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Risk maps for Antarctic krill under projected Southern Ocean acidification

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Marine ecosystems of the Southern Ocean are particularly vulnerable to ocean acidification[1]. Antarctic krill (*Euphausia superba*; hereafter krill) is the key pelagic species of the region and its largest fishery resource[2]. There is therefore concern about the combined effects of climate change, ocean acidification and an expanding fishery on krill and ultimately, their dependent predators—whales, seals and penguins[3,4]. However, little is known about the sensitivity of krill to ocean acidification. Juvenile and adult krill are already exposed to variable seawater carbonate chemistry because they occupy a range of habitats and migrate both vertically and horizontally on a daily and seasonal basis[5]. Moreover, krill eggs sink from the surface to hatch at 700–1,000 m (ref. 6), where the carbon dioxide partial pressure (p_{CO_2}) in sea water is already greater than it is in the atmosphere[7]. Krill eggs sink passively and so cannot avoid these conditions. Here we describe the sensitivity of krill egg hatch rates to increased CO_2, and present a circumpolar risk map of krill hatching success under projected p_{CO_2} levels. We find that important krill habitats of the Weddell Sea and the Haakon VII Sea to the east are likely to become high-risk areas for krill recruitment within a century. Furthermore, unless CO_2 emissions are mitigated, the Southern Ocean krill population could collapse by 2300 with dire consequences for the entire ecosystem.

To assess the sensitivity of krill embryonic development to ocean acidification, we experimentally exposed krill eggs to elevated seawater CO_2 levels (see Methods). Hatch rates were similar for krill eggs spawned at 380 and 1,000 µatm p_{CO_2}, but were significantly lower in the 1,250 µatm p_{CO_2} treatment. Hatch rates were roughly 20% of control levels at 1,500 µatm p_{CO_2} and almost no hatching was observed at 1,750 and 2,000 µatm p_{CO_2} (Fig. 1). Increased levels of CO_2 in the sea water also delayed embryonic development. At 8 days, embryos that had not hatched but were still alive had developed to mid limb-bud stage in the 1,250 and 1,500 µatm p_{CO_2} exposures but only to the late gastrula or early limb-bud stages in the 1,750 and 2,000 µatm p_{CO_2} exposures.

Exposure of embryos to 1,750 µatm p_{CO_2} during the first 3 days following spawning either completely inhibited hatching or substantially reduced hatching rates irrespective of the subsequent p_{CO_2} levels that they were reared in. Embryos that were transferred from 1,750 to 380 µatm p_{CO_2} after 3 days had similarly low hatch rates to those that remained at 1,750 µatm p_{CO_2} (Fig. 2). Embryos raised at 380 µatm p_{CO_2} for the first 3 days and then incubated at 1,750 µatm p_{CO_2} had a mean hatch rate of 0.65; the control treatment

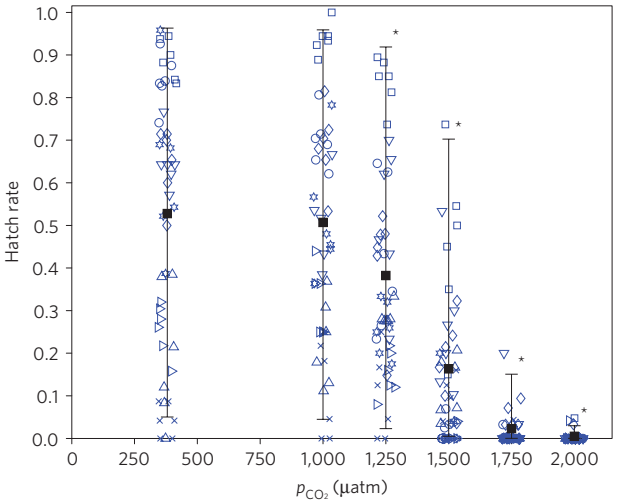

Figure 1 | Observed (open symbols) and modelled mean (black squares) krill egg hatch rates at six experimental p_{CO_2} levels. Differences in open symbols indicate different egg batches (8 in total). The error bars show the 95% credible intervals on the fitted means. Asterisks show hatch rates that differed from the control hatch rate (that is, a difference of zero between these two hatch rates was unlikely).

(exposed to 380 µatm p_{CO_2} throughout their development) had a mean hatch rate of 0.78. The model results showed good evidence that these two hatch rates were different (that is, a difference of zero between these two hatch rates was unlikely; mean estimated difference 0.13 with 95% credible interval 0.01–0.23). However, this reduction in hatch rate was small compared with groups exposed to 1,750 µatm p_{CO_2} for the first 3 days. The unhatched embryos in the groups exposed to 1,750 µatm p_{CO_2} for the first 3 days were mostly alive at the end of the experiment (8 days) but had developed only up to early to mid limb-bud stages. These results demonstrate a sharp decline of hatching success in seawater concentrations above 1,000 µatm p_{CO_2}, and that exposure to high CO_2 during the first 3-day period following spawning, until the late gastrula stage[6,8], significantly and irreversibly impacts embryonic development and hatch rates.

During the embryonic and larval stages, physiological regulatory mechanisms are still developing[9]. These stages are therefore thought to be more environmentally sensitive than adults[10]. Krill embryonic

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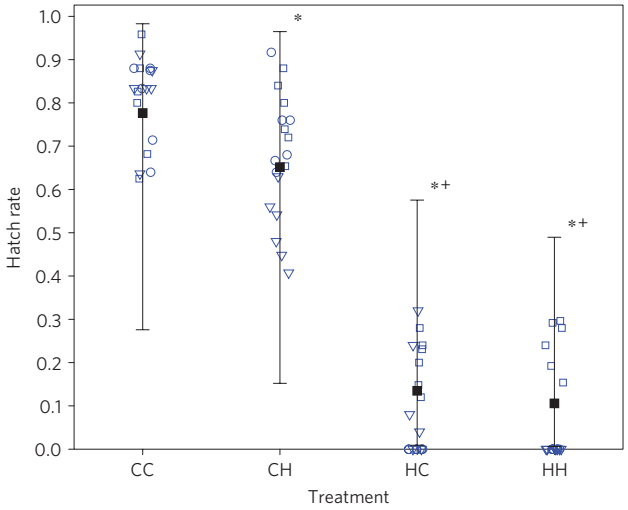

Figure 2 | Egg hatching success under different CO_2 treatments. CC, embryos reared at 380 µatm p_{CO_2} throughout an 8-day incubation period; CH, embryos reared at 380 µatm p_{CO_2} for 3 days and then exposed to 1,750 µatm p_{CO_2} for 5 subsequent days; HC, embryos reared at 1,750 µatm p_{CO_2} for 3 days and then exposed to 380 µatm p_{CO_2} for 5 subsequent days; HH, embryos reared at 1,750 µatm p_{CO_2} throughout an 8-day incubation period. Observed (open symbols) and modelled mean (black squares) hatch rates are shown. Different open symbols indicate different egg batches. The error bars show the 95% credible intervals on the fitted means. *: hatch rates that differed from the CC hatch rate; +: those that differed from CH (that is, a difference of zero between these two hatch rates was unlikely).

development has been shown to be completely interrupted at an early stage when reared in sea water at 2,000 µatm p_{CO_2} (pH 7.4; ref. 7). Our present study demonstrates that deleterious effects on embryonic development can occur in concentrations as low as 1,250 µatm p_{CO_2}. Present p_{CO_2} values at depth (~550 µatm p_{CO_2}) are already much higher than at the surface (Supplementary Fig. S1). However, krill recruitment still occurs, suggesting that embryonic development in the ocean may not be negatively affected at present CO_2 levels within their habitat[7]. Other pelagic crustaceans such as copepods were reported to be unaffected by the exposure to 2,000 µatm p_{CO_2} and exhibited reduced hatch rates only at 8,000 µatm p_{CO_2} (ref. 10).

Future seawater p_{CO_2} around the Antarctic continent could be highly heterogeneous both horizontally and vertically. Projections using a three-dimensional ocean carbon cycle model and the atmospheric CO_2 concentrations for the Representative Concentration Pathway (RCP) scenarios[11] (see Methods and Supplementary Methods for the details) show high p_{CO_2} values around the Weddell and the Haakon VII seas, off East Antarctica, and from the eastern Ross Sea to the western Antarctic Peninsula (Fig. 3 and Supplementary Fig. S1). These projections suggest that much of the present habitat for krill will be at damagingly high p_{CO_2} levels of above 1,000 µatm (Fig. 1) by 2100 under RCP 8.5 or by 2300 under RCP 6.0.

Krill lay fertilized eggs in the surface layer (0–200 m) during the austral summer season[5]. The embryos sink as they develop, then hatch out after 5–6 days at depths of 700–1,000 m (ref. 6). The larvae then swim upwards as they develop, and reach the surface some 30 days after the eggs were laid[12]. We have shown that the first 3 days following spawning is the critical period for exposure to high CO_2. Projected vertical profiles generally show relatively low p_{CO_2} levels similar to projected atmospheric CO_2 levels from the

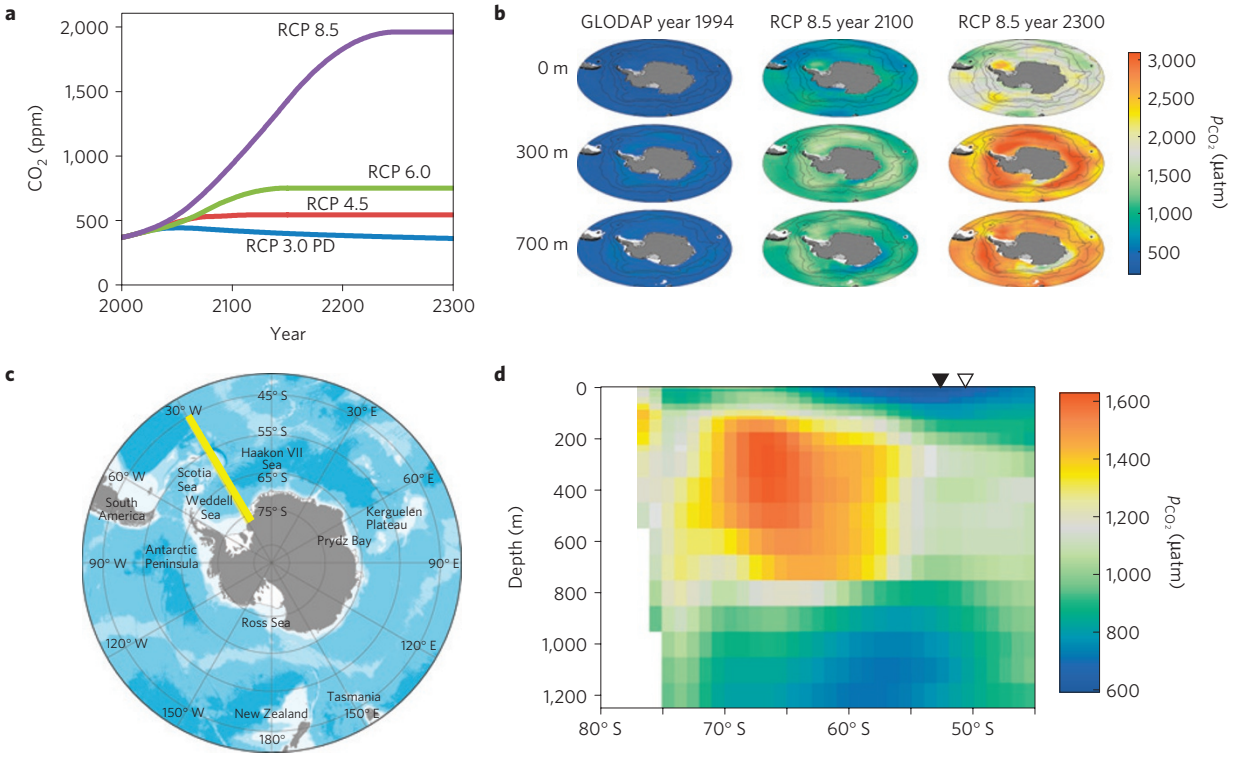

Figure 3 | Future projection of p_{CO_2} in the Southern Ocean. a, Trajectories of atmospheric CO_2 level under four RCP scenarios. **b**, Projection at different depth layers for year 1994, and years 2100 and 2300 under RCP 8.5. **c**, Map of the Southern Ocean. The bold yellow line indicates the 30° W line for which the vertical section is shown in **d**. **d**, p_{CO_2} along the 30° W section under RCP 8.5 at year 2100. The filled triangular marker denotes the position of the northern branch of the Southern Antarctic Circumpolar Current Front (approximately the northern limit of krill habitat[30]) and the open triangular marker denotes the position of the middle branch of the Polar Front.

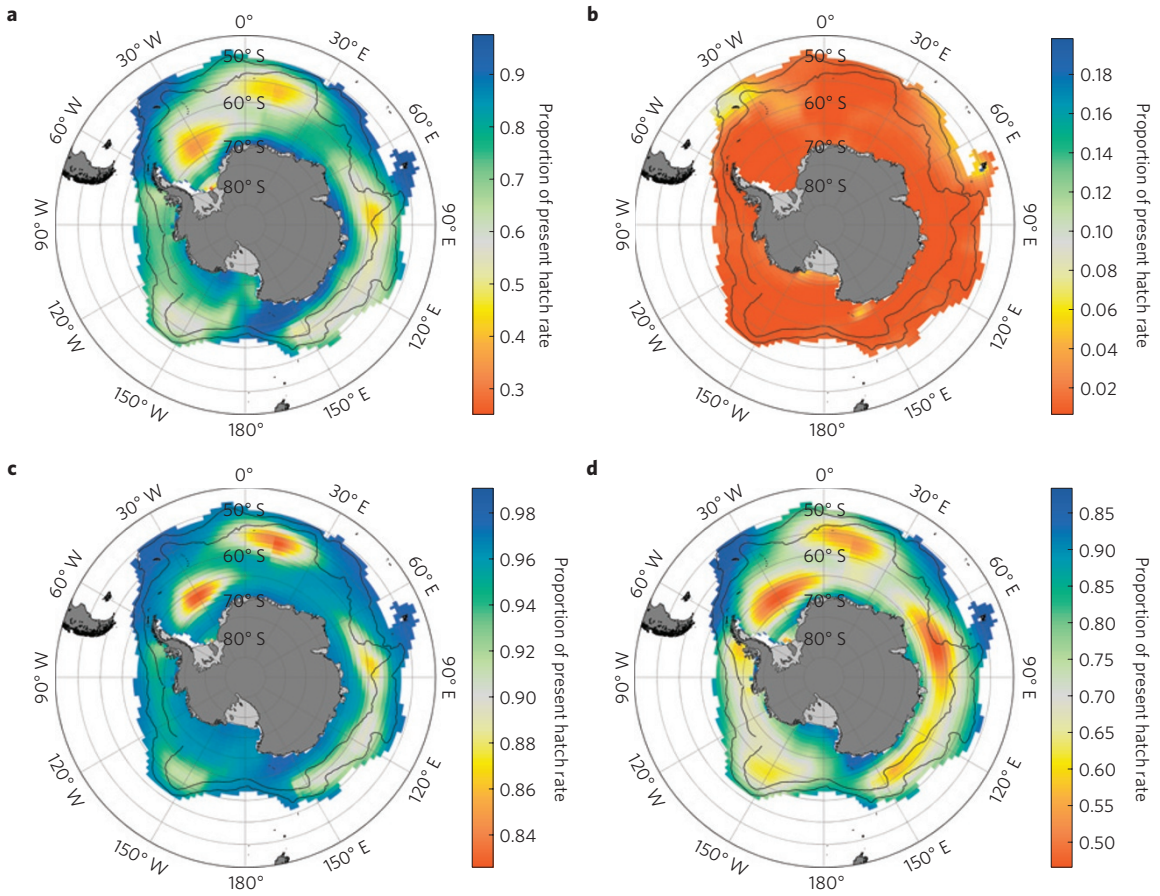

Figure 4 | Circumpolar risk maps of krill hatching success under projected future p_{CO_2} levels. **a**–**d**,Hatching success under the RCP 8.5 emission scenario for 2100 (**a**) and 2300 (**b**); and under the RCP 6.0 emission scenario for 2100 (**c**) and 2300 (**d**). Note the different colour scales on each panel. The southern-most black line shows the northern branch of the Southern Antarctic Circumpolar Current Front, and the northern-most line shows the middle branch of the Polar Front.

ocean surface down to a depth of 100 m (Fig. 3 and Supplementary Fig. S1). If krill spawn near the surface and the embryos sink slowly the embryos may experience only benign p_{CO_2} levels (that is, CO_2 levels similar to the atmosphere) for the first 3 days after spawning and hatching success might not be affected. However, this seems highly unlikely because krill embryos are reported to sink down to below 100 m within the first 12 h after spawning and to reach 1000 m before hatching[6].

We generated risk maps for the hatching success in a future acidified Southern Ocean based on p_{CO_2} projections of the water layers that krill embryos sink through during the first 3 days. The Weddell Sea and the Haakon VII Sea are identified as the first areas where krill egg hatching success is most likely to be at risk (Fig. 4). The predicted risk for the RCP 6.0 scenario (medium–high emission) is much milder compared with that for the RCP 8.5 scenario (high emission without mitigation), but still with hatching success by the year 2300 being as low as 45% of the present level. Under the RCP 4.5 and 3.0-PD scenarios, risks were minimal with reduction of less than 10% by year 2300 (Supplementary Fig. S2). Under the RCP 8.5 scenario most of krill habitat will suffer at least 20% lower hatching success by 2100, with reductions of up to 60–70% in the Weddell Sea. The entire habitat may be unsuitable for hatching by the year 2300 (Fig. 4b) and this would lead to the collapse of the krill population. The results of our study can be incorporated into existing models of the dynamics of krill populations[13] as a factor to scale recruitment success, thereby allowing assessment of regional impacts of ocean acidification on the dynamics of those populations. This approach can then be used to inform ecosystem and krill fishery management models under various carbon emission scenarios.

Hatching success is but one of the many population parameters that would be affected by ocean acidification. After 6 days of sinking, even if they successfully hatch out, krill larvae need to swim upwards through the p_{CO_2} maximum again. Any delay in their development rate or a compromised swimming performance could be fatal because they may sink to a depth where they cannot successfully swim back to the surface before exhausting their internal energy store. The exact mechanism whereby embryonic development is disrupted is yet to be clarified, but because early embryonic development does not involve calcification, the effect may be associated with hypercapnia and/or the intracellular acid–base balance becoming too extreme for protein function[14], slowing down[15] and/or causing irregular embryonic development[7], especially within the first 3 days of its development.

After hatching, krill pass through 12 larval stages, the first 3 of which are non-feeding stages when they solely rely on inherited maternal energy. During the following 9 larval stages, spanning several months, they are not able to store energy and need to continuously eat to meet their metabolic demand and to grow and develop[16]. Further, post-larval krill have been demonstrated to respond to elevated CO_2 by increasing ingestion rates, nutrient release rates and metabolic activity, reflecting enhanced energetic requirements[17]. Increased metabolic costs due to high CO_2 will be a great risk to them especially during the food-scarce winter period. Krill might acclimatize to future environmental conditions; however, their poor ionoregulatory capacity[18] suggests that krill will

face a considerable challenge in an acidifying ocean environment[14]. Unfortunately, the genetic homogeneity of krill at large spatial scales[19] indicates that rapid adaptation through natural selection of more tolerant genotypes is a rather remote possibility.

The accuracy of the risk map generated in this study relies on the ability of the model to predict the future environment as well as the wider applicability of the experimental results. Nevertheless, these maps do not account for the cumulative effects of increased CO_2 across life stages and generations. Therefore, our predictions of the time course of the population responses of these impacts may well be conservative.

The krill population is already experiencing a number of stresses due to a changing climate. Seawater temperature near the Antarctic Peninsula is rising[20]. It has been suggested that the krill population in the South Atlantic has already declined as a result of productivity changes caused by the decline in sea ice[21]. Declining sea ice cover further allows increased access to krill by predators and the fishery[22]. Ocean acidification is likely to put further pressure on the krill population. Although information is still very limited the multiple stressors are likely to impose synergistic, rather than additive, impacts on krill population.

Although various trends have been reported in the physical and chemical properties of the ocean, there is little information on the corresponding implications for the ocean's biota. This study has explored the likely impacts of ocean acidification on krill at a circumpolar scale. The data revealed that substantial declines in the viability of major populations of krill in the region may occur within the next 100 years, which is on the trajectory of change that could result in catastrophic consequences for dependent marine mammals and birds of the Southern Ocean.

Methods

The experimental population of krill was collected from the Indian Ocean sector of the Southern Ocean at 64° 09′ S, 100° 46′ E during the 2010/2011 field season. The krill were maintained in the Australian Antarctic Division's marine research aquarium, where they matured and spawned naturally[23]. Details of the experimental set-up are described in Supplementary Methods and Table S1.

Hatching experiment. Fertilized eggs were obtained in January 2012 from females that spawned in the laboratory. A total of eleven egg batches, each originating from different females, were used. Each batch was randomly distributed into experimental jars, with approximately 20–30 eggs per jar. Two types of experiment were conducted.

Detailed response of hatch rates against increasing CO_2. For eight batches of eggs, the embryos were incubated at: 380 (control), 1,000, 1,250, 1500, 1,750 and 2,000 µatm p_{CO_2}. Approximately 20–30 eggs from each batch were randomly assigned to each of the p_{CO_2} treatment levels.

Critical timing of high-CO_2 exposure. Seawater p_{CO_2} level was switched after 3 days of exposure to determine critical timings of exposure to a high CO_2 environment that significantly affects hatching success. Three batches of eggs were exposed to four different treatments: CC, 380 µatm p_{CO_2} throughout a total of 8 days (control); CH, 380 µatm p_{CO_2} for the first 3 days followed by 1,750 µatm p_{CO_2} exposure for subsequent 5 days; HC, 1,750 µatm p_{CO_2} for the first 3 days followed by 380 µatm p_{CO_2} exposure for subsequent 5 days; and HH, 1,750 µatm p_{CO_2} throughout a total of 8 days. Three days was chosen to switch treatment because that is the time when krill embryo gastrulation completes and organogenesis starts[6,8].

Hatch rates were determined for each jar 8 days after spawning on the basis of a number of studies indicating that hatching of krill embryos occurs within 5 to 6 days from spawning[6]. Even if embryos hatched after 8 days, in the wild those embryos may have already sunk out of the depth range in which they can successfully complete their developmental ascent[12]. There were 6 replicates from each batch for each treatment. Embryonic stages were classified at the end of each experiment[8].

Circumpolar p_{CO_2} projection. To estimate oceanic p_{CO_2} under the future CO_2 elevated condition, we computed oceanic p_{CO_2} using a three-dimensional ocean carbon cycle model developed for the Ocean Carbon-Cycle Model Intercomparison Project[24,25] and the projected atmospheric CO_2 concentrations. The model used, referred to as the Institute for Global Change Research model in the Ocean Carbon-Cycle Model Intercomparison Project, was developed on the basis of that used in ref. 26 for the study of vertical fluxes of particulate organic matter and calcite. It is an offline carbon cycle model using physical variables such as advection and diffusion that are given by the general circulation model.

The model was forced by the following four atmospheric CO_2 emission scenarios and their extensions to year 2300. RCP8.5: high emission without any specific climate mitigation target; RCP6.0: medium–high emission; RCP 4.5: medium–low emission; and RCP 3.0-PD: low emission[11] (see Supplementary Method for details). Simulated perturbations in dissolved inorganic carbon relative to 1994 (the Global Ocean Data Analysis Project (GLODAP) reference year) were added to the modern dissolved inorganic carbon data in the GLODAP data set[27]. To estimate oceanic p_{CO_2}, temperature and salinity from the World Ocean Atlas data set[28] and alkalinity from the GLODAP data set were assumed to be constant.

Modelling of hatch rates. Experimental hatch rates were modelled using binomial mixed models with treatment (p_{CO_2} level) as a factor and a random effect of egg batch. The models were fitted using WinBUGS 1.4.3 (ref. 29), with a burn-in of 1,000 iterations and parameter estimates obtained after a further 20,000 iterations with a thinning rate of 10. Diffuse normal priors with a mean of zero and precision of 10^{-6} were used for the treatment effects, and a diffuse gamma prior with shape and rate values of 0.001 for the random effect of batch.

Risk maps. The effect of p_{CO_2} level (380, 1,000, 1,250, 1,500, 1,750 or 2,000 µatm p_{CO_2}) on hatch rate was modelled as described above. Risk maps of predicted changes in hatch rates were based on the circumpolar p_{CO_2} projections from 0 to 400 m depth (the depth range that embryos experience in the first 3 days of their development), and the fitted treatment effects from the hatch rate model. That is, the projected p_{CO_2} values were transformed using the curve shown in Fig. 1 to obtain predicted hatch rates under the various climate change scenarios (see Supplementary Method for details).

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Author contributions

This study was initiated, designed, coordinated and analysed by S.K. Ocean carbon model projection was undertaken by A. Ishida. Experimental system was designed and assembled by R.K. Statistical modelling and analyses were undertaken by B.R. Experiments were undertaken by N.W. All authors made intellectual contribution. The manuscript was written by S.K. and edited by A. Ishida, R.K., B.R., A.C., S.N., M.W. and A. Ishimatsu.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to S.K.

Competing financial interests

The authors declare no competing financial interests.