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Food web changes under ocean acidification promote herring larvae survival

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Ocean acidification—the decrease in seawater pH due to rising CO_2 concentrations—has been shown to lower survival in early life stages of fish and, as a consequence, the recruitment of populations including commercially important species. To date, ocean-acidification studies with fish larvae have focused on the direct physiological impacts of elevated CO_2, but largely ignored the potential effects of ocean acidification on food web interactions. In an in situ mesocosm study on Atlantic herring (*Clupea harengus*) larvae as top predators in a pelagic food web, we account for indirect CO_2 effects on larval survival mediated by changes in food availability. The community was exposed to projected end-of-the-century CO_2 conditions (~760 µatm pCO_2) over a period of 113 days. In contrast with laboratory studies that reported a decrease in fish survival, the survival of the herring larvae in situ was significantly enhanced by 19 ± 2%. Analysis of the plankton community dynamics suggested that the herring larvae benefitted from a CO_2-stimulated increase in primary production. Such indirect effects may counteract the possible direct negative effects of ocean acidification on the survival of fish early life stages. These findings emphasize the need to assess the food web effects of ocean acidification on fish larvae before we can predict even the sign of change in fish recruitment in a high-CO_2 ocean.

The survival of fish larvae represents a critical bottleneck for recruitment and fish stock development and is thus also important for commercially exploited species[1,2]. Despite the key role larval survival plays in stock recruitment, few studies have investigated the sensitivity of fish larval survival to projected ocean acidification. While survival of the larvae of Atlantic silverside and Atlantic cod decreased when exposed to ~1,100 µatm pCO_2, no effect was detected in the larvae of yellowtail kingfish and summer flounder at ~880 µatm and ~4,700 µatm pCO_2, respectively[3–5]. Notwithstanding these direct CO_2 responses, next to nothing is known about ocean-acidification effects on fish larval survival in a pelagic food web context. In benthic communities, altered competitive dynamics under ocean acidification led to changes in food web productivity and ecosystem shifts[6,7], highlighting the importance of accounting for trophic interactions in ocean change biology. The most prominent and consistent alteration in pelagic communities exposed to elevated CO_2 is the stimulation of eukaryotic picophytoplankton[8,9]. Increased growth and biomass of picophytoplankton at the expense of larger phytoplankton speeds up the microbial loop and shifts primary production away from efficient transfer to higher trophic levels up to fish[9]. CO_2 stimulation of picoeukaryotes also occurred during this mesocosm study[10], making it an ideal test bed for examining the combined direct physiological and indirect food web effects of ocean acidification on fish larval survival.

The present study was part of a large-scale mesocosm experiment in which a fully functional pelagic ecosystem (organism size <3 mm) was enclosed and exposed to projected end-of-the-century CO_2 levels. Ten mesocosms (~50 m^3 each) were deployed in the Gullmarsfjord on the west coast of Sweden (Supplementary Fig. 1), five of which were left untreated as controls (~380 µatm pCO_2) and the remaining five were set to elevated CO_2 levels (~760 µatm pCO_2; between the Intergovernmental Panel on Climate Change's representative concentration pathways 6.0 and 8.5; ref. [11]). The experiment lasted for 113 days, from 7 March to 28 June 2013, and the enclosed water column was sampled regularly for a comprehensive set of physical, chemical and biological parameters[10]. Fertilized herring eggs were added to all mesocosms during the onset of a phytoplankton bloom on 22 April, after fertilization of the eggs on 18 April (Fig. 1). Fertilization was performed under treatment conditions, whereas the first four days of egg development happened at ambient conditions before the eggs were moved to a specific treatment. During embryonic development (from 4 days post-fertilization onwards) and from hatch on 11 May until final sampling on 21 June (41 days post-hatch; DPH), the herring larvae lived in the mesocosms (see the video in ref. [12]) and fed exclusively on the enclosed community. Prey abundances in the mesocosms[13] were similar to other nursery areas of Atlantic herring, such as the Kiel Fjord[14]. Survival rates of herring larvae were calculated based on the initial number of hatched larvae, dead larvae collected in the sediment traps over time, living larvae collected during the experiment and survivors at the end of the experiment. Since only a few larvae were caught alive during the experiment, the survival rates for certain time points mainly represent the relationship between the cumulative number of dead larvae from the sediment trap until this day and the number of hatched larvae at the start of the experiment. It is assumed that all dead fish ended up in the sediment trap because no fish larvae predator was present. Before 25 May, 14 DPH, the dense sediment material and small larval sizes made visual detection unreliable; therefore, larval abundance for 25 May was back-calculated from the abundance of larvae collected dead and alive during the remainder of the experiment. Herring larval survival was split into two phases, differing in mortality over time

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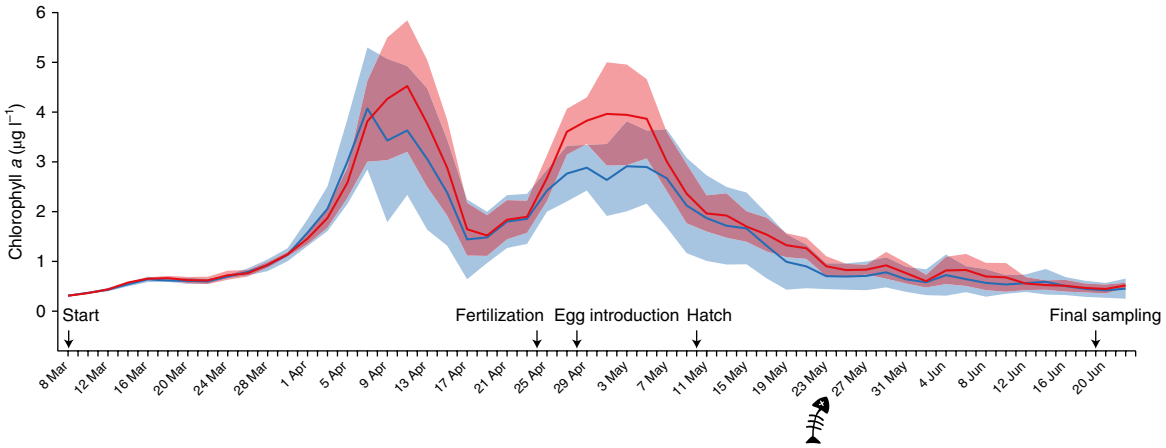

Fig. 1 | Chronology of major events during the experiment. Mean chlorophyll *a* concentration over time (blue and red colours depict ambient (five replicates) and high CO_2 levels (five replicates), respectively) and dates of introduction, hatch and final sampling of the herring larvae. The shaded area depicts the s.d. around the mean (five data points per treatment every second day). The fish bone depicts the start of every-second-day counting of dead larvae detected in the sedimented matter.

(Fig. 2). The first phase (P1) lasted for 16 DPH until 27 May, covering the larvae's critical first feeding period[2,15], and was characterized by high mortality. The second phase (P2), with comparatively low mortality, lasted from 27 May until 21 June, the last day of sampling for fish larvae.

Results and discussion

In contrast with our expectation, herring larvae experienced on average 19 ± 2% higher survival under elevated CO_2 levels compared with the controls (Cox proportional hazards model[16]: $P < 0.001$, hazard value (E) = 0.81, s.e. = 0.02) (Fig. 2). At the end of the experiment, significantly more larvae had survived in the elevated CO_2 treatment (3.2 ± 1.5%) compared with the ambient CO_2 treatment (1.2 ± 1.0%) (t-test: $P < 0.05$, $t = 2.45$, d.f. = 7.08). This significant difference in survival between CO_2 treatments developed mostly during P1 and thus in the first days after hatch (t-test: $P < 0.05$, $t = 2.53$, d.f. = 7.97).

The current literature suggests that herring larvae are either robust or negatively affected by CO_2 levels >900 µatm[17–21], thus a direct positive effect of elevated CO_2 on herring larval survival seems unintuitive. To elucidate whether food web effects were responsible for the difference in larval survival, we analysed plankton community stocks and production rates. Chlorophyll *a*, a proxy of phytoplankton biomass, as well as primary production were increased under elevated CO_2 conditions[10,22] (Fig. 1). This also stimulated secondary production as depicted by an increased abundance of nauplii, copepodites and adult copepods in the high CO_2 treatment[23,24] (Fig. 2b,c). A positive effect of increased food availability on larval survival is indicated by a significant correlation with prey abundances (that is, particles in the size range 100–300 µm), as well as the sum of nauplii and copepodite abundances during P1 of larval development (Fig. 3 and Supplementary Table 1). Microzooplankton such as ciliates are another important food source for herring larvae[25]. However, in the presented mesocosm study, no correlation between microzooplankton and larval survival was found, probably because microzooplankton was not affected by elevated CO_2, but was top-down controlled by copepods[26]. During P2, survival was similar in both treatments and no correlation between survival and prey abundance was detectable (Supplementary Table 1). Aside from prey abundance, CO_2-induced changes in food quality[27] could also have contributed to higher survival rates under elevated CO_2 conditions. However, the essential fatty acid composition (docosahexaenoic acid and eicosapentaenoic acid) of the surviving herring larvae showed no significant differences between treatments (Supplementary Fig. 2), discounting changes in food quality as the primary CO_2 effect on larval survival.

The first days after hatch of the herring larvae mark a critical phase in their development because a sufficient abundance of suitable prey items is needed to initiate successful feeding[2]. The CO_2-induced stimulation of primary and, consequently, secondary production appears to have improved the food supply for herring larvae during this early life stage. The decline in the abundance of nauplii and copepodites during P1 and of copepodites and adult copepods during P2 (Fig. 2b,c) probably reflects grazing loss due to herring larvae feeding and the size switch of developing herring larvae from smaller (P1) to larger prey items (P2)[28]. Top-down control by herring larvae on their prey items may also explain why no significant correlations between survival and prey abundances were found at later time points in the experiment.

A positive, bottom-up effect of elevated CO_2, from primary to secondary producers and from secondary producers to secondary consumers, has been shown before for benthic fish[7]. Elevated food availability was also found to compensate for negative ocean-acidification effects in invertebrates[29]. The study presented here shows that ocean acidification has the potential to improve the food supply higher up the food web. Ocean acidification has generally been found to stimulate primarily picophytoplankton (0.2–2.0 µm), accelerating the microbial loop and channelling primary production away from higher trophic levels[10]. Also in this study, picoeukaryotic phytoplankton showed a positive CO_2 response at multiple stages of the succession (see also ref. [30]). Similarly, positive CO_2 effects occurred in the nano- and microplankton size range, primarily in diatoms, when biomass build-up was supported by remineralized nutrients[30]. This bloom event preceded the start of larval feeding by about 10 days, which may be sufficient time for the CO_2-stimulated production signal to be transferred to mesozooplankton early life stages (the preferred prey of early-stage herring larvae). Thus, aside from increased prey availability, the timing of the plankton communities' CO_2 response may also have been critical for its effect on larval survival.

Despite the positive turnout for the herring larvae under high CO_2 conditions, the findings of this study should not be extrapolated to imply a bright future for fish recruitment in an acidifying ocean. Whereas herring larvae were shown to be tolerant to CO_2 levels projected for the end of this century[21], larval survival in other fish species, including the Atlantic cod *Gadus morhua*, is negatively

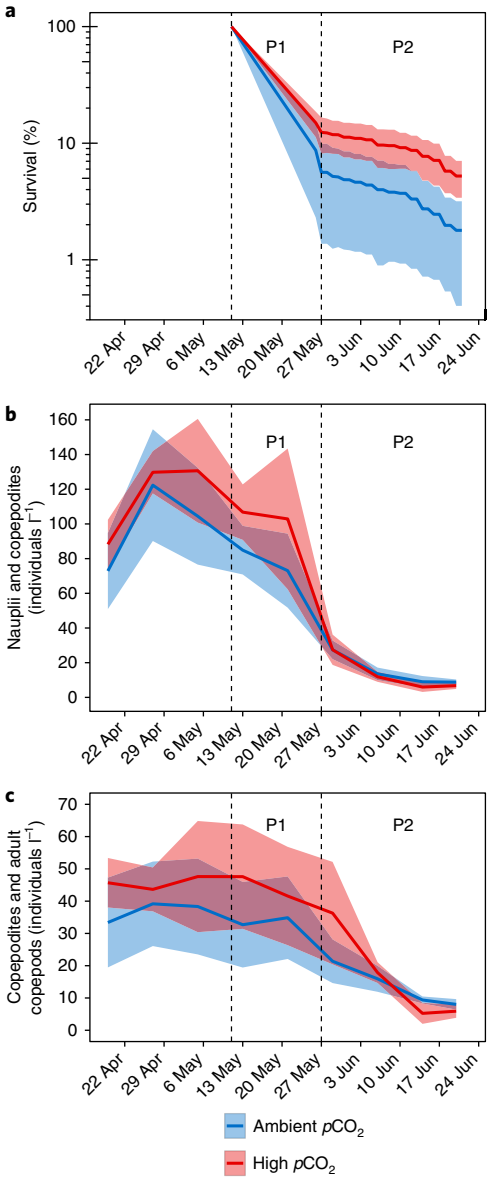

Fig. 2 | Development over time in ambient and high CO_2 treatments. **a**, Herring larval survival. **b**, The sum of nauplii and copepodite abundances, relating to particle sizes of 100–300 µm, which represents the main prey of herring larvae in P1. **c**, The sum of copepodite and adult copepod abundances, relating to particle sizes of 300–800 µm, which represents the main prey of herring larvae in P2. Blue represents ambient CO_2 and red high CO_2 (five replicates each). The shaded area depicts the s.d. around the mean. Dashed lines separate the two phases of survival, with P1 and P2 relating to the time of high and comparatively low larval mortality, respectively.

affected under projected ocean-acidification scenarios[5,31–33]. Also, biodiversity of fish may be affected, as shown at natural volcanic vents, where changes in food availability and predation have benefitted dominant fish species[34]. Whether a positive CO_2 effect on food supply can compensate for the negative effect of ocean acidification on larval physiology remains to be seen. Clearly, these considerations emphasize the need for further community-level studies to test the combined physiological and trophic effects of ocean acidification on fish larval survival. This information will be critical in developing and implementing ecosystem and fisheries management strategies to mitigate climate change impacts.

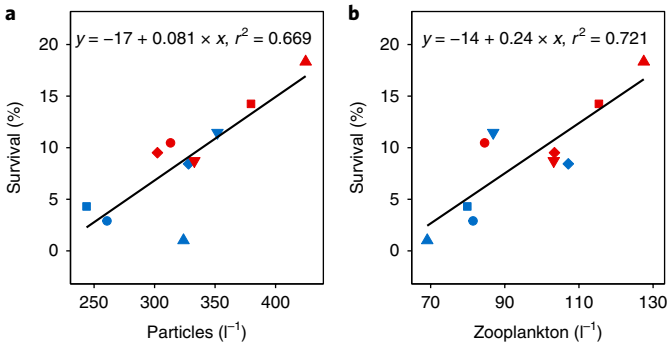

Fig. 3 | Relationship between larval survival and the abundance of food items in the ten mesocosms. a,**b**, Survival in P1 (11–27 May) versus the concentration of particles in the size range 100–300 µm (**a**) and the concentration of nauplii and copepodites (**b**) on 13 May. Blue and red colours depict individual mesocosms of ambient and high CO_2 levels, respectively.

Methods

Experimental set-up. The mesocosm CO_2 enrichment experiment took place from 7 March until 28 June 2013 in Gullmarsfjord, a sill fjord located on the Swedish west coast (58.26635° N, 11.47832° E). The endemic plankton community from Gullmarsfjord was enclosed in 10 mesocosms[35] and the development was monitored for 113 days. Each mesocosm consisted of a floating frame holding a translucent polyurethane bag 2 m in diameter and 17 m in length, with a conical sediment trap of 2 m length attached at the bottom, yielding an enclosure volume of ~50 m^3. CO_2 treatment levels were set to ambient and elevated conditions (~380 and ~760 µatm CO_2, respectively), with each treatment replicated 5 times. Regular sampling every two days was conducted for various parameters; for example, phytoplankton biomass, primary production and carbonate chemistry. For further details of the study; for example, CO_2 manipulation and community responses, see ref. [10]. The chronology of major events related to the development of fish larvae in the mesocosms, such as the introduction of eggs, hatch and final sampling, is shown in Fig. 1.

Fertile herring were caught using a gillnet at a depth of ~30 m on 22 April 2013 in the Oslo Fjord, south off Søndre Kaholmen, in collaboration with the Biological Station Drøbak (University of Oslo). To allow for genetic variation, the sticky eggs of 5 females were strip-spawned on each of 20 plastic plates and gently mixed with the sperm of 5 males, resulting in 2,262 ± 757 fertilized eggs per plate. Fertilization was performed in the laboratory at two CO_2 levels (ambient CO_2: ~470 µatm; and high CO_2: ~900 µatm), similar to the CO_2 levels in the mesocosms at that time[10], to allow investigation of the possible effect of CO_2 on fertilization success and sperm motility. Before introduction into the mesocosms, egg plates were kept in a flow-through tank with seawater at ambient (~470 µatm) CO_2 levels for 4 days, to synchronize the time of hatching[17] (F. Dahlke, personal communication).

Animal welfare was assured by performing the experiment according to the ethical permission (number 332–2012) issued by the Swedish Board of Agriculture 'Jordbruksverket'). To minimize stress, specimens were anaesthetized using MS-222 before handling and fixation. The species used (*C. harengus*) is not endangered and was obtained from a local registered and licensed fisherman (license ID = 977 224 357).

On 26 April, each mesocosm received two of the egg plates with, on average, 4,523 ± 528 eggs. The egg plates were kept in 'egg cages'—spherical mesh-cages that allowed for a protected environment with optimal water exchange. The egg cages were kept at a depth of 3 m until 1 May then 6 m until 12 May to save the eggs from wave action while preventing changes in abiotic variables such as temperature, CO_2 and salinity[10]. To check on development and estimate the time of hatching, the egg cages were briefly lifted out of the water every two days for all mesocosms. The time of peak hatch, 0 DPH, was estimated for 11 May based on optical inspection. The hatched larvae were allowed to swim directly from the egg cages into the surrounding mesocosms. The initial number of hatched larvae (mean: 1,608 ± 237 larvae $mesocosm^{-1}$) was calculated by comparing the abundances of eggs counted from photographs of each egg plate after fertilization and after hatch. The few detached eggs and dead larvae in the egg cages were counted and subtracted from the numbers of hatched larvae.

Abiotic factors, such as salinity, temperature and oxygen concentration inside the mesocosms, were measured every two days with a conductivity–temperature–density probe (Sea and Sun Technologies) and were close to the natural conditions surrounding the mesocosms. Temperature fluctuated between 8.5 and 11.6 °C (11 May to 8 June), followed by an increase in temperature to 15.5 °C on 21 June. The mean oxygen concentration for all mesocosms was relatively stable at ~100 µmol kg^{-1} (A. Ludwig, unpublished observation), whereas the mean salinity of

all mesocosms slightly increased due to evaporation, from 29.3 at hatch to 29.4 at final sampling[10].

Sampling. Since herring larvae could not be caught in the Apstein nets used for zooplankton (as described below), additional larval sampling was performed using light traps (BellaMare), taking advantage of the positive phototactic behaviour of the larvae. In total, <70 specimens per mesocosm were removed during the experiment using light traps. The larvae sampled by light traps were used to gain information on herring larval growth, which will be shown and discussed in detail in a separate manuscript. Sampled larvae were accounted for in the calculation of larval survival, as described in the section 'Statistical analysis'. Survivors were sampled on 21 June (41 DPH) (Fig. 1) by carefully pulling a ring-net of 1,000 µm mesh size through the full length of the enclosed water column, thereby sampling all remaining fish larvae from the mesocosms. For this purpose, the net was attached to a 'cleaning ring', which was used to wipe the inner side of the mesocosms and thus had exactly the same diameter as the mesocosm bags[35]. The net was lowered in a folded manner so that fish larvae were not caught on the way down. By pulling a rope at the deepest position of the ring (the last segment of the bag above the sediment trap), the net unfolded with the same diameter as the cleaning ring so that no fish could escape when it was pulled upwards. Fish larvae were prevented from escaping into the sediment trap by releasing air bubbles at the lowest part of the trap via the sediment sampling tube. This was verified through visual inspection of the sediment trap by lowering an underwater camera connected to a monitor.

Sedimented matter was retrieved every 2 days following an established procedure[36] and was visually inspected in rectangular black trays (70 cm × 50 cm × 10 cm) before regular sediment processing. The material was gently screened with forceps and dead larvae were collected. The first sighting of dead larvae in the sediment material was on 25 May (14 DPH), depicted by the fish bone in Fig. 1. Before 14 DPH, the dense sediment material and small larval sizes made visual detection unreliable. It was assumed that all dead fish ended up in the sediment trap because no effective fish larvae predator was present. The small sizes of the hydromedusae occurring in the mesocosm and no detection of predation of these on the herring larvae[37] supported this assumption. All larvae classified as dead or alive were incorporated within the survival analysis. The number of dead larvae before 25 May (X)—that is, the time when dead larvae were first detected in the sedimented material—was determined indirectly by the difference between the number of hatched larvae (H), the number of survivors at the end (E), the sum of larvae sampled alive (A) and the sum of dead larvae from the sediment between 25 May and the end of the experiment (D):

$$X = H - (E + A + D).$$

Here, X represents the sum of dead larvae between 11 May and 25 May and thus cannot be assigned to specific sampling days. For the statistical analysis, 25 May was set as the sampling day for this sum of dead larvae (X).

To assess the influence of prey abundances on larval survival, zooplankton samples from each mesocosm were collected every eight days. The preferred prey of the herring larvae, that is, from various life stages of copepods (nauplii, copepodites and adult copepods), was quantified using an Apstein net (mesh size: 55 µm; diameter 17 cm). The majority (>90%) of the adult copepods belonged to the species *Pseudocalanus acuspes*[23]. Particle abundances of the different size classes were obtained via an image-based analysis of plankton samples (the 'ZooScan method'[38]), where a subsample from the regular zooplankton net hauls was scanned using a flatbed scanner and automatically categorized and size measured. Prey size spectra, in terms of particle size, between 100 and 300 µm were considered for P1 and those of between 300 and 800 µm were considered for P2. These assumptions are based on prey size spectra in relation to herring larval standard length[39]. In terms of zooplankton groups, the abundance of copepod nauplii and copepodites was included for P1, whereas copepodites and adult copepods were considered as prey in P2 (ref. [28]). Due to the dominance of copepod species to the zooplankton community, other prey items are likely to have contributed minimally to the fish larval diet. Additional correlative analyses between smaller size classes of prey (ciliates) and fish larval survival did not improve the relationship.

Statistical analysis. We applied a Cox proportional hazards model[16] for the survival analysis over the whole period of the experiment. We calculated survival curves for the two treatments using the Kaplan–Meier estimator, which is a non-parametric statistic that includes censored (incomplete) observations. These censored observations allow the inclusion of fish for which there was incomplete information on survival (for example, because they were not dead at the end of the study or because they were sampled before it had ended). Survival curves for the two treatments, each containing five replicates/mesocosms, were analysed for significant differences ($P < 0.05$). The given hazard value 'E' represents the risk of a treatment group dying relative to a control group; for example, a value of $E = 0.8$ for the treatment group would imply a 20% higher mean survival than the control group. For the survival analysis of the two separate phases, the survival at the end of the respective phase was calculated and checked for significance using a Welch two-sampled t-test. The same values were used to check for Pearson's product-moment correlation between survival and particle abundances in the respective phases. For all statistical tests, a P value of 0.05 was considered the threshold of significance.

Life Sciences Reporting Summary. Further information on experimental design is available in the Life Sciences Reporting Summary.

Data availability. Data generated during this study are deposited in the PANGEA database (https://doi.pangaea.de/10.1594/PANGAEA.882406).

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Author contributions

M.S., U.R. and C.C. designed the experiment. M.S., M.H.S., F.J., L.T.B., M.A.-M., U.R. and C.C. performed the experiment. M.S. performed the survival analysis. M.A.-M. performed the zooplankton analysis. J.T. performed the particle analysis. L.T.B. performed the chlorophyll *a* analysis. M.S. and C.C. analysed the data. M.S., C.C. and U.R. wrote the paper. All authors discussed the results and implications, and commented on the manuscript at all stages.

Competing interests

The authors declare no competing interests.

Additional information

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Experimental design

1. Sample size

Describe how sample size was determined.

The sample size for the mesocosms was determined by the availability of these large floating mesocosms (55000m3). From the total number of 10 being avialable, 5 were used for control and 5 were used for high CO2 treatments. For the chlorophyll data, samples were taken from each mesocosm every 2 days to be able to follow the developmental patterns. Zooplankton samples were taken every 8 days from each mesocosm. A more intense sampling scheme was not possible, since it would have affected the mass balance determinations from other experiments connected to this study too much.
Numbers of fish eggs were calculated based on estimated survival rates with the aim of having 50 -100 herring larvae surviving at the end of the experiment.

2. Data exclusions

Describe any data exclusions.

No data were excluded from the analyses

3. Replication

Describe whether the experimental findings were reliably reproduced.

The experimental setup using 10 mesocosms and two treatments led to 5 replicates for all parameters analysed.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

The mesocosm were randomly distributed in the study area in the fjord. The striped spawned herring egg from the different parents were randomly distributed on each of the egg plates allowing for a random distribution of the larvae in the mesocosms .

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Blinding was not possible, since CO2 manipulation of selected mesocosms was needed.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed
☐	☒ The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☐	☒ A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
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☒	☐ A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒ The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
☐	☒ A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☐	☒ Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.

All statistical analyses were run in the programs R (Version 3.3.2) (R Core Team (2016). R: A language and environmental for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org) and RStudio (Version 1.0.136) (RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA, USA, www.rstudio.com). Graphics were done in the R package ggplot2 (H.Wickham. ggplot2: Elegant Graphics for Data Analysis. Springer Verlag New York, 2009).

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

There are no restrictions on material availability

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

No cell lines were used.

b. Describe the method of cell line authentication used.

Describe the authentication procedures for each cell line used OR declare that none of the cell lines used have been authenticated OR state that no eukaryotic cell lines were used.

c. Report whether the cell lines were tested for mycoplasma contamination.

Confirm that all cell lines tested negative for mycoplasma contamination OR describe the results of the testing for mycoplasma contamination OR declare that the cell lines were not tested for mycoplasma contamination OR state that no eukaryotic cell lines were used.

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.

Provide a rationale for the use of commonly misidentified cell lines OR state that no commonly misidentified cell lines were used.

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

The brood stock herring originated from the Oslo-Fjord close to the Biological Station Drøbak, University of Oslo and were caught using a gillnet on April, 22nd 2013 at a depth of ~30m, at the southern tip of Søndre Kaholmen, roughly located at 59°40'29" N and 10°36'22" E. The dead ready-to-spawn herring were transported on ice to the Sven Lovén Centre, where fertilization was performed four hours later.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

There was no human research participation.

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