marine Biodiversity at the University of Oldenburg (HIFMB), 26129 Oldenburg, Germany. [3]Alfred-Wegener-Institute, Helmholtz Centre for Polar and Marine Research (AWI), 27570 Bremerhaven, Germany. [4]Marine Evolutionary Ecology, GEOMAR Helmholtz Centre for Ocean Research Kiel, 24105 Kiel, Germany.
*These authors contributed equally to this work

‡Author for correspondence (lisa.spiecker@uni-oldenburg.de)

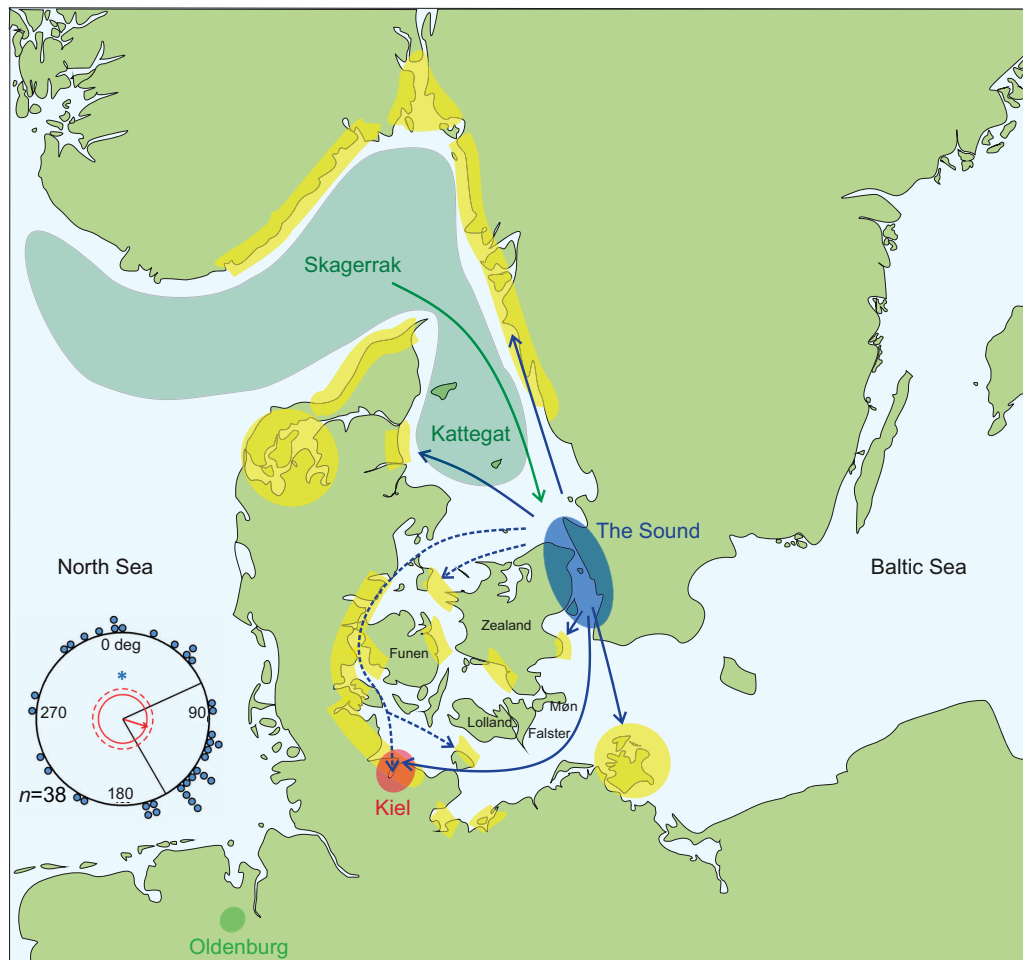L.S., 0000-0003-1801-4630; A.F., 0000-0003-0963-2971; C.C., 0000-0003-4102-7341; G.G., 0000-0001-5246-944X

While orientation based on olfactory and auditory cues is usually limited to a few kilometers (e.g. leaving a fjord), magnetic and sun compass orientation is mostly used for long-distance migration (e.g. herring migration between spawning and feeding grounds). To be able to effectively use the sun as a compass, animals must observe the path of the sun and link the sun's azimuth at different time points during the day to their circadian clock (reviewed in Mouritsen, 2018).

Western Baltic spring-spawning herring (WBSSH) migrate from their overwintering grounds to their coastal spawning grounds to lay benthic eggs in shallow, low-saline areas such as Greifswald Bay and Kiel Canal mainly between February and May (Fig. 1; Biester, 1989, Clausen et al., 2015, Paulsen et al., 2014, Polte et al., 2017). After spawning, adult herring leave the area. Yolk-sac larvae are found close to the spawning beds. Pre-flexion and flexion stage larvae are then observed in pelagic areas and post-flexion larvae return to shallow littoral areas where they remain until after their metamorphosis to the juvenile stage (Polte et al., 2017). It is assumed that juveniles initially stay near the coast and only start migrating to offshore nursery areas between Germany and Denmark in July/August (Oeberst et al., 2009; Payne et al., 2009; Polte et al., 2017). However, the exact path during the first migration of juvenile herring (age 0) is unknown.

To date, only Atlantic herring larvae have been tested in various orientation experiments between 14 and 28 days post-hatch (Cresci et al., 2020), weeks before they begin their first long-distance migration. Results of this study propose the potential use of a sun compass, but could not exclude the use of other orientational cues. To date, there are no published data on orientation mechanisms in juvenile herring as they embark on their first long-distance migration. In this study, we caught juvenile WBSSH in summer (July and August) 2021 in the Kiel Fjord and investigated whether they use a sun compass to orient towards offshore nursery areas and the Sound, where Baltic herring overwinter (Fig. 1; Payne et al., 2009).

MATERIALS AND METHODS
Experimental animals

All animal procedures were approved by the Animal Care and Use Committees of the Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit (LAVES, Oldenburg, Germany), Az.: 33.19-42502-04-17/2721 and performed in accordance with the relevant guidelines and regulations. Permission for scientific fishing using fishing rods, fish traps and sink nets was granted by the Schleswig–Holstein State office for agriculture, environment and rural areas to GEOMAR.

The experiments were performed at the University of Oldenburg, Germany, from August to October 2021. Juvenile herring were caught in the Kiel Fjord (54°19′46.0″N, 10°08′58.1″E) in July and August 2021 from the pier in front of the GEOMAR Helmholtz

Fig. 1. Map showing the suggested seasonal migrations of adult western Baltic spring-spawning herring (WBSSH) and the orientation of juveniles.
The summer feeding areas are located in Kattegat, Skagerrak and the eastern North Sea (dark green). Overwintering takes place in the Sound (blue); from there, herring migrate to different coastal areas for spawning (yellow); dashed lines show routes that are less known to be used. Juveniles for our experiment were caught in the Kiel Fjord (red) and tested in Oldenburg (green). Map modified from Aro (1989), Clausen et al. (2015), Nielsen et al. (2001). Circular diagram (left corner) shows the sun compass orientation of juvenile herring tested under normal conditions; each dot represents the mean direction of one fish tested 2–6 times; red arrow indicates the group's mean vector (ESE).

Centre for Ocean Research Kiel west shore building using large hand nets. Fish were kept in a flow-through tank (with Baltic Sea water) for 2 weeks and fed 2–3 times a day with *Artemia* sp. shrimp or natural plankton (caught in the Kiel Fjord) before being transported to Oldenburg (180 km SE) in plastic cooling boxes filled with continuously aerated Baltic Sea water (according to Kiel Fjord conditions: 15 PSU and 17°C).

After arriving in Oldenburg, fish were separated into two groups (sun compass and time-shift sun compass) and transferred into 200 l glass aquaria with water conditions matching those in Kiel Fjord. The tanks were filled with natural seawater, temperature was controlled by a TECO Aquarium Cooler TK 500 and for continuous filtration, an external filter was used (Eheim Professional). The light cycle was set to 14 h light:10 h dark with lights on between 06:00 h and 20:00 h for normal sun compass experiments and between 00:00 h and 14:00 h for time-shift sun compass experiments. The time-shifted tank was covered with opaque curtains to prevent external light from influencing the light:dark cycle. Once per day, when the light was on for both groups, the juveniles were fed *Artemia* sp. shrimp, enriched with Aqua Biotica Orange+ (Mrutzek Meeres-Aquaristik). The time-shift sun compass group was clock-shifted for 7 days before starting the experiments.

Subsequent to performing the orientation test, the body length of all fish in each experimental group was measured. In the normal sun compass group, the juveniles measured 5.8±1.7 cm (mean±s.d.) and in the time-shift sun compass group they were 5.2±0.8 cm. Animals tested in September (second cohort) had a standard length of 8.0±0.8 cm.

Sun compass orientation tests
In total, 79 fish were tested, with 38 juvenile herring in the normal sun compass experiment and 41 juveniles in the time-shift sun compass experiment. A clock-shift is necessary to exclude the use of additional omnipresent cues like the earth's magnetic field. Each individual fish was tested at least twice (2–6 times) in each condition, respectively. This multiple-testing method is also used in migratory birds (Hein et al., 2011; Wiltschko et al., 1993) to gain reasonable accuracy on the intended mean orientation direction. Additionally, multiple testing of the same individuals can significantly reduce the total number of experimental animals needed, which complies with the 3Rs principle. All of the tests were performed between 08:00 h and 13:00 h for time-shifted fish and between 08:00 h and 16:00 h for normal sun compass experimental fish.

During the experiments, juvenile herring were transferred into testing bowls (Ø 30 cm) filled with 5 l of sea water (temperature and salinity similar to housing tank water) and placed on top of a 10 l bucket that was positioned outside in the field with a clear, unhindered view to the sky and no visible landmarks. After 5 min of acclimatization, each herring was tested individually; pictures were taken every 10 s for 20 min using a GoPro camera (GoPro Hero 4 silver) placed on the bottom of the bucket aligned to the north (see Fig. 2A). The position of the fish's head relative to the center of the testing bowls was assessed by uploading the recording in ImageJ (National Institutes of Health, Bethesda, Maryland, USA) and clicking on the fish's head every 30 s (in every 3rd frame). By choosing 30 s intervals, we made sure to have no correlation between the successive data points due to lag of time in between them (autocorrelation). The resulting 40 captured positions per tested fish were then translated into compass directions. In addition to the orientation direction, three different people assessed cloud cover in 5% steps based on the recorded sky during the experiments (cameras were placed under the testing bowls and pointed at the sky). We averaged these judgments of cloud cover.

After each experimental run, the juvenile herring were removed from the experimental setup and placed in the shade to rest for at least 30–45 min before being tested again.

Correction of time-shift sun compass data

It is not known yet if fish are able to exactly measure the sun's azimuth or if they just estimate the azimuth in accordance to their internal clock – assuming a steady shift throughout the day. Therefore, we used two different methods to correct for the sun position at different times of the day and consequently correct the raw data that have been collected during the time-shift sun compass experiments. One is the generalized correction and the other is the accurate correction.

Using the generalized correction, a 15 deg change in sun azimuth per hour is assumed (Lambrinos et al., 1997), leading to a 90 deg shift in 6 h. These 90 deg were added to every mean vector that had been calculated using the 40 positional data points of each significant experimental run to get a generalized corrected mean vector.

For the accurate correction, the exact position of the sun at the specific location, day and time of each experimental run (at a time point mid-experiment, meaning after 10 min of the 20 min trial) was determined using www.sunearthtools.com (October 2020, based on Michalsky, 1988, see Fig. 2B). Afterwards, the position of the sun 6 h after each experimental run was also determined. The deviance of the two angles is calculated by subtracting the sun position during the actual experiment from the sun position of the expected experimental time. This deviance is then added to the original mean vector to get the accurate corrected mean vector.

Data analysis and statistics

All data were analysed using the circular statistics program Oriana (Kovach, 2011) as well as R (version 4.1.3) with ggplot2 (Wickham, 2016). From the 40 observed directions in the respective experimental run of each individual, we calculated the mean vector of orientation. We analyzed whether orientation preference was statistically different from a random distribution using the Rayleigh Uniformity Test [$P<0.05$ in our case corresponds to a length of mean vector ($\mathbf{r}$)>0.272]. The mean direction of a fish during one trial was averaged with the mean direction of the same fish during the following trials to gain only one direction per individual that was used to assess the groups' mean orientation direction.

To evaluate whether the fish were able to effectively use the sun as an orientation cue, the group result of the normal sun compass experiment was initially compared with that from the uncorrected time-shift experiment using a Mardia–Watson–Wheeler test. After proving that both data sets differed significantly, the data of the normal sun compass experiment were compared with those of the corrected time-shift data (generalized and accurate). We hypothesized that if the fish used a time-compensated sun compass, the sun compass direction and corrected time shift direction should be the same.

To analyze whether orientation depends on a clear view to the sky, the effect of relative 'cloud cover' on directionality [length of the mean vector ($\mathbf{r}$) of every individual experimental run] was determined using logit transformation of the $\mathbf{r}$ vectors, Bonferroni correction for multiple comparisons and paired t-tests.
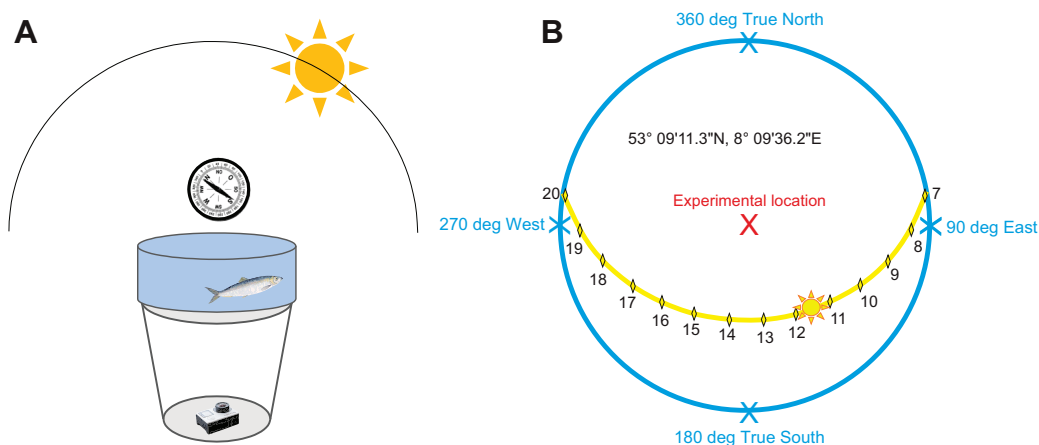

Fig. 2. Experimental setup for testing sun compass orientation and sun azimuth curve. (A) The experimental bowl containing 5 l of sea water as well as one experimental animal was placed on top of a bucket in the field, allowing a clear and unhindered view of the sky. A GoPro camera was placed at the bottom of the bucket, aligned towards north and used for recording time-lapse videos of the experimental runs. Schematic drawing of herring from Gervais et al., 1877. (B) Sun azimuth curve in Oldenburg in August 2021. Note that the sun azimuth moves very consistently at an average of ~15 deg h^{-1}. In northern Germany, the sun is never positioned directly overhead, which makes it possible to perform sun compass orientation tests at any time between sunrise and sunset. Illustration according to azimuth curve calculated by www.sunearthtools.com.
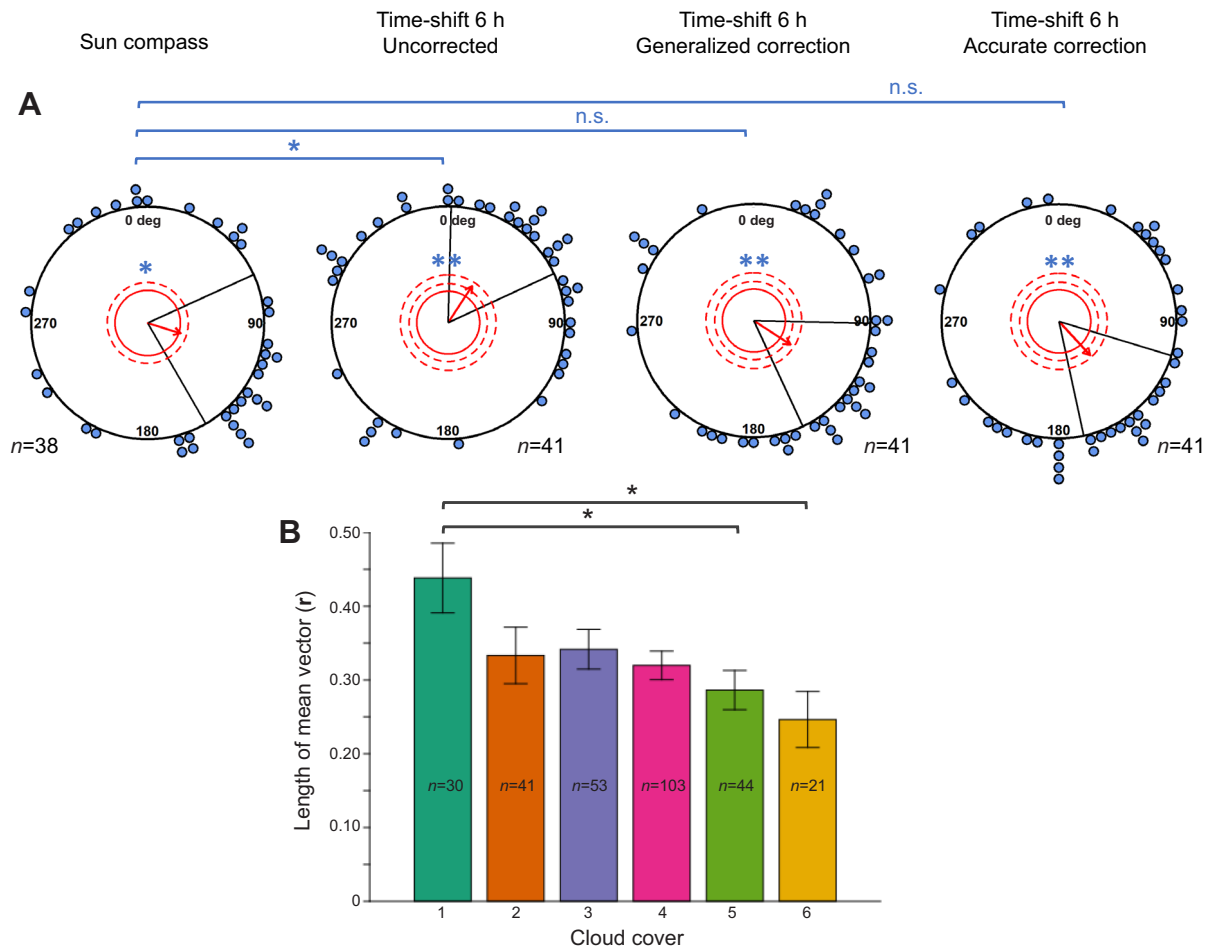
Fig. 3. Juvenile WBSSH are able to use a time-compensated sun compass for orientation. (A) 38 fish kept according to natural light/dark rhythm as well as 41 fish clock-shifted 6 h backwards were tested for their orientation direction under natural skies from August to October 2021. The normal sun compass group had a significant orientation towards ESE (mean direction: 108 deg, $P=0.033$) while the clock-shifted group oriented significantly towards NNE (mean direction: 33 deg, $P=0.003$). After correcting the time-shift data (generalized and accurate), the swimming direction of time-shifted juvenile herring points towards ESE (generalized; mean direction: 123 deg, $P=0.003$) or SE (accurate; mean direction: 137 deg, $P=0.002$). Every dot indicates the mean direction of one individual fish that oriented significantly at least twice in the given condition. Arrow (vector) indicates the group's mean direction. Red circles indicate the radius of the group mean vector necessary for significance according to the Rayleigh Test ($P<0.05$, solid circle; $P\leq0.01$, first dashed circle; $P\leq0.001$, second dashed circle). Solid black lines left and right of vector indicate 95% confidence intervals. Graphs created in R (version 4.1.3) using ggplot2 (Wickham, 2016). Group results were compared using a Mardia–Watson–Wheeler test (sun versus TS uncorrected: $P=0.014$). *$P<0.05$, **$P\leq0.01$; n.s., not significant. (B) Bar chart comparing the directedness of fish (indicated by the mean of the **r** vector in every experimental run of sun compass experiments) to the level of cloud. The cloud cover categories 1 to 6 indicate: 0–20% ($n=30$), >20–40% ($n=41$), >40–60% ($n=53$), >60–80% ($n=103$), >80–100% ($n=44$) and 100% ($n=21$) sky coverage, respectively. For statistics, **r** vectors were logit transformed (see Table S2). After Bonferroni correction for multiple comparisons, a paired t-test was performed. Orientation was significantly better at 0–20% cloud cover than at >80–100% or 100% cloud cover. No significant difference was found when cloud cover was between >20 and 100% (categories 2–6). Means±s.e.m.; *$P<0.003$.

RESULTS AND DISCUSSION

Herring expressed a significant sun compass orientation towards east-southeast (ESE) with a mean vector of 108 deg (see Fig. 3A) (for details, see Table S2). A 6 h clock-shift where the animals are tested before noon, when they think it is afternoon, should lead to a change in orientation when using a sun compass. Indeed, when clock-shifted 6 h backwards, fish showed a significant group orientation towards north-northeast (NNE), with a mean vector of 33 deg (see Fig. 3A) (for details, see Table S3). Comparison of these two datasets by performing a Mardia–Watson–Wheeler test showed a statistical difference ($W=8.507$, $P=0.014$). The change in mean vector was 75 deg.

To understand whether herring changed their directional swimming according to the time-shift, we used two different methods (generalized and accurate correction). First, we corrected by adding 90 deg (assuming 15 deg change per hour, see Fig. 2B)

and calculated a group swimming direction of time-shifted juvenile herring towards ESE, with a mean vector of 123 deg. By performing correction according to the accurate sun position (see Fig. 3A), herring showed a SE direction with a mean vector of 137 deg. Both these mean swimming orientations were statistically similar to the normal sun compass orientation direction when compared using a Mardia–Watson–Wheeler test (generalized: $W=0.309$, $P=0.857$, accurate: $W=1.9$, $P=0.387$). The change in mean vector after correction amounts to only 15 deg (generalized correction) and 29 deg (accurate correction), respectively.

To determine if cloud cover influences directional swimming, we tested whether clouds had an impact on the orientation ability of the fish.

We categorized cloud coverage from 1 to 6 [(1) 0–20%, (2) >20–40%, (3) >40–60%, (4) >60–80%, (5) >80–100% and (6) 100% cloudy] and calculated the mean **r** vector±s.e.m.

After logit transforming the **r** vectors and Bonferroni correction for multiple comparisons, the paired *t*-test showed that orientation was significantly higher at 0–20% cloudiness (**r**=0.439±0.04) than at >80–100% (**r**=0.286±0.01) or 100% cloud cover (**r**=0.246±0.05). No significant difference was found when the cloud cover was between >20 and 100% (see Fig. 3B and Table S1). It became apparent that the orientation ability of the fish decreased when the percentage of cloud coverage increased and the most successful tests were conducted when only 0–20% of the sky was covered with clouds.

Taken together, these facts demonstrate that juvenile Atlantic herring are able to use a time-compensated sun compass for orientation. This finding extends the results of Cresci et al. (2020), who used a transparent drifting *in situ* chamber (DISC) in which larvae at 14–16 and 25–28 days post-hatch were tested for their orientation ability in coastal areas of a Norwegian fjord. Cresci et al. (2020) found that both age groups display a significant orientation towards the southeast. However, fish larvae tested in a drifting DISC are exposed to many different environmental cues such as sound, olfactory cues or visual landmarks. Therefore, it is hard to determine the influence of one specific orientation cue. Cresci et al. (2020) suggest that larvae use the sun for orientation, since directionality decreased with increasing cloud cover. We performed experiments on juvenile herring during their first summer/autumn when they start to leave their shallow coastal nursery grounds and head towards offshore nursery or overwintering grounds; therefore, they should be in 'migration mode'. We tested the effect of body length on the individual bearing, but fish of the second cohort (which were older and larger) showed no significantly different bearing than juveniles tested in August. This confirms that the smaller fish from the first cohort were indeed already in 'migration mode' when caught. Furthermore, they were tested under controlled conditions, giving them no visual cues for orientation other than the sun. Clock-shifting the fish, which has not been done in the larval experiments, confirmed that herring juveniles use a time-compensated sun compass for orientation. This conclusion is based on the fact that they misinterpreted the sun's actual position and changed their orientation direction accordingly. In addition, orientation was more precise under sunny conditions than when clouds prevented the direct view of the sun.

Even though Table S1 and Fig. 3B show data collected at '100% cloud cover', which should lead to unoriented fish and therefore non-significant experimental runs, we still observed directional swimming. This could indicate that herring have further orientation capabilities, such as magnetic orientation or perhaps the use of a skylight polarization pattern (Hawryshyn, 1992; Waterman, 2006; Pomozi et al., 2001), but more analysis is needed to determine whether herring can indeed detect these cues. Even if celestial cues such as the sun were used as a primary compass sense in our experiment (as proven by the clock-shift), herring might use additional orientation mechanisms. The sun compass could be used collectively with other compass senses or be part of a cue cascade where one cue comes more into play if a higher ranked one is less available. Magnetic compass orientation would be plausible as this cue is omnipresent and has been demonstrated in a variety of fish species (Bottesch et al., 2016; Cresci et al., 2017; Putman et al., 2020). Whether herring can indeed use additional orientation mechanisms still needs to be determined. Even though herring larvae did not respond to rotations of the magnetic field (Cresci et al., 2020), magnetic orientation might develop in later life stages.

Juvenile Atlantic herring perform their first migration without the guidance of experienced adult herring. Similar difficulties are experienced by juvenile solitary migrating songbirds (e.g. the European blackcap *Sylvia atricapilla*), which use compass orientation during their first migration. When translocated, they do not find their way back to their migration route. However, as experienced adults, they have a map-based orientation and after translocation for several hundred kilometers, can adjust their direction accordingly (Merlin and Liedvogel, 2019). In a different study, we displaced juvenile coral reef fish (*Ostorhinchus doederleini*) by 180 km in a similar manner to the experiments on juvenile birds. We did not observe any change in orientation direction and conclude that they have no positional information and therefore no map-based orientation (L.S., F. Curdt, A. Bally, N. Janzen, P. Kraemer, B. Leberecht, M. J. Kingsford, H. Mouritsen, M. Winklhofer and G.G., unpublished results). Naive travelers, such as juvenile herring, coral reef fish or night-migratory songbirds seem to rely on simple inherited orientation mechanisms, such as a sun compass.

Juvenile Baltic herring start their journey at the end of summer, leaving the coastal areas to find areas of higher food availability (Kvamme et al., 2003). In our study, juveniles oriented to the east-southeast, which might indicate that they take the eastern route to reach the Sound (Fig. 1, solid blue line from the Sound to Kiel) or remain in shallower nursery areas at the German coast, potentially joining schools of similarly sized individuals from different spawning areas (e.g. Lübeck, Wismar, Greifswald) as suggested by Nøttestad et al. (1999). In future experiments, we plan to investigate additional compass- and map-based orientation mechanisms to further characterize the sensory orientation capabilities of Atlantic herring.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: L.S., M.L., G.G.; Methodology: L.S., M.L., G.G.; Validation: L.S., M.L., W.D.; Formal analysis: L.S., M.L., W.D.; Investigation: L.S., M.L., W.D.; Resources: A.F., C.C.; Data curation: L.S., M.L.; Writing - original draft: L.S., M.L., A.F.; Writing - review & editing: L.S., M.L., A.F., C.C., G.G.; Visualization: L.S., M.L.; Supervision: L.S., M.L., G.G.; Project administration: L.S., M.L., C.C., G.G.; Funding acquisition: G.G.

References
Aro, E. (1989). A review of fish migration patterns in the Baltic. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* **190**, 72-96.

Biester, E. (1989). The distribution of spring-spawning herring larvae in coastal waters of the German Democratic Republic. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* **190**, 109-112.

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

Clausen, L. A. W., Staehr, K. J., Rindorf, A. and Mosegaard, H. (2015). Effect of spatial differences in growth on distribution of seasonally co-occurring herring *Clupea harengus* stocks. *J. Fish Biol.* **86**, 228-247. doi:10.1111/jfb.12571

Cresci, A., Paris, C. B., Durif, C. M. F., Shema, S., Bjelland, R. M., Skiftesvik, A. B. and Browman, H. I. (2017). Glass eels (*Anguilla anguilla*) have a magnetic compass linked to the tidal cycle. *Sci. Adv.* **3**, e1602007. doi:10.1126/sciadv.1602007

Cresci, A., Allan, B. J. M., Shema, S. D., Skiftesvik, A. B. and Browman, H. I. (2020). Orientation behavior and swimming speed of Atlantic herring larvae (*Clupea harengus*) in situ and in laboratory exposures to rotated artificial magnetic fields. *J. Exp. Mar. Biol. Ecol.* **526**, 151358. doi:10.1016/j.jembe.2020.151358

Gerlach, G., Atema, J., Kingsford, M. J., Black, K. P. and Miller-Sims, V. (2007). Smelling home can prevent dispersal of reef fish larvae. *Proc. Natl. Acad. Sci. USA* **104**, 858-863. doi:10.1073/pnas.0606777104

Gervais, H., Boulart, R. and Gervais, P. (1877). *Les poissons: synonymie, description, moeurs, frai, pêche, iconographie des espèces composant plus particulièrement la faune francaise.* Paris: J. Rothschild.

Hawryshyn, C. W. (1992). Polarization vision in fish. *Am. Sci.* **80**, 164-175.

Hein, C. M., Engels, S., Kishkinev, D. and Mouritsen, H. (2011). Robins have a magnetic compass in both eyes. *Nature* **471**, E11-E12. doi:10.1038/nature09875

Kovach, W. L. (2011). Oriana–circular statistics for windows, ver. 4. Kovach Computing Services, Pentraeth.

Kvamme, C., Nottestad, L., Ferno, A., Misund, O. A., Dommasnes, A., Axelsen, B. E., Dalpadado, P. and Melle, W. (2003). Migration patterns in Norwegian spring-spawning herring: why young fish swim away from the wintering area in late summer. *Mar. Ecol. Prog. Ser.* **247**, 197-210. doi:10.3354/meps247197

Lambrinos, D., Maris, M., Kobayashi, H., Labhart, T., Pfeifer, R. and Wehner, R. (1997). An autonomous agent navigating with a polarized light compass. *Adapt. Behav.* **6**, 131-161. doi:10.1177/105971239700600104

Loyacano, H. A., Chappell, J. A. and Gauthreaux, S. A. (1977). Sun-compass orientation in juvenile largemouth bass, *Micropterus salmoides*. *Trans. Am. Fish. Soc.* **106**, 77-79. doi:10.1577/1548-8659(1977)106<77:SOIJLB>2.0.CO;2

Merlin, C. and Liedvogel, M. (2019). The genetics and epigenetics of animal migration and orientation: birds, butterflies and beyond. *J. Exp. Biol.* **222**, jeb191890. doi:10.1242/jeb.191890

Michalsky, J. J. (1988). The Astronomical Almanac's algorithm for approximate solar position (1950-2050). *Sol. Energy* **40**, 227-235. doi:10.1016/0038-092X(88)90045-X

Miethe, T., Grohsler, T., Böttcher, U. and Von Dorrien, C. (2014). The effects of periodic marine inflow into the Baltic Sea on the migration patterns of Western Baltic spring-spawning herring. *ICES J. Mar. Sci.* **71**, 519-527. doi:10.1093/icesjms/fst166

Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature* **558**, 50-59. doi:10.1038/s41586-018-0176-1

Mouritsen, H., Atema, J., Kingsford, M. J. and Gerlach, G. (2013). Sun compass orientation helps coral reef fish larvae return to their natal reef. *PLoS One* **8**, e66039. doi:10.1371/journal.pone.0066039

Nielsen, J. R., Lundgren, B., Jensen, T. F. and Stæhr, K. J. (2001). Distribution, density and abundance of the western Baltic herring (*Clupea harengus*) in the Sound (ICES Subdivision 23) in relation to hydrographical features. *Fish. Res.* **50**, 235-258. doi:10.1016/S0165-7836(00)00220-4

Nøttestad, L., Giske, J., Holst, J. C. and Huse, G. (1999). A length-based hypothesis to explain feeding migrations in pelagic fish. *Can. J. Fish. Aquat. Sci.* **56**, 26-34. doi:10.1139/f99-222

Oeberst, R., Klenz, B., Gröhsler, T., Dickey-Collas, M., Nash, R. D. M. and Zimmermann, C. (2009). When is year-class strength determined in western Baltic herring? *ICES J. Mar. Sci.* **66**, 1667-1672. doi:10.1093/icesjms/fsp143

Paulsen, M., Hammer, C., Malzahn, A. M., Polte, P., Von Dorrien, C. and Clemmesen, C. (2014). Nutritional situation for larval Atlantic herring (*Clupea harengus* L.) in two nursery areas in the western Baltic Sea. *ICES J. Mar. Sci.* **71**, 991-1000. doi:10.1093/icesjms/fst168

Payne, M. R., Clausen, L. W. and Mosegaard, H. (2009). Finding the signal in the noise: objective data-selection criteria improve the assessment of western Baltic spring-spawning herring. *ICES J. Mar. Sci.* **66**, 1673-1680. doi:10.1093/icesjms/fsp185

Polte, P., Kotterba, P., Moll, D. and Von Nordheim, L. (2017). Ontogenetic loops in habitat use highlight the importance of littoral habitats for early life-stages of oceanic fishes in temperate waters. *Sci. Rep.* **7**, 42709. doi:10.1038/srep42709

Pomozi, I. N., Horváth, G. B. and Wehner, R. D. (2001). How the clear-sky angle of polarization pattern continues underneath clouds: full-sky measurements and implications for animal orientation. *J. Exp. Biol.* **204**, 2933-2942. doi:10.1242/jeb.204.17.2933

Putman, N. F., Williams, C. R., Gallagher, E. P. and Dittman, A. H. (2020). A sense of place: pink salmon use a magnetic map for orientation. *J. Exp. Biol.* **223**, jeb218735. doi:10.1242/jeb.218735

Quinn, T. P. (1980). Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *J. Comp. Physiol.* **137**, 243-248. doi:10.1007/BF00657119

Radford, C. A., Stanley, J. A., Simpson, S. D. and Jeffs, A. G. (2011). Juvenile coral reef fish use sound to locate habitats. *Coral Reefs* **30**, 295-305. doi:10.1007/s00338-010-0710-6

Waterman, T. H. (2006). Reviving a neglected celestial underwater polarization compass for aquatic animals. *Biol. Rev.* **81**, 111-115. doi:10.1017/S1464793105006883

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis. Use R!* 2nd edn. Springer International Publishing.

Wiltschko, W., Munro, U., Ford, H. and Wiltschko, R. (1993). Red-light disrupts magnetic orientation of migratory birds. *Nature* **364**, 525-527. doi:10.1038/364525a0