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Ontogenetic differences in the response of the cold-water coral *Caryophyllia huinayensis* to ocean acidification, warming and food availability

Kristina K. Beck [a,b,*], Jan Nierste [a,c], Gertraud M. Schmidt-Grieb [a], Esther Lüdtke [a], Christoph Naab [a,d], Christoph Held [a], Gernot Nehrke [a], Grit Steinhoefel [a], Jürgen Laudien [a], Claudio Richter [a,b], Marlene Wall [a,e]

[a] *Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany*
[b] *University of Bremen, Bremen, Germany*
[c] *University of Rostock, Rostock, Germany*
[d] *University of Augsburg, Augsburg, Germany*
[e] *GEOMAR Helmholtz Centre for Ocean Research, Kiel, Germany*

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ABSTRACT

Cold-water corals (CWCs) are considered vulnerable to environmental changes. However, previous studies have focused on adult CWCs and mainly investigated the short-term effects of single stressors. So far, the effects of environmental changes on different CWC life stages are unknown, both for single and multiple stressors and over long time periods. Therefore, we conducted a six-month aquarium experiment with three life stages of *Caryophyllia huinayensis* to study their physiological response (survival, somatic growth, calcification and respiration) to the interactive effects of aragonite saturation (0.8 and 2.5), temperature (11 and 15 °C) and food availability (8 and 87 μg C L^{-1}). The response clearly differed between life stages and measured traits. Elevated temperature and reduced feeding had the greatest effects, pushing the corals to their physiological limits. Highest mortality was observed in adult corals, while calcification rates decreased the most in juveniles. We observed a three-month delay in response, presumably because energy reserves declined, suggesting that short-term experiments overestimate coral resilience. Elevated summer temperatures and reduced food supply are likely to have the greatest impact on live CWCs in the future, leading to reduced coral growth and population shifts due to delayed juvenile maturation and high adult mortality.

1. Introduction

Many cold-water coral (CWC) species have a wide geographical range, mainly between 200 and 1000 m depth (Freiwald et al., 2004; Roberts et al., 2006). However, in high latitude fjord environments, CWCs also occur at shallower depth (Försterra and Häussermann, 2003; Wisshak et al., 2005). Their calcium carbonate skeletons form three-dimensional frameworks, which support complex and diverse ecosystems (Freiwald et al., 2004). Their distribution is determined by several abiotic and biotic factors, such as carbonate chemistry, temperature, salinity, oxygen, current velocity and the availability of food and hard substrate (Georgian et al., 2016a; Georgian et al., 2014; Juva et al., 2020). However, CWCs are threatened by several ongoing environmental changes.

Ocean acidification has long been considered a severe threat for

CWCs (Roberts et al., 2006), as rising atmospheric carbon dioxide (CO$_2$) decreases carbonate ion concentrations (Guinotte et al., 2006; Orr et al., 2005) and seawater pH (Cyronak et al., 2016), potentially reducing calcification (Büscher et al., 2017; Georgian et al., 2016b; Gómez et al., 2018; Martínez-Dios et al., 2020; Movilla et al., 2014a) and enhancing skeletal dissolution (Hennige et al., 2015). Surface ocean pH has already declined by 0.1 units (Orr et al., 2005) and may decrease by a total of 0.16–0.44 units until 2100 compared to pre-industrial times (Kwiatkowski et al., 2020), with similar changes in the deep sea (Gehlen et al., 2014; Sweetman et al., 2017). The higher solubility of CO$_2$ in cold and deep waters reduces the seawater pH and aragonite saturation (Ω_{arag}) in natural CWC habitats (Guinotte et al., 2006; Orr et al., 2005). Due to the rise of the aragonite saturation horizon, about 70 % of CWCs are predicted to occur at aragonite undersaturation ($\Omega_{arag} < 1$) by 2100 (Guinotte et al., 2006). Some CWCs already occur at $\Omega_{arag} \leq 1$ in Chilean

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fjords (Fillinger and Richter, 2013), the Gulf of Mexico (Georgian et al., 2016a), SW Australia (Thresher et al., 2011) and the N Pacific Ocean (Baco et al., 2017). Previous studies indicate that CWCs may be able to maintain their calcification (Gori et al., 2016; Hennige et al., 2014) and respiration rates (Carreiro-Silva et al., 2014; C. Maier et al., 2016) over large pCO$_2$ ranges and even at $\Omega_{arag} < 1$ (Form and Riebesell, 2012; Hennige et al., 2015). However, the duration of exposure to low pH influences their physiological response (Form and Riebesell, 2012; Kurman et al., 2017). CWCs up-regulate genes for the calcification process (Carreiro-Silva et al., 2014), the pH in their calcifying fluid (McCulloch et al., 2012; Wall et al., 2015) and likely use lipid reserves (Hennige et al., 2014) to maintain these physiological processes at low pH. However, pH up-regulation is an energy-demanding process (McCulloch et al., 2012) and sufficient energy reserves must be available to mobilise lipid reserves.

Temperature is an important environmental driver of CWC distribution (Morato et al., 2020), affecting physiological processes (Dorey et al., 2020; Gori et al., 2016; Naumann et al., 2014). To date, surface water temperatures have already increased by 0.6–0.9 °C (IPCC, 2014) and are projected to increase further by 1.2–2.6 °C until 2100 (Mora et al., 2013), while below the pycnocline, water temperatures are predicted to increase by 0.2–1 °C (Mora et al., 2013; Sweetman et al., 2017). The thermal optimum of most scleractinian CWC species is most likely around 12–14 °C (Brooke et al., 2013; Chapron et al., 2021; Lunden et al., 2014). They can tolerate exposures beyond their thermal optimum for hours to days (Brooke et al., 2013; Dorey et al., 2020) and many CWC species in the deep sea currently live below their thermal optimum (Dorey et al., 2020; Gori et al., 2014; Naumann et al., 2013; Naumann et al., 2014). However, tolerance ranges are species-specific, with a lower thermal range (approx. 6–15 °C) observed for *Caryophylliidae* and *Oculinidae* (Brooke et al., 2013; Büscher et al., 2017; Chapron et al., 2021; Gori et al., 2016; Naumann et al., 2014) with mortalities at 15–17 °C (Brooke et al., 2013; Chapron et al., 2021), compared to the higher thermal range of *Dendrophylliidae* (approx. 10–21 °C) (Gori et al., 2014; Naumann et al., 2013; Reynaud et al., 2021).

Food availability is a key parameter for the physiological performance of CWCs (Baussant et al., 2017; Larsson et al., 2013; Naumann et al., 2011) and their ability to cope with environmental changes (Büscher et al., 2017; Gómez et al., 2018; Maier et al., 2016; Martínez-Dios et al., 2020). CWCs are opportunistic feeders (Mueller et al., 2014), but only zooplankton provides sufficient energy to sustain their metabolism (Höfer et al., 2018; Maier et al., 2021; Naumann et al., 2011). Primary productivity in surface waters (Mora et al., 2013; Sweetman et al., 2017) and particle flux to deep waters (Jones et al., 2014) are expected to decline in the future, which in turn can affect the entire food web at depth, including the zooplankton community (Capuzzo et al., 2018). Therefore, food availability for CWCs is likely to decrease in the future and it is unknown if sufficient energy will be available for CWCs to counteract potential negative effects of abiotic changes.

Most previous studies investigated the effect of a single stressor on CWCs and multiple stressor studies are still scarce, but it is important to explore if one stressor may enhance, reduce or reverse the effect of another (Kroeker et al., 2017). While CWCs may be able to tolerate changes in temperature (Dorey et al., 2020; Naumann et al., 2013), Ω_{arag} (Carreiro-Silva et al., 2014; Form and Riebesell, 2012; Gori et al., 2016; Hennige et al., 2015; Maier et al., 2013; Movilla et al., 2014b; Rodolfo-Metalpa et al., 2015) or food supply (Baussant et al., 2017; Larsson et al., 2013) to some degree, the combination of factors can reveal unexpected negative effects (Büscher et al., 2017). So far, the combined effects of warming and acidification on calcification and respiration rates of *Desmophyllum dianthus* and *Desmophyllum pertusum* (syn. *Lophelia pertusa*) have not shown consistent results (Büscher et al., 2017; Gori et al., 2016; Hennige et al., 2015). Therefore, the interactive effects of ocean acidification and warming on CWCs are still unclear, presumably because *ad libitum* feeding in these studies may have offset the effect of the other factors.

All studies to date have focused on adult CWCs and little is known about how early life stages of CWCs respond to future conditions. Even if adult corals were able to cope with environmental changes, the lower resilience of early life stages may be a bottleneck for survival of the population and species. In tropical and temperate coral recruits, low pH leads to reduced calcification rates (Albright and Langdon, 2011; Albright et al., 2008; Albright et al., 2010; Carbonne et al., 2022; Foster et al., 2015; Jiang et al., 2018) and skeletal deformations (Cohen et al., 2009; Foster et al., 2016). However, feeding has been found to mitigate these negative effects to some extent in juvenile corals (Drenkard et al., 2013; Edmunds, 2011). Elevated temperature increases calcification rates (Jiang et al., 2018), however, in combination with reduced pH, either a significant reduction in calcification rates (Anlauf et al., 2011; Carbonne et al., 2022) or no effect on survival and calcification (Edmunds, 2011; Foster et al., 2015; Jiang et al., 2018) was found. In general, early life stages of marine organisms (Albright, 2011; Byrne and Przeslawski, 2013; Kroeker et al., 2010; Kurihara, 2008) are expected to be particularly sensitive to future changes and the same might be true for CWCs. In this context, calcification of small, and therefore presumably younger, polyps of *D. pertusum* and *D. dianthus* is more affected by low pH than larger polyps (Maier et al., 2009; Martínez-Dios et al., 2020; Movilla et al., 2014a), providing a first indication of higher sensitivity of younger CWC life stages. This clearly underscores the need for a more detailed assessment of the response of early CWC life stages.

The aim of the present study is therefore to investigate the response of different CWC life stages to single and interactive effects of key environmental factors. In a six-month aquarium experiment with a fully crossed factorial design, three life stages (early juveniles, late juveniles and adult corals) of the solitary CWC *Caryophyllia huinayensis* were exposed to a combination of aragonite saturation ($\Omega_{arag} < 1$ and $\Omega_{arag} > 1$), temperature (11 °C and 15 °C) and feeding (8 and 87 µg C L^{-1}). We examined the survival, calcification and respiration rates after one, three and six months to identify temporal changes in their response. As responses to environmental changes are often context-specific, the treatments are based on environmental conditions in their natural habitat in Comau Fjord (Chile) and also represent potential future scenarios.

2. Material and methods

2.1. Study species and sampling

The solitary CWC *C. huinayensis* occurs in the SE Pacific Ocean and in Chilean fjords on and below overhangs, where it is associated with *Desmophyllum dianthus* and *Tethocyathus endesa,* two coral species from the same family Caryophylliidae (Cairns et al., 2005; Försterra and Häussermann, 2003). In Chilean fjords, *C. huinayensis* can reach densities of >4000 individuals m^{-2} (Cairns et al., 2005). In Comau Fjord (Northern Patagonia, Chile), it occurs as shallow as 11 m depth and down to >800 m on the continental slope, but is most abundant in the euphotic zone between 20 and 45 m (Cairns et al., 2005). Here, they are mostly subjected to aragonite oversaturation, while undersaturation occurs in deep waters and the fjord head, covering a pH range of 7.4 to 8.0 (Beck et al., 2022a; Fillinger and Richter, 2013). Water temperature ranges between 11 and 16 °C with highest values and short-term fluctuations in shallow waters (Beck et al., 2022a). Zooplankton biomass in Comau Fjord is four times higher in summer than in winter and decreases with water depth (Garcia-Herrera et al., 2022). To date, no study has investigated the physiological performance of *C. huinayensis*, neither under its natural environmental conditions nor in terms of future predictions, probably due to its small distribution range. However, the close taxonomic proximity to *D. pertusum* and *D. dianthus* from the same family Caryophylliidae, two of the most studied CWC species, suggests that these species are likely to respond similarly to future environmental conditions as *C. huinayensis*.

In 2014 and 2015, specimens of *C. huinayensis* were collected and transported to the culturing aquarium facility at the Alfred Wegener

institute (AWI, Germany). The corals were transferred to 1 L plastic bags containing 500 mL of seawater and pure oxygen. They were placed into an insulated Zarges box and transported from Chile to Germany within two days. We observed no instant or delayed mortality due to the shipment. At AWI, the corals were kept in artificial seawater (Dupla Marin Premium Reef Salt, Dohse Aquaristik GmbH & Co. KG; water exchange of 30 % per week). Until the experiment in 2020, corals were maintained at a temperature of 12.2 ± 0.9 °C, a salinity of 31.9 ± 0.5, a pH of 8.0 ± 0.1 and Ω_{arag} of 2.29 ± 0.50, reflecting mean annual *in situ* conditions (Beck et al., 2022a). However, the carbonate chemistry of the artificial seawater differs from natural seawater because the mean total alkalinity (TA) and dissolved inorganic carbon (DIC) are approx. 26 % higher than in Comau Fjord (Table 1) (Beck et al., 2022a), with increased TA values facilitating coral calcification. Corals were fed with freshly hatched *Artemia persimilis* nauplii (Aquakultur Genzel GmbH) three times per week and with thawed juvenile krill *Euphausia pacifica* (Zierfischfutterhandel Norbert Erdmann e.K.) once a week.

The corals have reproduced since 2014, which provided the opportunity to investigate the response of different life stages of the same population to environmental changes. The life cycle of *C. huinayensis* has recently been studied (Heran et al., 2023) and the corals were divided into three ontogenetic stages depending on their size (Supplementary Methods). Corals with a calyx diameter of 10.0 ± 2.0 mm were considered adults, while smaller corals were divided into early (diameter: 3.0 ± 0.5 mm) and late (diameter: 4.5 ± 0.8 mm) juveniles. Four weeks before the start of the experiment (September 2020), a total of 144 specimens were selected (48 early juveniles, 48 late juveniles, 48 adults) and glued on labelled polyethylene screws using Preis Easy Glue Underwater (Preis Aquaristik KG). To enable structural and geochemical analyses of the skeletons (not part of this study), corals were also stained with 50 mg L^{-1} fluorescent Calcein for 16–17 h at the same time.

2.2. Experimental design and setup

2.2.1. Experimental design

The experiment was run for six months from October 2020 until April 2021 in a dark, thermostatically controlled room. The experimental design was a three-factor design with a combination of two scenarios of Ω_{arag}, temperature and food availability. The effects of temperature and Ω_{arag} were examined individually and in combination in four experimental units with the following treatments (Fig. 1): 1) ambient: Ω_{arag} >

1 (pH_T 8.0) and 11 °C, 2) Ω: Ω_{arag} < 1 (pH_T 7.5) and 11 °C, 3) temperature: Ω_{arag} > 1 (pH_T 8.0) and 15 °C and 4) combined: Ω_{arag} < 1 (pH_T 7.5) and 15 °C. The Ω_{arag} treatments represent present-day pH_T conditions and the IPCC climate change scenario SSP5–8.5 with a −0.44 drop in pH in the euphotic zone until 2100 (Kwiatkowski et al., 2020). Each of the four experimental units for the physico-chemical treatments consisted of one large sump tank (80 L) and four aquarium tanks (36 L, Fig. 1). Two of these aquaria were used for the low feeding regime and two for the high feeding regime with *A. persimilis* nauplii (LF: 8.4 μg C L^{-1} and HF: 86.8 μg C L^{-1}, see below). Due to the complexity of eight treatments and the available control system for temperature and Ω_{arag} conditions, it was not possible to have truly independent aquaria for each treatment. Even though this is a pseudo-replicated design (Hurlbert, 1984), the advantage was to conduct a long-term experiment with simultaneous manipulation of eight combinations of temperature, Ω_{arag} and feeding conditions. Each aquarium tank contained nine corals, three individuals per life stage (Supplementary Methods).

2.2.2. Experimental setup

The water flow rate between the sump tank and the four aquarium tanks was 5–10 L min^{-1}. A small pump in each aquarium ensured constant water circulation. The same artificial seawater as in the culturing facility was used to facilitate rapid acclimation of the corals. Approx. 25 L of the water was changed per week (10 % of total volume). To achieve target conditions, the Ω_{arag} was lowered by injecting pure CO_2 gas into a separate container within the sump tank (targeting low pH within this container). Water from this container was then injected in small amounts into the sump of the recirculating experimental units. The supply of CO_2 gas and of low pH water into the experimental units was manipulated with a digital control system (iks aquastar, iks Computer-Systeme GmbH) and pH sensors that were calibrated once a week with pH buffers 7 and 9 (VWR). The iks pH sensors were cross-referenced with an additional pH meter (WTW pH 3310, Xylem Analytics), which was calibrated to the total scale with TRIS-HCl buffer. The water temperature was also controlled by the iks system with a heater submerged in the sump tank. In addition, water parameters were regularly monitored with the iks system (temperature and pH), additional sensors (pH, oxygen and salinity) and temperature loggers. Furthermore, we took water samples for TA and nutrients once per week (Supplementary Methods). Constant treatment conditions prevailed during the experiment with an ambient temperature of 11.2 ± 0.1 °C and an elevated

Table 1

Water parameters of four experimental treatments and in Comau Fjord, Chile.

Experimental temperature, salinity, oxygen pH_T (total scale) were measured daily and total alkalinity (TA) weekly. Dissolved inorganic carbon (DIC), pCO_2 and aragonite saturation (Ω_{arag}) were calculated from TA and pH_T using CO2SYS (Pierrot et al., 2006). *In situ* data are from Beck et al. (2022a). All values are stated as mean ± standard deviation (SD).

| Treatment	Salinity	Oxygen (mg L^{-1})	Temperature (°C)	pH_T	TA (μmol kg^{-1})	DIC (μmol kg^{-1})	pCO_2	HCO_3^- (μmol kg^{-1})	CO_3^{2-} (μmol kg^{-1})	CO_2 (μmol kg^{-1})	Ω_{arag}
Ambient	31.6 ± 0.2 (31.1; 32.0)	8.94 ± 0.09 (8.98; 9.12)	11.2 ± 0.1 (11.0; 11.3)	8.06 ± 0.03 (7.99; 8.16)	2730 ± 79 (2602; 2848)	2532 ± 75 (2398; 2634)	476 ± 36 (369; 552)	2353 ± 71 (2222; 2455)	158 ± 11 (136; 186)	20 ± 2 (16; 24)	2.44 ± 0.16 (2.09; 2.86)
Ω	31.5 ± 0.1 (31.2; 31.9)	8.93 ± 0.10 (8.96; 9.11)	11.2 ± 0.1 (10.6; 11.4)	7.54 ± 0.04 (7.45; 7.64)	2719 ± 64 (2619; 2808)	2719 ± 63 (2621; 2830)	1725 ± 160 (1396; 2064)	2591 ± 60 (2498; 2694)	53 ± 5 (47; 66)	74 ± 7 (59; 88)	0.82 ± 0.08 (0.72; 1.02)
Temperature	31.6 ± 0.1 (31.3; 32.1)	8.37 ± 0.23 (8.16; 8.44)	15.0 ± 0.1 (14.8; 15.4)	8.05 ± 0.02 (8.00; 8.12)	2648 ± 34 (2566; 2701)	2427 ± 29 (2361; 2475)	473 ± 23 (424; 522)	2238 ± 26 (2183; 2282)	172 ± 8 (155; 193)	18 ± 1 (16; 20)	2.67 ± 0.12 (2.41; 3.00)
Combined	31.6 ± 0.2 (31.2; 32.0)	8.33 ± 0.23 (8.17; 8.47)	15.1 ± 0.1 (14.9; 15.3)	7.50 ± 0.04 (7.42; 7.58)	2671 ± 48 (2587; 2737)	2666 ± 50 (2597; 2746)	1902 ± 186 (1585; 2175)	2538 ± 47 (2471; 2613)	56 ± 5 (48; 66)	72 ± 7 (60; 82)	0.86 ± 0.08 (0.75; 1.03)
In situ	31.9 ± 1.0	6.66 ± 0.90	12.3 ± 0.7	7.81 ± 0.11	2136 ± 53	2046 ± 70	707 ± 201	1938 ± 74	78 ± 15	30 ± 8	1.2 ± 0.2
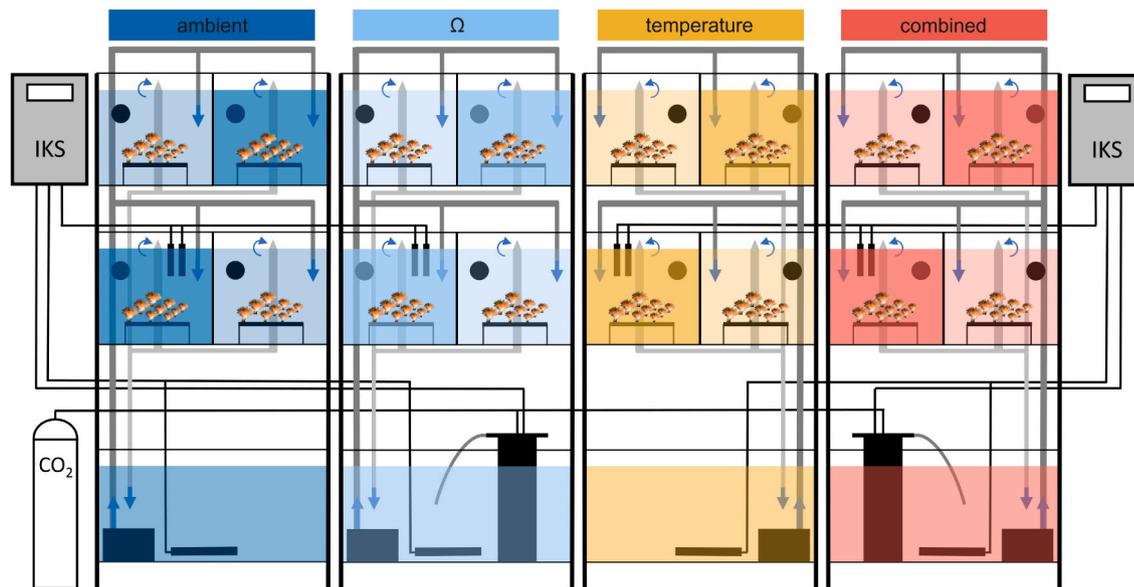
Fig. 1. Experimental setup. Each recirculating experimental unit for the four physico-chemical treatment combinations consisted of one sump tank (80 L) at the bottom and four aquarium tanks (35 L each) on top. Water flow out of the sump and into the aquarium tanks is indicated by blue arrows. Temperature and pH were controlled by computer systems (one for two aquarium systems) and measured in one of the four aquaria of each system. The sump was equipped with a heater to maintain the temperature at ambient or elevated temperature conditions and a CO_2 gas mixing device in the experimental units with aragonite undersaturation, where low pH water was added from a separate container in the sump. Two aquaria in each experimental unit were used for the low feeding regime (light colours) and two for the high feeding regime (dark colours). Each aquarium was equipped with one small water circulation pump (circle) and contained nine corals (three early juveniles, three late juveniles and three adults).

temperature of 15.1 ± 0.1 °C (Table 1, Fig. S1). The Ω_{arag} was 2.4 ± 0.2 and 2.7 ± 0.1 in the two treatments at ambient Ω_{arag} (pH_T: 8.06 ± 0.03 and 8.05 ± 0.02; pCO_2: 476 ± 36 and 473 ± 23) and 0.8 ± 0.1 and 0.9 ± 0.1 in the low Ω_{arag} treatments (pH_T: 7.54 ± 0.04 and 7.50 ± 0.04; pCO_2: 1725 ± 160 and 1902 ± 186; Table 1, Fig. S1). TA and DIC ranged from 2648 ± 34 μmol kg^{-1} to 2730 ± 79 μmol kg^{-1} and 2427 ± 29 μmol kg^{-1} to 2719 ± 63 μmol kg^{-1}, respectively, in the four treatments. The nutrient concentrations (silicate, phosphate, nitrate, nitrite and ammonium) were similar in all four experimental treatments, with silicate of 5.52 ± 2.49 μmol L^{-1}, phosphate of 1.68 ± 1.41 μmol L^{-1}, nitrate of 52.25 ± 35.67 μmol L^{-1}, nitrite of 0.29 ± 0.30 μmol L^{-1} and ammonium of 1.01 ± 0.92 μmol L^{-1} in all treatments (Table S1).

2.2.3. Experimental feeding conditions

We used *A. persimilis* nauplii as food source and aimed for low (LF) and high (HF) food supply. In a short-term pilot study, the ratio between HF and LF was determined (Supplementary Methods), confirming the previously used approx. 10-fold difference in food supply (12). High food concentrations were similar to the conditions in the culturing aquarium system (but without additional krill) and to maximum food availability in the photic zone of Comau Fjord in summer, whereas low food concentrations resembled minimum food availability in the aphotic zone in winter (calculated after Garcia-Herrera et al., 2022). However, the *in situ* zooplankton biomass data (Garcia-Herrera et al., 2022) was determined from mesozooplankton and is therefore a conservative estimate because larger plankton and euphausiids were not considered. Food availability was governed by concentration (nauplii per volume) and exposure time (feeding days), with nominally twelve times lower food availability in LF compared to HF. Corals in the LF regime were fed once per week, while HF corals were fed three times per week. A total of

0.5 g and 2 g dry cysts were used for LF and HF, respectively (Supplementary Methods). This resulted in 235 ± 63 nauplii L^{-1} for LF and 810 ± 303 nauplii L^{-1} for HF, corresponding to 940 ± 250 nauplii coral^{-1} and 3240 ± 1213 nauplii coral^{-1}, respectively, during each feeding period. We assume (1) a type I functional response for all Caryophyllidae (Höfer et al., 2018), (2) continuous feeding of corals, (3) well-mixed aquaria and (4) the food exposure being equivalent to concentration. This corresponds to an effective ten times difference in food supply of 8.4 ± 2.3 μg C L^{-1} (33.6 ± 8.9 μg C coral^{-1}) for LF and 86.8 ± 32.5 μg C L^{-1} (347.1 ± 130.0 μg C coral^{-1}) for HF (Supplementary Methods).

2.2.4. Experimental timeline

The corals were acclimatised to the experimental aquarium system for 20 days before the conditions were changed. During acclimatisation, all corals received the same amount of *A. persimilis* nauplii (2 g dry cysts for all corals) three times per week, which corresponds to half the amount of food of the HF regime. The four physico-chemical treatments were started consecutively over a period of two weeks, ensuring that the physiological measurements always took place in the same time interval after starting the experiment. Water parameters were gradually adjusted from ambient to experimental conditions over five days, with a change of 0.05 pH units and 0.5 °C every 12 h and simultaneous changes of feeding (Fig. 2).

2.3. Physiological measurements

Coral conditions were monitored by regular photo-documentation and an assessment of physiological performance (calcification and respiration) after one (T_1), three (T_2), and six (T_3) months. Photo documentation was used to assess the survival, health status and somatic
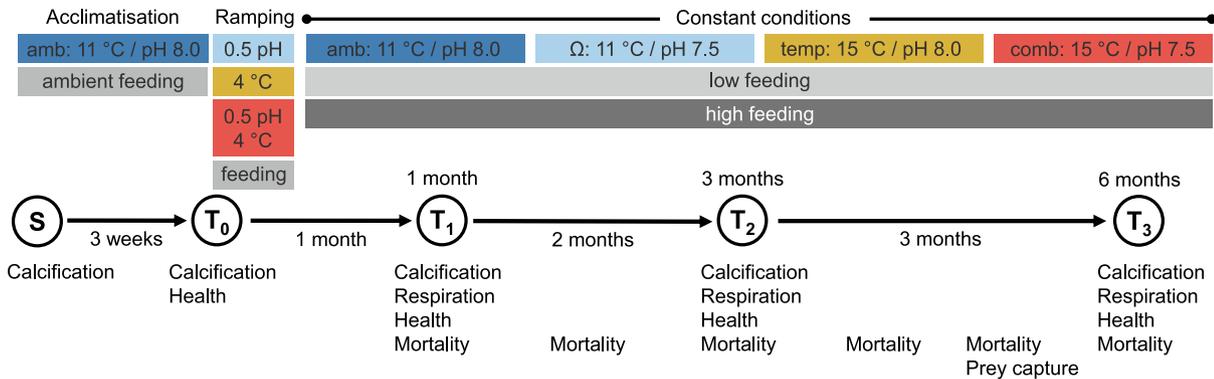
Fig. 2. Experimental timeline. During the acclimatisation period of 20 days, the conditions in the experimental units were 11 °C and pH 8.0 and *Caryophyllia huinayensis* was fed three times per week with the same amount of *Artemia persimilis* nauplii in all experimental aquaria. Following the acclimatisation period, water parameters were gradually adjusted from ambient to final experimental conditions over five days with changes of 0.05 pH units and 0.5 °C every 12 h to target conditions of: 1) amb (dark blue): 11 °C and $\Omega_{arag} > 1$, 2) Ω (light blue): 11 °C and $\Omega_{arag} < 1$, 3) temp (yellow): 15 °C and $\Omega_{arag} > 1$, 4) comb (red): 15 °C and $\Omega_{arag} < 1$, which were kept constant for six months. At the same time, feeding conditions were changed to the treatment conditions of low and high feeding with a twelve times difference in food concentration. The four physico-chemical treatments and the feeding regimes (including the acclimatisation period) were started in a staggered manner over two weeks. This ensured that the following physiological measurements of the corals always took place at the same time interval after the start of the experiment for all treatments. Corals were weighed before and after the acclimatisation period and after one, three and six months of the experiment to determine calcification rates. Respiration rates were also measured at the same three time points of the experiment. The health status of all corals was checked at the beginning of the experiment and after one, three and six months. Mortality rates were determined every month and prey capture rates were determined after five months.

growth.

2.3.1. Health status and survival

The lateral sides of the corals were photographed once a week using a digital camera (DSC-RX10M4, Sony Group Corporation). Pictures of the oral side of the corals were taken at the beginning and end of the experiment using a SLR camera (Nikon D3200 with a microscope adapter, Nikon Corporation) connected to a stereomicroscope (SteREO Discovery.V8, Carl Zeiss MicroImaging GmbH). We used the tissue covered surface area of the corals as proxy for their health status. Based on the lateral pictures, corals were classified into three health categories depending on the tissue coverage of their skeleton (Fig. 3) and survival rates were assessed monthly. The health categories were defined as: 1) calyx fully (or partly) covered with tissue on the lateral and oral side, 2) only oral side of calyx fully (or partly) covered with tissue, lateral side not covered with tissue, 3) dead, bare skeleton without tissue or only tissue remains. Dead corals were excluded from respiration and calcification measurements.

2.3.2. Somatic growth

The change in tissue covered surface area (%) between the start and end of the experiment was used to assess somatic growth. The tissue covered surface area of the corals was measured with a digital calliper (reading to 0.01 mm) and calculated geometrically after Naumann et al. (2009) using the formula of a truncated cone (Supplementary Methods) (Gori et al., 2014; Gori et al., 2016). To normalise the calcification and

respiration rates, the surface area was determined after one, three and six months.

2.3.3. Calcification

We used the buoyant weighing technique (Jokiel et al., 1978) to assess calcification rates with an electronic underfloor balance (Sartorius CPA 225D-OCE, Sartorius AG; precision: 0.01 mg) mounted above an aquarium. Seawater conditions were adjusted to treatment conditions and measured continuously for seawater density calculations (Jokiel et al., 1978). Skeletal dry mass was calculated using the densities of seawater and the skeleton of *C. huinayensis* (2.7397 ± 0.0437 g cm^{-3}; Supplementary Methods). Calcification rates were normalised to initial skeletal dry mass (% d^{-1}) and tissue covered surface area (mg cm^{-2} d^{-1}; Supplementary Methods).

2.3.4. Respiration

Respiration rates were measured in closed-cell incubations (15 and 25 mL; Fig. S2a) in a temperature-controlled water bath (11 °C and 15 °C) on a submergible magnetic stirring table (170 rpm; Fig. S2b) over 6–18 h (for full details see Supplementary Methods). Briefly, we used a fibre optic oxygen meter system (FSO2-4 and FSPRO-4, PyroScience GmbH) with contactless optical fibre oxygen sensors (SPFIB-BARE, PyroScience GmbH), oxygen sensor spots (OXSP5, PyroScience GmbH) and Pt100 temperature probes (TSUB21, PyroScience GmbH; Supplementary Methods).

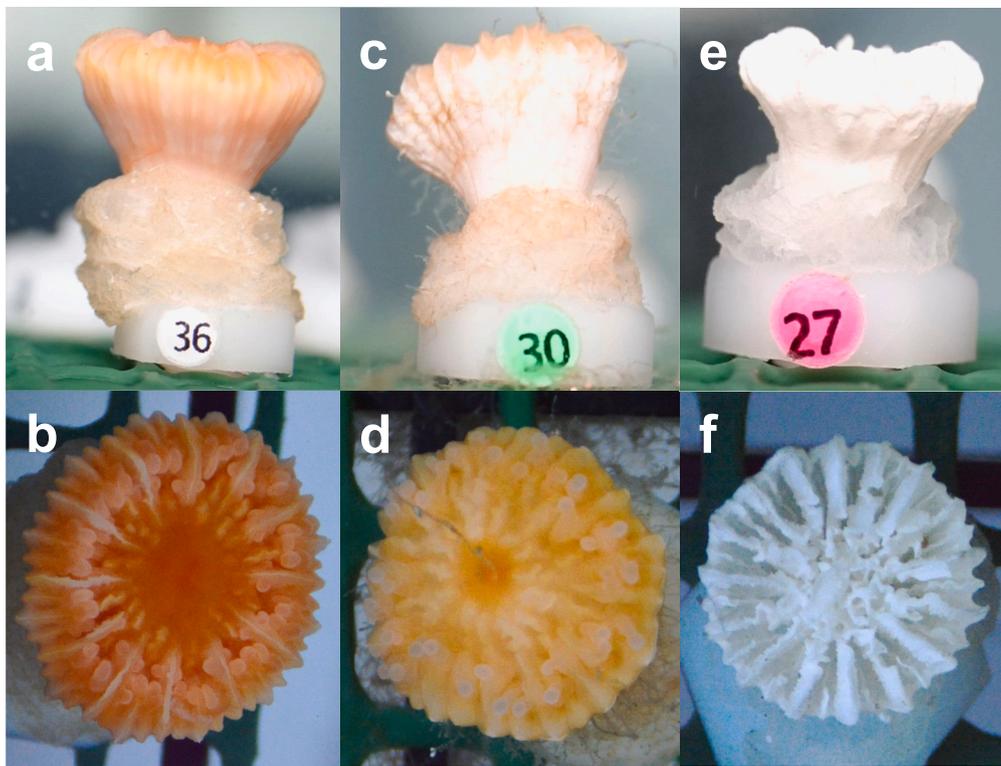All corals of the same life stage of one treatment were incubated at

Fig. 3. Health categories of *Caryophyllia huinayensis*. Photographs of the lateral (a, c, e) and oral side (b, d, f) of *C. huinayensis*. Corals were divided into three health categories depending on the tissue coverage of their skeleton after one, three and six months. Health categories are defined as: 1) calyx fully (or partly) covered with tissue on the lateral and oral side (a, b), 2) only oral side of calyx fully (or partly) covered with tissue, lateral side not covered with tissue (c, d), 3) dead, bare skeleton without tissue or only tissue remains (e, f). Dead corals were excluded from respiration and calcification measurements.

the same time after the start of the experiment ($\pm$ 1 day), resembling the applied shift in the start of the experimental conditions. To achieve this, the respiration procedure had to be adapted to other commonly used approaches. Instead of parallel background measurements in separate vials, each incubation vial was initially only filled with seawater from the respective experimental unit, closed hermetically and background measurements were conducted for 4 h. Afterwards, the corals were screwed in the lid of the incubation vials in their natural downward orientation and the oxygen measurements continued. The respiration rate of adult corals was measured in closed-cell incubations over 6 h, of late juveniles over 12 h and of early juveniles over 18 h in the dark. The oxygen concentration in the vials was measured in % air saturation by the software (PyroOxygenLogger Version 3.317 for FSO2-4 and Pyro-Workbench Version 1.2.0.1359 for FSPRO-4) in order to have a direct control on the respiration rate and ensure that it did not decrease too much (below 60 %). Respiration data in % were converted into mg L^{-1} and the respiration rate of the corals was calculated by linear regression of the oxygen depletion using the software R (R Core Team, 2021) and package *rMR* (Moulton, 2018). The slope of the respiration rates was analysed for 2 h intervals for late juveniles (six intervals over 12 h) and adults (three intervals over 6 h) and for 3 h intervals for early juveniles (six intervals over 18 h) and used to calculate the mean respiration rates over the whole time interval (Fig. S3). The script involved quality control steps and corrected for mean background respiration measured prior to the start of the incubations as well as for the incubation volume. Respiration rates were normalised to tissue covered surface area (mg O$_2$ cm^{-2} d^{-1}).

2.3.5. Prey capture rate

After five months, the prey capture rate was determined separately for each individual in incubation glass vials (volume: 110 mL). The vials were placed in a temperature-controlled water bath (11 °C and 15 °C) on a submersible magnetic stirring table (low speed of 180 rpm to avoid damaging the nauplii), where glass-coated magnetic stir bars kept the *Artemia* nauplii in suspension (Supplementary Methods). Freshly hatched nauplii were counted under a stereo microscope (475002-9902,

Carl Zeiss MicroImaging GmbH). LF and HF corals were fed 30 and 120 nauplii, respectively, corresponding to concentrations of 0.27 nauplii mL^{-1} and 1.09 nauplii mL^{-1}. Prey capture rate was expressed as the number of ingested nauplii coral^{-1} h^{-1}. The ash-free dry mass (AFDM) and organic carbon (C) content of nauplii were determined (Supplementary Methods). The uptake of nauplii organic matter (OM) was normalised to the coral surface area and expressed as mg OM cm^{-2} h^{-1} and C uptake in μmol C cm^{-2} h^{-1} and μmol C g^{-1} skeletal mass h^{-1} (Table S2).

2.4. Statistical analysis

All statistical analyses were performed using the software R (version 4.1.0) (R Core Team, 2021). Survival probability was calculated according to the Kaplan-Meier model using the package *survminer* (Kassambara et al., 2021). A generalized linear model (GLM; *glm*) was used to investigate differences in survival between treatments, life stages and feeding. Post-hoc comparisons were performed with the function *glht* of the package *emmeans* (Lenth, 2023). As the surface area change, prey capture, prey uptake, calcification and respiration were not normally distributed (Shapiro-Wilk test), we used linear mixed effect models (LMM; *lmer*) to examine the relationship between the response variables and treatments, life stages and feeding as fixed factors using the package *lme4* (Bates et al., 2015). For all parameters, one model was used with the data after six months, considering aquaria as random factor (1| aquarium) because of the pseudo-replicate design. A second model was used for calcification after one and three months to test for the delayed effect, with duration as fixed factor and (1|aquarium/coral_ID) as random factor because of the pseudo-replicate and repeated measures design. Post-hoc comparisons of significant effects were tested using the *lsmeans* function of the package *lsmeans* (Lenth, 2016). The effect size (mean difference) in calcification was calculated using the package *dabestr* (Ho et al., 2019).

3. Results

3.1. Health status and survival

Elevated temperature had the strongest negative effect on the health status of all life stages over six months (Fig. 4, Fig. S4, Table S3). This resulted in moribund corals and high mortality (47 %) after more than three months in adult and early juvenile corals (GLM, ambient – temperature: *p*-value <0.001; Tables S3–S5). Surprisingly, the combined effect of aragonite undersaturation and elevated temperature resulting in 28 % mortality appeared to be less severe than elevated temperature alone (GLM, ambient – temperature: *p*-value = 0.051; Tables S3–S5). Overall, mortality was highest in adult corals (18 of 48) compared to late juveniles (2 of 48), which represented the most resilient and healthy life stage (GLM, adult – late juvenile: p-value <0.001; Tables S3–S5). Food limitation deteriorated coral health and HF corals were overall healthier (42 corals in category 1) and had lower mortality (15 %) than LF corals (37 corals in category 1, 24 % mortality).

3.2. Somatic growth

Early and late juvenile corals maintained or even increased their tissue covered surface area by 35–60 % in the ambient and $\Omega < 1$ treatments under high food availability (LMM, feeding: *p*-value = 0.038; Fig. 5, Tables S3, S6 and S7). However, reduced food availability lead to only slight increases in the tissue covered surface areas of early juveniles and decreasing surface areas in late juveniles. Adult corals, by contrast, responded with an overall tissue retraction of 40 % in these two treatments with little to no differences between feeding regimes. This suggests that neither feeding regime provided enough energy to sustain the tissue covered surface area in adult corals (LMM, adult – early/late juvenile: *p*-value <0.001; Tables S3, S6 and S7). However, all life stages significantly retracted their tissue by an average of 70 % under elevated temperature (irrespective of aragonite saturation, except for late juveniles) compared to ambient temperature (LMM, ambient – temperature: *p*-value <0.001; Tables S3, S6 and S7) and not even the HF regime could compensate for this response.

3.3. Calcification

Throughout the experiment, a clear delay in response was apparent in the health status (Fig. 4) and calcification rates (Fig. 6). The treatment and feeding conditions did not affect the calcification rates in the first month, irrespective of the life stage. Subsequently, calcification rates declined under LF and elevated temperatures, with significantly lower rates after three months (LMM, *p*-value <0.001; Tables S3, S6 and S7). As expected and similar to somatic growth, calcification rates differed significantly between life stages after six months, with highest calcification in early juveniles and lowest in adult corals (LMM, p-value <0.001; Tables S3, S6 and S7). In general, net calcification rates (calcification minus dissolution) of adult corals were 3.4–6 times lower (1 month: 0.087 ± 0.066 mg cm^{-2} d^{-1}, 6 months: 0.055 ± 0.055 mg cm^{-2} d^{-1}) than in early and late juvenile corals (1 month: 0.363 ± 0.245 mg cm^{-2} d^{-1}, 6 months: 0.284 ± 0.234 mg cm^{-2} d^{-1}) throughout the whole experiment, leading to less pronounced treatment effects. Some adult corals even showed negative values after 3–6 months of the experiment, indicating that dissolution outweighed calcification under the respective treatment conditions.

Aragonite undersaturation alone had no significant effect on calcification rates of all three life stages of *C. huinayensis* over six months (LMM, ambient – Ω: p-value = 1; Fig. 6, Tables S3, S6 and S7). In contrast, low food availability and elevated temperature as single factors had the strongest effect on all life stages (Tables S3, S6 and S7). Under ambient conditions, calcification of early juveniles decreased by a factor of 4.4 from 0.513 ± 0.299 mg cm^{-2} d^{-1} to 0.118 ± 0.035 mg cm^{-2} d^{-1} due to food limitation, whereas it only decreased by a factor of 3.5 and

1.3 in late juvenile and adult corals, respectively (Table S3). Elevated temperature had an even stronger effect on calcification in juvenile corals than food limitation, with seven times lower calcification rates under HF (0.073 ± 0.092 mg cm^{-2} d^{-1} and 0.062 ± 0.059 mg cm^{-2} d^{-1} for early and late juveniles, respectively). However, warming had no clear effect on the calcification rates of adult corals. Food limitation in combination with elevated temperature further reduced calcification only in early juveniles by a factor of 1.8 (0.039 ± 0.122 mg cm^{-2} d^{-1}).

3.4. Respiration

Interestingly, respiration rates were similar between life stages and feeding regimes in the ambient and $\Omega < 1$ treatments (Fig. S5). However, respiration rates of early juveniles increased by a factor of up to 4.8 at elevated temperature (LMM, *e.g.* ambient – temperature: *p*-value <0.001; Fig. S5, Tables S3, S6 and S7). Respiration rates also became more variable, potentially as a result of reduced biomass and lower numbers of surviving individuals in the elevated temperature and combined treatments. Early and late juveniles reduced their respiration rates after six months under ambient conditions and at aragonite undersaturation (Fig. S5).

3.5. Prey capture rates

Prey capture rates did not differ between treatments and life stages, but between feeding regimes (LMM, p-value <0.001; Fig. S6a, Tables S2, S6 and S7), with four times higher captures rates under HF (HF: 18.25 ± 10.92 nauplii coral^{-1} h^{-1}, LF: 4.39 ± 3.83 nauplii coral^{-1} h^{-1}). The same amount of captured *Artemia* nauplii resulted in significant differences in OM and C uptake between life stages (LMM, p-value <0.001; Fig. S6b, Tables S2, S6 and S7). Early juveniles (0.259 ± 0.181 mg cm^{-2} h^{-1}) ingested 2.6 times more OM than late juveniles (0.100 ± 0.093 mg cm^{-2} h^{-1}) in the HF regime and as much as nine times more than adult corals (0.028 ± 0.019 mg cm^{-2} h^{-1}). Therefore, juveniles received relatively more energy than adult corals. The uptake rates were four times lower for juveniles in the LF than HF regime and even 5.6 times lower for adult corals in the LF regime, which is consistent with the four times higher food availability and capture rates (Table S2).

4. Discussion

This is the first study examining the response of different CWC life stages to the single and combined effects of ocean acidification, warming and reduced food availability. Importantly, none of the treatments resulted in severe short-term effects (≤ 3 months), but reduced feeding and warming negatively affected all life stages after six months. While juvenile corals mainly reduced their calcification rates, adult corals showed a stronger health decline and the highest mortality rates.

4.1. Response of life stages

Early life stages of CWCs were clearly characterized by faster calcification rates compared to adult corals, corroborating observations for the same species (T. Heran, pers. comm.) and other CWC species (Maier et al., 2013; Martínez-Dios et al., 2020; Movilla et al., 2014b). Most of the available energy in early life stages of tropical corals is allocated to calcification (Hughes and Jackson, 1985; Zilberberg and Edmunds, 2001) as high calcification rates are essential to quickly reach sexual maturity. In contrast, adult tropical corals invest a higher fraction of their energy into reproduction and less in maintaining calcification rates (Leuzinger et al., 2003; Leuzinger et al., 2012). In the present study, early juveniles were more sensitive than adults to reduced food supply and increased temperatures, almost halving their calcification rates based on absolute changes (but slightly less when expressed in relative changes; mean difference of -0.29 ± 0.05 and -0.27 ± 0.05 compared
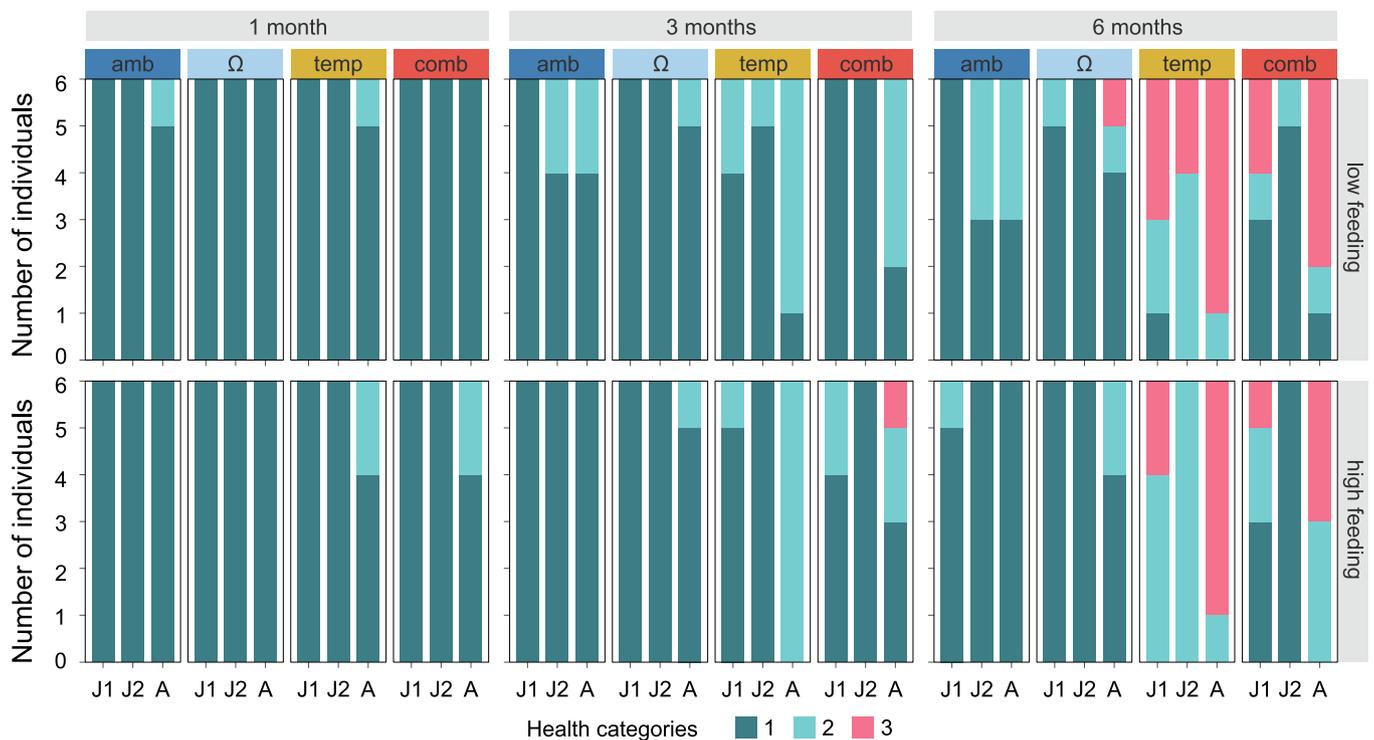
Fig. 4. Health status of three life stages of *Caryophyllia huinayensis* after one, three and six months under different Ω, temperature and feeding conditions. Health status of early juveniles (J1), late juveniles (J2) and adult corals (A) under low and high feeding. Treatment conditions: 1) amb (dark blue): 11 °C and $\Omega_{arag} > 1$, 2) Ω (light blue): 11 °C and $\Omega_{arag} < 1$, 3) temp (yellow): 15 °C and $\Omega_{arag} > 1$, 4) comb (red): 15 °C and $\Omega_{arag} < 1$. Three health categories: 1) calyx fully or partly covered with tissue on lateral and oral side, 2) only oral side of calyx fully or partly covered with tissue, 3) dead corals.

to -0.15 ± 0.04; Fig. 7). Calcification is the most commonly studied trait when investigating the effects of climate change on CWCs. However, in the present study, we also examined the general health status, survival and somatic growth of the corals and found a contrasting picture. While adult corals seem to be less vulnerable in terms of calcification, this impression differs for other traits. Adult corals showed poorer health, reduced somatic growth and higher mortality rates than juvenile corals under warming and reduced food availability. The reduced somatic growth rates suggest that adult corals invest less energy into the build-up of tissue and potentially also deplete their energy reserves as has been observed in *D. pertusum* and *M. oculata* in response to elevated temperatures (Chapron et al., 2021). Therefore, calcification is not the most appropriate trait to determine the sensitivity of adult CWCs to environmental changes due to their overall lower calcification rates.

This is also the first study revealing developmental trade-offs in CWCs and a shift from the predominant investment in calcification to tissue maintenance. Our findings are in contrast to the general assumption that early life stages are most vulnerable to environmental changes (Byrne and Przeslawski, 2013), as we clearly show that the response depends on the investigated traits. Our finding of reduced calcification rates in juvenile CWCs suggests a delayed maturation under future warming. This has further consequences for the maintenance of the whole population, suggesting that early life stages may be an important bottleneck for their persistence. In contrast, the smaller treatment effect on adult corals suggests a higher resilience of adult CWCs to environmental changes in terms of calcification. However, the stressful and limiting conditions of the present study pushed the adult corals to their tolerance limits as their higher energy demand for tissue maintenance and lower survival probability make them even more vulnerable to future changes. This could lead to a reduced number of mature corals in the future and thus reduce the reproductive output of the population.

4.2. Effect of reduced feeding

At ambient temperatures, reduced food availability clearly provided less energy for juvenile corals to maintain their calcification and respiration rates, while health and somatic growth rates of adult corals decreased. Even though the trend of decreasing respiration rates is small, this may indicate a downregulation of their metabolism at ambient temperature and reduced food uptake over the course of the experiment as has also been observed after long-term starvation periods in *D. pertusum* (Baussant et al., 2017; Larsson et al., 2013). This can either mean that less energy was available at the end of the present experiment or that the available energy was invested into other processes instead. Energy deficiency was apparent in both feeding regimes at elevated temperatures across life stages, even though prey capture rates were unaffected by treatment conditions. This is in accordance with findings for closely related Caryophyllidae (*D. dianthus* (Gómez et al., 2018; Gori et al., 2015) and *D. pertusum* (Baussant et al., 2017; Maier et al., 2016)), even though some other studies found an influence of treatment conditions in *D. pertusum* and *M. oculata* (Chapron et al., 2021; Georgian et al., 2016b; Gómez et al., 2022).

Efficient use of zooplankton are critical to meet the metabolic demands of CWCs (Höfer et al., 2018; Maier et al., 2016; Purser et al., 2010). However, most feeding studies did not find an effect of 10–15 times higher food availability on calcification rates of *D. pertusum* (Baussant et al., 2017; Büscher et al., 2017; Larsson et al., 2013), which is unexpected. One explanation may be that corals aim for a certain calcification rate, and once this is reached, no more energy can be channelled into calcification. This could also be a consequence of *ad libitum* feeding (see Höfer et al., 2018), where corals potentially start investing more energy into the build-up of energy reserves. Another explanation could be that corals in the feeding studies were not able to efficiently extract the provided food. Species-specific differences may also be an explanation as increasing calcification have only been reported in *D. dianthus* and *C. huinayensis* at 2.5–12 times higher food
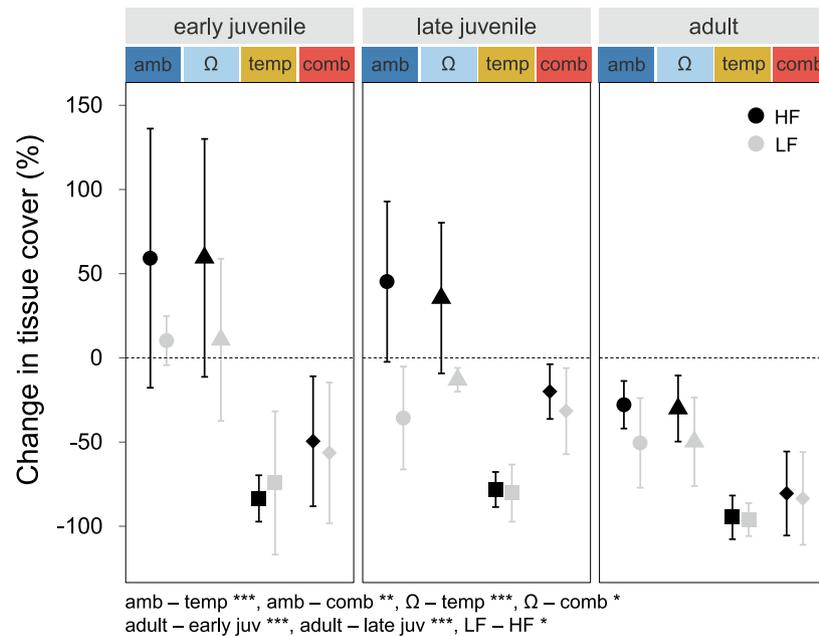
Fig. 5. Somatic growth of three life stages of *Caryophyllia huinayensis* after six months under different Ω, temperature and feeding conditions. Change in tissue cover (%) of early juveniles, late juveniles and adult corals under high (HF, black) and low (LF, grey) feeding ($N = 6$). Treatment conditions: 1) amb (dark blue): 11 °C and $\Omega_{arag} > 1$, 2) Ω (light blue): 11 °C and $\Omega_{arag} < 1$, 3) temp (yellow): 15 °C and $\Omega_{arag} > 1$, 4) comb (red): 15 °C and $\Omega_{arag} < 1$. Values are stated as mean ± standard deviation. Significant effects are indicated when present: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

availability (Martínez-Dios et al., 2020, this study). In the present study, a ten times higher food supply resulted in only 3.5–4.4 or 1.3 times increase in calcification at ambient temperature in juvenile and adult corals, respectively. This is in contrast to the five times higher calcification rates of *D. dianthus* under a 2.5-fold food increase (Martínez-Dios et al., 2020). Therefore, *C. huinayensis* appears to invest more into calcification under food limitation. In general, a direct comparison of feeding studies is difficult as different types of food are used and information on organic C uptake is barely provided. In the present study, C uptake in adult corals was within the range of Maier et al. (2016) when extrapolated to one week (1.92 and 11.7 μmol C g⁻¹ skeletal dry mass d⁻¹ for LF and HF, respectively; Table S2), which was insufficient to meet the metabolic demand of adult corals. As Maier et al. (2016) only found a short-term effect of feeding on calcification, this may indicate that the corals in both feeding regimes were not able to consume enough food in the long term and were starving.

Low feeding in the present study was chosen to mimic *in situ* oligotrophic conditions in Comau Fjord in winter (Garcia-Herrera et al., 2022), but discounted the natural zooplankton patchiness and likely occurrence of krill swarms (pers. obs.). This conservative estimate allowed us to evaluate the potential consequences of periods of resource limitations. However, this estimation of *in situ* food supply and the uniform diet of *Artemia* nauplii in our experiment seems to underestimate the actual *in situ* food intake, where CWCs likely feed on a range of different prey (Garcia-Herrera et al., 2022; Höfer et al., 2018; Maier

et al., 2021). This also shows that not only zooplankton abundance plays an important role, but also the type of food (Maier et al., 2021). *Desmophyllum pertusum* is well adapted to fluctuating feeding conditions and can cope with long periods of low food availability or complete food deprivation either by reduction of skeletal growth but preservation of fatty acids (Baussant et al., 2017) or maintenance of growth rates but reduction of its fatty acid content (Larsson et al., 2013). In contrast, other CWC species such as *C. huinayensis* and *D. dianthus* seem to be more negatively affected by prolonged low food availability and short-term starvation, as indicated by reduced calcification (Martínez-Dios et al., 2020; Naumann et al., 2011, this study). However, this only became apparent after three months in the present study, as CWCs seem to compensate for resource limitation by fuelling their metabolism by various supplementary energy sources over longer periods. This resulted in delayed responses until the limited available energy was channelled into core processes essential for survival. We therefore assume that the physiological performance of *C. huinayensis* will be negatively affected in the future by long periods of reduced food availability in winter.

4.3. Effect of elevated temperature

In addition to reduced feeding, elevated temperature had the most negative effect on *C. huinayensis*. Coral metabolism and health were strongly affected by long-term exposure to warming, even though the elevated temperature in the present study was only slightly higher than
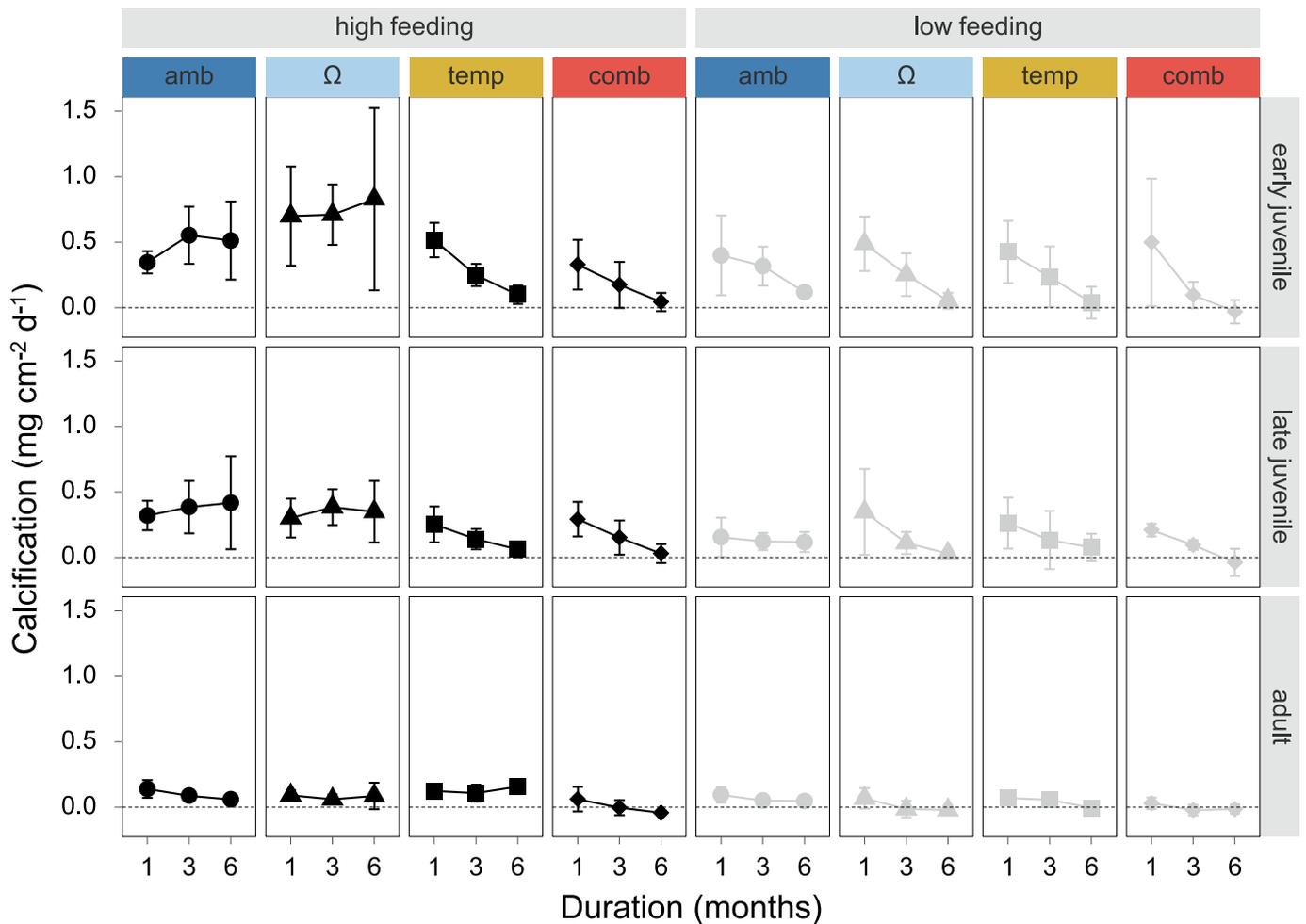
Fig. 6. Calcification of three life stages of *Caryophyllia huinayensis* after one, three and six months under different Ω, temperature and feeding conditions. Calcification rate of early juveniles, late juveniles and adult corals under high (HF, black) and low (LF, grey) feeding ($N = 1–6$). Treatment conditions: 1) amb (dark blue) = 11 °C and $\Omega_{arag} > 1$, 2) Ω (light blue): 11 °C and $\Omega_{arag} < 1$, 3) temp (yellow): 15 °C and $\Omega_{arag} > 1$, 4) comb (red): 15 °C and $\Omega_{arag} < 1$. Values are stated as mean ± standard deviation. Significant effects are indicated when present: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
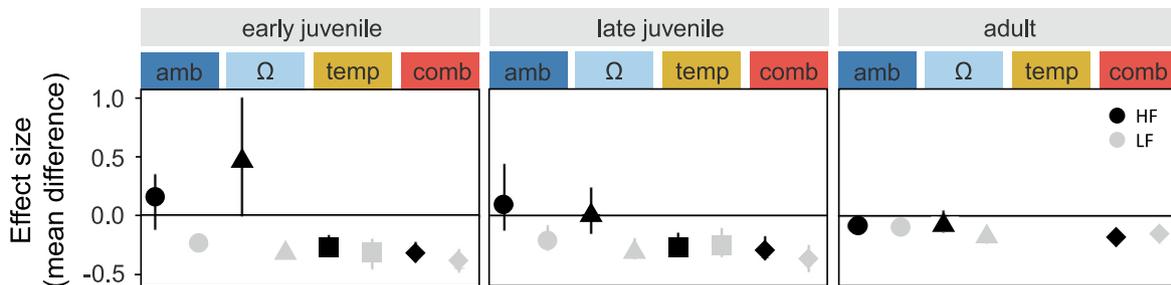

Fig. 7. Effect size (mean difference) in calcification of three life stages of *Caryophyllia huinayensis* after six months under different Ω, temperature and feeding conditions compared to initial ambient conditions. High feeding (HF) is shown in black and low feeding (LF) in grey ($N = 2–6$). Treatment conditions: 1) amb (dark blue): 11 °C and $\Omega_{arag} > 1$, 2) Ω (light blue): 11 °C and $\Omega_{arag} < 1$, 3) temp (yellow): 15 °C and $\Omega_{arag} > 1$, 4) comb (red): 15 °C and $\Omega_{arag} < 1$.

the maximum temperature for CWC habitats (14–15 °C) (Brooke et al., 2013; Freiwald et al., 2009). Elevated but also variable respiration rates of *C. huinayensis* at 15 °C provide evidence for an increased metabolic activity, as has also been shown for *D. pertusum* (Dorey et al., 2020; Gómez et al., 2022), albeit on much shorter timescales of a few days. It is known that CWCs can tolerate exposures beyond their thermal optimum for hours to days (Brooke et al., 2013; Dorey et al., 2020) and up to three

months (Naumann et al., 2013), but a further long-term increase by 1 °C above the current maximum temperature of CWC habitats may pose critical for their health as has been shown by the present study.

Potentially, thermal acclimatisation occurred in Comau Fjord, where CWCs in shallow waters are regularly exposed to short-term elevated temperatures (Beck et al., 2022a). However, the present study indicates that *C. huinayensis* can only tolerate 15 °C for up to three months, but not

for longer and particularly if coupled with resource limitation. Thus, the corals' nutritional condition plays a critical role for their ability to endure stressful conditions. Increased food availability was not able to sustain their health close to their upper thermal limit in the long term, as 15 °C seems to represent the long-term physiological limit of *C. huinayensis*.

4.4. Effect of aragonite undersaturation and combination with elevated temperature

Our study shows that all three life stages of *C. huinayensis* are able to withstand aragonite undersaturation for six months, with only a slight and non-significant reduction in their survival and calcification rates under food limitation. This confirms previous findings that CWCs are able to calcify under low pH conditions (Gori et al., 2016; Hennige et al., 2014) and even under aragonite undersaturation (Form and Riebesell, 2012; Hennige et al., 2015). This may be due to their ability to elevate the pH in their calcifying fluid (pH_{cf}), especially if sufficient energy is available (McCulloch et al., 2012), which was likely the case for juvenile corals in the HF regime. However, the slightly lower calcification rates in the LF regime at aragonite undersaturation may be a first indication that enhanced pH_{cf} up-regulation requires additional energy that under sufficient food supply can be compensated by calcifying organisms (Leung et al., 2022). We only measured higher skeletal dissolution than calcification rates of adult corals at aragonite undersaturation, as their tissue covered surface area decreased and therefore, the unprotected skeleton was in contact with seawater (Hennige et al., 2015; Hennige et al., 2020). In contrast, juvenile corals increased their tissue covered surface area, which protected their skeleton from dissolution. As ocean acidification does not generally have a large effect on CWCs, the elevated TA and DIC of the present study will most likely not have affected the calcification results. Here, elevated temperature and reduced food availability are clearly more relevant and have a stronger effect on coral physiology.

In contrast to aragonite undersaturation alone, the response to a combination of elevated temperature and aragonite undersaturation clearly differed between traits. While calcification rates decreased, both somatic growth and survival increased in the combined treatment. Similar mixed responses were found in previous multiple driver experiments ranging from additive, synergistic to antagonistic responses in *D. dianthus* (Gori et al., 2016) and *D. pertusum* (Büscher et al., 2017; Hennige et al., 2015). However, a combination of both parameters did not affect calcification (Büscher et al., 2017; Gori et al., 2016; Hennige et al., 2015), which is in contrast to the present study and may be a result of differences in the nutritional status of the corals between studies. In the present study, the combination of aragonite undersaturation and elevated temperature clearly affected the traits antagonistically, counteracting the negative response to elevated temperature and improved the overall corals' health status. Therefore, ocean acidification (both as single and combined stressor) will not severely affect live CWCs in the future, unlike warming and reduced food availability.

5. Conclusion

Our study clearly shows that elevated temperature and reduced food supply negatively affect the performance of juvenile and adult *C. huinayensis*, albeit in different ways. While calcification is reduced in juvenile corals, the survival probability of adult corals decreases, both of which affect the survival of the population. Overall, *C. huinayensis* is more sensitive to warming than ocean acidification, both as single and combined stressor. As sufficient feeding is an important factor determining the physiological response, CWCs may be able to tolerate short-term environmental changes if sufficient energy reserves are available and the conditions do not exceed their tolerance limits. However, long-term exposure (> 3 months) to 15 °C is clearly beyond the critical upper thermal limit of *C. huinayensis*. Currently, monthly average temperatures

in its natural habitat in shallow waters of Comau Fjord reach approx. 13 °C in summer and autumn, but can be as high as 16 °C over short time periods and fluctuate as much as 3.7 °C within one day (Beck et al., 2022a). The projections suggest an increase of almost 1 °C for the Gulf of Ancud by 2100 (van Leeuwen et al., 2021). Although this is still below the critical temperature of 15 °C, the combination of projected warming with strong environmental variability is expected to have a negative impact on their performance and could further restrict their physiological tolerance limits. Even though future temperature increases may primarily affect deep-water emergent CWC species in shallow waters, the food supply in CWC ecosystems in the deep sea is expected to decline. This will reduce the calcification rates of juvenile and the survival rate of adult CWCs and therefore, likely affect their ability to cope with long-term environmental changes in general.

CRediT authorship contribution statement

Kristina K. Beck: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Jan Nierste:** Methodology, Validation, Writing – review & editing. **Gertraud M. Schmidt-Grieb:** Conceptualization, Writing – review & editing, Funding acquisition. **Esther Lüdtke:** Investigation, Writing – review & editing. **Christoph Naab:** Investigation, Writing – review & editing. **Christoph Held:** Conceptualization, Writing – review & editing, Funding acquisition. **Gernot Nehrke:** Conceptualization, Writing – review & editing, Funding acquisition. **Grit Steinhoefel:** Conceptualization, Writing – review & editing, Funding acquisition. **Jürgen Laudien:** Resources, Writing – review & editing. **Claudio Richter:** Resources, Writing – original draft, Writing – review & editing. **Marlene Wall:** Conceptualization, Methodology, Software, Validation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data are available in the data repository PANGAEA: https://doi.org/10.1594/PANGAEA.949255 (Beck et al., 2022b).

Acknowledgements

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