Early life stages~~Viability~~ of fish ~~larvae~~ under ocean alkalinity enhancement in coastal plankton communities~~: from organisms to communities~~

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Abstract.

Ocean alkalinity enhancement (OAE) stands as a promising carbon dioxide removal technology. Yet, this solution to climate change entails shifts in ~~water chemistry~~environmental drivers with unknown consequences for marine fish that are critical to ecosystem health and food security. Fish and their supporting food webs may be stressed by the novel carbonate chemistry or the nutrients contained in the deployed minerals. With a mesocosm experiment on natural plankton communities, we studied early life stages of fish under alkalinity (+600 µmol kg^{-1}) and silicate (+75 µmol L^{-1}) addition. Larvae and young juveniles of temperate coastal species, including Atlantic herring (*Clupea harengus*) and cod (*Gadus morhua*), were exposed to direct physiological and indirect food web-mediated effects of OAE for 49 days. Neither in the shorter- nor in the longer-term did we find an impairment of fish growth and survival. Alkalization even led to an increase in fish biomass. ~~With a laboratory and mesocosm experiment, we show that early life stages of fish can be resistant to OAE. Neither direct physiological nor indirect food web-mediated impacts of OAE were apparent. growth and survival .~~ This resistance to OAE was despite using non-CO$_2$-equilibrated ~~OAE~~deployment ~~(ΔTA = +600 µmol kg^{-1})~~ that induces ~~strong~~more severe perturbations in carbonate chemistry (ΔpH = +0.7, pCO$_2$ = 75 µatm) compared to alternative ~~deployment~~ scenarios. ~~Still~~Overall, our ~~study across ecological scales (organism to community~~-level study~~)~~ ~~and exposure times (short- to long-term)~~ suggests that some fish populations, including key fisheries species, may be resilient to the water~~carbonate~~ chemistry changes under OAE. Whilst ~~our~~these results give cause for optimism regarding the large-scale application of OAE, other life history stages (embryos) and habitats (open ocean) may prove more vulnerable. ~~Still, our study across ecological scales (organism to community) and exposure times (short- to long-term) suggests that some fish populations, including key fisheries species, may be resilient to the carbonate chemistry changes under OAE.~~

1. Introduction

Ocean alkalinity enhancement (OAE) is being proposed as a carbon dioxide removal technology to help limit global warming to 1.5 °C (Renforth and Henderson, 2017; Rogelj et al., 2018). This ocean-based solution can be implemented through the accelerat~~ion of~~es a natural process – rock weathering – ~~by dissolving basic~~where alkaline minerals are dissolved in seawater. As alkalinity increases, so does the capacity of seawater to ~~store~~take up CO$_2$ from the atmosphere. The ~~storage~~sequestration

45 may be scalable, safe and cost-effective (Lackner, 2002). Besides ~~generating negative emission~~removing carbon to combat climate change, this approach would also counter ocean acidification that is widely recognized as major threat to marine life (Doney et al., 2020). While OAE indeed seems promising from a technological and economic perspective, an understanding of the potential environmental risks and side-effects is lacking (Gattuso et al., 2021; Nawaz et al., 2023; Bach et al., 2019). Research is needed to evaluate the ecosystem safety of OAE and guide its potential large-scale implementation.

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Biological processes are not affected by alkalinity itself but through the associated changes in various ~~it modifies~~ions and molecules ~~the carbonate system in seawater including known drivers of biological processes~~(Bach et al., 2019). Added alkalinity reduces CO_2 as carbon source for primary producers (Hansen, 2002), rises calcium carbonate saturation which

55 facilitates calcification (Renforth and Henderson, 2017) and increases pH concerning the acid-base balance of organisms (Tresguerres et al., 2020; Pörtner, 2008). Applied from stationary facilities or ships, the perturbation would initially be localized. A pH of up to 9 may be reached (Bach et al., 2019; Hartmann et al., 2023). Over ~~the~~ time~~frame of days to years~~, this 'OAE plume' would mix with surrounding water masses and absorb CO_2 from the atmosphere (equilibration), alleviating the perturbation (He and Tyka, 2023). Therefore, whilst at a global scale sequestering gigatons of CO_2 involves minor changes

60 in water chemistry (Renforth and Henderson, 2017), species communities at deployment sites could experience OAE as a stressor. In this sense, studying coastal regions is particularly relevant. They are not only most attractive economically for OAE deployment given the proximity to mineral and energy sources (He and Tyka, 2023) but also hotspots of biodiversity and ecosystem services.

Fishes are essential for the stability of coastal ecosystems and global food security (Fao, 2022). Physiological processes in fish

65 are highly sensitive to the concentrations of bicarbonate, CO_2 and H^+ (Tresguerres et al., 2020), which are all altered under OAE. To maintain homeostasis of body fluids and proper functioning of cells and tissues in variable environments, fish have evolved a sophisticated acid-base regulation (Perry and Gilmour, 2006). They are hence thought to cope well with mild changes in pH (i.e. H^+ concentration) and to be generally less sensitive than marine invertebrates (Melzner et al., 2009). Whether fishes can still compensate under scenarios of OAE that far exceed natural pH variability (Bach et al., 2019; Carstensen and Duarte,

70 2019; Hofmann et al., 2011) is, however, uncertain. There could be ~~Are there~~additional energetic costs for acid-base regulation that channel resources away from growth and reproduction~~? What are the~~ or pH thresholds beyond which physiological functions fail and threaten population viability.~~?~~

The related field of ocean acidification has taught us several lessons on the pH sensitivity of fishes. While they were mostly found to be robust to acidification, some ecosystems, species, life stages and traits were surprisingly vulnerable (Cattano et

75 al., 2018; Esbaugh, 2018; Nagelkerken and Connell, 2015). Physiological and behavioral impacts were observed related to metabolic rate, otolith calcification, sensory functioning, lateralization, swimming, foraging, predator avoidance and habitat selection. An OAE plume could entail a similarly large ~~magnitude of~~change in H^+ concentration~~–~~, albeit in the opposite direction, to that which ~~than what~~may impair fishes under end-of-century acidification (Bach et al., 2019; Hartmann et al., 2023). Unlike for global acidification, however, the exposure of fishes to OAE would be abrupt and spatially inconsistent

80 lowering the chances for phenotypic buffering and genetic adaptation (Sunday et al., 2014; Wong and Candolin, 2015; Blewett et al., 2022). An investigation into the shorter-term responses of fishes to OAE is thus needed.

OAE may prove particularly challenging for early life stages, a bottleneck for most fish populations. At the organism-level, larvae are highly sensitive to their abiotic environment (Melzner et al., 2009; Cattano et al., 2018) but lack the locomotory

capacity to avoid unfavorable water masses. This may facilitate direct physiological effects of OAE (Brownell, 1980; Parra and Yufera, 2002). At the community-level, larvae are tightly controlled by resources, competition and predation (Houde, 2008). OAE could change these food web interactions, for example via species-specific pH sensitivities, expanding calcifiers or CO_2 limited primary production, giving rise to indirect effects (Ockendon et al., 2014; Goldenberg et al., 2018). Only by combining these different ecological scales will we achieve a mechanistic understanding of impacts on larvae growth and survival and ultimately recruitment success (Fig. 1a).

Source minerals for OAE can introduce additional elements that may act as stimulators or stressors for fish. These include trace metals like iron and nickel (Morel and Price, 2003) but also macro-nutrients (Bach et al., 2019). The application of silicate minerals would, for instance, increase silicate concentrations (Si(OH)4) in seawater well above natural levels. This macro nutrient favors silicifying diatoms over other primary producers (Sarthou et al., 2005) with consequences for food web functioning (Sommer et al., 2002). On the one hand, the larger size of diatoms can make primary productivity directly accessible to copepods (Hansen et al., 1994), a primary food source for many fish larvae (Turner, 1984). On the other hand, strong silica cell walls (Pancic et al., 2019), toxic secondary metabolites (Ianora and Miralto, 2010) and low nitrogen content (Goldenberg et al., 2024) may reduce diatom palatability and nutritional value. Silicate minerals may hence cause changes at the bottom of the food web with either positive or negative knock-on effects for planktivorous fish.

Here, we study the sensitivity of early life stages of fish to OAE-induced increases in alkalinity and silicate. coastal fish larvae to OAE at both the organism- and community-level (Fig. 1). In temperate Western Norway, we employed two contrasting experimental approaches during the main spawning season in spring. First, in a controlled laboratory setting, we examined direct physiological effects on a major fisheries species, Atlantic herring (*Clupea harengus*) (Fao, 2022). Second, with large-scale mesocosms, we assessed the viability of a fish assemblage in the presence of indirect effects mediated via the plankton food web. Direct physiological as well as indirect food web-mediated effects were considered (Fig. 1a). For this, large-scale mesocosms were employed in coastal waters of temperate Western Norway during the main spawning season in spring. They enclosed natural plankton communities including larvae and young juveniles of major fisheries species such as Atlantic herring (*Clupea harengus*) and Atlantic cod (*Gadus morhua*) (Fao, 2022). Alkalinity was applied . nNon-CO_2-equilibrated OAE was appliewithd up to 600 µmol kg^{-1} of added alkalinity (Fig. 1), entailing strong perturbations in pH_T (increase by 0.7 units) and pCO_2 (decrease by 325 µatm) (Fig. 1c). A calcium-based mineral treatment served as baseline to establish the effects of extreme silicate availability (Fig. 1d). This intense yet realistic employment scenario (Bach et al., 2019; Hartmann et al., 2023; Renforth and Henderson, 2017) may reveal the maximum impact potential of OAE and facilitate the identification of response pathways in fish. Our findings on the resilience of fish larvae help establish an environmentally safe operating space of OAE for carbon dioxide removal.

(a) **Organism-level — Laboratory**

(b) **Community-level — Mesocosm**

Conceptual design

- model species in isolation (herring)
- controlled conditions in homogenious habitat
- direct effects only (food standardized)

- multiple, interacting fish species
- variable environment and depth layers (e.g. temperature, light, prey)
- direct and indirect effects via natural food web

growth & survival

physiology   behaviour

acid-base balance

OAE
pH stress

0.5 m (0.4 m³)

→ direct effects
- - → indirect effects
→ responses measured
in this study

growth & survival

predation & competition

OAE

pH stress

resources

CO_2 limitation & biomineralisation

20 m (60 m³)

Experimental design

OAE [ΔTA µmol kg⁻¹]

0   **600**

Ca

Ca

Ca

Mineral

OAE [ΔTA µmol kg⁻¹]

0   **150**   **300**   **450**   **600**

Ca

Mineral

Si

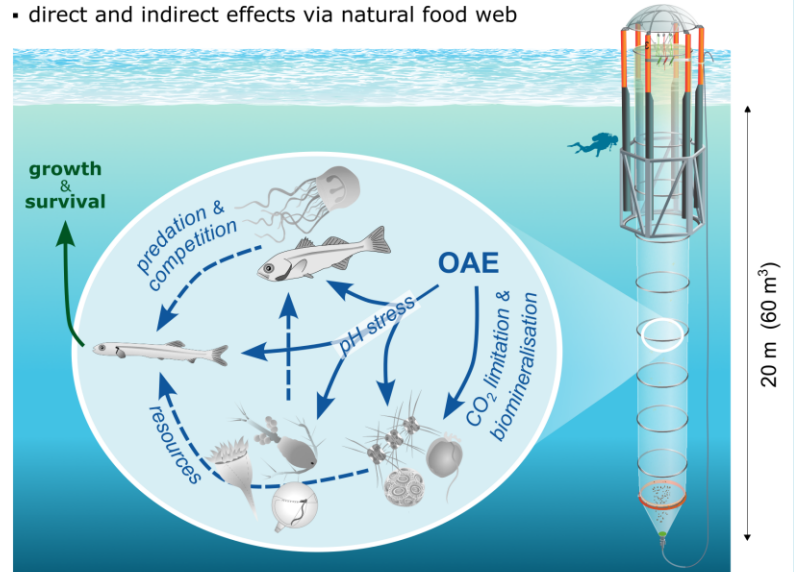
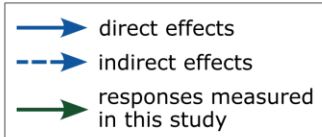
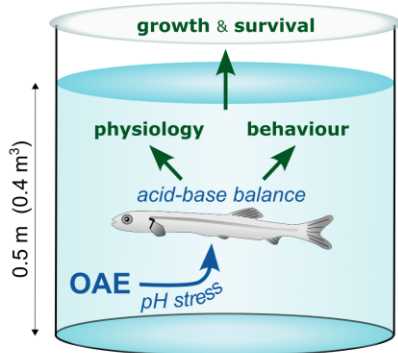
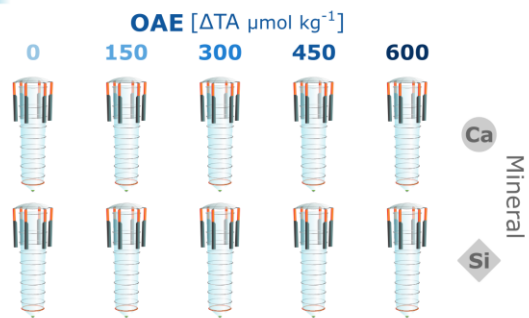
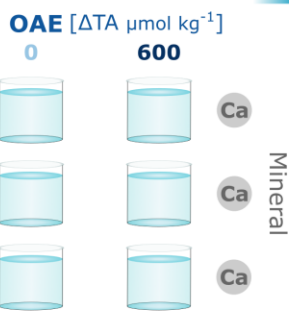
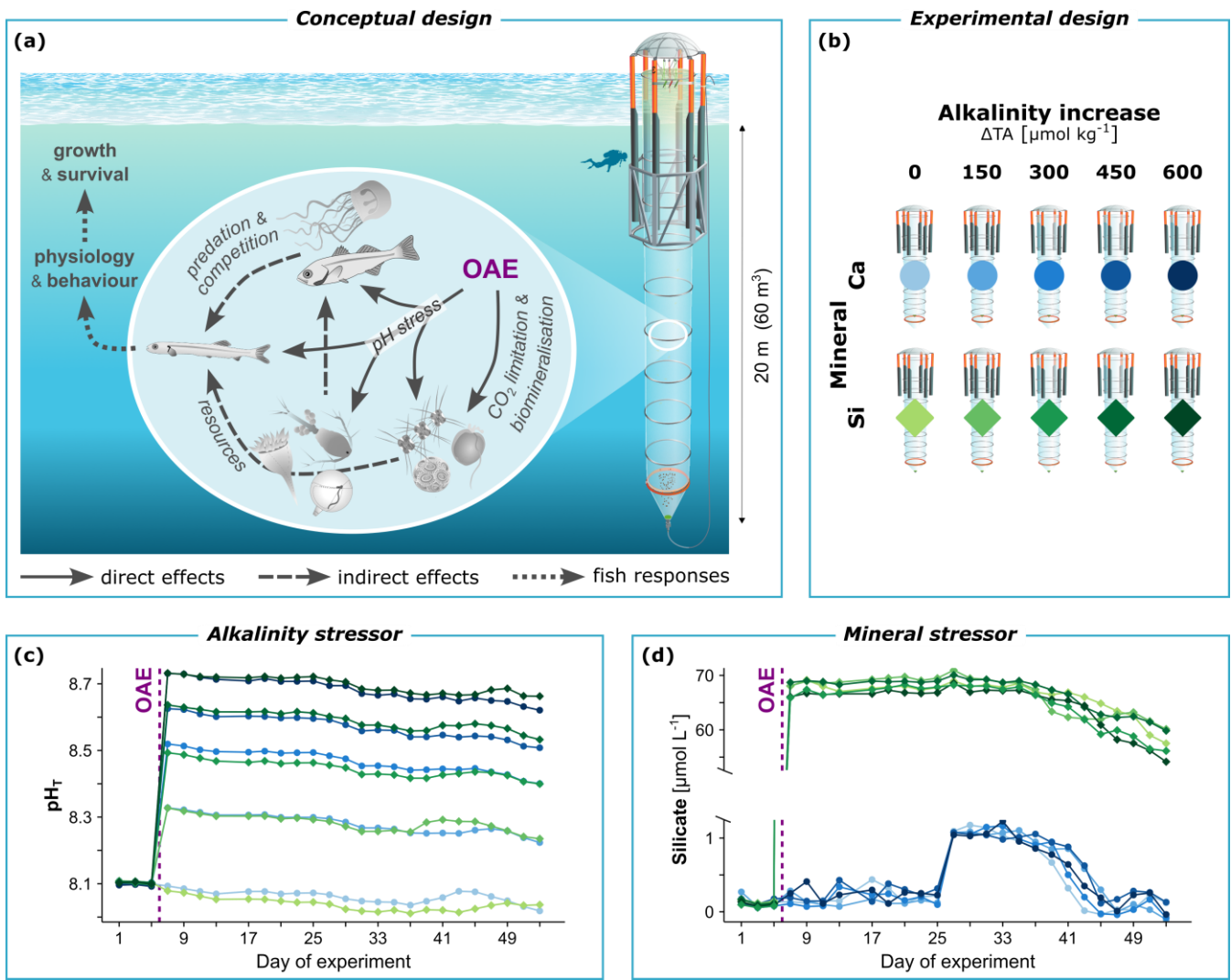



Figure 1: Conceptual and methodological framework of our mesocosm study on non-CO$_2$ equilibrated OAE. **a)** Potential pathways of change in fish in natural plankton communities. **b)** Water chemistry manipulations to simulate different scenarios of OAE. Using 10 mesocosm units, we tested increases in total alkalinity (ΔTA) under calcium-based (Ca) or silicate-based (Si) mineral addition. **c)** OAE-induced shifts in pH and **d)** silicate availability, as measured in each mesocosm throughout the experimental period. ~~OAE could affect fish larvae at different levels of ecological complexity. We address these by combining a laboratory **(a)** and mesocosm **(b)** experiment. The focus is on pure alkalinity as driver of biology during OAE, independent of the mineral used (Ca: calcium based, Si: silicate based).~~ Mesocosm symbol from Rita Erven, GEOMAR, and organism symbols partly from Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

2 Methods

2.1 Study system

~~Experiments~~ The experiment took place ~~in 2022 at the University of Bergen (laboratory) and the nearby Espegrend Marine Station~~ in Raunefjord ~~(mesocosm)~~ near Bergen, Norway (60°15'55" N, 5°12'21" E). This ~~is a~~ temperate mesotrophic region ~~is (60 °N)~~ characterized by a seasonal plankton succession with both calcifying and silicifying primary producers (Paulino et al., 2018). Here, spawning in many fish species coincides with the spring bloom. The subsequent survival of larvae and their growth into juveniles is vital for a balanced ecosystem and profitable fisheries. We studied the local assemblage of planktonic

larvae, comprised of various demersal and pelagic fish species. A particular focus was put on Atlantic herring. This small pelagic fish supports the largest fishery in Norway and the fourth largest in the world with an annual yield of ~1.7 Mt (Fao, 2022). As such, it holds a key role as trophic intermediary in transferring energy from zooplankton to larger predators (Toresen et al., 2019). Herring larvae had served us as model organisms during past laboratory (Sswat et al., 2018a; Maneja et al., 2015) and mesocosm work have proven on ocean acidification (Spisla et al., 2022; Sswat et al., 2018b). These studies suggested a certain tolerance of herring to pH decreases that already impacted larvae of other species such as cod (Stiasny et al., 2016).

to be ideal model organisms for the study of human impacts (Sswat et al., 2018a). 2.3.1 Experimental setup

Our second approach studied a fish assemblage of multiple species under close to natural conditions (Fig. 1b). As part of plankton communities in mesocosms, larvae were not only exposed to potential direct but also indirect effects of OAE. On May 7th 2022, ten floating KOSMOS mesocosms (Riebesell et al., 2013) were moored from RV ALKOR nearby Espegrend research station at a bottom depth of ~60 m (map in Spisla et al. 2022). The units consisted of 20 m long and 2 m wide transparent polyurethane bags that terminated in a 2 m long sediment trap (Fig. 1a). The lower end of the bags was extended to depth, while open at the bottom, to enclose ~60 m^3 of seawater including any planktonic organisms present. Then, the bottom was closed isolating the bags from the surrounding fjord water and marking the start of the experiment (day 0). Wall growth was removed regularly using brushes from the outside and a cleaning ring from the inside. Environmental conditions were assessed with CTD casts in two-day intervals. Average salinity was at ~33 and photosynthetically active radiation reduced to ~30% of surface radiation. Oxygen saturation stayed consistently above 100%. Temperature increased from 8.8 to 15.4 °C over the course of spring. These physiochemical conditions varied across the stratified water column from surface to depth.

A diverse, multi-trophic plankton food web was enclosed in the mesocosms. Larger organisms were removed at the start using a net with a mesh size of 3 mm that spanned the width of the mesocosms. The resulting community comprised of primary producers (e.g. diatoms and coccolithophores), grazers (e.g. copepods) and predators (e.g. jellyfish) as in previous experiments at this locality (Schulz et al., 2017; Spisla et al., 2022). Larvae of various fish species were also present including codfishes (mostly Atlantic cod *Gadus morhua*), gobies (mostly *Pomatoschistu* spp.) and flatfishes (mostly *Limanda* spp. and *Microstomus* spp.). On day 6, these naturally occurring larvae were supplemented with 95 laboratory-reared herring larvae per mesocosm (25 days post-hatch, 15 ± 1 mm). By the end of the experiment, the fish assemblage consisted of a mixture of larvae and young juveniles.

Primary production in the mesocosms was initially low as the experiment began shortly after the spring bloom with little inorganic nutrients remaining (Ferderer et al., 2024). To also consider bloom conditions in our study of OAE, nutrients were added on day 25 to all mesocosms leading to an increase in nitrate, phosphate and silicate of 3.8 ± 0.2, 0.20 ± 0.01 and 0.98 ± 0.06 µmol L^{-1}, respectively. During past experiments, this level of fertilization induced phytoplankton blooms in mesocosms (e.g. Schulz et al., 2017) that corresponded in intensity to those observed in the natural environment (Paulino et al., 2018).

2.2 Herring larvae rearing

The herring larvae had been reared under ambient conditions (i.e. without OAE) in the laboratories at the nearby University of Bergen. Following Folkvord et al. (2020), two wild-caught females (~356 g in size) and males (~297 g) were strip spawned onto plastic plates in two crosses. Fertilization success was 92%. Eggs were incubated at 7.1 ± 0.1 °C and a salinity of 33.4 ± 0.1 (mean ± SD). After hatching 17 days later (24th April), a total of 2400 larvae were distributed amongst two ~500 L rearing tanks. These were filled with water pumped from the fjord and aerated with ambient air. Temperature was continuously adjusted to match that of the outside fjord and averaged 6.5 ± 0.8 °C. Oxygen levels were 87.8 ± 4.7%, salinity 33.5 ± 0.3, total alkalinity 2523 ± 6 µmol kg^{-1} and pH$_{NBS}$ 7.94 ± 0.09. Artificial light mimicked the local diurnal light cycle. The larvae

were fed *ad libitum* with a diverse assemblage of zooplankton including nauplii and copepodites, regularly collected from the nearby fjord (Folkvord et al., 2015). Prey densities were closely monitored in the tanks and restocked daily to maintain high levels (2000 prey L^{-1}). Algae cultures were also added daily (*Rhodomonas* sp. and *Isochrysis* sp.). Over the rearing period, larvae survival was estimated at 99.8%.

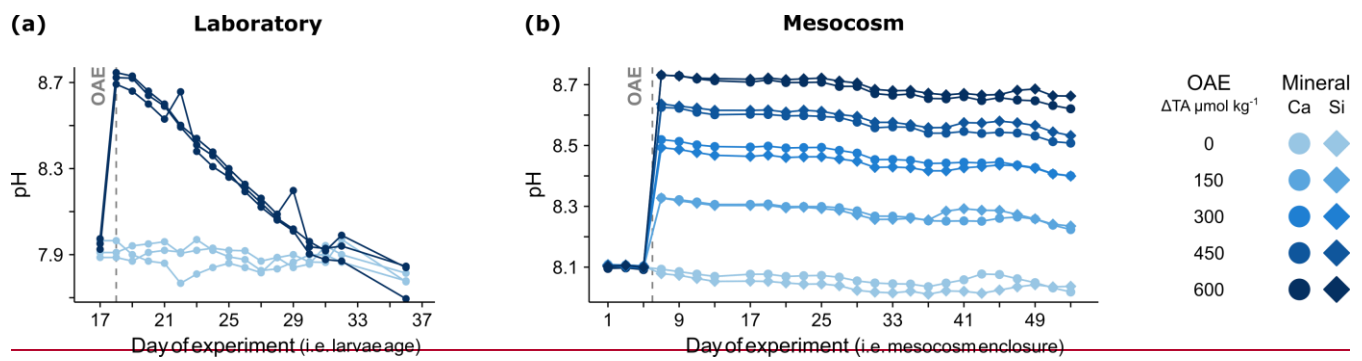
2.2 Laboratory experiment

2.2.1 Experimental setup

To investigate direct effects of OAE, herring larvae were reared under controlled environmental conditions (Fig. 1a). Following Folkvord et al. (2020), two wild-caught females (~356 g in size) and males (~297 g) were strip spawned onto plastic plates in two crosses. Fertilization success was 92%. Eggs were incubated at 7.1 ± 0.1 °C and a salinity of 33.4 ± 0.1 (mean $\pm$ SD). After hatching 17 days later (24th April), larvae were transferred to six aerated experimental tanks. Each tank held 0.25-0.4 m^3 fjord water with an estimated 1800 larvae at the start. Temperature was maintained at 8.5 ± 0.2 °C, oxygen levels at $88.5 \pm 5.2\%$ and salinity at 33.8 ± 0.7. Artificial light mimicked the local diurnal light cycle. The larvae were fed *ad libitum* with a diverse assemblage of zooplankton including nauplii and copepodites, regularly collected from the nearby fjord (Folkvord et al., 2015). Prey densities were closely monitored in the tanks and restocked daily to maintain high levels (2000 prey L^{-1}). Algae cultures were also added daily (2 L, *Rhodomonas* sp. and *Isochrysis* sp.).

2.2.2 OAE application

On day 18 post-hatch, alkalinity was enhanced (ΔTA) in three larval tanks by 600 µmol kg^{-1}, while the remaining three served as untreated controls (Fig. 1a). For this, one liter of alkaline solution that simulated calcium-based OAE was prepared with NaOH, CaCl$_2$ and Milli-Q water. The solution was then poured slowly into the center of each tank, where the current created by the aeration system assured rapid mixing. During the experiment, the equilibration of CO$_2$ with the atmosphere was slowed down through aeration with CO$_2$-reduced air (pCO$_2$ = ~100 µatm) using CO$_2$-scrubbers (absorption via Ca(OH)$_2$ and NaOH). To further minimize gas exchange with the laboratory room, tanks were covered by a transparent lid. The control tanks were instead treated with pure Milli-Q water and ambient air.

The application of non-CO$_2$-equilibrated OAE was successful. In each tank, total alkalinity (TA) was measured three times over the treatment period following the principles in Schulz et al. (2023). Water was filtered (PES, 0.2 µm) into glass bottles and stored at 4 °C until analysis on the following days via titration (Metrohm 862 Compact Titrosampler with Aquatrode Plus with PT1000) calibrated against certified reference material. pH was measured daily directly in the tanks with a handheld probe (WTW 3320 with sensor 662-1305, Xylem Analytics). Following the OAE manipulation, TA increased abruptly from 2519 ± 5 to 3082 ± 175 µmol kg^{-1} (mean $\pm$ SD) with corresponding increase in pH of ~0.7 units (Fig. 2a). Over the following 18-day test period, pH steadily decreased back towards ambient levels due to gas exchange and dilution by feed water. Our experiment may thus represent a scenario where larvae are exposed to a plume of intense OAE that subsequently mixes with ambient seawater and equilibrates with the atmosphere, slowly alleviating the perturbation.

~~2.2.3 Measured variables~~

~~The sensitivity of herring to OAE was assessed through different traits and at different exposure times (i.e. larvae ages). As basic physiological trait, routine metabolic rate was measured on five larvae per tank following Berg et al. (2020). Larvae were placed individually in glass vials (4 or 20 mL) before dawn to assure empty guts. Oxygen consumption was tracked for 1.5 h in darkness using a 4-channel fiber-optic oxygen meter (FireSting O$_2$, PyroScience GmbH). Then, larvae were anesthetized (0.1 g L^{-1}) followed by euthanizing (overdose) with MS222, photographed and freeze-dried to obtain dry mass. Finally, mass-specific routine metabolic rate was estimated. See supplementary information for further methodological details.~~

~~Swimming behavior while hunting for live prey was assessed directly in the tanks following Illing et al. (2018). Herring larvae are pause-travel predators that swim in bouts and pause to search for and target prey. An observer tracked 10 larvae per tank for 2 min, one larva at a time. Then, total time spent moving, pause frequency and duration of each pause were computed. Growth was also assessed regularly for ten larvae per tank via measures of standard length on euthanized larvae. At the end of the experiment, longer-term survival was evaluated by counting all larvae remaining in the tanks.~~

~~2.3 Mesocosm experiment~~

2.3.~~2~~ OAE application

On day 6, we established a ~~We tested a gradient in alkalinity enhance~~five-step gradient in alkalinity increase (ΔTA)~~ment~~ from 0 to 600 µmol kg^{-1} ~~using two different mineral sources (Fig. 1b)~~, with half of ~~. Half of~~ the mesocosms simulat~~ing~~ed calcium-based (Ca) and the other half silicate-based (Si) ~~OAE~~mineral addition (Fig. 1b). The Ca-based treatment only introduced elements that are already abundant in seawater and were thus unlikely to impact marine life beyond the alkalinity effect. It hence served as baseline to establish the effect of excess silicate. ΔTA was applied non-CO$_2$ equilibrated (Bach et al., 2019). This economically more feasible approach, only adds alkalinity and CO$_2$ sequestration occurs afterwards through natural equilibration with the atmosphere. In the alternative pre-CO$_2$ equilibrated approach, the to-be-sequestered CO$_2$ would instead be added together with the alkalinity leading to milder changes in seawater chemistry. We restricted ΔTA to 600 µmol kg^{-1} to avoid abiotic precipitation of calcium carbonate, which would signify a loss in alkalinity and thus a nonsensical OAE scenario (Hartmann et al., 2023). The gradient design with non-replicated treatment levels (Riebesell et al., 2023) was preferred for ΔTA to allow for a more informative study of biogeochemical processes that were also part of the multidisciplinary mesocosm project (e.g. Ferderer et al., 2024). For analysis, ΔTA could then be tested as continuous explanatory variable in the sense of linear regression. ~~to address two contrasting mineral addition scenarios (Renforth and Henderson, 2017; Bach et al., 2019). The Si-based treatment, on the other hand, adds a limiting nutrient with the potential to alter food webs.~~

235 The OAE ~~manipulation~~ application ~~was conducted on day 6 following~~followed the principles in Riebesell et al. (2023). NaOH was used as alkalizer with a proportional amount of $CaCl_2$ to simulate quick or hydrated lime (Ca-based) and $MgCl_2$ to simulate olivine (Si-based)~~(Ferderer et al., 2024)~~. Silicate was added in equal amounts of 75 µmol L^{-1} to all five Si-based mesocosms using Na_2SiO_3. ~~To~~ This allowed to separate the effects of alkalinity and silicate and ~~to prevent~~prevented mineral precipitation~~, Na_2SiO_3 was added in equal amounts (75 µmol L^{-1}) to all five Si-based mesocosms~~ (Ferderer et al., 2024). These salts were

240 dissolved in 40 L Milli-Q water per mesocosms and then mixed ~~enabled a homogeneous injection of the OAE solutions~~into the mesocosms using a special distribution device referred to as the 'spider' (Riebesell et al., 2013).

Carbonate chemistry and inorganic nutrients were monitored in two-day intervals based on depth-integrated water samples. For this, samplers equipped with a pressure-controlled motor (5 L, Hydro-Bios, Kiel, Germany) where lowered from the surface to the bottom of the mesocosms to collect water evenly across the water column. The resulting samples represented

245 mesocosm averages. In the laboratory, water was first sterile filtered using a 0.2 µm pore size polyethersulfone membrane. Carbonate chemistry was assessed following Schulz et al. (2023). TA was measured via titration (Metrohm 862 Compact Titrosampler with Aquatrode Plus with PT1000) calibrated against certified reference material (CRM batch 193) supplied by Prof. Andrew Dickson's laboratory and pH spectrophotometrically (Dickson et al., 2007). With the temperature and salinity provided by the CTD casts, in situ pH and pCO_2 could then be calculated using CO2SYS for Excel with constants from Luecker

250 et al. 2000 and Dickson 1990 (Pierrot et al., 2021). Silicate was determined spectrophotometrically following Hansen and Koroleff (1999).

Our OAE treatments produced the intended water chemistry changes. ~~ter). The manipulation created a clean gradient in TA from 2215 ± 5 to 2756 ± 7 µmol kg^{-1} and pH from 8.05 ± 0.02 to 8.69 ± 0.03 (Fig 2b). Across this gradient, pCO_2 dropped from 384 ± 22 to 75 ± 6 µatm and ΩCa rose from 3.2 ± 0.2 to 11.7 ± 0.2.~~ TA increased in a clean gradient (Fig. S1a), followed

255 by the expected increases in pH (Fig 1c) and ΩCa (from 3.2 ± 0.2 to 11.7 ± 0.2) and decreases in pCO_2 (Fig S1b). These OAE-induced shifts in carbonate chemistry were present across depth (as exemplified via pH, Fig. S1c). CO_2 ~~In contrast to the smaller laboratory tanks, e~~equilibration with the atmosphere was ~~negligible~~minimal throughout the experimental period given the large depth and stratified water column of the mesocosms. Silicate availability in the Si-based mineral treatments stayed in extreme excess between 55 and 70 µmol L^{-1}, while the Ca-based treatments remained well below 1 µmol L^{-1} for most of the

260 experiment suggesting silicate limitation (Fig. 1d). In conclusion, carbonate chemistry and silicate ~~p~~Perturbations ~~hence remained~~were relatively stable over 48 days of OAE; optimal conditions for the emergence of food web effects and their propagation to fish.

2.~~4~~3.3 ~~Measured~~ Biological variables

We monitored the fish assemblage closely. Mortality through processes other than predation was tracked over the entire experiment. For this, the sediment trap was sampled in two-day intervals via a tube connected to the surface (Fig. 1a~~b~~) and

265 immediately screened for dead fish. Carcasses were assigned to either herring, codfishes or flatfishes based on their distinct body shape. This method had proven successful in previous campaigns, especially in colder climates where fish carcasses disintegrate slowly (Spisla et al., 2022). At the end of the experiment, all live fish were caught with a net (1 mm mesh) spanning the width of the mesocosm. Fish were anesthetized (0.1 g L^{-1}) followed by euthanizing (overdose) with MS222 and preserved

270 at -80 °C. Finally, each individual fish ~~were~~was weighed for ~~(~~wet mass~~) and assigned to broad taxonomic groups~~. Predation on herring was estimated as the difference between the individuals initially introduced and the ones found later in the sediment trap and final sampling.

The wider plankton community was also monitored to better understand potential indirect effects on fish. Primary producer biomass and photosynthetic capacity was approximated every two days via chlorophyll a. For this, depth-integrated water

samples were filtered and analyzed on a fluorometer (Ferderer et al., 2024). Metazoan zooplankton was sampled every four days across the entire water column using a net with 55 µm mesh size (Apstein, Ø 17 cm) (Spisla et al., 2022). After preservation in 70% ethanol, copepods (main larval prey) and hydrozoans (potential larval competitors and predators) were counted under the microscope.

2.~~5~~4 Data analysis

To ~~For the laboratory, the responses of herring were tested based on measurements of individual larvae. Linear mixed models were employed with *OAE* as categorical fixed effect (ΔTA 0 vs. ΔTA 600) and larvae rearing *tank* as random effect. A separate analysis was conducted for each larval age.~~

~~For the mesocosm, fish responses were instead~~ assess the responses of fish and other functional groups to OAE, replicate measures within mesocosms (i.e. individuals or sampling days) were first ~~ed using~~ sum~~med or~~s ~~or~~ averaged. This provided one independent measure per mesocosm. Per capita size of fish had been $\log_{10}$ transformed to reduce the influence of large but rare individuals on the calculated average. The subsequent analyses were conducted at a significance level of $\alpha = 0.05$ with R version 4.0.5 (R Core Team, 2021).

For univariate responses, ~~s across all individuals.~~ ~~l~~Linear ~~regressions~~ models were employed with *ΔTA* (continuous), *mineral* (categorical) and their interaction (*ΔTA × mineral*) as explanatory variables (type III test). ~~OAE as continuous explanatory variable (ranging from ΔTA 0 to ΔTA 600). To align with the laboratory experiment, we only focused on *alkalinity* as OAE driver. This simplification was acceptable given that the thereby omitted factor *mineral* showed no effect (Table S1).~~ Unexplained variability was particularly high at the level of single taxa (Fig. S2~~1~~) likely due to random differences in starting numbers and sizes. We therefore restricted our main analyses to the whole fish assemblage. Here, across all fishes, some of the variability was compensated for by competition for limited food resources. Model assumptions were addressed following Lüdecke et al. (2021). Normality of residuals was checked with normal Q-Q plots and homogeneity of variance with residual versus fitted plots.

~~P~~Finally, we ~~otential shifts in the~~ ~~assessed possible changes in~~ taxonomic composition of the fish assemblage ~~under OAE~~were assessed using multivariate analyses based on Bray-Curtis dissimilarity (vegan package, Oksanen et al., 2022). Differences in composition between mesocosms were illustrated via~~using~~ non-metric multidimensional scaling (nMDS) ~~based on Bray-Curtis dissimilarity.~~ ~~and~~Mantel tests with Pearson correlation were employed to test for *ΔTA* and permutational multivariate analysis of variance (adonis2 function) to test for *mineral* based on 999 permutations. ~~(Oksanen et al., 2022).~~

~~All analyses were conducted at a significance level of α = 0.05 with R version 4.0.5 (R Core Team, 2021). Model assumptions were addressed following Lüdecke et al. (2021). Normality of residuals was checked with normal Q-Q plots and homogeneity of variance with residual versus fitted plots. Per capita sizes of mesocosm fish were log 10 transformed. Some outlier individuals in the laboratory trials on physiology and behavior were excluded based on interquartile range.~~

3 Results

~~3.1 Organism-level responses in the laboratory~~

~~Our single-species test under controlled conditions suggests that Atlantic herring larvae may cope with OAE. Larvae under OAE maintained a similar routine metabolic rate than larvae under ambient conditions (Fig. 3a). Their activity pattern during hunting of live prey was also unaffected by OAE, including the time they spent swimming and how often and how long they paused (Fig. 3b). The absence of an OAE effect on metabolic rate and activity was consistent across exposure time (i.e. larval~~

age). To note, the pH perturbation slowly alleviated and reached ambient levels 13 days after OAE application (age 31, Fig. 2a). From then onwards, our data tested for the lasting after-effects of elevated pH.

Larvae developed normally despite OAE. Growth of treated larvae was indistinguishable from that of untreated ones (Fig. 3c) and averaged at 0.41 mm day⁻¹. Larval size structure was also maintained (Fig. 3d). Ultimately, similar numbers of larvae survived under OAE compared to ambient conditions until the end of the experiment 19 days after OAE application (Fig. 3e). This final assessment was based on 1800 individuals per treatment tank feeding on natural zooplankton prey. The estimated survival of 98 %, which corresponds to 99.95 % average daily survival, can be considered extremely high, given the vulnerability of this life stage, and suggests an optimal rearing environment. In conclusion, we found no evidence for a direct effect of OAE on herring larvae across different responses at the organism-level, from basic physiology and behavior to growth and survival.

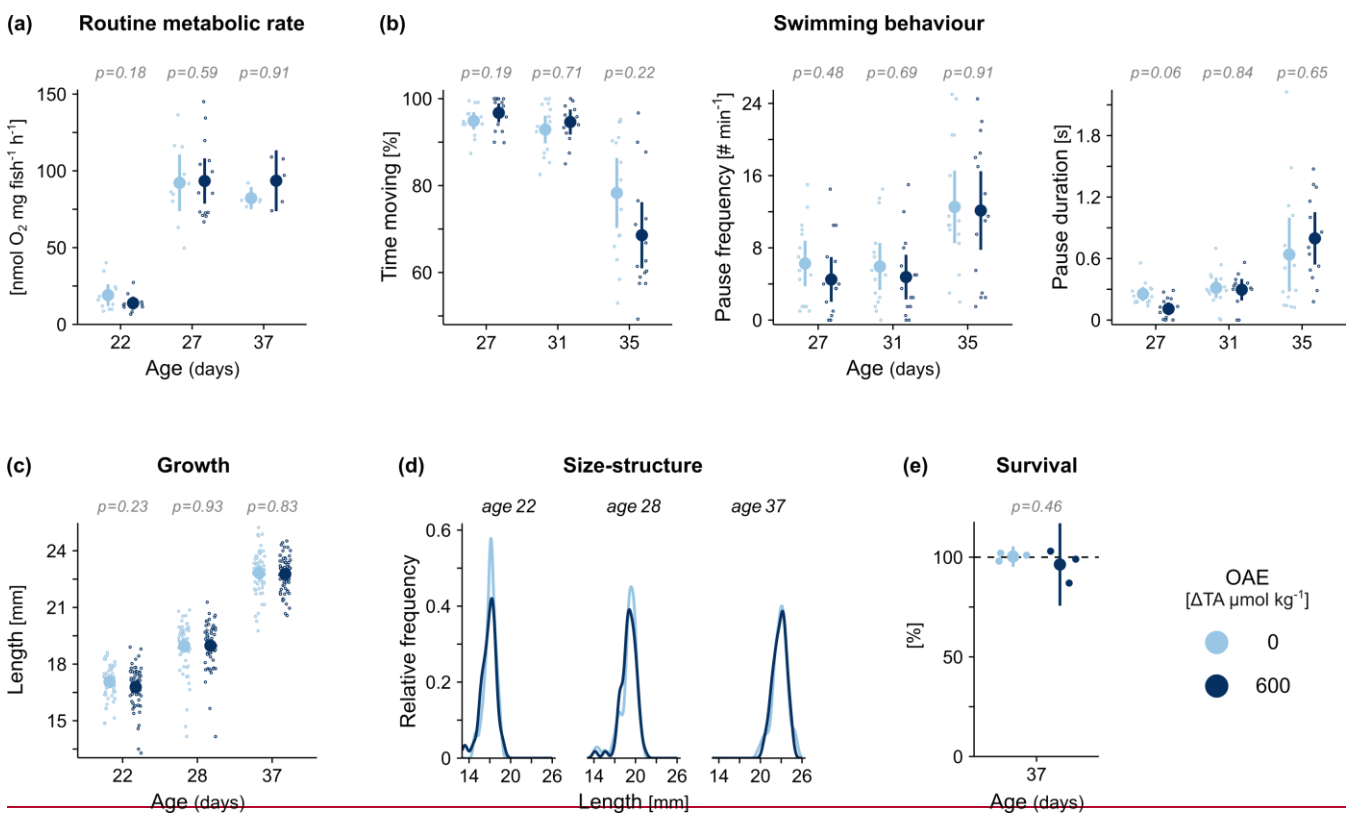



Figure 3: Organism-level responses of herring larvae to OAE, under controlled laboratory conditions. Basic physiology **(a)** and behavior **(b)**, growth via size at age **(c)**, size distribution **(d)** and long-term survival at the end of the experiment **(e)**. Shown are individual larvae (a-c) or treatment tanks (e) (small points) and averages (large points) with ±95% confidence intervals. At each age (days post-hatch), linear models (in grey) test for an OAE effect (details in Table S2). Larvae had been exposed to OAE since day 18.

3.2 Community-level responses in mesocosms

Our ~~experiment~~ study ~~of~~on fish in natural plankton communities considered changes in both water chemistry and food web interactions. We were nevertheless ~~was also not~~un-able to detect negative impacts of OAE, neither via increased alkalinity nor via a silicate-based mineral addition. ~~Here we studied~~ The fish assemblages comprised of larvae and young juveniles of different coastal ~~fishes~~species including the introduced herring and naturally enclosed species such as Atlantic cod. ~~In the mesocosms, these fish assemblages were shaped by both environmental conditions and food-web interactions.~~

During the experiment, ~~m~~fish mMortality by processes other than predation ~~-~~was monitored ~~-~~via carcasses that had sunk to the sediment trap. We found this mortality to be throughout unrelated to OAE. ~~It was assessed via carcasses that had sunk to the sediment trap and thus represented death via processes other than predation.~~ The abrupt changes in carbonate ~~water~~ chemistry following OAE application were not lethal to any of the species (Fig. 24a-left), including herring (Fig. 24b). These results indicate that elevated ~~OAE~~ pH did not impair physiology at the most basic level that leads to an immediate demise. Surviving the first shock, the fishes now had the chance to adjust to the novel water chemistry. At the end of our experiment, mortality still remained unaffected by OAE (Fig. 24a-right) and species-specific effects were not apparent (Fig. 24c). Hence, there was no sign of ~~a~~ physiological or behavioral disruption that rendered fish incapable of foraging for food~~-~~ causing starvation. To note, the unusually high mortality rates in two mesocosms (Ca ΔTA 300 and Si ΔTA 150, Fig 24a, b) were most likely caused by flappy walls that harmed some larvae during wave action.

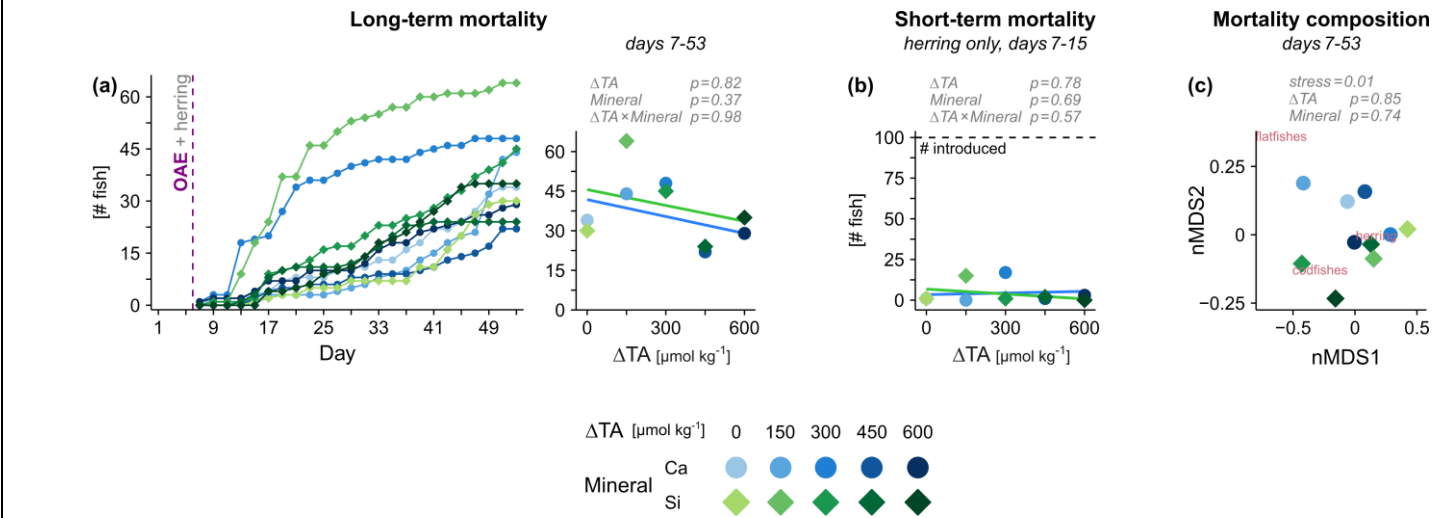



Figure 2: Fish mortality under OAE monitored via the sediment trap. **a)** Cumulative mortality over time across all species and **b)** immediately following the OAE perturbation for herring. **c)** Differences in taxonomic composition between mesocosms via non-metric multidimensional scaling (nMDS). Statistical tests in grey (details in Table S1).

We next assessed theThe assemblage of live fish individuals at the end of the 49-day experiment. Also here, our OAE-manipulations of varying alkalinity and mineral did not emerge asconfirmed that OAE was not a dominant stressors for fish. Neither total abundances (Fig. 34ad) nor taxonomic composition (Fig. 34be) provided evidence for an effect of followed any OAE related pattern. Besides physiological stress and starvation, abundances were also a product of predation by other fish and invertebrate predators. At this point, we have to acknowledge the high variability in some of the mesocosm data, especially at the level of individual fish species, which may have concealed less severe yet ecologically relevant impacts. The only significant response effect in our study was the increase in that average fish size, and consequently total fish biomass under alkalization, increased under OAE (Fig. 34df, g). Average fish size showed a similar, albeit non-significant, pattern (Fig. 3c). This positive effect of alkalinity seemed to be mostly driven by one taxon, the codfishes (Fig. S31). In contrast, the high availability of silicate under Si-based OAE seemed of no consequence for the fish assemblage, despite its potential to cause imbalances at the bottom of the food web.

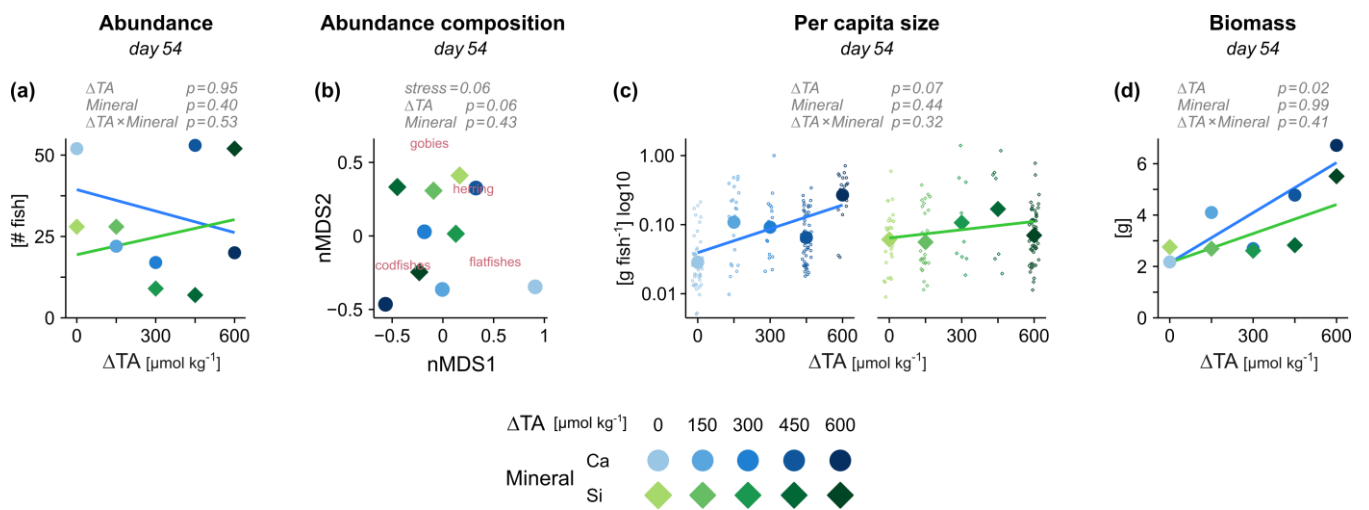



Figure 3: Fish growth and survival under OAE, assessed via the assemblage of live fish at the end of the experiment. **a)** Abundance, **c)** individual size and **d)** total biomass across all fish taxa. **c)** Differences in taxonomic composition between mesocosms via non-metric multidimensional scaling (nMDS). Larger points represent mesocosms and smaller points in **c** single individuals. Statistical tests in grey (details in Table S1).

FinallyLastly, we assessed functional changes groups in of the plankton food web that have with the potential to propagate indirect effects of OAE to fish. affect fish indirectly. PronouncedMajor changes in effects of OAE on lower trophic levels due to alkalinity increase or elevated silicate were not apparent, considering primary producers (chlorophyll a, Fig. 45a) and the main prey of fish larvae (copepod zooplankton, Fig. 45b). Invertebrate predators (jellyfish) that compete with fish for food and may prey on small larvae seemed also unaffected by OAE (Fig. 45c). There was no sign of an altered predation rate on herring (Fig. 45d), an estimate that also includes the potential predation from larger piscivorous fish present in the mesocosms (e.g.

cod juveniles). Overall, we found no evidence for an increased bottom-up or reduced top-down forcing that could explain the positive effect of OAE on fish biomass.

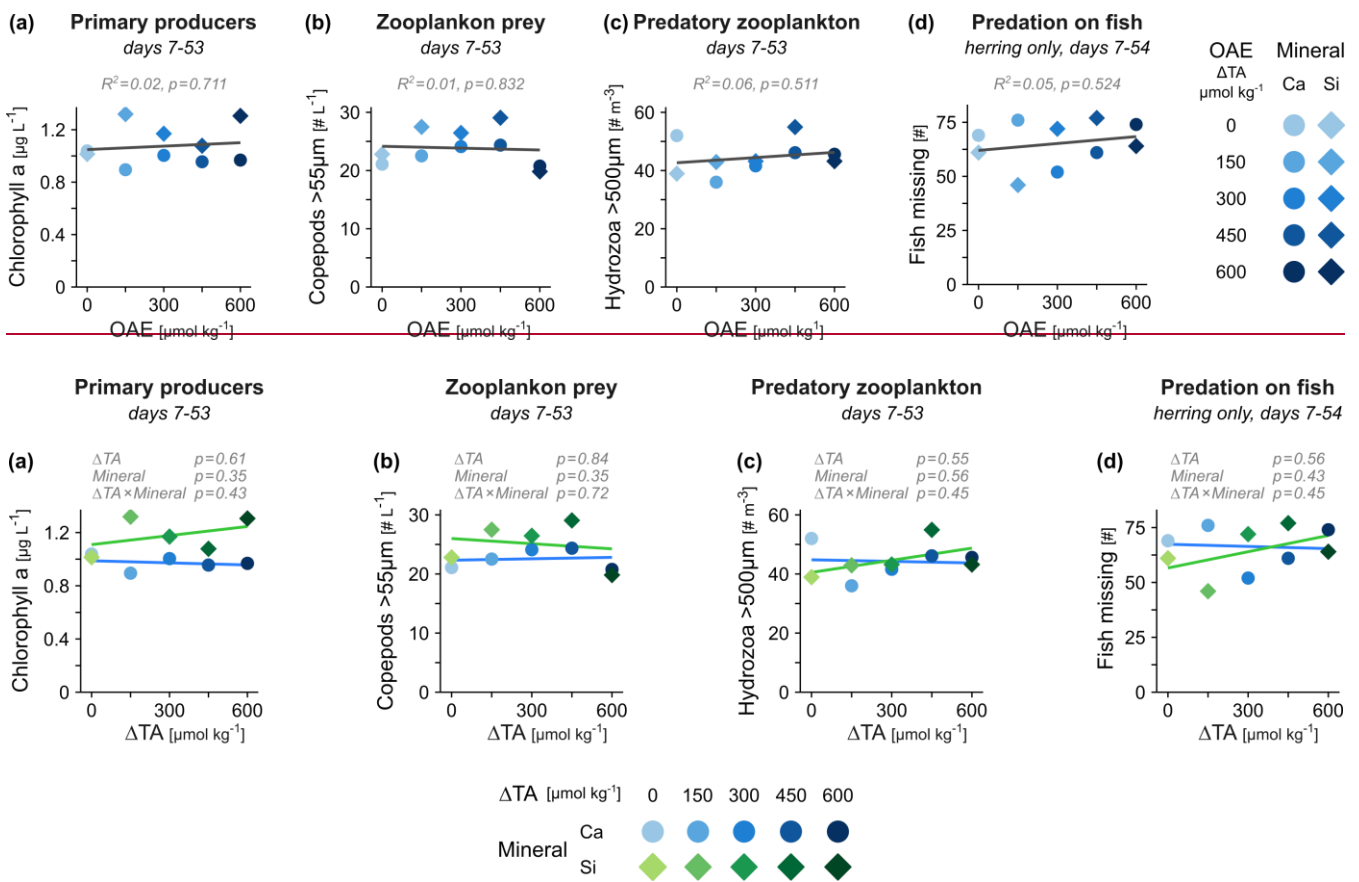



Figure 4~~5~~: Potential sources of indirect effects of OAE on fish mediated via species interactions. Abundance of other functional groups including **(a)** primary producers, **(b)** invertebrate grazers and **(c)** invertebrate predators. **d)** Predation on herring estimated via missing individuals. Averages across the treatment period are tested ~~with linear regressions~~ (in grey, details in Table S~~2~~4).

4. Discussion

Our study suggests that larvae and juveniles of some temperate coastal fishes may be viable under ocean alkalinity enhancement (OAE) for carbon dioxide removal. Negative impacts of ~~OAE~~ alkalinity and silicate were not apparent, neither ~~despite our thorough investigation across response types (physiology to survival), ecological scales (organism to community) and timeframes (~~in the shorter- ~~nto~~ or longer-term ~~exposure)~~. Early life stages from these fish populations may recruit successfully and continue to support fisheries in regions of OAE deployment.

During the first days of OAE exposure in our mesocosms, fish mortality was not elevated suggesting an absence of severe direct effects on their physiology. ~~Physiology and behavior of the tested fish larvae seemed resistant to the direct effects of OAE. Functional impairment, as reported in some cases for the opposing stressor ocean acidification (Cattano et al., 2018; Esbaugh, 2018; Nagelkerken and Connell, 2015), could not be observed.~~ In the local ecosystem, natural pH variability peaks at ~8.35 (Omar et al., 2016) and thus remains well below the ~8.7 of our highest ~~OAE~~ alkalinity scenario. The fishes were hence challenged by an instantaneous pH increase that considerably exceeded what their populations should have been pre-adapted to in this system. The ability to compensate despite the severity and abruptness of the perturbation confirms a powerful machinery for acid-base regulation in these vertebrates (Tresguerres et al., 2020). This result may have been expected for

herring based on its At least for Atlantic herring tolerance , this result should come as no surprise given the species' tolerance to moderate levels of the opposing stressor ocean acidification (Sswat et al., 2018a; Maneja et al., 2015; Franke and Clemmesen, 2011), but also see (Frommel et al., 2014). However, with cod that can experience high larvae mortality under similar conditions (Stiasny et al., 2016), we also included a supposedly more pH sensitive species. Interestingly, both species – herring and cod – can develop major organ damage at more extreme levels of acidification (Frommel et al., 2014; Frommel et al., 2012). We could have missed minor damages caused by OAE that did not pose an immediate threat to survival. (Stiasny et al., 2016; Frommel et al., 2012)Whilst our larvae experiments did not demonstrate adverse effects of OAE, Oother life history stages may prove more vulnerable to OAE, in particular reproductive cells and early embryos that lack specialized regulatory tissue (Melzner et al., 2009; Dahlke et al., 2020).

Ecosystems and fish species may differ in their sensitivity to OAEalkalization. We only know of two comprehensive studies on the viability of fish larvae under increased elevated pH (Brownell, 1980; Parra and Yufera, 2002). These investigated fFive species were investigated here in an aquaculture context. After only 24 h exposure to pH above ~8.5, the authors reported reduced first-feeding success and, in one species, even lethality. Interestingly, high pH was considerably more detrimental than low pH (Brownell, 1980; Parra and Yufera, 2002), further emphasizing the impact potential of OAE. Given these acute sensitivities that contrast our finding of tolerance, we can may infer a species-specific effect of increased of OAE pH on fish larvae. OAE could be more stressful for fishes that have adapted to stable environmental conditions, such as in the open ocean (Blewett et al., 2022; Hofmann et al., 2011), or for fishes that are already challenged physiologically, like in warm tropical waters (Vinagre et al., 2016; Pörtner, 2008). Our results on temperate coastal species at the organism level are clearly only a first step towards assessing the safety of OAE for fish populations.

Once fish survive the water chemistry perturbation itself, time would be given for food web-mediated impacts of OAE. In this context, sSeveral mechanisms were proposed through which alkalinity may with the potential to lower the quantity and quality of food prey for higher trophic levels. These include slowed primary production (Hansen, 2002), proliferation of heavily armored calcifiers (Renforth and Henderson, 2017) and pH stress in invertebrate prey (Melzner et al., 2009). Yet, in our mesocosms, we could not find evidence for these indirect effects of OAE on fish, not even after longer-term exposure. However, what we did observe was a positive effect of OAE alkalization on fish biomass. This unexpected result was not easily explained through major changes elsewhere in the community. Neither prey foodavailability seemed was enhanced nor the potential for competition with or predation by jellyfish reduced. Altered intraguild predation — larger fish eating smaller ones — seemed not to be responsible either. The biogeochemical perspective including inorganic nutrients and export of matter (Ferderer et al., 2024) provided also no clues as to how alkalization may have facilitated the build-up of fish biomass. With that we explored some of the more obvious bottom-up and top-down processes that can propagate environmental change to fish (Sswat et al., 2018b; Goldenberg et al., 2017; Spisla et al., 2022). Overall, it appears that our alkalinity manipulation did not cause major ecosystem shifts.

Addition of silicate mineral, in contrast, induced strong responses in our primary producers, as presented in Ferderer et al. (2024). The authors observed an increase in diatom cell silicification and a prominence of their shells in suspended matter. Other studies on silicate enrichment in Norway even described diatoms as low in nutritional value (Gilpin et al., 2004; Davidson et al., 2002) and poor food for zooplankton (Nejstgaard et al., 2001). It is thus surprising that the excess silicate in our mesocosms did not indirectly impact copepod grazers and their fish predators. This finding emphasizes the complexity of species interactions that will require careful consideration in the emerging research field of OAE.

Whilst our study may have ~~more subtle responses may have been~~ overseen more subtle responses, ~~our study~~the fishes ~~seemed~~ appeared able to maintain basic physiological and ecological capabilities under OAE. This is a significant first step towards the classification of OAE as a stressor, since under these circumstances fish populations are given an opportunity to adjust. At the organismal-level, individuals may avoid the OAE plume, acclimate physiologically (Pörtner, 2008) or simply persevere until the conditions improve. The perturbation will alleviate with time ~~mixing or equilibration alleviates the perturbation~~ through mixing with surrounding water masses (He and Tyka, 2023), CO_2 equilibration (Bach et al., 2019) as well as removal of nutrients and trace metals via the biological pump (Morel and Price, 2003; Ferderer et al., 2024). At the community-level, behavioral plasticity may enable individuals to react to changing resources and predation (Wong and Candolin, 2015; Mcmeans et al., 2016), while the selection of robust phenotypes over generations allows for genetic adaptation (Sunday et al., 2014). The basic survivability demonstrated in our study is a prerequisite for these compensatory mechanisms that could improve population resistance and recovery.

Over geological time scales, natural rock weathering and the resulting alkalization of the ocean has been buffering earth's climate. An artificial acceleration of this process could be accomplished through different scenarios, each one causing a distinct perturbation of seawater (Renforth and Henderson, 2017; Hartmann et al., 2023). We focused on changes in carbonate chemistry before CO_2-equilibration of the alkalized water. Our inability to detect severe impacts here may classify the alternative, pre-CO_2-equilibrated application as especially safe, given its stable CO_2 partial pressure and smaller increases in pH and calcium carbonate saturation. With silicate addition, we tested a secondary driver of OAE that is hypothesized to cause major ecosystem shifts (Bach et al., 2019). ~~While not subject of our study, secondary drivers of OAE including~~ There are several further drivers, however, such as trace metal toxicity/enrichment (Morel and Price, 2003) or suspended mineral particles (Affandi and Ishak, 2019) that are likely to play a role as well. A large-scale intervention such as OAE will inevitably bring about some level of environmental change, not just via the manipulation itself but also supporting activities on land and at sea. OAE has to be seen in relation to other carbon-dioxide removal technologies and the environmental, economic and social harm caused by unrestrained climate change. Our study on temperate coastal species helps to develop such a risk-benefit analysis towards the preservation of fish in marine ecosystems and the livelihoods they support.

Ethics

Fish research was approved by the Norwegian Animal Research Authority (NARA) via the University of Bergen (laboratory, FOTS ref 29008) and University of Agder (mesocosm, FOTS 28931).

Data availability

The raw data supporting the conclusions of this article are ~~being made available~~available at ~~via PANGAEA.~~ https://doi.org/10.1594/PANGAEA.967059

Competing interests

The authors declare that they have no conflict of interest.

Author contributions

SUG, MM, UR, MS, GB and AF conceptualized the study, all authors conducted the experiments, SUG and MM analysed the data, SUG wrote the manuscript with particular input from MM and DB, and all authors revised the manuscript.

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