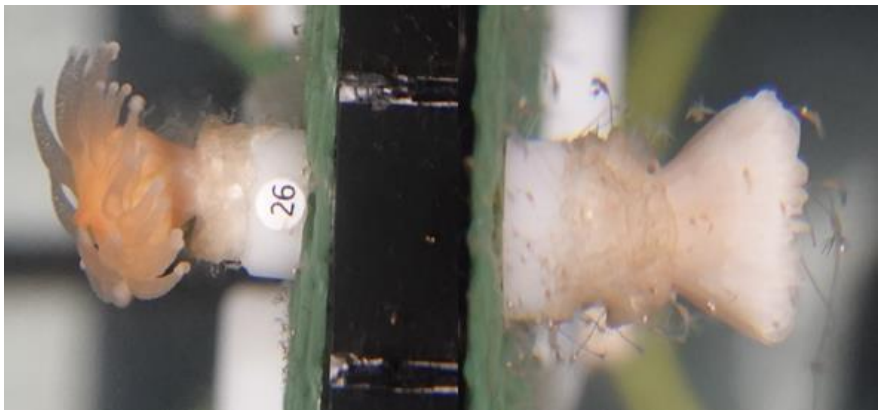
Effects of climate change and feeding on the energy budget of three life stages of the cold-water coral *Caryophyllia huinayensis*



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Jan Christoph Nierste

in the section bentho-pelagic processes at the

Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven.

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First supervisor:
Dr. Marlene Wall
Alfred Wegener Institue
Biosciences division
Section Bentho-pelagic processes
Am Alten Hafen 26
27568 Bremerhaven
Tel: +49 (471) 4831-1313
Email: marlene.wall@awi.de

Second supervisor:
Dr. Stefan Forster
Rostock University
Institut für Biowissenschaften
Section Marine Biology
Albert-Einstein-Str. 3
18059 Rostock
Tel: +49 (0) 381 4986053
Email: Stefan.forster@uni-rostock.de

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Summary

Cold-water corals (CWCs) lack the endosymbiotic algae found in tropical corals and are therefore dependent on heterotrophic feeding to meet their metabolic demands. They are important bioengineers providing a habitat for many species from the shallows down to the deep-sea. While it is widely understood that ocean acidification (OA) and rising water temperatures due to the anthropogenic climate change will severely impact CWCs in the near future not much is known about the actual effects on their physiology. Most studies conducted so far only implemented either ocean acidification or elevated temperature as stressors without considering the possible interactions between these two. The results of these studies showed that the response of CWCs to these stressors varies between species, populations and life stages.The aim of this thesis was to investigate how a 6-month exposure to OA (pH 7.5 & Ω_{arg} ~ 0.8) and elevated temperature (+ 4 °C) as single stressor as well as in combination influenced the metabolism of the solitary CWC species *Caryophyllia huinayensis* over three different life stages of the polyp. Two feeding regiments were implemented to test for potentially mitigating effects of a 12-fold increase in food availability. The results indicate that *Caryophyllia huinayensis* are able to calcify under ocean acidification with sufficient amounts of food as it predominately increases the energy demand for calcification, while elevated temperature alone increased metabolic rates beyond a point where enhanced food availability could compensate for the detrimental effects and induced mortality. In combination the interaction of OA and elevated temperature act antagonistic leading to metabolic rates similar to those measured at ambient conditions. However, the corals health still deteriorated with mortality rates only slightly lower than under elevated temperature and no mitigating effects of increased food availability. A trend for higher resilience in the intermediate life stage was detected but the response was not strong enough to acclimate to the stressors. This shows that *C. huinayensis* will most likely not be able to cope with the effects of climate change on the metabolism, threating the survival of this species in a changing ocean.

1. Introduction

Cold-water corals (CWCs) or azooxanthellate corals are characterized by the absence of zooxanthellae in their tissues. They can be found in all major oceans from shallow waters to over 6000 m depth and at temperatures between 0 and 13 °C (Freiwald *et al.*, 2004; Roberts *et al.*, 2006, Waller *et al.*, 2011). Like their tropical relatives, CWCs are important bioengineers, and some species can build extensive reefs similar in size and biodiversity to those known from tropical waters (Roberts *et al.*, 2006). Both tropical and cold-water reefs are susceptible to damages due to ocean acidification (OA) and rising water temperatures as consequences of climate change (Feely *et al.*, 2012 and references therein, Freiwald *et al.*, 2004; McCulloch *et al.*, 2012). To meet their metabolic demands, they utilize a wide array of food sources, including dissolved organic matter (DOM) and particulate organic matter (POM) sinking down from the productive surface layer as well as zooplankton (Höfer *et al.*, 2018; Naumann *et al.*, 2011; Soetart *et al.*, 2016). The input of food into deeper waters can be scarce and CWCs can downregulate their metabolism and utilize storage tissues to survive periods of nutrient limitation (Gori *et al.*, 2016; Maier *et al.*, 2019), and appear to be able to adapt their life cycle to variations in food input (Feehan *et al*. and references therein, 2019; Maier *et al.*, 2020).

The oceans absorb about one third of the anthropogenically released CO_2 (Feely *et al.*, 2012). This lowers their pH and increases the solubility of aragonite a polymorph of calcium carbonate ($CaCO_3$) which corals use to build their skeleton. This leads to a decrease in the saturation state of aragonite (Ω_{Arg}) and a rapid shoaling of the aragonite saturation horizon (the depth at which Ω_{Arg} is one) (Feely *et al.*, 2012; Lunden *et al.*, 2013). 70 % of currently known CWC populations are expected to be exposed to aragonite undersaturated waters by the end of the century (Guinotte *et al.*, 2006). In addition, global warming elevates the water temperature down to the deep sea and leads to enhanced stratification of the surface layer (Kwiatkowski *et al.*, 2020; Levin & Le Bris, 2015; Soetart et al, 2016). The enhanced stratification is expected to hinder the replenishment of nutrients in the surface layer leading to a reduction in primary production in the euphotic zone and thus the amount of POM sinking to deeper waters fueling the deep-sea food webs (Kwiatkowski *et al.*, 2020; Soetart et al, 2016).

The impact of climate change on CWCs has been studied for less than two decades (Roberts *et al.*, 2006), mostly with the cosmopolitan species *Lophelia pertusa* (Büscher *et al.*, 2017; Dodds *et al.*, 2007; Form & Riebesell, 2012; Georgian *et al.*, 2016; Gómez *et al.*, 2018, Form &

Riebesell, 2012 Hennige *et al.*, 2015; Maier *et al.*, 2013), *Madrepora oculata* (Maier *et al.*, 2013; Maier *et al.*, 2016) and *Desmophyllum dianthus* (Carreiro-Silva *et al.*, 2014; Gori *et al.*, 2016), testing their response to one or a combination of stressors like rising water temperatures, OA, and changes in food-availability.

In experiments lasting from three weeks to over a year CWCs have shown different reactions to OA depending on the severity (Gori *et al.*, 2018 and references therein; Form & Riebesell, 2012; Martínez-Dios *et al.*, 2020 and references therein). Differences could be observed between species (Movilla *et al.*, 2014) as well as between populations from different locations (Georgian *et al.*, 2016). Overall CWCs appear to be able to maintain calcification at Ω_{Arg} levels below one (Büscher *et al.*, 2012; Carreiro-Silva *et al.*, 2014; Form & Riebesell, 2012; Glazier *et al.*, 2020; Gori *et al.*, 2016; Hennige *et al.*, 2014) with detrimental effects on calcification observed at Ω_{Arg} levels below 0.8 (Gómez *et al.*, 2018; Maier *et al.*, 2016; Martínez-Dios *et al.*, 2020), while the respiration rates were either unaffected or decreased (Carreiro-Silva *et al.*, 2014; Form & Riebesell, 2012; Gori *et al.*, 2016; Hennige *et al.*, 2015; Maier *et al.*, 2016). In contrast, large, thriving populations of CWCs have been encountered in waters with Ω_{Arg} levels as low as 0.6 (Baco *et al.*, 2017; Fillinger & Richter, 2013; Thresher *et al.*, 2011). This resistance to OA has been attributed to the separation between the site of calcification and the surrounding seawater as well as the corals' ability to modify the conditions at the site of calcification. The coral tissue forms a barrier around the coral skeleton protecting it from dissolution. In addition, CWCs are able to upregulate the pH of their internal calcifying fluid to maintain calcification in corrosive waters (McCulloch *et al.*, 2012). This upregulation is achieved via a Ca^{2+}-ATPase transporting Ca^{2+} ions in and H^{+} ions out of the calcifying fluid. This process leads to an 10 % increase in energy demand for calcification when the pH drops by 0.1 units (McCulloch *et al.*, 2012). An increase in food concentration had a positive effect on calcification of *D. dianthus* at levels at or above 0.5 (Martínez-Dios *et al.*, 2020) but had no effect on the growth rates of the colonial species *L.pertusa* (Büscher *et al.*, 2017) and *M. oculata* (Maier *et al.*, 2016). CWC populations in aragonite undersaturated waters are believed to be able to grow due to a high input of food in these regions compensating for the increased energy demand for calcification (Gómez *et al.*, 2018, Martínez-Dios *et al.*, 2020).

The respiration of CWCs increases with temperature indicating that the metabolism of CWCs is more sensitive to changes in temperature than pH (Büscher *et al.*, 2017; Dodds *et al.* and references therein, 2007; Gori *et al.*, 2016) and even a minor elevation by 2 °C increased the

respiration rate of *L. pertusa* by 50 % (Dodds *et al.*, 2007). Calcification can be enhanced (Büscher *et al.*, 2017) or negatively affected by a prolonged exposure to elevated temperatures (Dodds *et al.*, 2017; Gori *et al.*, 2016). This might be connected to the thermal maximum of the involved enzymes (Dodds *et al.*, 2017 and references therein; Gori *et al.*, 2016 and references therein). When increased temperature stimulated calcification rates, higher amounts of food led to a further increased the growth rates (Büscher *et al.*, 2017).

Studies combining OA and elevated temperature are still scarce and show that a combination of both stressors can have different effects. The observed effects were either antagonistic compensating changes in respiration and calcification (Büscher *et al.*, 2017, Hennige *et al.*, 2015) or synergetic, further reducing respiration and calcification compared to single factor approaches (Gori *et al.*, 2016). Unlike in the single stressor approaches, corals subjected to a combination of both stressors were unable to utilize an increase in food availability (Büscher *et al.*, 2017).

Another aspect that needs further investigation is the ability of different life stages to adapt to climate change. OA experiments including early life stages suggest that they are more adversely affected than fully grown corals (Maier *et al.*, 2009; Martínez-Dios *et al.*, 2020; Movilla *et al.*, 2014). In comparison, the low growth rates of adult CWCs make them more resilient to an increase in the energy demand from calcification (Movilla *et al.*, 2014 and references therein). However, reproduction is energetically costly and an increase in overall metabolic demand coupled with insufficient food availability has the potential of threatening CWCs at this point of their life cycle (Maier *et al.*, 2020).

The studies conducted so far highlight the importance of multistressor approaches to assess the ability of CWCs to adapt to climate change. Further research into the role of food availability and different life stages is needed as these are key factors to the survivability of CWC species and population in a changing ocean.

This master thesis is embedded within a larger multistressor experiment focusing on the scleractinian CWC *Caryophyllia huinayensis*. It addresses the effects of OA at pH 8.1 and 7.5 and elevated temperature at 11 and 15 °C as single and combined factors on three different life stages under two different feeding regiments after six months of exposure. My thesis focuses on the effects on the metabolic turnover expressed in the feeding rate, respiration rate, calcification, and O:N ratios after six months. The aim is to understand how the treatment

conditions affect the metabolic turnover in *C. huinayensis*. I hypothesize based on observations from long term studies on the long-time studies performed with *L. pertusa* and *D. dianthus* (Büscher *et al.*, 2017; Gori *et al.*, 2016; Martínez-Dios *et al.*, 2020) due to the similar morphology and close association of *D. dianthus* and *C. huinayensis* in Comau Fjord (Cairns *et al.*, 2005) as well as the similarity of the treatments and duration to these experiments. As such, my hypotheses are as follows:

[1] Calcification of all low fed corals will decrease in the pH, temperature, and combined treatments with an increase in food availability compensating for adverse effects of single stressors, while it will be insufficient in the combined treatment.

[2] While the metabolic demand and thus respiration rates will increase in both single factor treatments, it will be more strongly influenced by elevated temperature than a decrease in pH. O:N ratios will increase for the low fed corals in the single factor treatments and both feeding regiments in the combined treatment.

[3] A combination of decreased pH and elevated temperature will act synergetic, decreasing the metabolic rate and thus respiration and calcification of *C. huinayensis* regardless of life stage and feeding.

[4] Adult corals will be more resilient to single and combined stressors, as I expect them to have higher feeding rates and more storage tissue as the younger stages due to their larger size.

2. Material & Methods

2.1 Sampling site and species

2.1.2 The Comau Fjord

The 34 km long Comau Fjord is located in Northern Chilean Patagonia and characterized by a distinct north-south orientation. The depth decreases from almost 600 m at the mouth to less than 50 m at the head (Häussermann & Försterra, 2009). In Comau Fjord deep-water species occur in shallow waters, a phenomenon known as deep-water emergence or eurybathy and therefore can easily be observed *in situ* and sampled by scuba divers (Häussermann & Försterra, 2009). The surface layer is strongly influenced by the freshwater input of adjacent rivers and high precipitation creating a low-salinity layer with salinity as low as 2 extending from the surface to up to ten meters depth. The salinity below is relatively stable at 32 (Jantzen *et al.*, 2013 and references therein). This, together with high tidal amplitudes of up to 7 m limit the distribution of cold-water corals and other stenohaline marine species to 18 m depth. Below dense aggregations of the scleractinian corals *Desmophyllum dianthus* and *Caryophyllia huinayensis* can be found with the highest abundance reported between 20 and 280 m depth (Fillinger & Richter, 2013), while only scattered specimens occur in the shallower regions (Cairns *et al.*, 2005; Häussermann & Försterra, 2009; Jantzen *et al.*, 2013). The pH values measured in the fjord by Jantzen *et al.* (2013) in March 2010 and February/March 2011 ranged from 8.3 in the surface layer to 7.4 and below around 200 m with the aragonite saturation horizon around 150 m. They observed a sharp vertical gradient in pH with a decrease of up to 0.5 pH units within 50 m below the halocline. In February 2012 Fillinger & Richter (2013) measured pH values from 8.42 below the low salinity layer to a minimum value of 7.71 below 300 m. In 1995, Silva (2008) measured the lowest pH in Comau Fjord at 7.6 without giving the depth of the measurements. Similar pH gradients have been reported from other fjords in the region (Silva, 2008; Torres *et al.*, 2011). As a result, corals at greater depths can be subjected to waters undersaturated with respect to aragonite. Nevertheless, dense coral banks can be found at depths where the aragonite saturation level is close to or below one (Jantzen *et al.* 2013). The temperature of the surface layer above the halocline is strongly influenced by seasonal changes in solar radiation ranging between 6 and 23°C while the water temperature below the pycnocline varies between 6 and 12 °C (Häussermann & Försterra, 2009, Häussermann & Försterra, 2012)

2.1.3 Caryophyllia huinayensis

Caryophyllia huinayensis (Cairns *et al.*, 2005) is a small, solitary scleractinian cold-water coral with a maximum height of about 2 cm. This species is endemic to the waters of Chile where it has been recorded from 11 to 800 m depth. In Comau Fjord, it can be found on portions of hard substrates protected from sedimentation to depths of at least 200 m in areas with moderate to high current velocities, where it is often associated with *D. dianthus* (Fig. 1) (Cairns *et al*. 2005, Fillinger & Richter, 2013, Häussermann & Försterra, 2009).

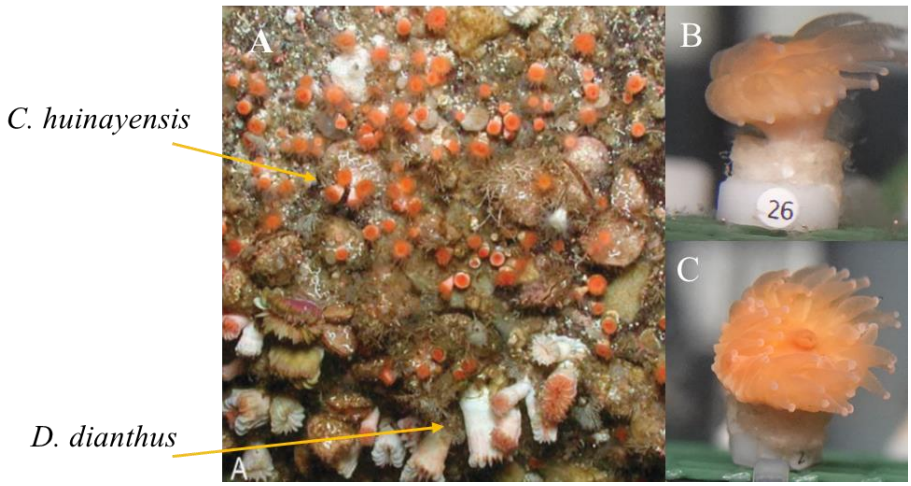

Figure 1: *Caryophyllia huinayensis*. A shows *C. huinayensis* and *D. dianthus* in the same habitat, changed after Cairns, Häussermann & Försterra (2005). B and C show two adult specimens of *C. huinayensis*. from the long-term experiment.

2.2 Coral maintenance and setup of the long-term experiment

The corals used in this experiment were sampled by scuba divers at the station CrossHuinay North at 21 m depth between in 2014 and 2015 and transported to the aquaria facility at the AWI. There they were maintained and reproduced over the past years.

The corals were assigned to one of three life stage based on their size. The tissue covered surface area of the different life stages at the beginning of the experiment were 0.25 ± 0.07 cm^2 for the "recruits", 0.51 ± 0.15 for the "juveniles" and 2.49 ± 0.82 for the "adults". Half of the adult corals were specimens born and brought up in the rearing facility of AWI.

The corals were glued onto plastic PVC screws using superglue and placed into a plastic rack s, which held them in an upright position (Fig. 2). A group of 24 corals kept in a separate culturing room at 11 °C and 8.0 pH was used to test different setup and procedures for the final incubations with the corals from the experiment. This group contained twelve recruits, six

juveniles and six adults with the mean tissue surface area of the life stages in that order being 0.22 ± 0.08, 0.37 ± 0.06 and 0.78 ± 0.14.

After the corals were transferred from the culturing to the experimental system and before the start of the experiment the corals were acclimated for three weeks at control conditions of 8.05 ± 0.04 pH and 11.0 ± 0.05 °C .During the acclimatization phase, they were fed twice per week with *Artemia persimilis* nauplii hatched from 2 g of frozen eggs incubated in an Artemio 1 breeding set (JBL GmbH & Co. KG, Neuhofen, Germany) filled with artificial sea water and kept at 27 °C with a bright light source. After the acclimatization period the pH and temperature of the treatments were adjusted to the final values by 0.05 pH units and 0.5 °C over five and six days, respectively. The experiment was set up in darkness with four different treatments each consisting of four 35 l tanks connected to one central 80 l technical tank receiving and distributing water to all four tanks. Each tank was housing nine corals, three of each life stage.100 µm nets on the inflow and outflow of the aquaria prevented particles from getting in or out of the tanks. The temperature- and pH-settings were controlled by an iks aquastar (iks ComputerSysteme GmbH, Karlsbad, Germany) Every Tuesday 25 to 30 l of the technical tanks volume was exchanged with a mixture of 75 % fresh artificial seawater made of distilled water mixed with reef salt (Aqua Medic GmbH, Bissendorf, Germany) and 25 % “old” water from other tanks. The “old” water was added to keep the nutrient levels stable because the nutrient concentrations of the fresh artificial seawater were below those of the treatments. The water parameters were set to resemble either ambient levels (8.1 pH, 11°C) or to the low pH and high temperature levels that had previously been measured in the waters of Comau Fjord (7.5 pH, 15.0 °C) but may also occur when the worst case scenario (RCP 8.5) occurs (IPCC, 2014). The temperature- and $pH_{(NBS)}$-settings were controlled by an iks aquastar unit (iks ComputerSysteme GmbH, Karlsbad, Germany). For further analysis, the measured pH values were converted from the NBS to the total scale. The values for temperature and $pH_{(total)}$ measured by the iks system over the course of the experiment were 8.09 ± 0.04 pH and 11.0 ± 0.04 °C for the ambient, 7.54 ± 0.04 pH and 11.1 ± 0.1 °C for the pH, 8.05 ± 0.02 pH and 15.0 ± 0.1 °C for the temperature, and 7.50 ± 0.04 pH and 15.0 ± 0.1 °C for the combined treatment. The salinity of the ambient, pH, temperature and combined treatment was 31.6 ± 0.2, 31.5 ± 0.1, 31.6 ± 0.1 and 31.6 ± 0.2, respectively. The oxygen concentration in (treatments in the same order as salinity) was 8.95 ± 0.11 mg/L, 8.94 ± 0.13 mg/L, 8.40 ± 0.25 mg/L and 8.36 ± 0.24 mg/L.

In addition, pH and temperature of the tanks were measured daily from Monday to Friday using a ProfiLine pH 3310 (Xylem Analytics Germany Sales GmbH & Co. KG, Weilheim, Germany) for pH and temperature and a ProfiLine Cond 3110 (Xylem Analytics Germany Sales GmbH & Co. KG, Weilheim, Germany) for salinity and temperature. Oxygen levels were measured using a Pro20i Dissolved Oxygen Meter (Xylem Analytics Germany Sales GmbH & Co. KG, Weilheim, Germany). Each treatment was subdivided into two feeding groups: The corals from the high feeding (HF) group fed on Monday, Wednesday, and Friday with *A. persimilis* nauplii hatched from 2 g of eggs while the corals assigned to the low feeding (LF) group were fed on Wednesday with nauplii hatched from 0.5 g of eggs. Before the feeding the inflow of water into the tanks was decreased. Feeding lasted for six hours with the HF corals fed half of their nauplii at the beginning and the rest after three hours to avoid clogging the nets on the outflow pipes. After these six hours the inflow was increased to wash the remaining nauplii into the nets which were then changed. The corals used for the test incubations were fed on the same days as the HF corals from the experiment.

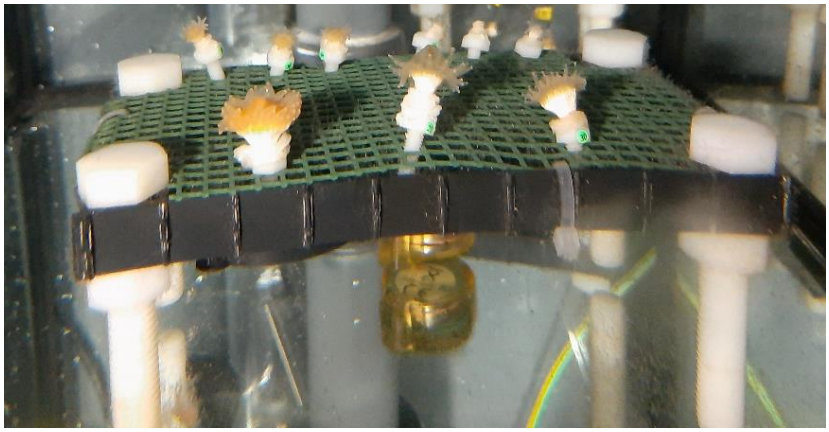

Figure 2: One of the racks holding the different life stages of *C. huinayensis* in the tanks.
The adults are in the foreground while the recruits (right) and juveniles (left) can be seen in the background.

2.3 Incubations

2.3.1 General setup

For the incubations, a water bath was set up in a plastic box. Temperature levels were set to 11 or 15 °C using a 230V-thermostat (SCHEGO Schemel & Goetz GmbH & Co. KG, Offenbach, Germany) controlled by a T-Computer (Aqua Medic GmbH, Bissendorf, Germany), while constant water movement was provided by Turbelle nanostream 6025 (Tunze Aquarientechnik GmbH, Penzberg, Germany) and a Pico Pumpe (Hydor USA Inc., Sacramento, California) in the corners of the water bath. Two magnetic stirring plates, a MIXdrive15 controlled by a

MIXcontrol 40 (2mag AG, München, Germany) and a Telesystem controlled by a Telemodul C (Variomag-USA, Daytona Beach, Florida) set at 180 rounds per minute (rpm) with glass coated magnetic stirrers providing water movement in the incubation chambers. For the test incubations a smaller water bath with only one stirring drive and a datalogger HOBO TidbiT v2 (CiK Solutions GmbH, Karlsruhe, Germany) to control the accuracy of the T-Computer was set up. Only the Pico Pump provided water movement in the small water bath while the setup for the temperature control remained unchanged. 15 Weck jars (J. Weck GmbH u. Co. KG, Wehr-Öflingen, Germany) with a volume of 130 ml and three acorn nuts glued onto the lid with two-component glue (UHU GmbH, Bühl, Germany) to hold the screws were used as incubation chambers for all incubations (Fig. 3). To prevent the surrounding water from entering the bottles during the incubations the water level was set to be just underneath the rubber band.

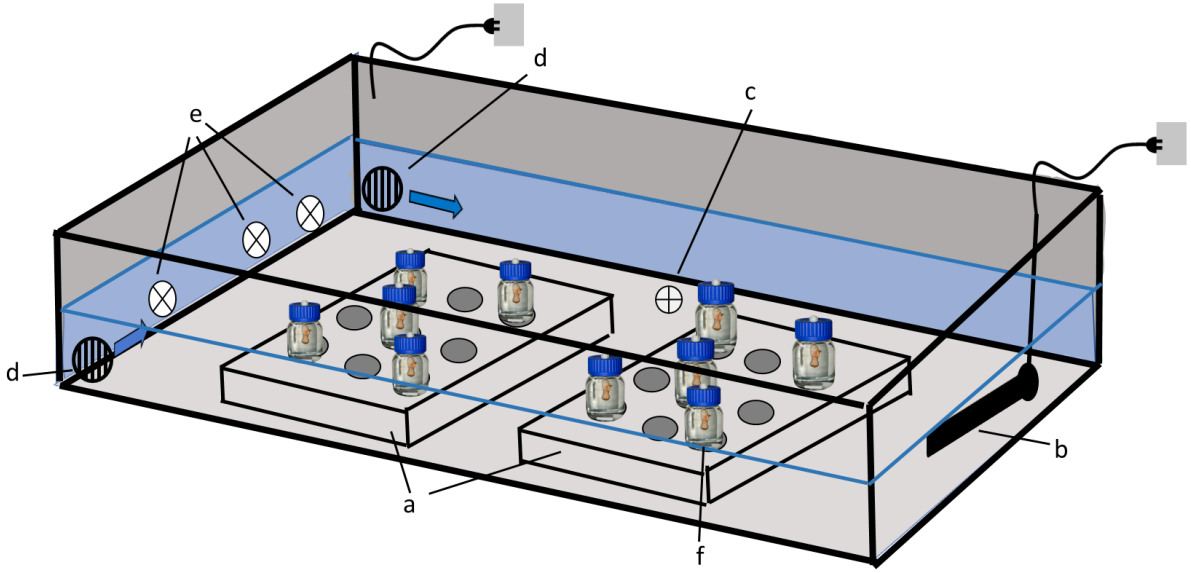

Figure 3: Incubation setup with the blue arrows indicate the outflow direction of the aquarium pumps. (A) shows one of the Weck-bottles without the oxygen sensors (B). a = magnetic stirring plates, b = thermostat, c = temperature sensor of the T-Computer controlling the thermostat, d = Aquarium pumps, the blue arrows indicate the outflow direction, e = position of the pt100 temperature sensors of the Firesting®, *F* = incubation chambers (Weck jars). Note that the used illustration does not use the actual Weck jars, but templates provided by Kristina Beck.

2.3.2 Incubations to determine the feeding rates

To evaluate the feeding rates of the corals, different approaches for the feeding incubations were tested. A total of five test incubations were conducted with freshly hatched *A. persimilis* nauplii from the same batch used to feed the corals in the long-term experiment. For the first four test incubations ten subsamples from a solution of nauplii and eggs were counted under a stereo microscope 475002-9902 (Carl Zeiss AG, Oberkochen, Germany) set at 1× magnification to calculate the total amount of nauplii and eggs in the solution and therefore the

necessary amount for the incubations. The nauplii needed for the fifth incubation were counted under the stereo microscope, transferred into snap-caps, and stored in a fridge at 5 °C for a day before being used. The number of nauplii and eggs in each bottle and the duration of the incubations can be seen in table 1. These tests were set with possible amounts of nauplii for the LF group in the final feeding incubations and conducted either on days when the corals would normally be fed or on the next day. In the latter case the corals were not fed the day before.

Table 1: Timeline and setup of the test incubations for feeding. The number of nauplii for the first four incubations were calculated as mean from ten subsamples while those from the fifth incubation were counted by hand to get an exact number.

Date of the incubation	Number of corals per bottle	Number of nauplii (±SD)	Number of eggs (±SD)	Duration (hours)
29.01	3 (recruits & juveniles) or 2 (adults)	323 (41.54)	7 (7.38)	6
16.02		404 (20.63)	149 (19.19)	6
24.02		252 (8)	Not counted	1 (jar 1), 2 (jar 2) or 3 (bottle 3 to 8)
26.02		250 (9.68)	Not counted	3 (jar 1 and 2) or 1 (jar 3 to 8)
05.03	1	30	Excluded	1

Figure 4: Dense overgrowth of hydrozoans on the skeleton of an adult coral from the temperature treatment. More hydrozoans can be seen growing on the rack.

From the results of these tests, incubating each coral individually for one hour with the amount of nauplii × ml^{-1} was set to resemble the one available to the corals in the tanks was chosen as the most suitable approach, because it eliminates the possibility of under- or overestimating the feeding rates due to the standard deviation. The incubation of all four treatments took two weeks because each set of incubations took place two days after the last feeding. Two days before the incubations, the *A. persimilis* eggs were put in the breeding sets and the screws and corals gently scrubbed with a toothbrush to remove hydrozoans growing on the screws and exposed parts of the coral skeleton (Fig. 4). On the next day, the nauplii needed for the incubations were counted and transferred into snap caps, 30 nauplii for the LF- and 120 for the HF-corals and stored in a fridge at 5 °C until the beginning of the incubations on the next day. For the incubations, each bottle was filled with 110 ml of water from the technical tank and the nauplii from the snap-caps. This volume was chosen so the corals would be completely submerged during the incubations while no water and thus nauplii could escape when closing the incubation chambers. The resulting initial

nauplii concentration was 0.27 nauplii × ml^{-1} and 1.09 nauplii × ml^{-1} for the LF and HF incubations, respectively, At the end of the incubations the amount of nauplii caught by hydrozoans was counted and later added to the remaining nauplii. In contrast to the corals from the test incubations, the corals from the treatments did not extend their tentacles within ten minutes after the incubation started. Depending on the extension of their tentacles at the end, the corals were assigned a percentage of tentacle extension relative to the polyp height with the three stages: < 25 %, 25 – 75 % and > 75 %. The corals were then transferred back into their tanks and the remaining nauplii filtered over a 100 µm net, transferred into plastic bottles and counted.

Two separate batches of nauplii were hatched to calculate the theoretical weekly intake of *Artemia* nauplii-derived POM, the C/N-ratio of the nauplii and the difference in these values between one- and two-day old nauplii. From the first batch 300 two-day old nauplii per filter were filtered onto six GF/F- and four GF/C-filters for POM- and C/N- measurements, respectively. The same was done with one- and two-day old nauplii from the second batch but this time with 500 nauplii per filter and three GF/F- and GF/C-filters on each day. For the POM measurements the GF/F filters were dried for at least 24 h at 60 °C, weighed, combusted at 500 °C and weighed again. The POM-values of two-day old nauplii from the second batch were used to calculate the theoretical hourly POM-intake of the corals during normal feeding events.

2.3.3 Incubations to determine the energetic turnover

Twelve of the 15 incubation chambers were equipped with OXSP5-SUB oxygen sensor spots (Pyroscience GmbH, Aachen, Germany) glued to the inside and spot adapters SPADBAS (Pyroscience GmbH, Aachen, Germany) glued to the outside for the respiration measurements with the FireSting®-PRO (Pyroscience GmbH, Aachen, Germany) sensors. Each FireSting®-PRO was equipped with four optical oxygen sensors SPFIB-BARE (Pyroscience GmbH, Aachen, Germany) and one external pt100 temperature sensor TSUB21 (Pyroscience GmbH, Aachen, Germany) to measure the temperature of the water bath. The remaining three chambers served as controls for changes in the concentration of nutrients, dissolved inorganic carbon (DIC), total organic carbon (TOC) and total alkalinity (TA). A rubber band between the bottle and the lid and three metal clamps sealed the bottles and prevented the exchange of air or water with the surroundings. The Firesting® sensors were calibrated using water depleted of oxygen with sodium dithionite and air saturated water for 0 % and 100 % oxygen saturation, respectively. The sensors measured the oxygen concentration and temperature every ten

seconds and displayed them in percent oxygen saturation and °C on the connected Notebook. The bottles, lids and rubber bands were completely submerged in the tanks and all air bubbles removed with a toothbrush. First the background respiration was measured for four hours with water from the technical tank. Water samples were taken to determine the start concentrations of nutrients, DIC, TA and TOC.

A total of three test incubations were conducted to determine the adequate duration of the incubations to get good values for the respiration measurements as well as the nutrient concentrations, DIC, TA and TOC. The Firesting® and the glass coated stirrers were only available for the last two test incubations so the first was conducted using plastic coated stirrers and a handheld oxygen meter to determine the oxygen concentration at the end of the incubations. Two of these three respiration measurements used the water from the tank the test corals were held in while the last one was performed with water from the ambient treatments technical tank. The first test incubation lasted for 24 hours, the following for 48 hours. The speed of the magnetic stirrers was set at 150, 100 and 180 rpm, with the last setting giving the best results for a smooth operation of the magnetic stirrers.

The final incubations took place three days after a regular feeding to prevent the influence of the specific metabolic action on the respiration rates. The corals were incubated in batches with one incubation chamber containing one life stage of one tank with at least two recruits, two juveniles or one adult to ensure that there would be sufficient changes in the measured values. Due to the high mortality in the temperature treatment only nine were holding corals while the remaining three monitored by the Firesting® were used for the controls. The corals were screwed onto the lid and the bottles sealed while fully submerged. The incubations lasted for a maximum of 42 hours. Some of the adults that were likely to come close to less than 50 % oxygen saturation beforehand were stopped after 24 hours to prevent of low oxygen concentrations on the metabolism. Afterwards the pH of the water in the bottles was measured and water samples were taken. The volume remaining in the bottles after sampling was measured to calculate the actual incubation volume.

At the end of the background measurements the pH, temperature and salinity of the technical tank was measured with a ProfiLine pH 3310 (Xylem Analytics Germany Sales GmbH & Co. KG, Weilheim, Germany) for pH and temperature and a ProfiLine Cond 3110 (Xylem Analytics Germany Sales GmbH & Co. KG, Weilheim, Germany) for salinity. The volumes of the samples taken from the technical tanks before and after the incubations ranged from 110 to 160

ml. During the first two test-incubations all samples were filtered over GF/F filters. This was changed to GF/C filter for all subsequent incubations as using the GF/F filters lead to problems with the C/N-analysis. In the final incubations the samples for organic carbon remained unfiltered due to the large variations encountered in POM and DOC-values during the test-incubations. All filters were washed in MiliQ® (Merck KGaA, Darmstadt, Germany), dried at 60 °C and stored in a desiccator before being used. The water samples for Nutrient, DIC, TA, DOC, POC and TOC-samples were attained and treated as follows:

For the nutrient analysis, 10 ml were filtered into a 15 ml Falcon-tube and stored in a freezer at – 20 °C. They were analyzed for concentrations of NO_x, NO_2, NO_3^-, PO_4^{3-} and Si using a QuAAtro nutrient analysator with a XY-2 sampler (SEAL analytical GmbH, Norderstedt, Germany) and NH_4^+ with a FP4025 fluorometer (JASCO Deutschland GmbH, Pfungstadt, Germany). For DIC, 4 ml were filtered into small, brown glass vials poisoned with mercury chloride ($HgCl_2$) without headspace, stored at about 5 °C and analyzed using a Gerät (Herteller) with reference material from the Dickson batch 102. For the TA measurement 60 ml were filtered without headspace into 50 ml falcon tubes and stored at about 5 °C. The inhouse standard of filtered North Sea water was used for the TA measurements. Each sample was divided into two 25 ml duplicates and measured with a TW alpha plus coupled to a TitroLine alpha plus (Xylem Analytics Germany Sales GmbH & Co. KG, Weilheim, Germany) using Gran titration (Gran, 1952). Samples for DOC were only taken during the test-incubations. For the final incubations, the filters were removed before transferring the water into the plastic bottles to measure TOC. In both cases the remaining volume, between 30 and 50 ml, was used. Both DOC and TOC were analyzed using a TOC-$L_{CPH/CPN}$ analyzer, (Shimadzu Corp., Tokyo, Japan). For POM, the filters were dried for at least 24 hours at 60 °C and weighted using a M2P Micro Balance (Sartorius AG, Göttingen, Germany). Afterwards the C/N-ratio of the POM was analyzed using an EA 3000 (Eurovector, Palavia, Italy).

2.3.4 Determination of coral surface area

The tissue surface of the corals was determined to a) normalize all changes in water parameters, respiration rates and POM-intake from feeding to the coral surface and b) to calculate the changes in the tissue coverage during the long-term experiment comparing start to end. This was done using the formula $A = ((\pi \times r^2) + ((r + R) \times \pi \times m))/100$, where A is the tissue surface in cm^2, r and R are the radius of the oral and aboral surface in mm respectively and m the length of the lateral surface in mm calculated with the equation $m = \sqrt{(r - R)^2 + h^2}$, where h is the

height of the coral in mm. The values for r, R and h were obtained using a digital caliper. When the coral was oblong shaped two radii were measured and the mean of the two values used for r and R. These measurements were taken at the beginning of the long-term experiment and, two weeks before it ended.

2.3.5 Coral fitness and behavior

Due to the variations in tissue surface area, the corals were divided into six different categories (1 = coral skeleton completely covered with tissue, 6 = no tissue visible) according to their tissue covered surface. Measurements from incubations performed with corals that were determined to be of the category 4 (tissue only on oral side with septa not covered) were excluded from any further data analysis to prevent an influence of decaying tissue.

To see how the corals reacted to the influx of zooplankton during normal feeding events they were filmed for short periods of time (3 – 5 min) with 1 to 3 hour intervals between each take using a camera DSC-RX10M4 (Sony Group Corporation, Tokyo, Japan) with a Vario Sonnar 2.4 – 4/8.8 – 220 objective (Sony Group Corporation, Tokyo, Japan) and an external light source Walimex pro LED Flat 200 (Samyang Optics, Masan, South Korea) set at 10 % intensity. To avoid a possible reaction by the corals to repeated handling and turning of the rack, one side of the rack was filmed for three hours (half the time of the feeding) after which the rack was turned around to film the other side for the remaining 3 hours. Filming started with the adults, since the tended to have their tentacles retracted most of the time while the recruits and juveniles often had their tentacles already extended before the feeding. Filming started 1 minute before the addition of the *A. persimilis* nauplii.

2.4 Data analysis

2.4.1 Respiration rates

The oxygen concentration in $mg \times l^{-1}$ and $\mu mol \times l^{-1}$ was calculated from the signal intensity, ambient pressure and water temperature measured by the Firesting® sensors using the Pyroscience® oxygen calculation tool FW4 excel spreadsheet from 2019. The mean respiration rates in $mg \times cm^{-2} \times d^{-1}$ and $\mu mol \times cm^{-2} \times d^{-1}$ were calculated for the first 18 hours of the incubations and corrected for background respiration, incubation volume and normalized to coral surface area. The 18-hour time frame was chosen due to the exponential increase in

respiration rates due to microbial growth in the incubations of the temperature and combined treatment after 18 and 24 hours, respectively.

2.4.2 Calcification rates

Calcification rates were calculated using the alkalinity anomaly technique which assumes that calcification takes up two Mols of bicarbonate (HCO_3^-) and therefore decreases TA by two Mol to produce one Mol of Calcium carbonate ($CaCO_3$), expressed in the formula $G_{TA} = -(\Delta TA/2)$ (Gazeau *et al.*, 2015). As TA is influenced by the concentration NH_4^+, PO_4^{3-} and NOx as well Gazeau *et al.* (2015) devised a formula that accounts for their influence: $G^*_{TA} = (\Delta NH_4^+ - \Delta TA - \Delta PO_4^{3-} - \Delta NO_x)/2$. Changes in TA, NH_4^+, PO_4^{3-} and NOx were corrected for the incubation volume and time and inserted into the formula. The resulting hourly growth rates were upscaled to changes per day and normalized to the total surface area of corals in the respective incubation chamber.

2.4.3 Carbonate chemistry

The properties of the Carbonate-system and the aragonite saturation were calculated using the CO2Sys_v2.1 exel tool from Pierrot *et al.* (2006) with the constants from Lueker *et al.* (2000), $KHSO_4$ from Dickson, total pH scale and $[B]_T$-values from Upstrom (1974). The input variables used where $pH_{(total)}$, DIC concentrations, temperature, salinity, Si- and PO_4^{3-}-concentration and the pressure in dbar during the incubation measured by the Firesting®.

2.4.4 O:N ratio

To determine the primary energy source (Gori *et al.*, 2016), O:N ratios were calculated from the daily respiration rates and changes in NH_4^+ concentrations in µmol per day corrected for the incubation volume and tissue surface.

2.5 Statistical analysis

All statistical analysis were conducted using the R software version 4.1.0 (R Core Team, 2020). For batch incubation comparisons were done between experimental treatments only and not individual life stages. Normal distribution of the residuals was tested with the Shapiro-Wilk-Test using the command shapiro.test. Homogenity of variance for respiration and ammonium excretion was tested with the Levene test using the command LeveneTest from the car-package.

If normality of residuals or variance of homogeneity was not given, the data was transformed with logarithmic, square root or cube root transformation. All data sets that met the conditions with or without being transformed were tested for significance with ANOVA using the command Anova() from the car-package.

If the conditions for the ANOVA could not be met, significance was tested with the untransformed data using the Kruskal-Wallis test with the command kruskal.test() for one factor and the generalized least of squares (GLS) model using the command gls() from the nlme-package for multiple factors.

If significant differences were detected, post-hoc tests were conducted with the pairwise wilcoxon rank-sum test with the command pairwise.wilcox.test for nonparametric tests and the lsmeans function from the emmeans-package (formerly lsmeans) using the adjust method “tukey” for significant differences detected by the ANOVA.

3. Results

3.1. Changes over the course of the long-time experiment

3.1.1 Water parameters and carbonate system

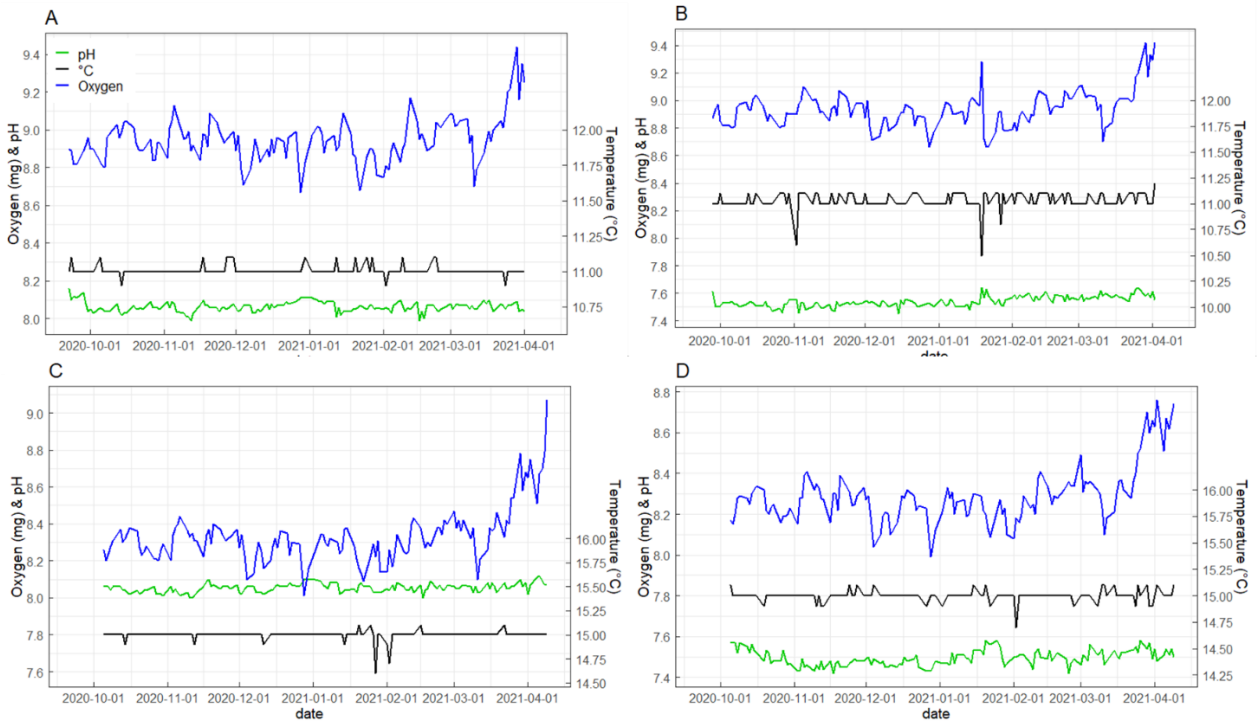

Figure 5: $pH_{(total)}$, temperature(°C) measured daily by the iks system and oxygen concentration (mg/l) measured daily with the hand-held oxygen meter in the tanks during then experiment. Treatments from A to D are: Ambient, pH, temperature, combined. The increase in oxygen concentrations at the end of the experiment is due to a new oxygen meter.

Over time, the pH and temperature of the different treatments were relatively constant with deviations rarely exceeding 0.1 pH units or 0.25 °C (Fig. 5). In comparison, O_2 concentrations were fluctuating more strongly but always stayed above 8.5 mg x l^{-1} in the ambient and pH treatment (Fig. 5 A, B) and 8.0 mg x l^{-1} in the temperature and combined treatment (Fig. 5 C, D). These values led to Ω_{arg} levels of 1.46 ± 0.03, 0.63 ± 0.001, 1.78 ± 0.05 and 0.71 ± 0.02 for the ambient, pH, temperature and combined treatment, respectively.

3.1.2 Changes in tissue surface area and mortality after 6 months

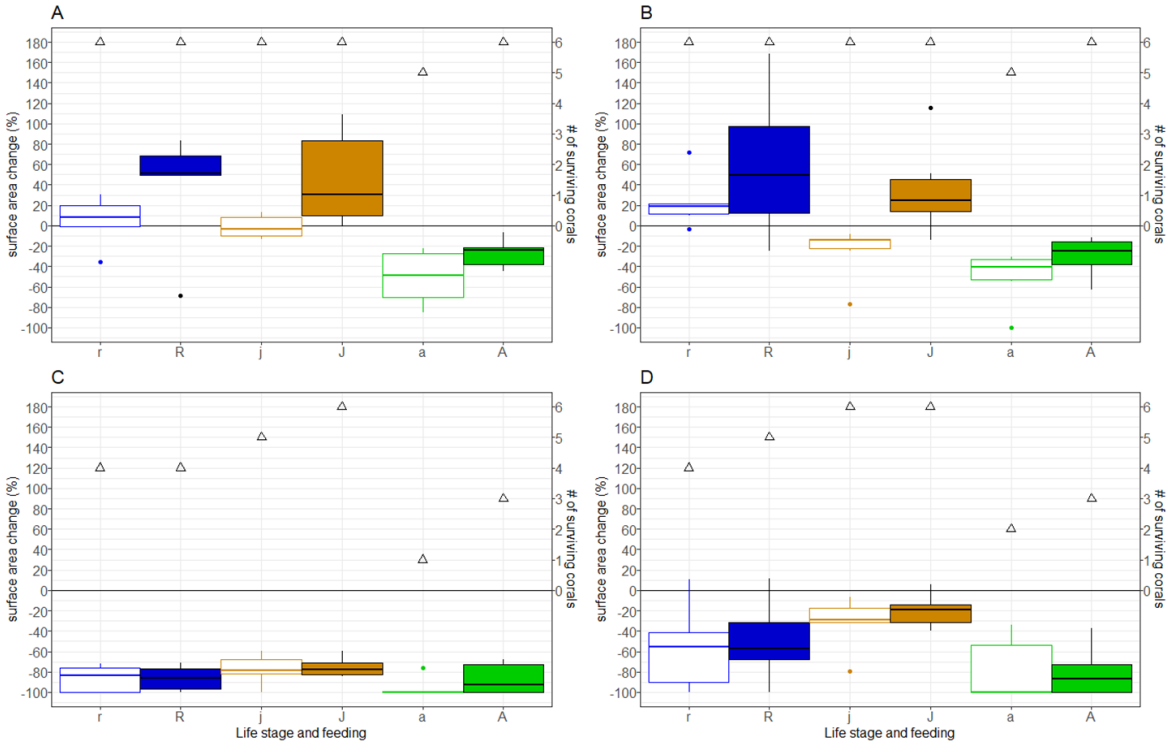

Figure 6: Change in tissue surface area in % and mortality over 6 months. Treatments from A to D: Ambient, pH, temperature, combined. The number of corals for each plot is 6. LF corals are represented by lowercase letters and HF corals by uppercase letters. "r" stands for recruits, "j" for juveniles and "a" for adults.

3.1.2.1 Mortality

25 (17.4 %) of the 144 corals died before the end of the long-time experiment. With 17 out of the 25 dead polyps, the adults represented 68 % of all dead corals, followed by the recruits with 7 dead polyps (28 %) and one dead juvenile (4 %). Mortality was highest in the temperature treatment with 13 corals (36.1 %, Fig. 6 C) followed by the combined treatment with ten corals (27.8 %, Fig.6 D) and the pH and ambient treatment with one adult each (2.7 %, Fig. 6 A & B).

3.1.2.2 Changes in tissue surface area.

Table 2: Four-way ANOVA testing the influence of the treatment, life stage and feeding group on tissue growth rates over 6 months. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Factors	Df	*F*-value	*p*-value
Intercept	1	128.144	< 0.0001 ***
Treatment	3	57.527	< 0.0001 ***
LS	2	29.682	< 0.0001 ***
Feeding	1	13.919	0.0003 ***
Treatment:LS	6	3.827	0.0016 **
Treatment:Feeding	3	3.898	0.011 *
LS:Feeding	2	0.814	0.446
Treatment:LS:Feeding	6	0.505	0.804
Residuals	120		

The treatments had a significant influence on the corals surface extension and therefore growth rates over the course of the experiment (Tab. 2), with values ranging from 171.14 to – 85.01 % in the ambient treatment, (Fig. 6 A) 168.63 to – 100 % in the pH treatment (Fig. 6 B), 9.17 to – 100 % in the temperature treatment (Fig. 6 C) and 11.20 to – 100 % in the combined treatment (Fig. 6 D).The overall changes differed greatly between treatments and were only similar between the ambient and the pH treatment (Tukey's HSD, t-ratio = 0.374, p = 0.982). The corals in the temperature treatment lost high proportions of their tissue surface area (Fig. 6C) resulting in significantly lower growth rates compared to the ambient (Tukey's HSD, t-ratio = – 10.937, $p < 0.0001$), pH (Tukey's HSD, t-ratio = – 10.562, $p < 0.0001$) and combined (Tukey's HSD, t-ratio = t-ratio = – 3.667, $p = 0.0021$) treatment. The same but with less severity (Fig. 6 D) applies for the corals from the combined treatment in comparison to the ambient (Tukey's HSD, t-ratio = – 7.270, $p < 0.0001$) and pH (Tukey's HSD, t-ratio = – 6.895, $p < 0.0001$) treatment.

Feeding had a significant effect on tissue surface extension (Tab. 2) with a 12-fold increase in food availability leading to increased tissue growth rates in the ambient (Tukey's HSD, t-ratio = 3.658, p = 0.009, Fig. 6 A) and pH treatment (Tukey's HSD, t-ratio = 3.459, p = 0.017, Fig. 6 B), but had no effect in the temperature (Tukey's HSD, t-ratio = – 0.151, p = 1.00, Fig. 6 C) and combined treatment (Tukey's HSD, t-ratio = 0.496, p = 0.999, Fig. 6 D).

There were significant differences in tissue extension rates between life stages overall (Tab. 2) and within the treatments (Tab. 2). The adults in the ambient treatment had lower tissue extension rates than the recruits (Tukey's HSD, t-ratio = – 5.149, $p = 0.0001$) and the juveniles (Tukey's HSD, t-ratio = – 4.412, $p = 0.0013$). In the pH treatment the only significant differences were between the adults and the recruits (Tukey's HSD, t-ratio = – 5.873, $p < 0.0001$) while all other life stages had similar extension rates.

In the temperature treatment, tissue retraction was similar between the life stages, while differences occurred in the combined treatment, where tissue retraction was less severe in the juveniles than in the adults (Tukey's HSD, t-ratio = 3.904, $p = 0.0084$), but both life stages did not differ significantly from the recruits.

3.2 Physiological response of the test corals to different incubation procedures.

3.2.1 Feeding rates as response to different food concentrations.

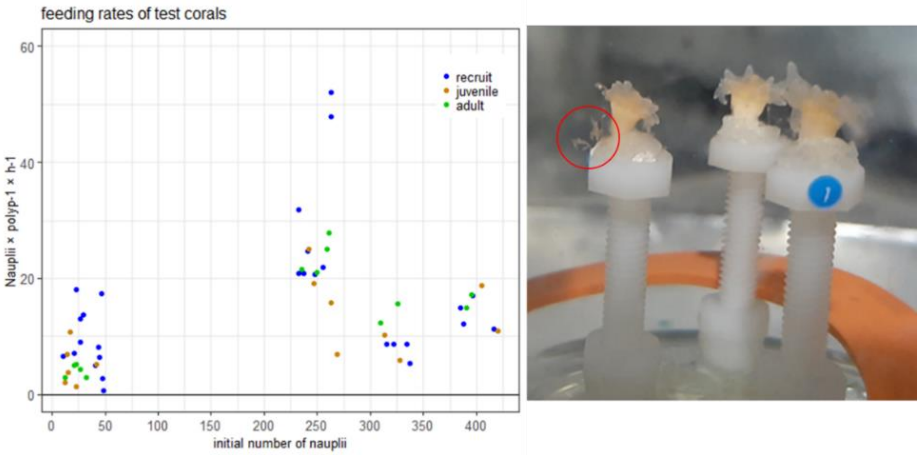

Figure 7: Measured hourly feeding rates of the test corals to assess an adequate duration and initial number of nauplii for the feeding experiments with the corals from the longtime experiment. For the test with 30 nauplii the corals were incubated individually (n = 23) while all other tests were conducted with two to three corals per bottle (n of recruits = 4, n of juveniles and adults = 2). The picture on the right shows recruits after the incubation with 250 nauplii, groups of nauplii caught by hydrozoans or mucus can be seen in the red circle.

Table 3: Two-way ANOVA testing the influence of the different amounts of nauplii ("group") and life stage on the feeding rate of the test corals. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Factors	Df	*F*-value	*p*-value
Intercept	1	1784.84	< 0.0001 ***
Group	4	19.90	< 0.0001 ***
LS	2	2.48	0.096
Group:LS	8	1.23	0.30
Residuals	40		

The feeding rates differed between the different incubations but not between the life stages (Tab. 3) with no clear correlation between the initial amount of nauplii and feeding rates (Fig. 7). This may have been due to methodological errors like the outflow of nauplii upon closing of the bottles, mucus secretion or hydrozoans capturing nauplii that were not eaten during the incubation (Fig. 7) or the standard deviation in the actual number of nauplii. The individual incubations with 30 nauplii show the different feeding rates of individual polyps which might be masked in the other incubations with two to three polyps per bottle.

3.2.2 Physiological response to different incubation durations and procedures.

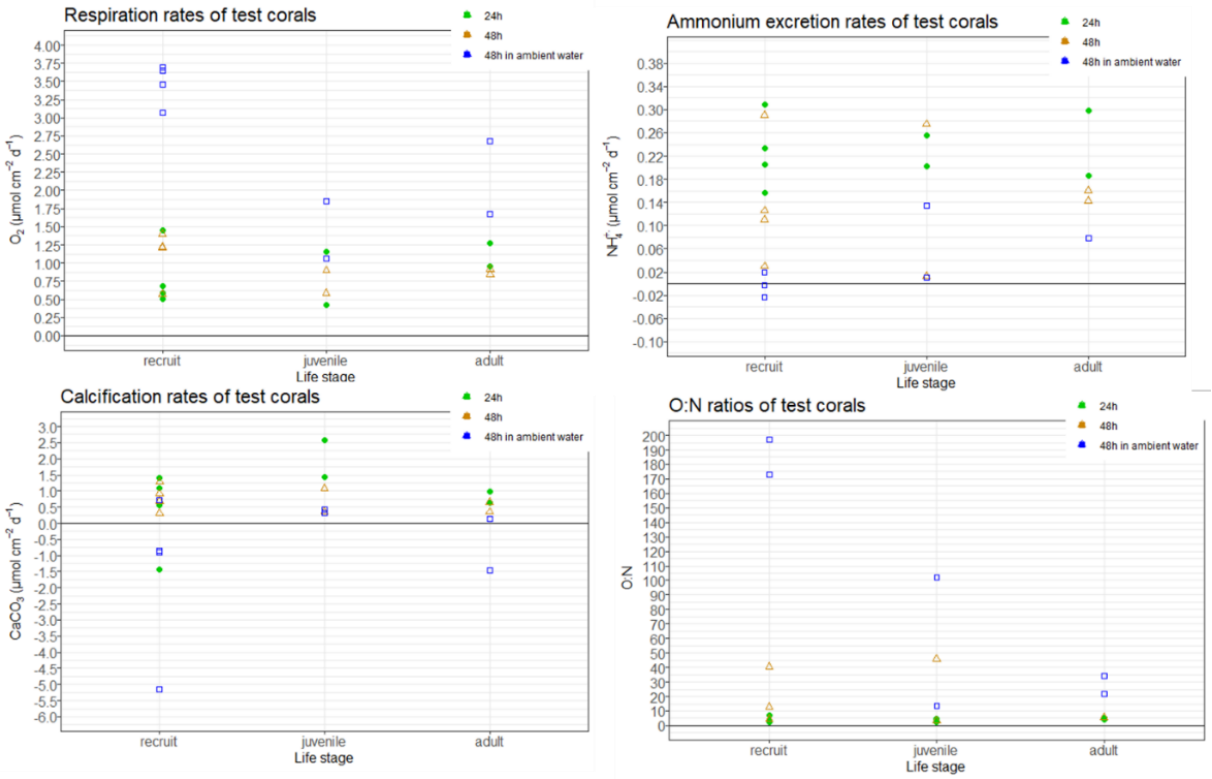

Figure 8. Daily respiration, ammonium excretion and calcification rates normalized to the tissue surface and O:N ratios of the test corals during three separate test incubations. The third incubation was performed with water from the ambient treatment.

Table 4: One-way ANOVA testing for significant differences in respiration rates, ammonium excretion rates and O:N ratios between the incubations with the test corals. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Measured value	**Df**	***F*-value**	***p*-value**
Respiration rate	2	17.02	< 0.0001
Ammonium excretion	2	14.40	0.0001
O:N ratio	2	16.81	< 0.0001

All tested procedures yielded measurable results (Fig. 8). Significant differences in respiration and ammonium excretion rates and O:N-ratios(Tab. 4) as well as calcification rates (Kruskal-Wallis , Df = 2, $p = 0.01$) were always due to the third incubation conducted with water from the ambient treatment differing from the other two. This indicates that in this last incubation the corals metabolism may have been negatively affected by the sudden change in water parameters.

3.3 Physiological response of the corals to the treatment conditions

3.3.1 Feeding rates and weekly nauplii-derived POM intake under different food densities

Table 5: Feeding rates in nauplii × h^{-1} of the different treatments within the feeding groups. n gives the number of corals used for the feeding incubations.

	Low feeding				High feeding			
Treatment	**Min.**	**Max.**	**Mean (±SD)**	**n corals**	**Min.**	**Max.**	**Mean (±SD)**	**n corals**
Ambient	0	11	3.2 (3.8)	18	0	30	11.4 (8.5)	18
pH	0	14	5.0 (4.1)	18	6	46	21.6 (11.5)	18
Temperature	2	11	4.3 (3.4)	9	0	53	19.4 (13.2)	13
Combined	0	13	5.2 (3.7)	11	3	33	17.5 (7.9)	14
All	0	14	4.4 (0.9)	56	0	53	17.5 (4.4)	63

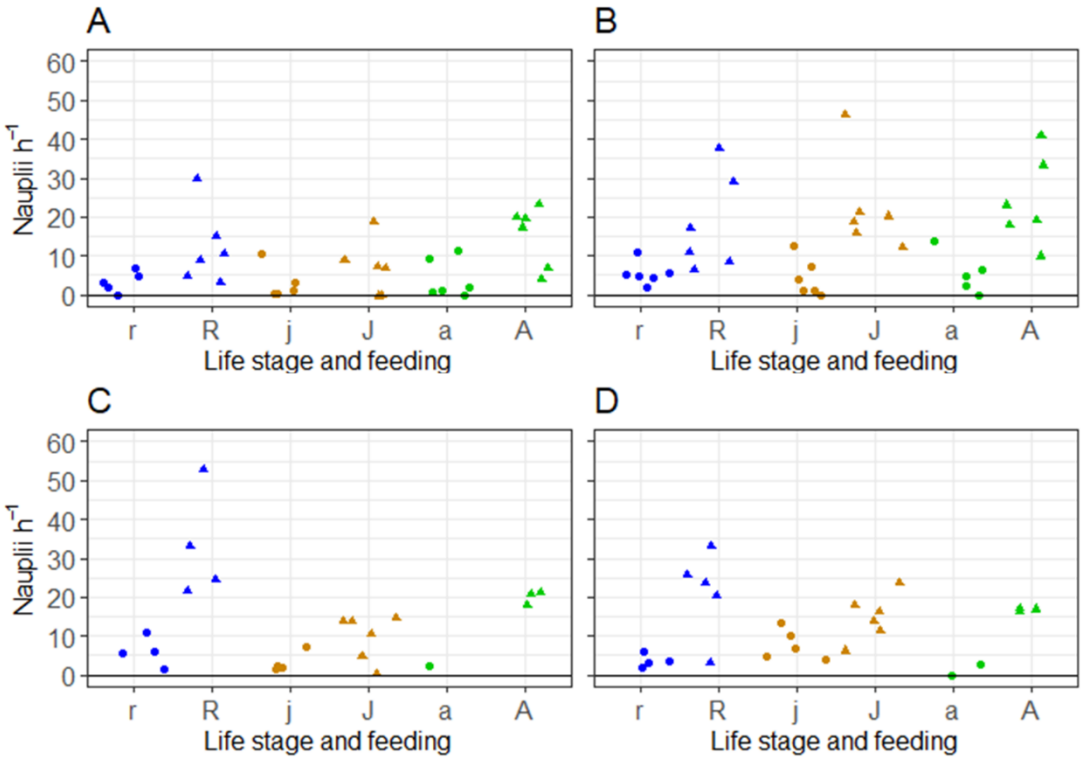

Figure 9: Individual feeding rates of the corals over one hour. Treatments from A to D are: Ambient, pH, temperature, combined. LF corals are represented by lowercase letters and HF corals by uppercase letters. “r” stands for recruits, “j” for juveniles and “a” for adults.

Table 6: Four-way ANOVA testing the effects of the different stressors on the feeding rates of the corals.

Factors	Df	*F*-value	*p*-value
Intercept	1	846.306	< 0.0001 ***
Temperature	1	2.195	0.141
pH	1	5.513	0.021 *
Life stage	2	2.804	0.065
Feeding	1	87.440	< 0.0001 ***
Temperature:pH	1	2.830	0.095
Residuals	111		

A four-fold increase in food concentration led to a corresponding (Tab. 5), significant increase in feeding rates (Tab. 6, Tukey's HSD, *t*-ratio = 9.351, $p < 0.0001$), while the feeding rates of the different life stages were similar to each other (Tab. 6, Fig. 9).

The amount of POM per individual *Artemia persimilis* nauplii was 3 ± 0.3 µg for both one- and two-day old nauplii with similar carbon (1.2 ± 0.05 µg and 1.1 ± 0.2 µg) as well as nitrogen (0.2 ± 0.005 µg and 0.2 ± 0.017 µg) content for one- and two-day old nauplii, respectively and a C/N ratio of 5.04 ± 0.14 and 4.81 ± 0.44 in one- and two-day old nauplii, respectively (Wilcoxon-Mann-Whitney test, p = 0.64, 0.06, 0.08 and 0.08 for POM, C, N and C/N, respectively).

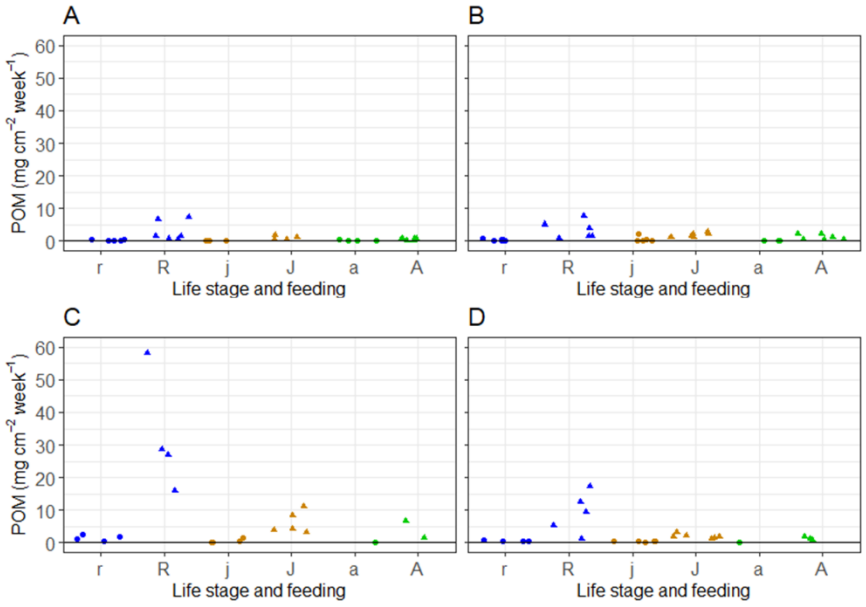

Figure 10: Theoretical weekly nauplii-derived POM intake of the individual corals normalized to the tissue surface during the feeding incubations calculated using the mean POM of two-day old *A. persimilis* nauplii. Treatments from A to D are: Ambient, pH, temperature, combined. LF corals are represented by lowercase letters and HF corals by uppercase letters. "r" stands for recruits, "j" for juveniles and "a" for adults.

Table 7: Three-way ANOVA testing the effect of treatment, life stage and feeding group on the weekly POM intake per cm^2.

Factores	Df	*F*-value	*p*-value
Intercept	1	19.262	< 0.0001
Treatment	3	15.390	< 0.0001
Life stage	2	22.852	< 0.0001
Feeding	1	189.033	< 0.0001
Treatment:Life stage	6	0.852	0.533
Residuals	92		

The increase in weekly nauplii derived POM intake between the two feeding groups was statistically significant (Tab. 7). With an average of 4.93 ± 9.18 mg POM × cm^{-2} × $week^{-1}$, the HF corals ingested considerably higher amounts than the LF corals with 0.41 ± 0.5 mg POM × cm^{-2} × $week^{-1}$ (Tukey's HSD, *t*-ratio = 13.75, $p < 0.0001$). The effects of life stage and treatment on the weekly POM intake were tested and found to be important factors (ANOVA, $F = 22.95$, $p < 0.0001$, DF = 2 for Life stage and $F = 14.26$, $p < 0.0001$, DF = 3 for treatment). As the hourly feeding rates did not differ significantly between the life stages and feeding, this is most likely an effect of the differences in surface area (Fig. 10).

The adults had significantly less POM available per week than the juveniles (Tukey's HSD, *t*-ratio = – 3.08, $p = 0.008$) and recruits (Tukey's HSD, *t*-ratio = – 6.447, $p < 0.0001$). The juveniles in turn had less POM available per week than the recruits (Tukey's HSD, *t*-ratio = – 4.332, $p = 0.0001$).

At 0.91 ± 1.71 mg POM × cm^{-2} × $week^{-1}$, the weekly POM intake from the ambient treatment was slightly lower than that of the pH treatment at 1.28 ± 1.63 mg POM × cm^{-2} × $week^{-1}$, but still similar (Tukey's HSD, *t*-ratio = – 2. 337, $p = 0.098$), while significantly lower than the 2.68 ± 4.29 mg POM × cm^{-2} × $week^{-1}$ of the combined treatment with (Tukey's HSD, *t*-ratio = – 3.096, $p = 0.014$).

The corals from the combined treatment also took in more POM per cm^2 than those from the pH treatment, but the overall rates were close to each other (Tukey's HSD, *t*-ratio = 0.39, $p = 0.40$).

Compared to the corals from the temperature treatment with 8.86 ± 14.39 mg POM × cm^{-2} × $week^{-1}$, the ambient (Tukey's HSD, *t*-ratio = – 1.98, $p < 0.0001$), pH (Tukey's HSD, *t*-ratio = -1.42, $p < 0.0001$) as well as the combined treatment (Tukey's HSD, *t*-ratio = – 1.03, $p = 0.009$) all had significantly lower amounts of POM per cm^2.

3.3.1.2 Tentacle extension in response to the input of *Artemia* nauplii.

Table 8: Feeding rates in nauplii × h^{-1} of the different life stages within the feeding groups and estimated extension rates in %. Total n of LF corals = 56; Total n of HF corals = 63.

		< 25 %				**25 – 75 %**				**> 75 %**			
	Life stage	Min	Max	Mean (±SD)	n corals	Min	Max	Mean (±SD)	n corals	Min	Max	Mean (±SD)	n corals
LF	Recruit	0	11	5.44 (3.81)	9	2	7	4 (1.91)	7	2	11	5.20 (3.49)	5
	Juvenile	0	4	1.38 (1.77)	8	0	7	2.17 (2.56)	6	2	13	8 (3.92)	7
	Adult	0	14	4.73 (4.78)	11	0	2	1.33 (1)	3				0
	n total				28				16				12
HF	Recruit	10	36	22.8 (10.71)	5	3	53	19.93 (13.91)	14	9	33		2
	Juvenile			12	1	0	46	13.41 (11.24)	17	7	20	14 (15.10)	6
	Adult	7	41	20.64 (9.54)	11	4	23	16.33 (6.50)	6			20	1
	n total				17				37				9

During the feeding incubations, recruits and juveniles tended to extend their tentacles further than the adults (Tab. 8). An increase in food availability led to more corals extending their tentacles to the intermediate stadium (Tab. 8, 25 – 75 %), while corals that fully extended their tentacles mostly belonged to the LF group (Tab. 8, > 75 %). Differences between the feeding rates based on the tentacle extension (Kruskal Wallis, $p < 0.0001$) were mainly due to the higher feeding rates in the HF corals compared to the LF corals. Within the feeding groups, the feeding rates of the corals with fully extended tentacles caught more nauplii than those in the intermediate stadium (Wilcoxon rank sum test, $p = 0.007$), while there was no difference compared to those with retracted tentacles (Wilcoxon rank sum test, $p = 0.08$).

While in their tanks, food input led to different reactions, from already extended tentacles with no change extension over the duration of the feeding (Fig. 11 A, Fig. 12 A, B) to fully retracted tentacles that were not extended (Fig. 11 D – F, Fig. 12 D)

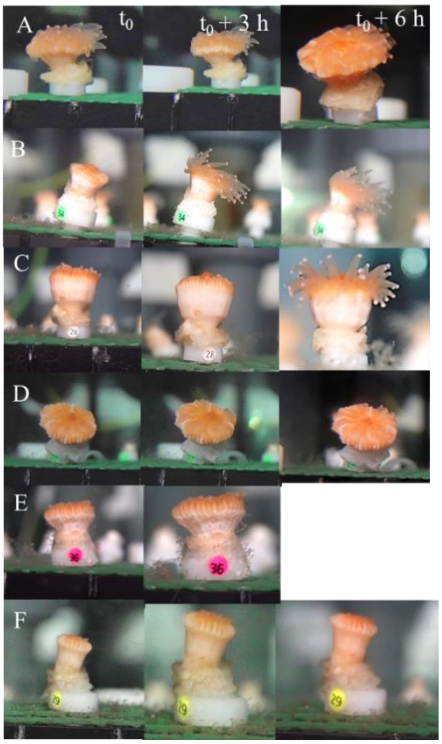

Figure 11: Examples for adult corals from the ambient (A, C), pH, (B, D), temperature (F) and combined (E) treatment exhibiting differences in tentacle extension during feeding in the tanks.

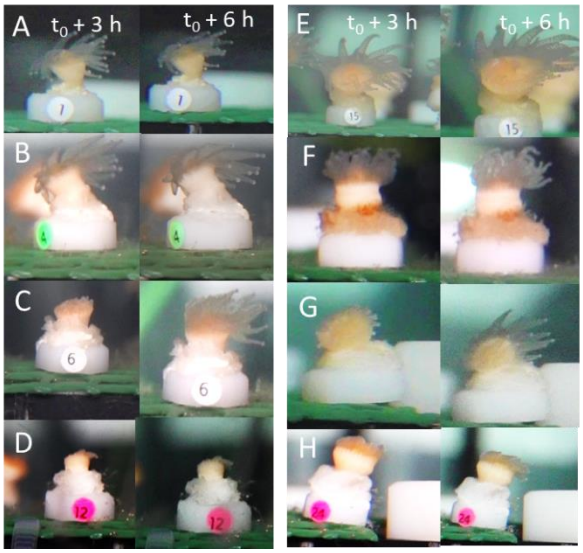

Figure 12: Examples for recruits (A – D) and juveniles (E – H) from the ambient (A, C, E, F), pH, (B, G), and combined (D, H) treatment exhibiting differences in tentacle extension during feeding in the tanks.

3.3.2 Calcification, respiration and ammonium excretion rates during the incubations

3.3.2.1 Changes in the carbonate system during the incubations

The initial $pH_{(NBS)}$ measured in the technical tanks before the incubations was 7.836 in the ambient treatment, 7.571 in the pH treatment, 8.027 in the temperature treatment and 7.539 in the combined treatment. Changes during the incubations ranged from – 0.135 to 0.286 in the control and – 0.309 to 0.264 in the coral chambers.

Changes in Ω_{arg} ranged from – 0.43 to 0.26 in the control and – 0.87 to 0.49 in the coral chambers.

3.3.2.2 Differences between rates measured in the control chambers

Changes in the control chambers in NO_x, PO_4, NH_4^+ and oxygen concentrations per hour were similar between the treatments, while some differences occurred between the changes in TA concentrations (ANOVA, $F = 13.08$, $p = 0.003$, DF = 3). This was due to significantly lower rates in the ambient (Tukey's HSD, t-ratio = 5.97, $p = 0.002$) and combined treatment (Tukey's HSD, t-ratio = 4.29, $p = 0.015$) compared to the pH treatment.

Table 9: Daily calcification, respiration and ammonium excretion rates of the different treatments and feeding groups normalized to tissue surface area. Calcification rates are given in µmol $CaCO_3$ d^{-1} cm^{-2}. Respiration rates are given in µmol O_2 d^{-1} cm^{-2}. Ammonium excretion rates are given in µmol NH_4^+ d^{-1} cm^{-2}.

	Feeding group ->	**Low feeding**			**High feeding**		
Measured Variable	**Treatment**	**Min.**	**Max.**	**Mean (± SD)**	**Min.**	**Max.**	**Mean (± SD)**
Calcification	Ambient	0.48	6.18	2.56 (2.45)	0.26	4.47	3.21 (4.04)
	pH	– 11.60	– 0.74	– 4.71 (4.02)	– 4.36	3.89	– 0.48 (2.85)
	Temperature	– 5.75	– 2.33	– 3.50 (1.54)	– 4.43	– 2.09	– 2.86 (1.36)
	Combined	– 0.33	2.95	0.97 (1.32)	0.26	3.66	1.05 (1.46)
Respiration	Ambient	0.895	2.240	1.564 (0.429)	1.597	3.328	2.505 (0.670)
	pH	0.962	2.091	1.590 (0.490)	1.450	2.472	2.050 (0.422)
	Temperature	4.715	6.119	5.593 (0.633)	6.090	11.326	8.558 (2.631)
	Combined	1.958	3.973	2.795 (0.801)	1.999	4.861	3.155 (1.239)
Ammonium excretion	Ambient	0.015	0.164	0.088 (0.052)	0.064	0.268	0.15 (0.084)
	pH	- 0.045	0.149	0.036 (0.073)	0.101	0.317	0.168 (0.082)
	Temperature	- 0.129	0.712	0.246 (0.371)	- 0.849	0.591	0.109 (0.829)
	Combined	0.046	0.273	0.130 (0.085)	0.061	0.341	0.204 (0.101)

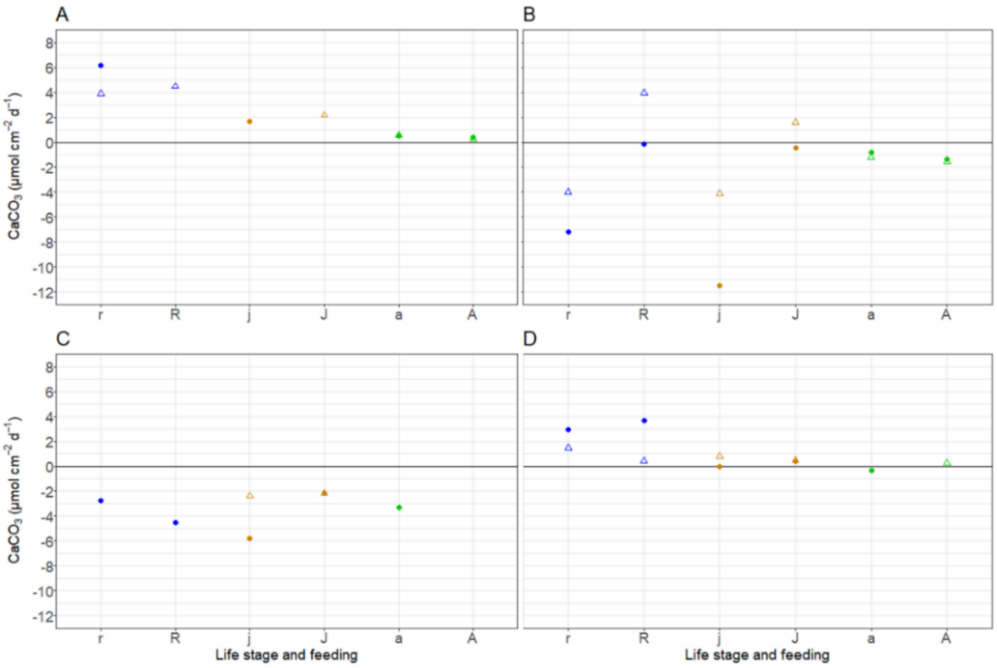

Figure 13: Daily calcification rates normalized to the tissue surface area. Treatments from A to D are: Ambient, pH, temperature, combined. The circles and triangles show which values belong to which bottle. Those in green represent the excretion rates while those in blue represent the respiration rates. LF corals are represented by lowercase letters and HF corals by uppercase letters. "r" stands for recruits, "j" for juveniles and "a" for adults

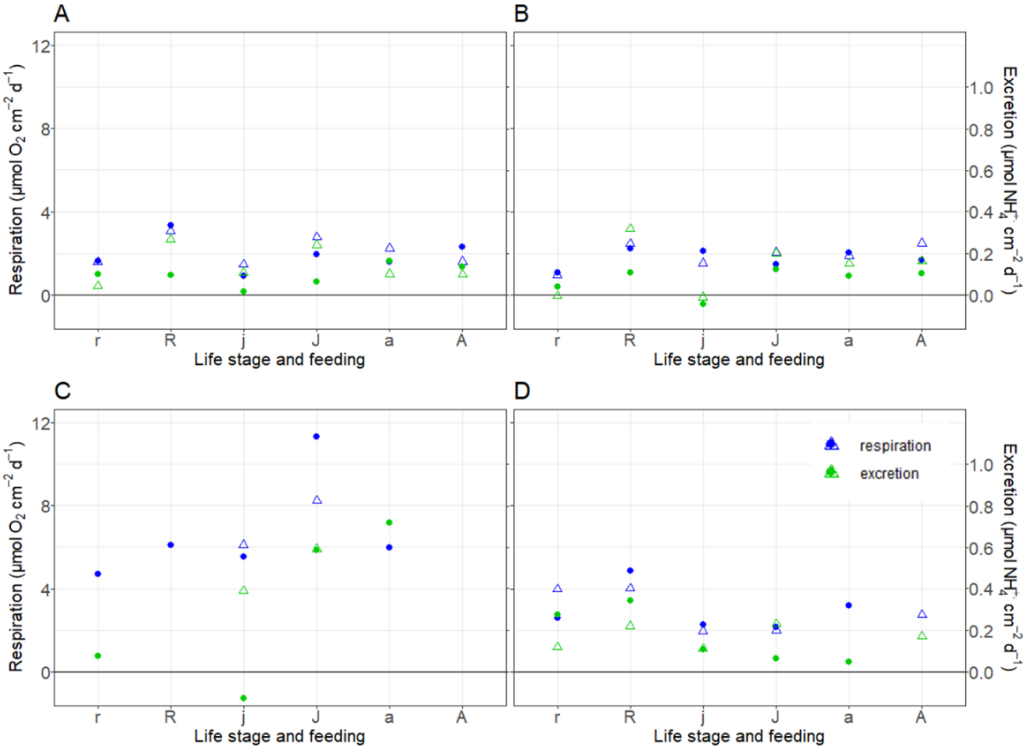

Figure 14: Daily rates for respiration and ammonia excretion normalized to the tissue surface area. Treatments from A to D are: Ambient, pH, temperature, combined. The circles and triangles show which values belong to which bottle. Those in green represent the excretion rates while those in blue represent the respiration rates. LF corals are represented by lowercase letters and HF corals by uppercase letters. "r" stands for recruits, "j" for juveniles and "a" for adults.

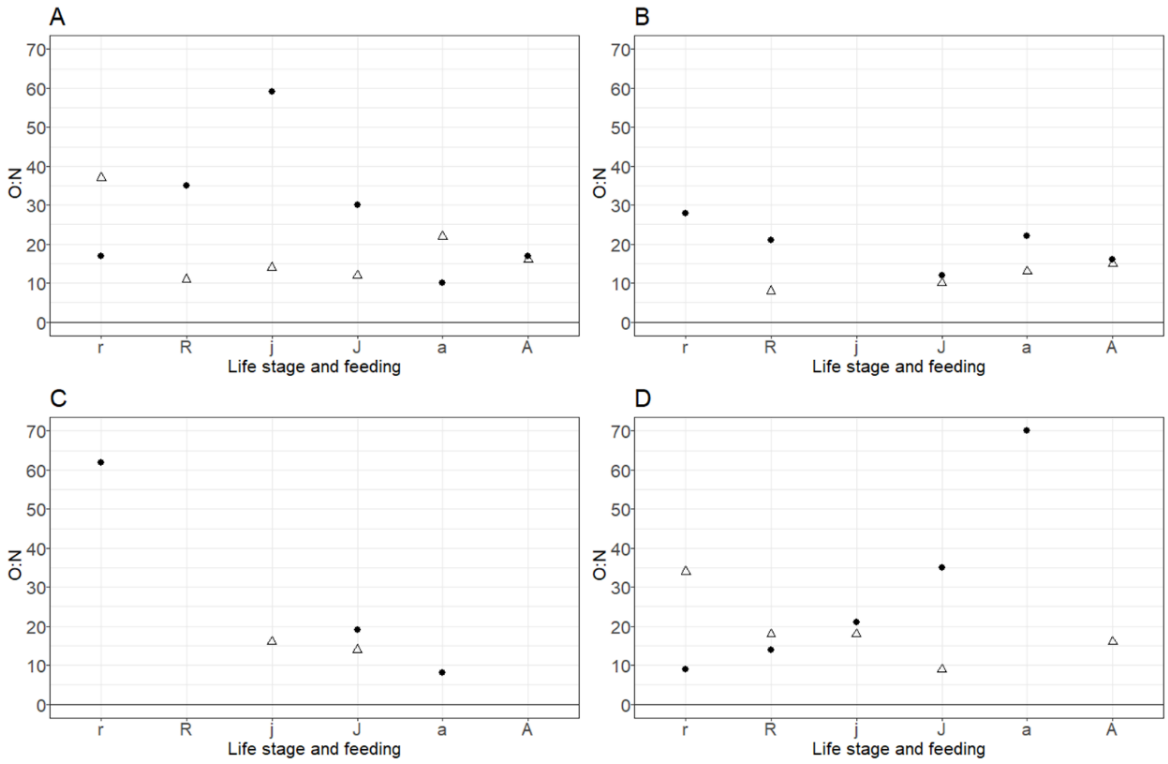

Figure 15: O:N ratios of the different treatments calculated from the daily respiration and ammonium excretion rates normalized to the tissue surface area. Treatments from A to D are: Ambient, pH, temperature, combined. The circles and triangles show which values belong to which bottle. LF corals are represented by lowercase letters and HF corals by uppercase letters. “r” stands for recruits, “j” for juveniles and “a” for adults.

Table 10: Three-way ANOVA testing the influence of the applied stressors on calcification, respiration and ammonium excretion rates. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Measured Variable	Factors	Df	F-value	p-value
Calcification	Intercept	1	2.001	0.166
	Temperature	1	1.058	0.311
	pH	1	0.216	0.645
	Feeding	1	2.451	0.127
	Temperature:pH	1	27.450	< 0.0001 ***
	Residuals	33		
Respiration	Intercept	1	2718.220	< 0.0001 ***
	Temperature	1	89.228	< 0.0001 ***
	pH	1	26.794	< 0.0001 ***
	Feeding	1	11.376	0.002 *
	Temperature:pH	1	17.360	0.0002 ***
	Residuals	36		
Ammonium excretion	Intercept	1	17.992	0.001 ***
	Temperature	1	4.088	0.051
	pH	1	1.942	0.172
	Feeding	1	3.301	0.078
	Temperature:pH	1	0.056	0.814
	Residuals			
O:N ratio	Intercept	1	864.969	< 0.0001 ***
	Temperature	1	0.074	0.787
	pH	1	0.085	0.773
	Feeding	1	2.439	0.128
	Temperature:pH	1	0.750	0.393
	Residuals	31		

3.3.2.3 Calcification rates

All coral batches in the ambient treatment showed positive net calcification rates, while the calcification rates in the temperature treatment were always negative (Tab. 9, Fig. 13 A, C). Positive as well as negative calcification rates occurred in the pH and combined treatment (Tab. 9, Fig. 13. B, D). Neither pH nor temperature applied as single stressor had a significant effect on calcification rates, while there were clear differences between the treatments (Tab. 10).

Between the treatments, the calcification rates of the ambient treatment were close to those of the combined treatment (Tukey's HSD, t-ratio = 1.075, p = 0.707), while being higher than

those of the pH (Tukey's HSD, *t*-ratio = 4.275, $p = 0.008$) and the temperature treatment (Tukey's HSD, *t*-ratio = 4.112, $p = 0.0013$).

The calcification rates of the pH treatment were similar to the temperature treatment (Tukey's HSD, *t*-ratio = 0.391, $p = 0979$) and lower than those of the combined treatment (Tukey's HSD, *t*-ratio = – 3.252 $p = 0.013$).

Like the comparison with the ambient treatment, calcification rates in the temperature treatment were significantly lower than those of the combined treatment (Tukey's HSD, *t*-ratio = – 3.199 $p = 0.015$).

While the measured effect was not significant, a 12-fold increase in food availability led to enhanced calcification in the recruits and juveniles of the pH treatment (Tab. 13, Fig. 13 B).

3.3.2.4 Respiration rates

Temperature and pH, both as single stressor and in combination, had a significant influence on respiration rates (Tab. 10). Respiration rates were negatively affected by a decrease in pH (Tukey's HSD, *t*-ratio = – 5.176, $p < 0.0001$) and increased with temperature (Tukey's HSD, *t*-ratio = 9.446, $p < 0.0001$).

Between the treatments, the respiration rates of the ambient treatment were close to those of the pH treatment (Tukey's HSD, *t*-ratio =0.528, $p = 0.952$) and the combined treatment (Tukey's HSD, *t*-ratio = – 2.173, $p = 0.150$), while being significantly lower than those of the temperature treatment (Tukey's HSD, *t*-ratio = – 10.069, $p < 0.0001$).

Respiration rates in the pH treatment were also similar to the combined treatment (Tukey's HSD, *t*-ratio = – 2.676, $p = 0.051$) and lower than that in the temperature treatment (Tukey's HSD, *t*-ratio = – 10.522, $p < 0.0001$).

Like the comparison with the ambient and the pH treatment, respiration rates in the temperature treatment were significantly higher than those of the combined treatment (Tukey's HSD, *t*-ratio = 7.832 $p < 0.0001$).

3.3.2.5 Ammonium excretion

While an increase was measured in the older life stages of the temperature treatment (Fig. 14 C), none of the applied stressors had a significant effect on the ammonium excretion rates (Tab 10.).

3.3.2.6 O:N ratios

O:N ratios were not influenced by pH or temperature as single or combined stressors as well as feeding (Tab. 10). O:N ratios of the different life stages and feeding groups were similar to each other and showed high variations within life stages and feeding groups (Fig. 15) with the exception of the temperature treatment, were the increase in ammonium excretion in the older life stages is visible in correspondingly decreasing O:N ratios (Fig. 15 C).

4. Discussion

4.1 Evaluation of the method

Unlike the much larger *D. dianthus*, *C. huinayensis* remains rather small throughout its life cycle (Häussermann & Försterra, 2005), making it harder to achieve good ratios of tissue surface area to incubation volume when planning to sample multiple water parameters. The Weck jars used as incubation chambers for the incubations worked reasonably well for this task. The volume was small enough to get measurable changes in almost all samples except DOC, POC and TOC, for which a greater volume might be needed (Dr. Marlene Wall, personal communication) and enabling exact feeding essays with hand-counted nauplii with a reasonable amount of work. They were also big enough to allow for prolonged incubations without risking hypoxia and containing just enough water to take the different water samples used for the different measurements. Deterioration of the rubber bands and two-component glue after prolonged use due to contact with salt water might be problem.

4.2 Feeding rates across treatments and life stages

Having to rely on heterotrophic feeding to meet their metabolic demands, CWCs efficiently utilize available zooplankton showing a linear increase in feeding rates as in response to increased prey availability (Höfer *et al.*, 2018; Naumann *et al.*, 2011; Tsounis *et al.*, 2010). *C. huinayensis* exhibited the same reaction with feeding rates correlating significantly with the food density in the incubation chambers. The mean feeding rates of the HF corals were 3.95 times higher in the HF than in the LF corals, increasing with about the same order of magnitude as the food concentration in the incubation chambers, indicating that the maximum feeding rate was not reached. The feeding rates of *C. huinayensis* were unaffected by the treatments while studies investigating the response of *L. pertusa* to low pH levels reported either reduced or enhanced feeding rates depending on the site of origin (Georgian *et al.*, 2016) or no change (Gomez *et al.*, 2018). The feeding rates during the incubations were similar between the three life stages. Consequently, the available energy from feeding on *A. persimilis* nauplii relative to the tissue surface area decreased with size and therefore age of the polyp.

The increase in food availability and uptake in the HF corals stimulated the metabolism in all treatments, visible in the significant increase in respiration rates across all treatments (Naumann *et al.*, 2011).

CWCs are known to utilize DOC and detritus as food sources as well (Naumann *et al.*, 2011 and references therein). Unfortunately, the high variations in DOC, POC and TOC measurements from the incubations rendered these measurements unusable to determine their turnover and role in the energy budget of *C. huinayensis* under the different stressors.

The slow response of some polyps, visualized as extension of the tentacles, to the input of *A. persimilis* nauplii observed in the tanks and the feeding incubations is perplexing, considering that the importance of this food source to the metabolism of CWCs (Naumann *et al.*, 2011) would make a fast reaction paramount for a species dependent on a fluctuating input of food. But as the feeding rates were mostly unaffected by the tentacle extension, it appears that the tentacles are not needed to overpower small prey items like *Artemia* nauplii. During an experiment with adult *A. salina* as food items *L. pertusa* produced mucus nets to catch them (Murray *et al.*, 2019). Therefore, it might be energetically more reasonable to keep the tentacles retracted when feeding exclusively on small prey items, especially for the adults who lost tissue surface area in all treatments indicating energetic imbalance.

However, *C. huinayensis* is able to catch prey items like euphausiid shrimps almost as big as the polyp itself (Dr. Jürgen Laudien, personal communication). Since mucus alone would most likely be insufficient to incapacitate large, mobile prey items of this size class, retracting the tentacles to conserve energy might negatively impact the ability of *C. huinayensis* to utilize different groups of zooplankton therefore affecting their energy budget and ability to cope with increased metabolic demands. Therefore it would be interesting to know how different composition of the zooplankton could influence the responses of the corals.

4.3 Physiological response to the different treatment conditions and metabolic implications.

4.3.1 Respiration, calcification and tissue extension.

Calcification rates in the corals from the ambient treatment were always positive with no visible influence of higher food availability. This has also been shown to be the case in *L. pertusa* where skeletal growth rates were unaffected by differences in food density at ambient temperature (Büscher *et al.*, 2017; Larsson *et al.*, 2013), while calcification the rates of *D. dianthus* were enhanced by a higher food availability (Martínez-Dios *et al.*, 2020). However, the significant increase in tissue growth rates for the HF corals over the course of the long-time

experiment shows that the surplus energy was used to facilitate higher growth rates. Both calcification and tissue growth rates showed a visible decline with polyp size and therefore age, which has been shown to be the case in zooxanthellate corals as well as CWCs (Elahi & Edmunds, 2006; Movilla *et al.*, 2014 and references therein). Faster growth rates are believed to be important for small polyps to "overcome the strong selective pressure at early life stages" (Martínez-Dios *et al.*, 2020).

In comparison to the corals at ambient conditions, respiration rates were unaffected by the pH treatment, which has been shown for other species of CWCs as well (Carreiro-Silva *et al.*, 2014; Hennige *et al*., 2015; Maier *et al*., 2016), while the exposure to low pH and the resulting low Ω_{arg} levels resulted in a significant reduction of calcification rates. Studies working with comparable pH and Ω_{arg} levels over 6 months or longer yielded similar detrimental effects of OA on calcification rates of different CWC species (Georgian *et al.*, 2016; Gomez *et al.*, 2018; Maier *et al.*, 2016; Martínez-Dios *et al.*, 2020), while studies working with Ω_{arg} levels close to or above one often reported no detrimental effects on calcification (Carreiro-Silva *et al.*, 2014; Gori *et al.*, 2016; Maier *et al.*, 2013; Martínez-Dios *et al.*, 2020).

Although the effect was not statistically significant, an increase in food availability had a positive effect on calcification rates in the younger life stages, indicating that the surplus energy in the HF group was used to fuel the increased energy demand for the variety of mechanisms (McCulloch *et al.*, 2012) responsible for maintaining calcification in undersaturated waters. Calcification rates in the adults were unaffected by increased food intake. An increase in food availability had a positive effect on calcification of *D. dianthus* until a threshold around 7.5 pH and Ω_{arg} levels of around 0.8 (Martínez-Dios *et al.*, 2020), while no such effect could be observed for *M. occulata* (Maier *et al.*, 2016) and *L.pertusa* (Büscher *et al.*, 2017). It has been speculated that this may be due to the differences in physiology between solitary and colonial corals and the effect this has on the ability of individual polyps to react to changes in the environment (Martínez-Dios *et al.*, 2020).

Assuming that the 10 % increase in energy demand for calcification for every drop in pH by 0.1 units (McCulloch *et al.* 2012) holds true for *C. huinayensis*, then the resulting increase in energy demand for calcification must have been about 60 % higher in the pH treatment at 7.5 pH compared to ambient treatment at 8.1 pH. Since neither respiration nor tissue extension rates differed significantly from those in the ambient treatment it appears that even more severe OA and the resulting aragonite undersaturation does not have a strong impact on the overall

metabolism of *C. huinayensis*. It appears that the additional energy demand for calcification can be satisfied with a sufficient increase in food availability. This, together with the positive effect of increased food availability on calcification and tissue growth fits the assumptions that CWC populations can thrive in aragonite undersaturated waters, like they have been encountered in Comau Fjord (Fillinger & Richter, 2013), due to high surface productivity and therefore influx of food to deeper waters compensating for the increased energy demand for calcification (Gomez *et al.*, 2018; Gori *et al.*, 2016).

In contrast to low pH, a 4 °C increase in temperature led to significant increase in respiration rates indicating an increase in the overall metabolic rates and therefore energy demand in response to the rising temperature (Dodds *et al.*, 2007; Newell & Branch, 1980). Elevated temperature significantly decreased both calcification and tissue growth rates with no difference between the life stages or mitigating effects of increased food availability. Higher temperature and the subsequent increase in metabolic rates have been shown to lead to higher calcification rates in CWCs if the temperature was within the range normally encountered in their natural habitat (Büscher *et al.*, 2017, Naumann *et al.*, 2014) with a further enhancement when more food was available (Büscher *et al.*, 2017). While CWCs are able to tolerate short-term exposure to temperatures beyond their upper thermal limit (Brooke *et al.*, 2013; Naumann *et al.*, 2014) a prolonged exposure significantly reduced calcification and respiration rates in *D. dianthus* (Gori *et al.*, 2016) and induced mortality in *L. pertusa* (Brooke *et al.*, 2013). Gori et al. (2016) presumed that the lower calcification rates of *D. dianthus* under elevated temperature were due to the involved enzymes exceeding their thermal range at 15 °C. In contrast to Gori et al. (2016), respiration rates of *C. huinayensis* increased under elevated temperature indicating enhanced metabolic activity. Therefore, it appears that the enzymes responsible for calcification were still within their thermal range, but the increased energy demand forced *C. huinayensis* to allocate all available energy to processes meant to keep the polyp alive until more favorable conditions occurred.

When applying both stressors in combination, respiration rates were slightly increased compared to the ambient and the pH treatment, but the effect was not significant. While low pH and high temperature applied as single stressors negatively affected calcification rates, no such effect was measured under a combination of both stressors with the corals exhibiting the same pattern of higher calcification rates in younger life stages observed in the ambient treatment, albeit not as distinct.

It must be kept in mind that most of the corals in the ambient treatment extended their tissue surface area therefore protecting their skeleton from dissolution (McCulloch *et al.*, 2012), while almost all corals in the combined treatment retracted their tissue, exposing the underlying skeleton to the acidic surrounding water. This means that the actual calcification rates of the combined treatment had to be substantially higher than those of the ambient treatment since they first had to compensate for dissolution of the exposed parts of the coral skeleton to get to the positive calcification rates measured during the incubations (Büscher *et al.*, 2017).

In contrast to the mostly positive calcification rates, most of the corals lost tissue surface area growth rates under the combination of both stressors with no mitigating effect of higher food availability but with lower mortality in the HF group. This means that energy was allocated to calcification despite the overall tissue surface retraction and mortality suggesting that the energy intake in both feeding groups was insufficient to combat detrimental effects of the combined stressors on the coral's physiology. No definitive answer to the reason of these contrasting responses can be made based on the available data. Perhaps the positive calcification rates could be a sign for higher resilience of the surviving corals to the treatment conditions.

The conspicuous mismatch between calcification and tissue growth rates, especially evident in the combined treatment and the adults in the ambient treatment, brings to question how the corals divide their available energy between calcification and tissue growth. It appears that even though the retraction of the tissue surface and high mortality indicated that the energy intake was insufficient to fuel basic metabolic needs, energy was still being allocated to calcification. Other studies observed similar patterns with tissue growth rates responding more strongly to changes in the corals' environment than calcification (Anthony *et al.*, 2002; Larsson *et al.*, 2013 and references therein). Anthony *et al.* (2002) concluded that the higher sensitivity of tissue growth to environmental stressors makes it better suited to assess the coral health than calcification rates, which appears to be the case here as well and might explain why the corals health deteriorated despite the similarities to the corals from the ambient treatment.

Overall, it appears that, like it has been observed in *D. dianthus* (Gori *et al.*, 2016), the metabolism of *C. huinayenis* is more strongly affected by the elevated temperature than low pH levels implemented in the long-time experiment. In combination low pH and elevated temperature had an antagonistic effect on the metabolism of *C. huinayensis*, leading to similar respiration and calcification rates compared to ambient conditions. This has also been reported for the colonial species *L. pertusa* (Büscher *et al.*, 2017; Hennige *et al.* 2015) while the effect

on the morphologically more similar *D. dianthus* was synergistic (Gori *et al.*, 2016), leading to a significant decrease in calcification and respiration rates. While the calcification and respiration rates suggest that *C. huinayensis* is able to acclimate to a combination of OA and elevated temperature, the severe tissue retraction and increased mortality in the combined treatment contradict this interpretation. Although there were less severe than under elevated temperature as single stressor, they suggest that the combined effects of climate change affected the metabolism of *C. hunayensis* in a way where even a marked increase in food availability cannot compensate for the higher energy demand or other detrimental effects.

4.3.2 Energy source for additional metabolic demands

Some of the batch incubations from the pH and the temperature treatment exhibited negative ammonium excretion rates. To the authors knowledge there are no known energetic pathways in corals or any other metazoans utilizing ammonium and the ammonium excretion rates measured in other studies were always positive (Carreiro-Silva *et al.*, 2014; Gori *et al.*, 2016, Naumann et al., 2011). Since the excretion rates were always positive in the batch incubations from the combined treatment, where the respiration rates indicate an exponential bacterial growth the most likely explanation is either a methodical or measurement error.

Like in other studies conducted with *D. dianthus* (Carreiro-Silva *et al.*, 2014; Gori *et al.*, 2016) the ammonium excretion rates were not significantly affected by low pH and elevated temperature as single or combined stressors. They were relatively stable all life stages. While a small increase in ammonium excretion rates can be seen for the HF corals of the ambient and the pH treatment is visible, this most likely just reflects the higher input due to the increased feeding rates. In contrast to the experiment conducted with *D.dianthus* resulting in a clear switch in the main energy source for the metabolism from a mixed use of proteins and carbohydrate or lipids to a protein dominated catabolism visible in lower O:N ratios (Gori *et al.*, 2016), the O:N ratios of *C. huinayensis* during the incubations were similar between the treatments and life stages. The large variability within the treatments showed no significant correlation with the life stage or feeding group. Based on the O:N rations, no clear answer can be given to how the prolonged exposure to single and combined stressors influenced the nature of the predominant energy source. Considering that the measurements were taken towards the end of the long-time experiment at a point where the corals in the temperature and combined treatment had already lost large portions of their tissue surface, there simply may have been no substantial amounts of storage tissues left leaving the corals with only the energy they gained

by utilizing the organic matter they took in from the nauplii and perhaps the surrounding water to fuel their metabolism.

4.4 Ontogenetic effects of low pH and increased temperature

The decline in calcification and tissue growth rates with polyp age observed at ambient conditions is in agreement with the findings of other studies investigating the effects of size and age on the growth rates of CWCs (Maier *et al.*, 2013 and references therein; Movilla *et al.*, 2014). While the inverse relationship between polyp size and calcification rates was still visible in tissue growth rates under OA, it was inversed in the measured calcification rates of the LF corals, showing a greater vulnerability of young life stages to OA. This has been attributed to OA further increasing the already high energy demand for calcification in younger polyps (Movilla *et al.*, 2014).

No differences in calcification and tissue growth rates between the life stages occurred under elevated temperature. It appears that all available energy was allocated to other metabolic processes, possibly to keep up with the increased metabolic demand (Dodds *et al*., 2007).

The inverse relationship of calcification rates and polyp size occurred again when both stressors were applied in combination, while tissue growth rates where similar to those exhibited under elevated temperature. In this treatment however the juveniles were the least affected life stage in terms of relative loss in tissue area.

Representing more than two thirds of all corals that died over the course of the experiment while also losing tissue surface area in all treatments and feeding groups, the adults of *C. huinayensis* were the most affected of the three life stages used in the long-time experiment. While this contradicts the findings of higher resilience to OA in adult CWCS (Movilla *et al.*, 2014; Martínez-Dios *et al.*, 2020) it may be an effect of the comparatively higher metabolic demand due to the larger tissue area increased further by low pH and elevated temperature.

Even though the pH and temperature values in the ambient treatment were set to represent values common in the natural habitat of *C. huinaynesis* and the corals being reared at these conditions for a prolonged time the adults still lost tissue surface area. While the higher food availability in the HF group did not lead to positive tissue growth rates for the adults it led to slower losses compared to the LF group. As one would expect them to thrive at these conditions,

this leads to the question whether the observed effect of the stressors on the adults physiology may be (partly) due to insufficient energy acquisition in both feeding groups.

While the juveniles exhibited lower tissue growth rates than the recruits at ambient conditions and OA as single stressor, the effect of OA on calcification rates was similar for both life stages. Under elevated temperature they were statistically indistinguishable from each other in both calcification and tissue growth rates. While there was a trend towards slower tissue area losses under the combination of both stressors in the juveniles compared to the recruits, the difference was not statistically significant. However, the fact that the juveniles lost only one polyp over the duration of the long-time experiment while the recruits lost seven indicates, that the juveniles were slightly more resilient to the applied stressors than the recruits. This may be due to their lower energy demand for calcification and tissue growth as has been shown in the ambient treatment, while also having a lower base metabolic rate and more energy from feeding available per cm^2 tissue than the adults due to their smaller tissue surface area.

Overall, while some mitigation by feeding could be observed under low pH and Ω_{arg} levels around 0.8, all three life stages showed detrimental effects of increased temperature and a combination of both stressors on their physiology that would threaten their survival. This could not be mitigated by the 12-fold increase in food availability implemented in the long-term experiment. If the effects on the adults were entirely due to the effects of the stressors, then the results suggest that the combined effects of OA and elevated temperature will lead to an erosion at the ontogenetic borders of the population, threatening the polyps at the beginning and end of their life cycle.

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Appendix

Glossary

AWI: Alfred-Wegener-Institute

CWC: Cold-water coral

DIC: Dissolved inorganic carbon

DOM: Dissolved organic matter

OA: Ocean acidification

POM: Particulate organic matter

TOM: Total organic matter

TA: Total alkalinity

Ω_{arg}: Saturation state of aragonite

Supplementary data

Supplementary A: Long-time experiment.

Table A1: Water parameters during the long-time experiment measured by the iks system (pH and °C) and the handheld oxygen meter.

Treatment ->	Ambient			pH			Temperature			Combined		
date	$pH_{(total)}$	oxygen (mg/l)	°C	$pH_{(total)}$	oxygen (mg/l)	°C	$pH_{(total)}$	oxygen (mg/l)	°C	$pH_{(total)}$	oxygen (mg/l)	°C
22.09.2020	8.16	8.90	11.00									
23.09.2020	8.10	8.89	11.10									
24.09.2020	8.12	8.82	11.00									
25.09.2020	8.11	8.82	11.00									
28.09.2020	8.14	8.89	11.00	7.61	8.87	11.00						
29.09.2020	8.08	8.92	11.00	7.50	8.94	11.00						
30.09.2020	8.04	8.96	11.00	7.50	8.97	11.00						
01.10.2020	8.05	8.90	11.00	7.51	8.85	11.10						
02.10.2020	8.03	8.90	11.00	7.53	8.82	11.00						
05.10.2020	8.06	8.83	11.10	7.53	8.82	11.00	8.06	8.26	15.00	7.57	8.17	15.10
06.10.2020	8.05	8.81	11.00	7.54	8.80	11.00	8.06	8.20	15.00	7.57	8.15	15.00
07.10.2020	8.04	8.80	11.00	7.52	8.81	11.00	8.06	8.24	15.00	7.57	8.20	15.00
08.10.2020	8.04	8.96	11.00	7.52	8.95	11.00	8.04	8.28	15.00	7.52	8.28	15.00
09.10.2020	8.04	8.98	11.00	7.50	8.97	11.00	8.06	8.31	15.00	7.57	8.29	15.00
12.10.2020	8.08	9.03	11.00	7.52	8.99	11.00	8.06	8.37	15.00	7.55	8.28	15.00
13.10.2020	8.04	8.96	11.00	7.53	8.94	11.10	8.04	8.30	15.00	7.52	8.25	15.00
14.10.2020	8.02	8.99	10.90	7.54	8.93	11.00	8.04	8.32	14.90	7.56	8.30	15.00
15.10.2020	8.03	9.04	11.00	7.53	9.01	11.00	8.03	8.35	15.00	7.53	8.32	15.00
16.10.2020	8.03	9.05	11.00	7.51	9.04	11.10	8.02	8.38	15.00	7.52	8.34	15.00
19.10.2020	8.07	9.01	11.00	7.51	8.96	11.00	8.04	8.36	15.00	7.48	8.32	14.90
20.10.2020	8.05	8.93	11.00	7.54	8.91	11.00	8.02	8.27	15.00	7.53	8.22	15.00
21.10.2020	8.05	8.90	11.00	7.50	8.85	11.00	8.03	8.23	15.00	7.52	8.20	15.00
22.10.2020	8.06	8.89	11.00	7.50	8.90	11.00	8.04	8.25	15.00	7.47	8.23	15.00
23.10.2020	8.05	8.89	11.00	7.47	8.88	11.00	8.04	8.28	15.00	7.48	8.25	15.00

26.10.2020	8.09	8.95	11.00	7.49	8.80	11.10	8.06	8.21	15.00	7.48	8.16	15.00
27.10.2020	8.06	8.84	11.00	7.46	8.82	11.10	8.02	8.21	15.00	7.53	8.19	15.00
28.10.2020	8.06	8.84	11.00	7.52	8.81	11.10	8.02	8.20	15.00	7.49	8.19	15.00
29.10.2020	8.06	8.93	11.00	7.52	8.91	11.00	8.02	8.26	15.00	7.46	8.20	15.00
30.10.2020	8.05	8.93	11.00	7.55	8.90	11.10	8.01	8.29	15.00	7.47	8.23	15.00
02.11.2020	8.09	8.85	11.00	7.56	8.90	10.60	8.06	8.20	15.00	7.43	8.15	15.00
03.11.2020	8.06	9.01	11.00	7.46	8.97	11.10	8.03	8.34	15.00	7.43	8.28	15.00
04.11.2020	8.09	9.05	11.00	7.53	9.00	11.10	8.05	8.38	15.00	7.49	8.28	15.00
05.11.2020	8.08	9.13	11.00	7.53	9.10	11.10	8.03	8.40	15.00	7.45	8.39	15.00
06.11.2020	8.04	9.08	11.00	7.48	9.08	11.10	8.01	8.44	15.00	7.46	8.41	15.00
09.11.2020	8.03	8.95	11.00	7.50	9.00	11.00	8.03	8.36	15.00	7.43	8.32	15.00
10.11.2020	8.01	8.96	11.00	7.53	9.01	11.10	8.00	8.33	15.00	7.46	8.35	14.90
11.11.2020	8.01	8.99	11.00	7.53	8.97	11.10	8.00	8.35	15.00	7.44	8.33	15.00
12.11.2020	7.99	8.89	11.00	7.50	8.91	11.00	8.01	8.31	14.90	7.48	8.28	14.90
13.11.2020	8.03	8.92	11.00	7.49	8.92	11.00	8.03	8.31	15.00	7.44	8.27	14.90
16.11.2020	8.07	8.84	11.00	7.52	8.85	11.00	8.06	8.22	15.00	7.48	8.16	15.00
17.11.2020	8.10	8.98	11.10	7.48	8.94	11.10	8.09	8.34	15.00	7.42	8.30	15.00
18.11.2020	8.07	8.97	11.00	7.47	8.96	11.00	8.10	8.37	15.00	7.47	8.30	15.00
19.11.2020	8.07	8.91	11.00	7.54	8.89	11.00	8.06	8.29	15.00	7.48	8.22	15.00
20.11.2020	8.06	9.09	11.00	7.51	9.07	11.10	8.07	8.40	15.00	7.45	8.39	15.00
23.11.2020	8.06	9.04	11.00	7.53	9.03	11.00	8.05	8.37	15.00	7.45	8.33	15.00
24.11.2020	8.04	9.00	11.00	7.53	8.99	11.10	8.06	8.34	15.00	7.47	8.31	15.10
25.11.2020	8.06	8.96	11.00	7.52	8.88	11.10	8.06	8.31	15.00	7.48	8.24	15.00
26.11.2020	8.06	8.93	11.00	7.54	8.93	11.10	8.06	8.32	15.00	7.49	8.25	15.00
27.11.2020	8.05	8.95	11.10	7.52	8.98	11.00	8.05	8.33	15.00	7.48	8.29	15.10
30.11.2020	8.08	8.99	11.10	7.53	8.98	11.00	8.07	8.37	15.00	7.48	8.33	15.00
01.12.2020	8.06	8.89	11.00	7.54	8.87	11.10	8.03	8.27	15.00	7.49	8.27	15.00
02.12.2020	8.04	8.97	11.00	7.54	9.00	11.00	8.02	8.34	15.00	7.50	8.29	15.00
03.12.2020	8.05	8.79	11.00	7.53	8.81	11.00	8.05	8.23	15.00	7.46	8.15	15.00
04.12.2020	8.07	8.71	11.00	7.54	8.71	11.00	8.06	8.10	15.00	7.49	8.04	15.10
07.12.2020	8.07	8.79	11.00	7.50	8.74	11.00	8.06	8.13	15.00	7.47	8.10	15.00
08.12.2020	8.03	8.86	11.00	7.54	8.81	11.00	8.03	8.23	15.00	7.48	8.19	15.00

09.12.2020	8.03	8.95	11.00	7.54	8.88	11.00	8.03	8.30	15.00	7.45	8.21	15.00
10.12.2020	8.05	8.89	11.00	7.52	8.87	11.00	8.03	8.25	15.00	7.45	8.20	15.00
11.12.2020	8.04	8.83	11.00	7.50	8.78	11.10	8.02	8.16	14.90	7.46	8.10	15.00
14.12.2020	8.08	8.90	11.00	7.53	8.83	11.00	8.04	8.20	15.00	7.45	8.16	15.00
15.12.2020	8.05	8.86	11.00	7.45	8.88	11.00	8.04	8.28	15.00	7.47	8.22	15.00
16.12.2020	8.08	8.95	11.00	7.55	8.91	11.00	8.06	8.32	15.00	7.46	8.29	15.00
17.12.2020	8.06	8.88	11.00	7.52	8.91	11.00	8.07	8.27	15.00	7.50	8.28	15.00
18.12.2020	8.07	8.96	11.00	7.56	8.97	11.00	8.06	8.36	15.00	7.48	8.32	15.00
21.12.2020	8.07	8.94	11.00	7.54	8.94	11.10	8.06	8.35	15.00	7.49	8.29	15.00
22.12.2020	8.09	8.85	11.00	7.53	8.82	11.10	8.08	8.23	15.00	7.51	8.22	15.00
23.12.2020	8.08	8.96	11.00	7.50	8.89	11.10	8.07	8.30	15.00	7.45	8.24	15.00
26.12.2020	8.09	8.99	11.00	7.52	8.88	11.00	8.06	8.29	15.00	7.43	8.23	14.90
28.12.2020	8.11	8.67	11.00	7.53	8.66	11.00	8.10	8.01	15.00	7.43	7.99	15.00
30.12.2020	8.11	8.83	11.10	7.50	8.77	11.00	8.10	8.16	15.00	7.48	8.12	15.00
02.01.2021	8.11	8.97	11.00	7.56	8.88	11.00	8.10	8.26	15.00	7.47	8.21	14.90
04.01.2021	8.10	9.02	11.00	7.51	8.99	11.00	8.09	8.34	15.00	7.47	8.33	15.00
05.01.2021	8.09	9.01	11.00	7.52	8.98	11.10	8.07	8.34	15.00	7.46	8.28	15.00
06.01.2021	8.09	8.98	11.00	7.56	8.96	11.00	8.06	8.30	15.00	7.52	8.31	15.00
07.01.2021	8.08	8.88	11.00	7.54	8.90	11.10	8.05	8.28	15.00	7.47	8.20	15.00
08.01.2021	8.09	8.94	11.00	7.51	8.90	11.10	8.08	8.32	15.00	7.51	8.26	15.00
11.01.2021	8.09	8.97	11.00	7.50	8.92	11.10	8.08	8.30	15.00	7.51	8.27	15.00
12.01.2021	8.01	8.89	11.10	7.51	8.83	11.10	8.02	8.24	15.00	7.49	8.19	15.00
13.01.2021	8.06	8.91	11.00	7.52	8.87	11.00	8.03	8.26	15.00	7.49	8.20	15.00
14.01.2021	8.02	9.01	11.00	7.48	8.99	11.00	8.04	8.37	14.90	7.47	8.26	15.00
15.01.2021	8.04	9.09	11.00	7.54	9.02	11.00	8.04	8.38	15.00	7.53	8.30	15.10
18.01.2021	8.04	8.98	11.00	7.52	8.96	11.00	8.05	8.28	15.00	7.53	8.29	15.00
19.01.2021	8.05	8.87	11.00	7.64	9.28	10.50	8.03	8.21	15.00	7.51	8.22	15.00
20.01.2021	8.05	8.86	11.10	7.57	8.72	11.10	8.07	8.16	15.10	7.58	8.20	15.10
21.01.2021	8.06	8.75	11.00	7.63	8.66	11.10	8.08	8.13	15.00	7.57	8.13	15.00
22.01.2021	8.07	8.68	11.00	7.58	8.67	11.00	8.06	8.09	15.00	7.56	8.09	14.90
25.01.2021	8.05	8.86	11.10	7.52	8.77	11.10	8.06	8.22	15.10	7.58	8.22	15.00
26.01.2021	8.07	8.90	11.00	7.56	8.91	11.10	8.03	8.29	15.00	7.55	8.27	15.00

27.01.2021	8.07	8.90	11.10	7.52	8.92	10.80	8.03	8.22	14.60	7.49	8.20	15.00
28.01.2021	8.05	8.87	11.00	7.51	8.79	11.10	8.03	8.31	15.00	7.45	8.23	15.00
29.01.2021	8.06	8.76	11.00	7.55	8.78	11.00	8.03	8.14	15.00	7.47	8.10	15.00
01.02.2021	8.05	8.75	11.00	7.57	8.79	11.10	8.05	8.14	14.90	7.50	8.08	15.00
02.02.2021	8.06	8.81	10.90	7.59	8.84	11.00	8.04	8.26	14.70	7.50	8.18	14.70
03.02.2021	8.05	8.79	11.00	7.56	8.78	11.10	8.07	8.17	15.00	7.51	8.16	15.00
04.02.2021	8.03	8.89	11.00	7.59	8.89	11.10	8.04	8.24	15.00	7.51	8.20	15.00
05.02.2021	8.07	8.93	11.00	7.57	8.92	11.10	8.08	8.34	15.00	7.51	8.29	15.00
08.02.2021	8.10	8.83	11.00	7.60	8.84	11.00	8.06	8.25	15.00	7.47	8.23	15.00
09.02.2021	8.07	8.90	11.10	7.57	8.90	11.10	8.04	8.24	15.00	7.44	8.25	15.00
10.02.2021	8.04	8.93	11.00	7.54	8.89	11.00	8.04	8.25	15.00	7.52	8.20	15.00
11.02.2021	8.06	9.07	11.00	7.58	9.01	11.00	8.06	8.40	15.00	7.54	8.38	15.00
12.02.2021	8.05	9.17	11.00	7.55	9.07	11.10	8.03	8.43	15.00	7.50	8.41	15.00
15.02.2021	8.09	9.05	11.00	7.61	9.04	11.10	8.07	8.38	15.10	7.49	8.34	15.00
16.02.2021	7.99	8.95	11.00	7.58	8.98	11.10	8.00	8.32	15.00	7.53	8.30	15.00
17.02.2021	8.04	8.98	11.00	7.55	8.90	11.00	8.04	8.27	15.00	7.48	8.25	15.00
18.02.2021	8.00	8.95	11.00	7.53	8.94	11.10	8.05	8.30	15.00	7.50	8.29	15.00
19.02.2021	8.07	8.89	11.00	7.59	8.96	11.00	8.09	8.28	15.00	7.52	8.28	15.00
22.02.2021	8.07	8.92	11.10	7.58	8.95	11.10	8.05	8.38	15.00	7.50	8.32	15.00
23.02.2021	8.05	9.04	11.10	7.54	9.07	11.00	8.07	8.38	15.00	7.49	8.34	15.00
24.02.2021	8.04	9.03	11.00	7.59	9.05	11.10	8.05	8.34	15.00	7.42	8.36	15.00
25.02.2021	8.05	9.01	11.00	7.55	9.01	11.10	8.04	8.42	15.00	7.47	8.34	15.00
26.02.2021	8.06	9.04	11.00	7.57	9.01	11.00	8.07	8.40	15.00	7.49	8.34	14.90
01.03.2021	8.08	9.09	11.00	7.55	9.10	11.00	8.06	8.47	15.00	7.46	8.49	15.00
02.03.2021	8.05	9.08	11.00	7.59	9.11	11.00	8.05	8.38	15.00	7.51	8.31	15.00
03.03.2021	8.07	9.02	11.00	7.54	9.06	11.00	8.05	8.42	15.00	7.50	8.36	15.00
04.03.2021	8.08	9.03	11.00	7.57	9.02	11.00	8.06	8.36	15.00	7.48	8.35	15.00
05.03.2021	8.07	9.05	11.00	7.56	9.04	11.10	8.07	8.42	15.00	7.56	8.36	15.00
08.03.2021	8.07	9.06	11.00	7.58	9.03	11.00	8.06	8.32	15.00	7.51	8.32	14.90
09.03.2021	8.05	8.93	11.00	7.56	8.93	11.00	8.03	8.38	15.00	7.52	8.30	15.00
10.03.2021	8.07	8.97	11.00	7.62	8.97	11.10	8.06	8.23	15.00	7.54	8.23	15.10
11.03.2021	8.05	8.70	11.00	7.58	8.70	11.10	8.03	8.10	15.00	7.46	8.10	15.10

12.03.2021	8.05	8.79	11.00	7.60	8.80	11.00	8.03	8.21	15.00	7.48	8.18	15.00
15.03.2021	8.10	8.88	11.00	7.57	8.84	11.00	8.08	8.26	15.00	7.53	8.21	15.10
16.03.2021	8.08	8.94	11.00	7.58	8.95	11.00	8.05	8.38	15.00	7.51	8.30	15.00
17.03.2021	8.10	8.99	11.00	7.59	8.99	11.00	8.08	8.36	15.00	7.49	8.36	15.00
18.03.2021	8.07	8.94	11.00	7.57	9.01	11.10	8.06	8.38	15.00	7.52	8.37	15.00
19.03.2021	8.04	9.00	11.00	7.57	9.01	11.00	8.03	8.46	15.00	7.52	8.32	15.00
22.03.2021	8.08	9.05	11.00	7.54	9.01	11.10	8.08	8.33	15.10	7.53	8.28	15.00
23.03.2021	8.07	9.01	11.00	7.60	8.99	11.10	8.05	8.42	15.00	7.53	8.36	15.00
24.03.2021	8.05	9.10	10.90	7.59	9.01	11.10	8.05	8.40	15.00	7.55	8.40	14.90
25.03.2021	8.07	9.20	11.00	7.63	9.17	11.00	8.06	8.54	15.00	7.52	8.50	15.10
26.03.2021	8.07	9.22	11.00	7.64	9.20	11.10	8.06	8.54	15.00	7.58	8.52	15.00
29.03.2021	8.09	9.44	11.00	7.58	9.42	11.10	8.10	8.78	15.00	7.54	8.70	15.10
30.03.2021	8.04	9.16	11.00	7.60	9.17	11.00	8.06	8.58	15.00	7.57	8.60	14.90
31.03.2021	8.05	9.35	11.00	7.57	9.33	11.00	8.08	8.68	15.00	7.49	8.66	14.90
01.04.2021	8.04	9.25	11.00	7.61	9.29	11.00	8.02	8.65	15.00	7.54	8.63	15.00
02.04.2021				7.55	9.42	11.20	8.07	8.75	15.00	7.48	8.76	15.10
05.04.2021							8.11	8.51	15.00	7.51	8.51	15.00
06.04.2021							8.12	8.67	15.00	7.54	8.67	15.00
07.04.2021							8.09	8.70	15.00	7.51	8.62	15.00
08.04.2021							8.07	8.79	15.00	7.54	8.68	15.00
09.04.2021							8.07	9.07	15.00	7.50	8.74	15.10

Table A2: Total and relative surface area change of *C. huinayensis* in the long-time experiment over the 6-month duration. Blank fields indicate complete tissue loss. Corals marked with a * grew, while corals marked with a † died before the end of the experiment

Treatment ->	ambient					pH					temperature					combined				
Life stage	Coral ID	surface area (cm^2), t0	surface area (cm^2)	change (cm^2)	change (%)	Coral ID	surface area (cm^2), t0	surface area (cm^2)	change (cm^2)	change (%)	Coral ID	surface area (cm^2), t0	surface area (cm^2)	change (cm^2)	change (%)	Coral ID	surface area (cm^2), t0	surface area (cm^2)	change (cm^2)	change (%)
recruit	1	0.32	0.32	-0.004	-1.24	1*	0.27	0.33	0.06	21.29	1*	0.15	0.16	0.01	9.17	1†	0.18		-0.18	-100.00
	2	0.24	0.07	-0.16	-68.52	2	0.27	0.21	-0.07	-24.84	2†	0.20		-0.20	-100.00	2†	0.27		-0.27	-100.00
	3	0.27	0.17	-0.10	-35.63	3	0.38	0.37	-0.01	-3.55	3	0.22	0.06	-0.16	-71.79	3*	0.15	0.17	0.02	10.93
	4*	0.17	0.25	0.08	49.82	4*	0.18	0.24	0.06	34.13	4	0.38	0.05	-0.33	-87.09	4	0.18	0.14	-0.04	-24.38
	5*	0.30	0.30	0.001	0.39	5*	0.19	0.32	0.13	71.55	5†	0.37		-0.37	-100.00	5†	0.20		-0.20	-100.00
	6*	0.23	0.35	0.12	51.40	6*	0.34	0.36	0.02	5.36	6	0.25	0.06	-0.18	-74.57	6	0.29	0.14	-0.15	-52.61
	7*	0.17	0.21	0.04	21.73	7*	0.25	0.30	0.05	20.85	7	0.28	0.05	-0.23	-83.14	7	0.28	0.14	-0.14	-49.91
	8*	0.28	0.51	0.23	83.36	8*	0.20	0.42	0.22	107.89	8	0.29	0.08	-0.21	-71.13	8	0.29	0.11	-0.18	-61.07
	9*	0.32	0.41	0.10	30.73	9*	0.28	0.33	0.05	17.62	9†	0.20		-0.20	-100.00	9	0.34	0.13	-0.20	-60.98
	10*	0.32	0.53	0.22	68.12	10*	0.28	0.47	0.19	65.44	10	0.28	0.04	-0.24	-84.49	10	0.35	0.10	-0.25	-70.45
	11*	0.18	0.21	0.03	15.44	11*	0.34	0.38	0.03	9.69	11	0.25	0.06	-0.19	-76.03	11	0.22	0.13	-0.08	-38.43
	12*	0.17	0.46	0.29	171.14	12*	0.15	0.41	0.25	168.63	12†	0.25		-0.25	-100.00	12*	0.18	0.20	0.02	11.20
juvenile	13*	0.86	0.95	0.09	10.80	13	0.25	0.06	-0.19	-76.53	13	0.44	0.15	-0.29	-65.47	13	0.34	0.07	-0.27	-79.56
	14*	0.58	0.60	0.02	3.51	14*	0.51	0.57	0.06	11.53	14	0.59	0.24	-0.35	-59.38	14	0.55	0.48	-0.07	-13.55
	15	0.96	0.95	-0.01	-0.69	15	0.43	0.33	-0.11	-24.67	15	0.28	0.11	-0.17	-59.96	15	0.51	0.35	-0.16	-30.77
	16	0.43	0.43	0.00	-0.65	16	0.58	0.50	-0.08	-14.28	16	0.38	0.07	-0.31	-82.11	16	0.52	0.40	-0.12	-23.08
	17*	0.68	0.77	0.09	12.74	17	0.42	0.38	-0.04	-8.73	17†	0.88		-0.88	-100.00	17	0.58	0.54	-0.04	-6.47
	18*	0.39	0.52	0.13	32.87	18*	0.42	0.51	0.09	22.30	18	0.33	0.10	-0.23	-70.57	18	0.47	0.31	-0.16	-34.10
	19	0.51	0.45	-0.07	-12.97	19	0.56	0.49	-0.07	-13.01	19	0.56	0.10	-0.45	-81.67	19	0.54	0.47	-0.08	-13.95
	20*	0.38	0.79	0.41	108.85	20*	0.70	0.88	0.19	26.69	20	0.44	0.07	-0.37	-84.10	20	0.60	0.37	-0.24	-39.40
	21	0.49	0.46	-0.03	-6.03	21	0.41	0.35	-0.06	-14.93	21	0.62	0.15	-0.46	-75.04	21	0.44	0.32	-0.12	-26.59
	22*	0.32	0.64	0.32	99.69	22*	0.51	0.76	0.26	51.07	22	0.51	0.14	-0.37	-72.89	22	0.39	0.33	-0.06	-15.70
	23	0.34	0.30	-0.04	-10.85	23	0.39	0.34	-0.05	-12.96	23	0.52	0.10	-0.42	-81.52	23	0.46	0.31	-0.15	-32.19
	24*	0.69	0.88	0.19	27.37	24*	0.42	0.91	0.49	115.98	24	0.56	0.09	-0.47	-83.36	24*	0.59	0.63	0.04	5.96
adult	25	3.27	1.16	-2.11	-64.45	25	4.06	2.80	-1.25	-30.93	25†	2.93		-2.93	-100.00	25†	3.29		-3.29	-100.00
	26	1.87	1.47	-0.41	-21.71	26	3.21	2.85	-0.36	-11.28	26†	2.46		-2.46	-100.00	26	2.01	0.54	-1.46	-72.86
	27	2.85	1.90	-0.95	-33.28	27	2.30	1.04	-1.25	-54.56	27†	3.48		-3.48	-100.00	27†	1.05		-1.05	-100.00
	28	3.37	1.86	-1.51	-44.76	28	1.26	1.10	-0.17	-13.06	28	2.56	0.79	-1.77	-69.08	28†	1.23		-1.23	-100.00
	29	1.58	1.17	-0.41	-25.86	29	3.23	2.12	-1.11	-34.44	29	1.08	0.26	-0.82	-76.10	29	1.91	1.26	-0.65	-34.20
	30	2.20	1.27	-0.93	-42.45	30	1.68	0.97	-0.71	-42.52	30	1.16	0.17	-0.99	-85.27	30†	2.23		-2.23	-100.00
	31†	2.92	0.81	-2.11	-72.17	31	2.11	1.43	-0.68	-32.32	31†	3.46		-3.46	-100.00	31†	2.11		-2.11	-100.00
	32	3.39	2.63	-0.77	-22.62	32	2.91	2.17	-0.74	-25.45	32	2.55	0.81	-1.74	-68.22	32	2.95	0.80	-2.14	-72.75
	33	2.23	0.33	-1.90	-85.01	33†	3.20	0.00	-3.20	-100.00	33†	1.27		-1.27	-100.00	33†	2.42		-2.42	-100.00
	34	3.26	2.44	-0.82	-25.17	34	1.10	0.83	-0.27	-24.90	34†	3.95		-3.95	-100.00	34†	4.01		-4.01	-100.00
	35	2.31	1.79	-0.52	-22.33	35	2.73	1.46	-1.27	-46.54	35†	2.46		-2.46	-100.00	35	2.38	1.45	-0.93	-38.91
	36	3.06	2.86	-0.20	-6.58	36	2.72	1.01	-1.71	-62.99	36†	2.04		-2.04	-100.00	36	1.72	1.07	-0.65	-37.54

Supplementary B: Feeding incubations

Table B1: Mean concentration of *Artemia* nauplii calculated from subsets counted by M.Sc. Christoph Naab. Values are given for subsets that were counted before the feeding incubations and could therefore be used to extrapolate the number of nauplii for the feeding incubations.

Date	Feeding group	Mean Nauplii per ml
30.09.2020	LF	0.33
02.10.2020	HF	0.79
05.10.2020	HF	0.61
07.10.2020	LF	0.19
07.10.2020	HF	1.03
09.10.2020	HF	0.99
12.10.2020	HF	0.65
14.10.2020	LF	0.25
14.10.2020	HF	0.68
16.10.2020	HF	0.55
19.10.2020	HF	0.95
21.10.2020	LF	0.18
21.10.2020	HF	1.15
23.10.2020	HF	0.74
26.10.2020	HF	0.87
28.10.2020	LF	0.17
Mean (±SD) of *Artemia* nauplii per ml of all days	LF	0.23 (0.07)
	HF	0.78 (0.23)

Table B2: Dry weight, ash-free dry weight and OM content of the two batches of *Artemia persimilis* batches. The data from the second batch was used to calculate the corals' nauplii-derived POM intake.

n nauplii	age	mg nauplii	mg per nau	mg AFDW	mg OM	mg OM per nauplii
300	2 days	1.306	0.004	0.382	0.924	0.003
		1.177	0.004	0.329	0.848	0.003
		1.196	0.004	0.322	0.874	0.003
		1.003	0.003	0.031	0.972	0.003
		1.721	0.006	0.613	1.108	0.004
		0.892	0.003	0.213	0.679	0.002
500	1 day	1.742	0.003	0.394	1.348	0.003
		2.732	0.005	1.118	1.614	0.003
		1.850	0.004	0.390	1.460	0.003
500	2 days	2.706	0.005	1.280	1.426	0.003
		2.894	0.006	1.459	1.435	0.003
		1.434	0.003	0.278	1.156	0.002

Table B3: Carbon and nitrogen content of the *A. persimilis* nauplii.

Number of nauplii	Age	mg N INT per nauplii	mg C INT per nauplii	C/N INT per nauplii
300	2 days	0.00024	0.00108	4.47
		0.00021	0.00095	4.45
		0.00022	0.00096	4.39
		0.00018	0.00083	4.51
500	1 day	0.00023	0.00114	5.02
		0.00023	0.00115	4.91
		0.00023	0.00122	5.20
500	2 days	0.00021	0.00089	4.33
		0.00021	0.00092	4.35
		0.00021	0.00092	4.38

Table B4: Feeding rates of the coral batches using the test corals. Blank columns are due to the eggs not being counted in the later incubations. The controls were there to test the accuracy of the calculation for mean artemia from ten subsamples.

Life stage	duration (h)	#nauplii t0	#eggs t0	#nauplii t	#eggs t	Δ nauplii	Δ eggs	nauplii/coral	eggs/polyp	nauplii/polyp/h
recruit	6	323	7	164	10	159	-3	53	-1	9
				228	14	95	-7	32	-2	5
				166	8	157	-1	52	0	9
				165	11	158	-4	53	-1	9
juvenile				212	10	111	-3	37	-1	6
				141	12	182	-5	61	-2	10
adult				137	8	186	-1	93	0	16
				101	8	222	-1	74	0	12
control				196	15	127	-8			
recruit	6	404	149	104	69	300	80	100	27	17
				130	61	274	88	91	29	15
				210	145	194	4	65	1	11
				192	158	212	-9	71	-3	12
juvenile				204	138	200	11	67	4	11
				58	89	346	60	115	20	19
adult				219	151	185	-2	92	-1	15
				203	134	201	15	100	8	17
control				380	118	24	31			
recruit	1	252		155		97		32		32
	2			124		128		43		21
	3			64		188		63		21
				53		199		66		22
juvenile				112		140		47		16
				83		169		56		19
adult				105		147		74		25
				60		192		64		21
control				272		-20				
				240		12				
				227		25				
recruit	3	250		27		223		74		25
	3			58		192		64		21
	1			107		143		48		48
	1			94		156		52		52
juvenile	1			230		20		7		7
	1			174		76		25		25
adult	1			207		43		22		22
	1			165		85		28		28
control				243		7				
				255		-5				
				254		-4				

Table B5: Feeding rates of the individual corals during the final feeding incubation using the test corals.

Life stage	duration (h)	Nauplii t0	Nauplii t	Nauplii/h
recruit	1	30	24	6
			13	17
			23	7
			22	8
			21	9
			23	7
			17	13
			12	18
			29	1
			16	14
			25	5
			27	3
juvenile			19	11
			28	2
			26	4
			25	5
			29	1
			23	7
adult			26	4
			27	3
			25	5
			25	5
			27	3

Table B6. Feeding rates and POM-uptake of the individual corals during the feeding incubations. Treatments from 3 to 6 are: Ambient, pH, temperature, combined. Tanks x.1 and x.4 always belonged to the LF group, while x.2 and x.3 belonged to the HF group. Blue rows represent recruits, yellow juveniles and green adults.

Tank Nr.	Coral ID	Extension (%)	Nauplii/h	ntake POM (mg)	mg POM/cm^2	Tank Nr.	Coral ID	Extension (%)	Nauplii/h	ntake POM (mg)	mg POM/cm^2
	w 1	< 25	0	0.000	0.000		g 1	< 25	6	0.018	0.055
	w 3	< 25	2	0.006	0.035		g 3	< 25	5	0.015	0.041
	w 5	25 - 75	7	0.021	0.069		g 5	> 75	5	0.015	0.047
	w 13	< 25	11	0.033	0.035		g 13	> 75	7	0.021	0.362
3.1 (LF)	w 15	25 - 75	3	0.009	0.009	4.1	g 15	< 25	0	0.000	0.000
	w 17	25 - 75	0	0.000	0.000		g 17	> 75	12	0.036	0.095
	w 25	< 25	1	0.003	0.003		g 25	< 25	2	0.006	0.002
	w 27	25 - 75	2	0.006	0.003		g 27	< 25	14	0.042	0.040
	w 29	< 25	0	0.000	0.000		g 29	< 25	6	0.018	0.009
	w 7	25 - 75	3	0.009	0.043		g 7	< 25	11	0.033	0.110
	w 9	> 75	5	0.015	0.036		g 9	25 - 75	4	0.012	0.037
	w 11	> 75	2	0.006	0.029		g 11	25 - 75	2	0.006	0.016
	w 19	< 25	0	0.000	0.000		g 19	< 25	1	0.003	0.006
3.4 (LF)	w 21	25 - 75	1	0.003	0.006	4.4	g 21	< 25	4	0.012	0.034
	w 23	< 25	0	0.000	0.000		g 23	25 - 75	1	0.003	0.009
	w 31	< 25	1	0.003	0.004		g 31	< 25	0	0.000	0.000
	w 33	< 25	11	0.033	0.099		g 33				
	w 35	< 25	9	0.027	0.015		g 35	< 25	5	0.015	0.010
	w 2	< 25	10	0.030	0.400		g 2	< 25	29	0.087	0.422
	w 4	25 - 75	30	0.090	0.362		g 4	25 - 75	17	0.051	0.208
	w 6	> 75	9	0.027	0.076		g 6	25 - 75	9	0.027	0.076
	w 14	25 - 75	19	0.057	0.096		g 14	< 25	12	0.036	0.063
3.2 (HF)	w 16	> 75	9	0.027	0.063	4.2	g 16	25 - 75	19	0.057	0.114
	w 18	25 - 75	0	0.000	0.000		g 18	> 75	20	0.060	0.118
	w 26	25 - 75	20	0.060	0.041		g 26	< 25	19	0.057	0.020
	w 28	25 - 75	23	0.069	0.037		g 28	< 25	10	0.030	0.027
	w 30	> 75	20	0.060	0.047		g 30	< 25	18	0.054	0.056
	w 8	25 - 75	3	0.009	0.018		g 8	25 - 75	11	0.033	0.078
	w 10	25 - 75	15	0.045	0.085		g 10	25 - 75	6	0.018	0.038
	w 12	25 - 75	5	0.015	0.033		g 12	25 - 75	38	0.114	0.281
	w 20	25 - 75	7	0.021	0.026		g 20	25 - 75	16	0.048	0.054
3.3 (HF)	w 22	25 - 75	0	0.000	0.000	4.3	g 22	25 - 75	21	0.063	0.082
	w 24	> 75	7	0.021	0.024		g 24	25 - 75	46	0.138	0.153
	w 32	25 - 75	4	0.012	0.005		g 32	< 25	23	0.069	0.032
	w 34	< 25	7	0.021	0.009		g 34	< 25	33	0.099	0.120
	w 36	25 - 75	17	0.051	0.018		g 36	< 25	41	0.123	0.122
	y 1	> 75	11	0.033	0.20		r 1				
	y 3	< 25	6	0.018	0.29		r 3	< 25	6	0.018	0.105
	y 5						r 5				
	y 13	< 25	2	0.006	0.04		r 13				0.000
5.1	y 15	> 75	2	0.006	0.05	6.1	r 15	25 - 75	7	0.021	0.059
	y 17						r 17	> 75	13	0.039	0.073
	y 25	25 - 75	2	0.006	0.02		r 25	25 - 75			
	y 27						r 27				
	y 29						r 29		0	0.000	0.000
	y 7	25 - 75	6	0.018	0.39		r 7	25 - 75	4	0.012	0.084
	y 9						r 9	25 - 75	2	0.006	0.046
	y 11	< 25	2	0.006	0.10		r 11	> 75	3	0.009	0.067
	y 19				0.00		r 19	< 25	4	0.012	0.026
5.4	y 21	25 - 75	1	0.003	0.02	6.4	r 21	> 75	5	0.015	0.046
	y 23	> 75	7	0.021	0.22		r 23	> 75	10	0.030	0.095
	y 31						r 31	< 25			
	y 33						r 33				
	y 35						r 35		3	0.009	0.006
	y 2						r 2				
	y 4	25 - 75	53	0.159	3.24		r 4	25 - 75	24	0.072	0.527
	y 6	< 25	33	0.099	1.59		r 6	< 25	3	0.009	0.065
	y 14	> 75	14	0.042	0.18		r 14	> 75	16	0.048	0.101
5.2	y 16	25 - 75	14	0.042	0.62	6.2	r 16	25 - 75	14	0.042	0.106
	y 18	25 - 75	15	0.045	0.47		r 18	> 75	18	0.054	0.176
	y 26	< 25		0.000			r 26		17	0.051	0.094
	y 28		106	0.318			r 28				
	y 30		21	0.063	0.37		r 30	25 - 75			
	y 8	< 25	25	0.075	0.89		r 8	25 - 75	26	0.078	0.685
	y 10	25 - 75	22	0.066	1.50		r 10	> 75	33	0.099	0.952
	y 12						r 12	25 - 75	20	0.060	0.294
	y 20	25 - 75	5	0.015	0.22		r 20	25 - 75	11	0.033	0.090
5.3	y 22	25 - 75	11	0.033	0.24	6.3	r 22	25 - 75	6	0.018	0.055
	y 24	25 - 75	0	0.000	0.00		r 24	25 - 75	24	0.072	0.114
	y 32	< 25	21	0.063	0.08		r 32	25 - 75	16	0.048	0.060
	y 34						r 34				
	y 36	< 25	18	0.054			r 36	< 25	17	0.051	0.048

Figure B1: Screenshots from the videos of the HF adults from the ambient (A, B) and pH (C, D) treatment during feeding events in the tanks.

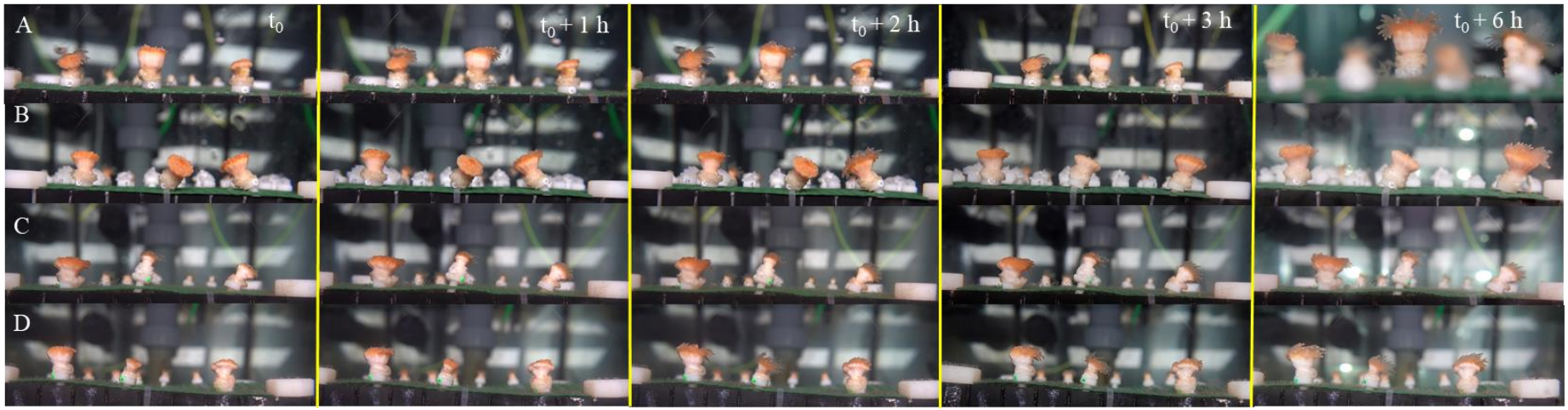


Figure B2: Screenshots from the videos of the LF adults from the ambient (A, B) and pH (C, D) treatment during feeding events in the tanks.

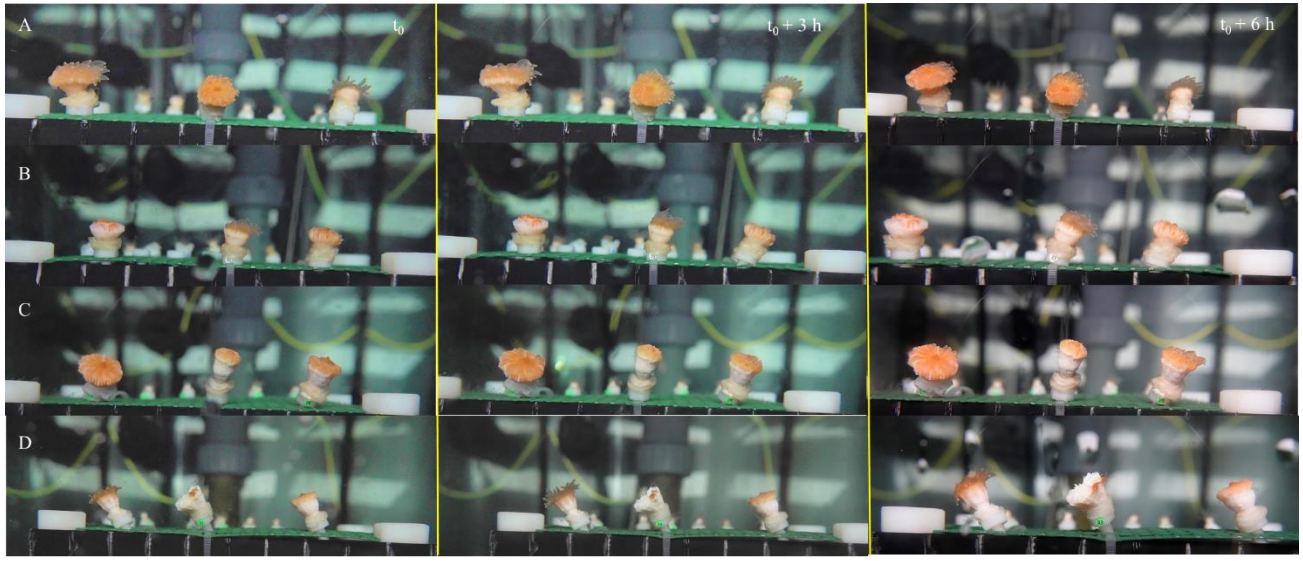


Figure B3: Screenshots from the videos of the HF adults from the temperature (A, B) and combined (C, D) treatment during feeding events in the tanks.

Figure B4: Screenshots from the videos of the LF adults from the temperature (A) and combined (B) treatment during feeding events in the tanks. Only two tanks were filmed due to the high mortality.

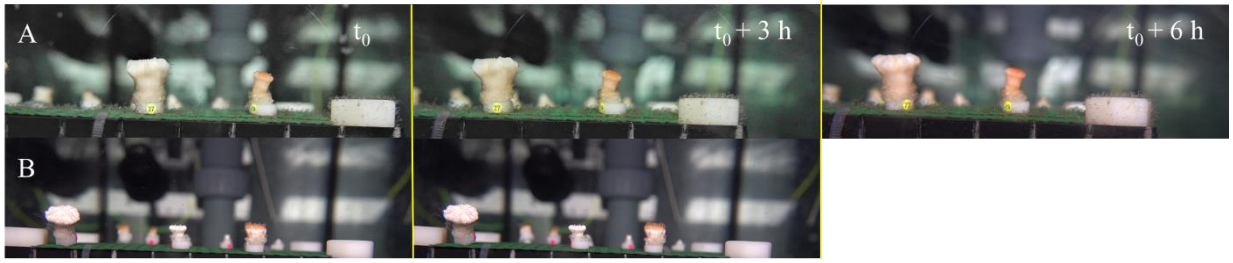


Figure B5: Screenshots from the videos of the HF recruits (left) and juveniles (right) from the ambient (A, B) and pH (C, D) treatment during feeding events in the tanks.

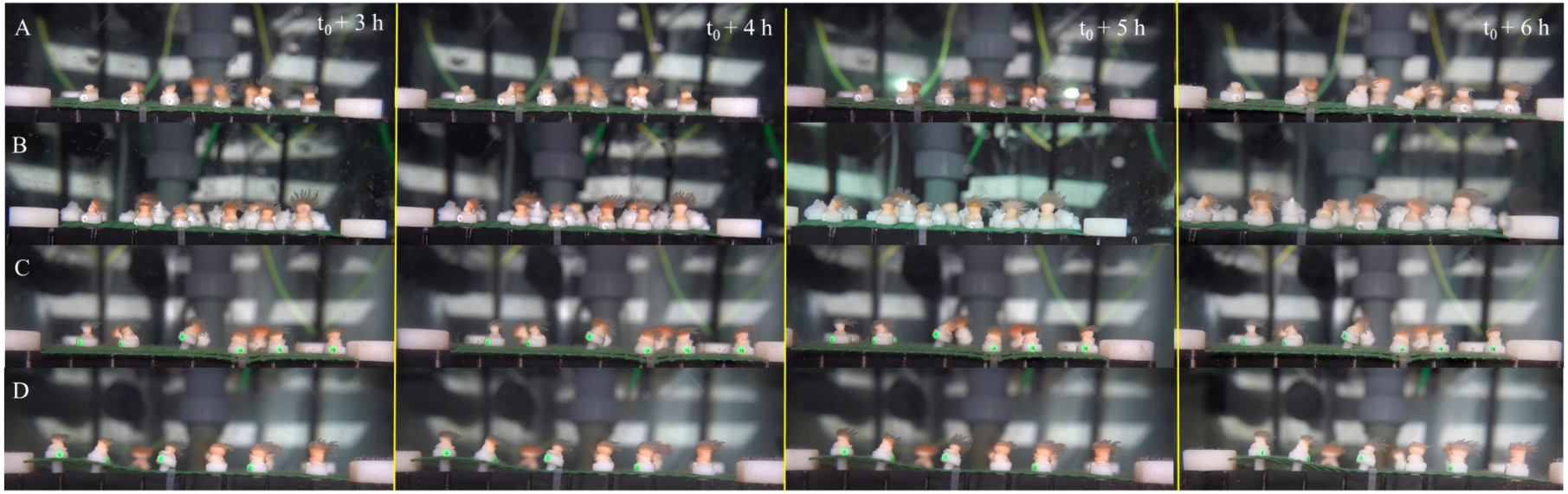


Figure B6: Screenshots from the videos of the LF recruits (left) and juveniles (right) from the ambient (A, B) and pH (C, D) treatment during feeding events in the tanks.

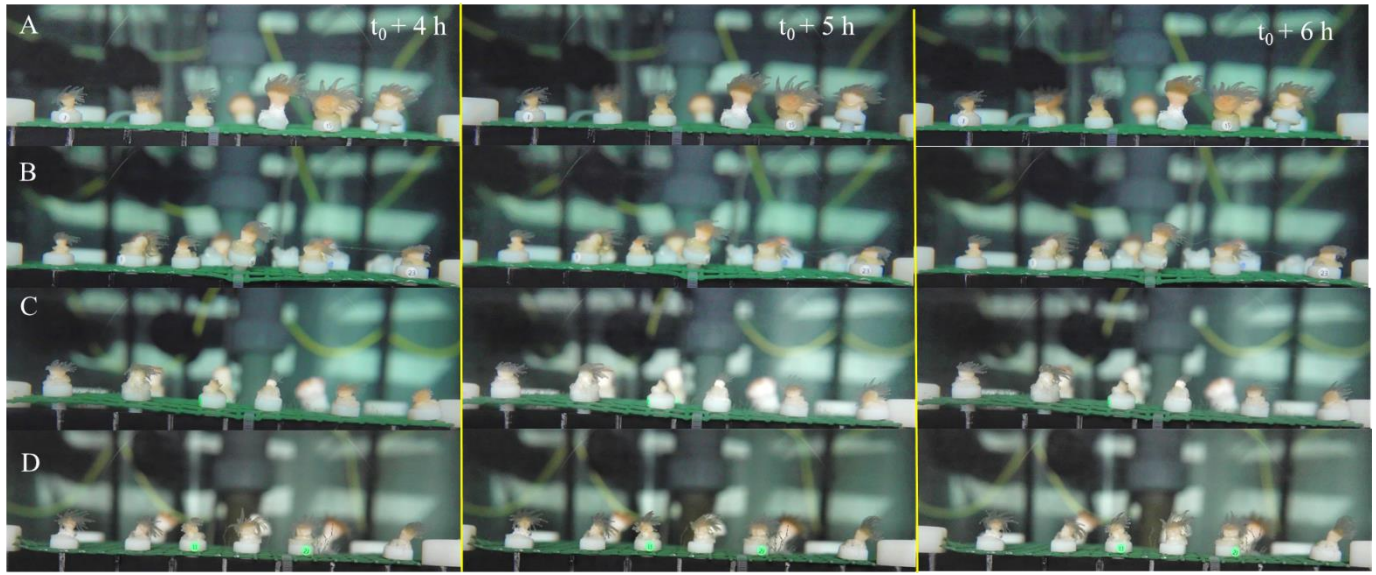


Figure B7: Screenshots from the videos of the HF recruits (left) and juveniles (right) from the temperature (A, B) and combined (C, D) treatment during feeding events in the tanks.

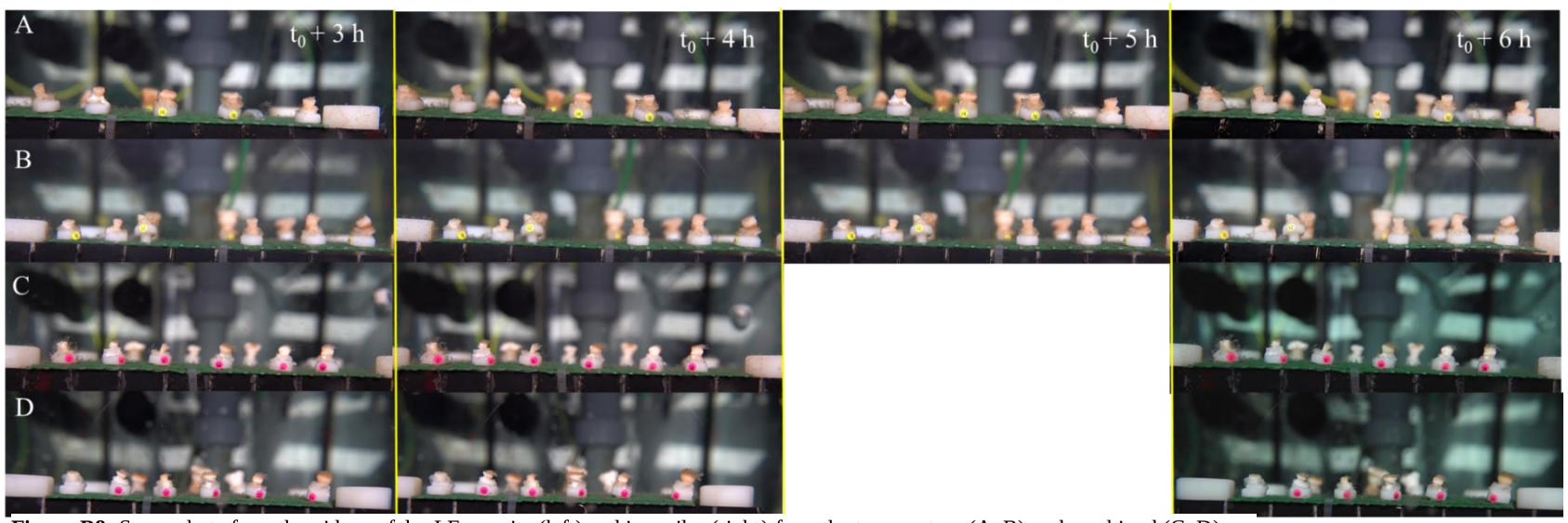
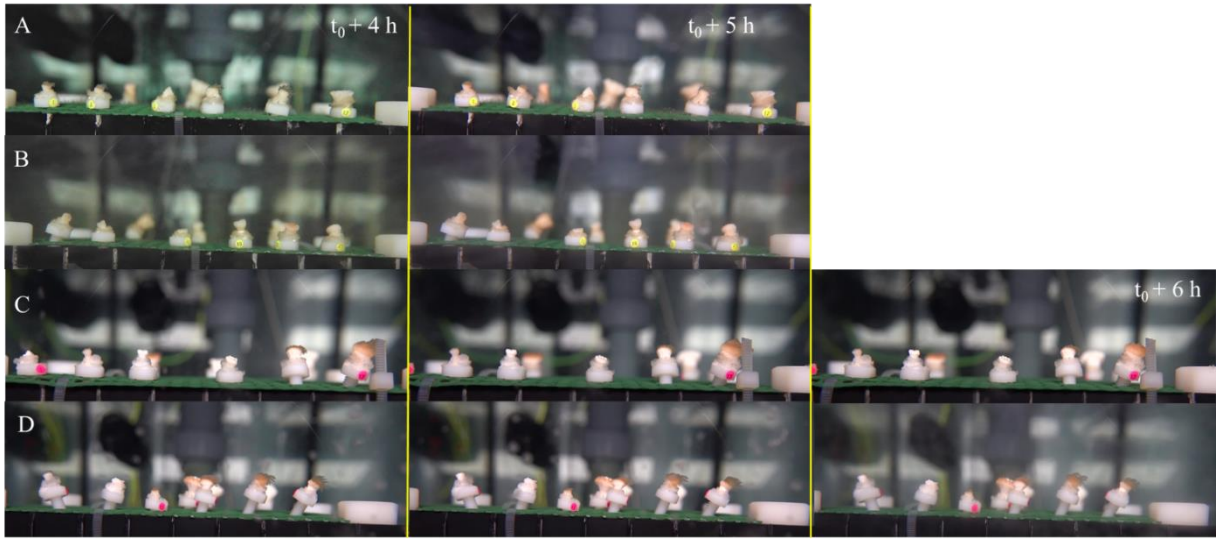


Figure B8: Screenshots from the videos of the LF recruits (left) and juveniles (right) from the temperature (A, B) and combined (C, D) treatment during feeding events in the tanks.



Supplementary C: Incubations to determine the energetic turnover.

Table C1: Raw data obtained from the incubation with the test corals. Values in red were not used for calculations due to large deviations from the mean. Blank columns indicate that the affected variable was not measured during the incubation.

Incubation time	Life stage	Bottle ID	Coral ID	Coral tissue per bottle (cm^2)	Volume per bottle (L)	density (kg/L)	t0	t	duration (h)	Nox (µmol/L)	Silikat (µmol/L)	Nitrit (µmol/L)	Phosphat (µmol/L)	Ammonium (µmol/L)	Nitrat (µmol/L)	TA corr. (µmol/kg)	$pH_{(NBS)}$	O_2 (mg/L)	ΔO_2 (µmol d^{-1} cm^{-2})	DIC (µmol/L)	NPOC (µmol/L)	TDN (µmol/L)
24 hours	tank					1.0242				32.361	12.388	0.091	0.628	0.379	32.292	3070.00		8.83		2681.42	51.06	48.08
						1.0242				41.084	15.166	0.109	0.778	0.211	41.001	3093.96		8.83		2506.38	31.62	49.43
						1.0242				29.735	10.949	0.086	0.642	0.827	29.664	3072.46		8.83		2518.02	31.21	50.53
	recruit	1	1, 3, 5	1.06	0.13	1.0243	10:06:00	10:18:00	24.2	46.941	16.676	0.185	0.980	2.243	46.775	3032.41		8.34		2547.12	84.35	60.93
		2	7, 9, 11	0.76	0.13	1.0243	10:17:00	10:27:00	24.2	44.234	17.083	0.207	0.914	2.162	44.041	3069.18		8.20		3121.21	97.60	62.76
		3	13, 15, 17	0.99	0.13	1.0243	10:28:00	10:37:00	24.1	48.979	16.440	0.279	0.966	2.734	48.709	3027.60		8.33		2527.60	119.14	69.86
		4	19, 21, 23	0.80	0.13	1.0243	10:34:00	10:42:00	24.1	45.312	16.516	0.221	0.930	2.855	45.098	3045.54		8.34		3063.33	73.84	61.03
	juvenile	5	2, 4, 6	1.18	0.13	1.0243	10:39:00	10:48:00	24.1	40.379	14.663	0.230	0.862	2.802	40.155	3031.52		8.35		2523.18	96.08	60.98
		6	8, 10, 12	1.28	0.13	1.0243	10:41:00	10:58:00	24.3	38.744	14.396	0.219	0.916	3.510	38.528	3009.06		8.10		2523.65	132.92	65.13
	adult	7	14, 18	1.93	0.13	1.0243	10:46:00	11:03:00	24.3	47.583	16.395	0.258	0.897	5.447	47.329	3024.03		7.86		3074.63	101.64	64.42
		8	20, 22, 24	2.50	0.13	1.0243	10:51:00	11:14:00	24.4	48.255	16.412	0.228	1.014	4.587	48.030	3026.47		7.88		2523.66	92.08	63.92
	control	9			0.13	1.0243	10:52:00	11:18:00	24.4	48.199	16.604	0.292	0.873	0.956	47.910	3047.46		8.47		2532.52	94.73	59.40
48 hours	tank					1.0242				20.956	8.148	0.056	0.569	0.160	20.901	3041.80				3227.84	27.57	42.58
						1.0242				36.216	13.897	0.108	0.775	0.306	36.114	3035.50	7.84	8.87		3346.67	28.79	42.76
						1.0242				22.943	9.414	0.071	0.570	0.451	22.879	3034.64				3575.77	27.59	43.48
	recruit	1	1, 3, 5	1.06	0.13	1.0244	11:42:00	11:42:00	48.00	34.300	13.257	0.140	0.929	5.432	34.173	3005.35	7.77	7.78		3402.55	128.68	52.74
		2	7, 9, 11	0.76	0.13	1.0244	11:48:00	11:52:00	48.07	35.858	13.815	0.134	0.726	2.158	35.751	3001.43	7.77	8.20		3290.18	75.71	51.99
		3	13, 15, 17	0.99	0.13	1.0244	11:52:00	12:01:00	48.15	31.992	11.919	0.156	0.719	2.372	31.862	3017.61	7.74	7.73		3238.21	101.80	57.35
		4	19, 21, 23	0.80	0.13	1.0244	11:56:00	12:09:00	48.22	36.565	13.864	0.156	0.882	1.057	36.443	2989.92	7.73	7.93		3289.94	84.66	55.02
	juvenile	5	2, 4, 6	1.18	0.13	1.0244	11:59:00	12:15:00	48.27	36.704	13.065	0.138	0.816	0.919	36.605	3007.39	7.74	8.07		3292.30	64.65	51.39
		6	8, 10, 12	1.28	0.13	1.0244	12:03:00	12:22:00	48.32	35.363	13.164	0.148	0.926	6.146	35.256	2984.69	7.68	7.84		3354.58	79.96	49.88
	adult	7	14, 18	1.93	0.13	1.0244	12:07:00	12:26:00	48.32	37.984	13.611	0.197	0.859	5.496	37.827	2985.19	7.70	7.53		3267.40	96.07	57.36
		8	20, 22, 24	2.50	0.13	1.0244	12:10:00	12:43:00	48.55	37.083	13.518	0.160	0.995	6.257	36.961	2998.49	7.70	7.36		3332.32	71.87	55.11
	control	9			0.13	1.0244	12:12:00	12:48:00	48.60	35.331	14.088	0.181	0.495	0.687	35.181	3021.96	7.79	8.41		3416.78	71.18	50.54
48 hours with ambient water	tank					1.0241				58.744	4.658	0.088	2.214	0.698	58.722	2769.13	8.04			3386.98	67.61	108.23
						1.0241				72.670	5.958	0.100	2.290	0.674	72.656	2776.82	8.04			2964.55	73.42	104.00
						1.0241				83.493	6.741	0.092	2.781	1.103	83.451	2765.99	8.04			3108.05	103.43	103.43
	recruit	1	11, 3, 5	1.02	0.13	1.0241	14:32:00	15:43:00	49.18	66.779	6.500	0.108	1.923	0.960	66.684	2799.20	8.06	0.10	3.07	2944.99	162.40	114.13
		2	1, 7, 9	0.80	0.13	1.0241	14:40:00	15:51:00	49.18	70.590	6.038	0.128	1.820	0.695	70.522	2894.92	8.18	0.12	3.65	2939.98	183.80	108.30
		3	13, 15, 17	0.99	0.13	1.0241	14:48:00	15:57:00	49.15	65.871	5.453	0.129	2.702	1.296	65.786	2797.43	8.06	0.12	3.69	2678.72	115.81	115.81
		4	19, 21, 23	0.80	0.13	1.0241	14:54:00	16:08:00	49.23	68.808	5.812	0.164	1.984	1.258	68.730	2751.77	7.92	0.11	3.46	3220.10	89.59	106.90
	juvenile	5	2, 4, 6	1.18	0.13	1.0241	15:01:00	16:17:00	49.27	76.422	7.155	0.066	2.322	1.197	76.389	2749.84	7.93	0.03	1.06	2715.02	93.90	105.50
		6	8, 10, 12	1.28	0.13	1.0241	15:07:00	16:28:00	49.35	77.054	6.554	0.137	2.690	3.744	76.971	2745.98	7.88	0.06	1.85	2950.22	116.10	112.50
	adult	7	14, 18	1.93	0.13	1.0241	15:13:00	16:38:00	49.42	79.696	6.726	0.230	2.370	3.383	79.528	2751.84	7.89	0.05	1.68	2777.78	107.90	113.80
		8	20, 22, 24	2.50	0.13	1.0241	15:21:00	16:48:00	49.45	81.832	8.284	0.260	0.458	4.078	81.670	2874.01	8.14	0.09	2.68	3002.03	129.10	107.30
	control	9			0.13	1.0241	15:24:00	16:57:00	49.55	70.961	5.612	0.114	1.923	1.007	70.890	2767.09	8.01			2527.40	114.10	104.45

Table C2: Hourly and daily rates for changes in the measured values in the coral chambers during the incubations with the test corals. Δ-values are those corrected for values measured in the corals' tank before the incubations.

Incubation time	Life stage	Coral ID	ΔO_2 (µmol d^{-1} cm^{-2})	ΔTA (µmol/h) - control	ΔNOx (µmol/h) - control	ΔPhosphat (µmol/h) - control	ΔAmmonium (µmol/h) - control	Δammonium - control (µmol d^{-1} cm^{-2})	O/N	µmol CaCO3 d^{-1} cm^{-2}
24 hours	recruit	1, 3, 5	0.5	-0.08	-0.0060	0.0006	0.0069	0.156	3	1.1
		7, 9, 11	1.5	0.12	-0.0205	0.0002	0.0065	0.205	7	-1.4
		13, 15, 17	0.6	-0.11	0.0051	0.0005	0.0096	0.233	3	1.4
		19, 21, 23	0.7	-0.01	-0.0146	0.0003	0.0103	0.308	2	0.6
	juvenile	2, 4, 6	0.4	-0.09	-0.0412	-0.0001	0.0100	0.203	2	1.4
		8, 10, 12	1.2	-0.21	-0.0502	0.0002	0.0137	0.256	5	2.6
	adult	14, 18	1.3	-0.13	-0.0028	0.0001	0.0241	0.299	4	1.0
		20, 22, 24	0.9	-0.11	0.0004	0.0008	0.0194	0.186	5	0.6
48 hours	recruit	1, 3, 5	1.2	-0.05	-0.0025	0.0012	0.0129	0.290	4	0.7
		7, 9, 11	0.6	-0.06	0.0017	0.0006	0.0040	0.126	5	0.9
		13, 15, 17	1.4	-0.01	-0.0088	0.0006	0.0046	0.110	13	0.3
		19, 21, 23	1.2	-0.09	0.0035	0.0010	0.0010	0.030	41	1.3
	juvenile	2, 4, 6	0.6	-0.04	0.0039	0.0009	0.0006	0.013	46	0.4
		8, 10, 12	0.9	-0.10	0.0002	0.0012	0.0147	0.275	3	1.1
	adult	14, 18	0.9	-0.10	0.0073	0.0010	0.0129	0.161	6	0.7
		20, 22, 24	0.8	-0.06	0.0047	0.0013	0.0149	0.143	6	0.4
48 hours with ambient water	recruit	11, 3, 5	3.1	0.09	-0.0111	0.0000	-0.0001	-0.003	-1120	-0.9
		1, 7, 9	3.7	0.35	-0.0010	-0.0003	-0.0008	-0.024	-150	-5.2
		13, 15, 17	3.7	0.08	-0.0135	0.0020	0.0008	0.019	197	-0.8
		19, 21, 23	3.5	-0.04	-0.0057	0.0002	0.0007	0.020	173	0.7
	juvenile	2, 4, 6	1.1	-0.05	0.0144	0.0010	0.0005	0.010	102	0.3
		8, 10, 12	1.9	-0.06	0.0160	0.0020	0.0072	0.135	14	0.4
	adult	14, 18	1.7	-0.04	0.0230	0.0012	0.0063	0.078	22	0.1
		20, 22, 24	2.7	0.29	0.0286	-0.0039	0.0081	0.078	34	-1.5

Table C3: Coral health categories to assess the physiological status of the corals devised by M.Sc. Kristina Beck

Category	1	2	3	4	5	6
Criteria	(almost) completely covered with tissue	tissue retracted/ lateral side of calyx partly covered with tissue	only oral side of calyx covered with tissue	tissue only on oral side but septa not covered with tissue	almost dead/tissue remains inside of calyx (aboral side)	dead (no tissue visible)

Table C4: Raw data obtained from the incubation with the corals from the ambient treatment. Values in red were not used for calculations due to large deviations from the mean.

Tank Nr	Bottle Nr.	Coral ID	Life stage	Feeding	Coral tissue per bottle (cm^2)	Volume per bottle (l)	density (kg/l)	t_0	t	duration (hours)	NOx (µmol/l)	Silikat (µmol/L)	Nitrit (µmol/L)	Phosphat (µmol/L)	Ammonium (µmol/L)	Nitrat (µmol/L)	TA corr. (µmol/kg)	$pH_{(NBS)}$	ΔO_2 (mg/d/cm-2)	ΔO_2 (µmol/d/cm-2)	DIC (µmol/kg)	TOC (µmol/L)	TDN (µmol/L)
							1.024				97.091	6.879	0.125	3.834	0.240	96.968	2720.604				2457.37	55.570	111.500
technical			start				1.024										2707.201	7.966			2516.24	118.048	118.048
							1.024				88.026	6.702	0.090	3.336	0.526	88.004	2697.719				2403.00	61.330	116.100
3.1	1	1,3,5	recruit	LF	0.79	0.124	1.024	14:14:00	10:16:00	44.03	76.902	6.827	0.096	3.381	1.422	76.854	2639.65	7.963	0.052	1.628	2306.47	128.58	128.58
3.1	2	13,15,17	juvenile	LF	2.67	0.121	1.024	14:21:00	10:22:00	44.02	74.434	6.546	0.160	2.730	0.884	74.354	2653.43	7.939	0.029	0.895	2480.28	125.33	125.33
3.4	3	7,9,11	recruit	LF	0.83	0.125	1.024	14:29:00	10:28:00	43.98	99.782	7.932	0.244	3.712	0.791	99.636	2665.37	8.015	0.050	1.572	2329.69	171.90	128.60
3.1	4	25,27,29	adult	LF	4.24	0.124	1.024	14:35:00	16:18:00	25.72	90.047	6.854	0.168	4.071	6.318	89.945	2715.11	7.92	0.051	1.584	2550.62	123.20	121.30
3.2	5	2,4,6	recruit	HF	0.68	0.124	1.024	14:42:00	10:35:00	43.88	102.446	8.058	0.227	3.831	1.217	102.219	3582.30	7.943	0.106	3.328	2424.54	121.97	121.97
3.2	6	14,16,18	juvenile	HF	1.55	0.123	1.024	14:47:00	10:41:00	43.90	99.426	8.592	0.318	3.656	1.752	99.240	3626.81	7.889	0.062	1.943	2257.41	127.23	127.23
3.2	7	26,28,30	adult	HF	4.59	0.125	1.024	14:56:00	16:32:00	25.60	88.637	7.707	0.165	4.218	5.658	88.533	2719.84	7.824	0.074	2.319	2479.29	99.24	122.50
3.4	8	19,21,23	juvenile	LF	1.21	0.124	1.024	15:01:00	10:48:00	43.78	92.778	7.181	0.165	3.714	2.192	92.673	3649.75	7.97	0.047	1.463	2495.64	127.01	127.01
3.3	9	8,10,12	recruit	HF	1.50	0.124	1.024	15:08:00	10:55:00	43.78	100.014	7.919	0.195	4.472	6.177	99.881	2569.81	7.688	0.098	3.072	1944.57	112.50	129.50
3.3	10	20,22,24	juvenile	HF	2.31	0.127	1.024	15:14:00	11:01:00	43.78	91.652	7.052	0.170	4.266	8.238	91.535	2631.07	7.657	0.089	2.772	2045.88	103.70	134.80
3.3	11	32,34,36	adult	HF	7.92	0.116	1.024	15:21:00	16:46:00	25.42	96.287	7.290	0.215	4.335	7.433	96.128	2709.31	7.753	0.051	1.597	2519.77	128.20	127.00
3.4	12	33.35	adult	LF	2.13	0.123	1.024	15:26:00	11:10:00	43.73	88.644	7.193	0.164	3.704	3.428	88.523	2736.74	7.85	0.072	2.240	2368.17	136.19	136.19
	13					0.130	1.024	15:37:00	11:32:00	43.92	107.498	8.435	0.158	4.605	0.344	107.424	2759.06	7.967			2515.03	179.10	124.50
technical	14		control		0	0.130	1.024	15:39:00	11:42:00	44.05	93.407	7.305	0.096	3.780	0.767	93.360	2735.45	7.926			2426.91	183.00	133.90
	15					0.130	1.024	15:41:00	11:51:00	44.17	86.457	7.311	0.125	3.077	0.207	86.334	2799.35	8.083			2407.66	199.60	123.60

Table C5: Raw data obtained from the incubation with the corals from the pH treatment. Values in red were not used for calculations dueto large deviations from the mean.

Tank Nr	Bottle Nr.	Coral ID	Life stage	Feeding	Coral tissue per bottle (cm2)	Volume per bottle (l)	density (kg/l)	kg	t	t_0	duration(h)	NOx (µmol/l)	Silikat (µmol/L)	Nitrit (µmol/L)	Phosphat (µmol/L)	Ammonium (µmol/L)	Nitrat (µmol/L)	TA corr. (µmol/kg)	pH	ΔO_2 (mg/d/cm^{-2})	ΔO_2 (µmol/d/cm^{-2})	DIC (µmol/kg)	TOC (µmol/L)	TDN (µmol/L)
						0.130	1.024					91.076	7.358	0.170	2.252	0.667	91.008	2797.01				2610.947	63.84	107.70
technical			start			0.130	1.024					83.747	7.107	0.129	2.529	1.202	83.669	2794.56	7.571			2619.084	66.80	102.00
						0.130	1.024					81.372	7.048	0.184	2.206	0.555	81.236	2789.80				2611.587	60.95	111.23
4.1	1	1,3,5	recruit	LF	1.02	0.126	1.024	0.123	15:30:00	11:39:00	44.2	100.056	9.677	0.113	2.607	2.409	99.965	2812.90	7.512	0.034	1.057	2518.872	120.40	120.40
4.1	2	13,15,17	juvenile	LF	0.77	0.125	1.024	0.122	15:34:00	11:48:00	44.2	93.416	9.348	0.134	3.987	1.358	93.323	2903.97	7.835	0.067	2.091	2573.935	123.87	123.87
4.4	3	7,9,11	recruit	LF	1.00	0.126	1.024	0.123	15:39:00	11:55:00	44.3	89.312	8.271	0.119	2.399	1.782	89.241	2797.31	7.634	0.031	0.962	2556.278	130.50	109.30
4.1	4	25,27,29	adult	LF	5.96	0.119	1.024	0.116	15:45:00	17:41:00	25.9	91.444	7.574	0.196	2.522	6.264	91.366	2768.69	7.428	0.064	2.015	2624.616	108.70	127.10
4.2	5	2,4,6	recruit	HF	0.81	0.127	1.024	0.124	15:58:00	12:03:00	44.1	90.419	7.862	0.150	2.540	3.077	90.324	2776.66	7.616	0.071	2.233	2614.211	107.80	111.10
4.2	6	14,16,18	juvenile	HF	1.58	0.123	1.024	0.120	16:02:00	12:12:00	44.2	83.136	7.371	0.165	2.337	4.739	83.094	2791.45	7.624	0.046	1.450	2591.564	168.50	109.30
4.2	7	26,28,30	adult	HF	4.92	0.125	1.024	0.122	16:05:00	17:53:00	25.8	93.585	7.745	0.179	2.811	5.627	93.419	2790.62	7.524	0.053	1.655	2633.393	160.50	126.34
4.4	8	19,21,23	juvenile	LF	1.18	0.127	1.024	0.124	16:09:00	12:21:00	44.2	94.127	8.139	0.188	2.412	1.646	94.037	2786.36	7.535	0.049	1.527	2535.787	135.20	122.42
4.3	9	8,10,12	recruit	HF	1.30	0.126	1.024	0.123	16:15:00	12:30:00	44.3	82.818	7.541	0.167	2.549	7.869	82.689	2594.60	7.371	0.078	2.450	2479.885	102.30	117.70
4.3	10	20,22,24	juvenile	HF	2.55	0.127	1.024	0.124	16:18:00	12:40:00	44.4	82.956	7.270	0.154	2.524	9.293	82.858	2624.91	7.347	0.065	2.039	2500.476	129.92	129.92
4.3	11	32,34,36	adult	HF	4.00	0.123	1.024	0.120	16:21:00	18:03:00	25.7	94.362	7.770	0.249	3.017	7.032	94.113	2768.72	7.446	0.079	2.472	2635.895	94.01	114.10
4.4	12	31.35	adult	LF	2.89	0.125	1.024	0.122	16:24:00	12:50:00	44.4	90.908	7.235	0.138	2.595	8.261	90.783	2768.27	7.516	0.060	1.886	2521.099	106.30	117.10
	13					0.130	1.024	0.127	16:40:00	12:59:00	44.3	76.206	6.596	0.141	2.078	1.772	76.103	2753.87	7.66			2540.25	99.94	114.30
technical	14		control		0	0.130	1.024	0.127	16:43:00	13:07:00	44.4	81.912	6.770	0.254	2.070	1.055	81.730	2763.76	7.69			2582.45	113.12	113.12
	15					0.130	1.024	0.127	16:47:00	13:15:00	44.5	85.709	8.139	0.254	2.172	1.878	85.506	2766.41	7.74			2555.60	115.47	115.47

Table C6: Raw data obtained from the incubation with the corals from the temperature treatment. Values in red were not used for calculations due to large deviations from the mean. Values underlined in yellow came from corals of the health category 4 and were not used for further analysis.

Tank Nr	Bottle Nr.	Coral ID	Life stage	Feeding	Coral tissue per bottle (cm2)	density (kg/l)	Volume per bottle (l)	t	t_0	duration(h)	Nox (µmol/l)	Silikat (µmol/L)	Nitrit (µmol/L)	Phosphat (µmol/L)	NH_4^+ (µmol/L)	Nitrat (µmol/L)	MW TA corr. (µmol/kg)	pH	ΔO_2 (mg/d/cm^{-2})	ΔO_2 (µmol/d/cm^{-2})	DIC	TOC (µmol/L)	TDN (µmol/L)
technical	start					1.023	0.130	start			108.394	7.234	0.360	2.684	0.641	108.148	2635.84	8.027		8.558	2188.33	60.78	138.54
						1.023	0.130				111.056	7.187	0.311	2.994	0.963	110.816	2629.38			2.63093307	2299.84	144.48	144.48
						1.023	0.130				140.295	9.464	0.456	3.852	0.507	139.875	2630.83				2276.57	140.45	140.45
5,1&5,4	1	1,3,7	recruit	LF	0.27	1.023	0.127	15:16:00	10:32:00	43.3	120.974	9.056	0.194	2.562	1.722	120.890	2647.39	8.04	0.15	4.715	2390.984	110.90	148.51
5.1	2	13.15	juvenile	LF	0.26	1.023	0.126	15:18:00	10:40:00	43.4	104.580	7.316	0.172	2.274	0.947	104.506	2684.54	8.09	0.18	5.552	2277.649	202.60	152.88
5.1	3	29	adult	LF	0.26	1.023	0.121	15:20:00	10:48:00	43.5	132.543	8.681	0.306	2.628	4.254	132.251	2641.83	8.00	0.19	5.984	2338.755	158.37	158.37
5.2	5	4,6,	recruit	HF	0.11	1.023	0.127	15:26:00	11:06:00	43.7	119.438	8.420	0.222	2.368	0.076	119.384	2640.49	8.01	0.19	6.090	2332.740	151.20	151.20
5.2	6	14,16,18	juvenile	HF	0.40	1.023	0.125	15:29:00	11:17:00	43.8	119.349	8.844	0.111	3.176	4.892	119.238	2654.81	7.99	0.36	11.326	2343.476	124.40	149.74
5.4	7	21.23	juvenile	LF	0.25	1.023	0.127	15:32:00	11:26:00	43.9	117.731	8.228	0.203	2.592	2.849	117.689	2647.26	7.95	0.20	6.119	2379.321	170.80	149.63
5.3	9	8,10,	recruit	HF	0.13	1.023	0.127	15:37:00	11:44:00	44.1	119.975	8.129	0.204	2.949	2.259	119.841	2639.67	7.97	0.14	4.237	2345.777	157.70	157.70
5.3	10	20,22,24	juvenile	HF	0.30	1.023	0.121	15:40:00	11:52:00	44.2	120.513	7.943	0.168	3.153	4.182	120.353	2647.56	8.01	0.26	8.257	2303.072	145.49	145.49
5.3	11	32	adult	HF	0.81	1.023	0.125	15:43:00	12:01:00	44.3	118.628	7.949	0.311	2.760	6.051	118.317	2640.60	7.99	0.47	14.605	2332.960	105.30	140.78
	4					1.023	0.130	15:22:00	10:57:00	43.6	105.885	6.791	0.288	2.340	2.445	105.603	2651.45	7.955	0.01		2310.480	108.20	147.39
technical	8	control			0	1.023	0.130	15:35:00	11:34:00	44.0	102.711	6.861	0.240	2.663	1.650	102.545	2638.61	7.892	0.02		2317.237	141.50	159.71
	12					1.023	0.130	15:44:00	12:10:00	44.4	134.003	9.476	0.398	3.494	1.194	133.760	2637.62	7.990	0.01		2325.490	121.20	152.00

Table C7: Raw data obtained from the incubation with the corals from combined treatment. Values in red were not used for calculations due to large deviations from the mean. Values underlined in yellow came from corals of the health category 4 and were not used for further analysis.

Tank Nr	Bottle Nr.	Coral ID	Life stage	Feeding	Coral tissue per bottle	Volume per bottle (l)	density (kg/l)	t	t_0	duration(h)	Nox (µmol/l)	Silikat (µmol/L)	Nitrit (µmol/L)	Phosphat (µmol/L)	Ammonium (µmol/L)	Nitrat (µmol/L)	TA corr. (µmol/kg)	pH	ΔO_2 (mg/cm-2)	ΔO_2 (µmol/d/cm-	DIC	TOC (µmol/L)	TDN (µmol/L)
technical	start					0.130	1.023	start			106.35	7.902	0.192	2.002	0.807	106.272	2707.30	7.539		3.155	2491.76	121.18	121.18
						0.130	1.023				86.19	6.710	0.222	1.730	0.614	86.024	2706.67			1.23931957	2402.10	74.59	120.51
						0.130	1.023				98.06	7.402	0.188	1.962	0.816	97.986	2697.84				2356.32	77.43	119.70
6,1&6,4	1	3,7	recruit	LF	0.31	0.127	1.023	14:38:00	09:51:00	43.2	90.14	7.080	0.245	1.865	2.142	89.957	2725.54	7.605	0.083	2.588	2536.137	115.50	136.53
6,1&6,4	2	15.17	juvenile	LF	0.89	0.126	1.023	14:41:00	09:59:00	43.3	95.50	7.802	0.105	1.832	2.280	95.457	2747.55	7.611	0.073	2.267	2528.851	142.35	142.35
6.1	3	29	adult	LF	1.26	0.125	1.023	14:45:00	10:06:00	43.3	85.23	7.316	0.254	1.294	1.756	85.088	2768.74	7.647	0.102	3.189	2547.185	162.40	129.70
6.4	4	9,11	recruit	LF	0.27	0.123	1.023	14:48:00	10:14:00	43.4	116.28	9.521	0.159	2.286	1.394	116.243	2714.95	7.560	0.127	3.973	2558.271	284.30	141.34
6.2	5	4,6	recruit	HF	0.28	0.127	1.023	14:52:00	10:22:00	43.5	97.11	8.058	0.180	1.782	2.264	96.984	2716.79	7.533	0.156	4.861	2496.475	106.60	127.79
6.2	6	14,16,18	juvenile	HF	1.18	0.125	1.023	14:55:00	10:30:00	43.6	81.71	6.615	0.111	2.042	1.980	81.614	2747.82	7.562	0.069	2.153	2596.936	128.80	129.10
6.2	7	26	adult	HF	0.54	0.111	1.023	14:57:00	10:40:00	43.7	106.88	8.523	0.150	2.085	2.678	106.791	2728.10	7.497	0.167	5.210	2447.310	207.20	135.10
6.4	8	19,21,23	juvenile	LF	1.11	0.127	1.023	15:00:00	10:52:00	43.9	105.23	8.535	0.138	2.166	2.661	105.153	2712.50	7.546	0.063	1.958	2476.893	174.40	142.80
6.3	9	8,10,12	recruit	HF	0.42	0.127	1.023	15:03:00	11:01:00	44.0	106.40	8.004	0.128	2.129	2.270	106.274	2730.54	7.556	0.128	4.011	2504.391	116.60	137.42
6.3	10	20,22,24	juvenile	HF	1.32	0.124	1.023	15:05:00	11:09:00	44.1	101.07	7.790	0.102	3.144	5.441	101.031	2724.76	7.501	0.064	1.999	2575.253	136.98	136.98
6.3	11	36	adult	HF	1.07	0.126	1.023	15:07:00	11:17:00	44.2	97.20	7.808	0.149	1.908	3.588	97.095	2738.81	7.514	0.088	2.753	2537.016	120.30	139.33
6.4	12	35	adult	LF	1.45	0.126	1.023	15:10:00	11:25:00	44.3	93.73	6.954	0.176	1.914	3.914	93.552	2743.14	7.500	0.081	2.519	2546.419	116.90	130.70
	13					0.130	1.023	15:32:00	11:35:00	44.1	95.59	8.115	0.170	1.590	0.768	95.511	2838.27	7.825			2550.52	465.90	130.30
technical	14	control			0	0.130	1.023	15:34:00	11:42:00	44.1	98.41	7.623	0.114	3.300	2.429	98.354	2739.19	7.560			2566.75	133.39	133.39
	15					0.130	1.023	15:36:00	11:49:00	44.2	103.65	8.237	0.138	1.752	1.080	103.580	2743.51	7.590			2543.59	170.00	138.54

Table C8: Properties of the carbonate system before and after the incubations calculated using the CO2Sys_v2.1 excel spreadsheet (Pierrot *et al.*, 2006)

Treatment	Chamber ID.	Life stage	Feeding	pCO2 (µatm)	HCO_3 (µmol/kgSW)	CO_3^{2-} (µmol/kgSW)	CO_2 (µmol/kgSW)	Ω_{Arg}	xCO2 (dry at 1 atm) (ppm)
Ambient		Technical		781.604	2329.285	94.767	33.319	1.457	791.950
				800.329	2385.088	97.037	34.117	1.492	810.923
				764.309	2277.744	92.670	32.582	1.425	774.427
	4	adult	LF	902.078	2424.198	87.534	38.885	1.345	913.747
	7	adult	HF	1097.099	2363.577	68.419	47.291	1.051	1111.290
	11	adult	HF	1314.062	2404.033	59.095	56.643	0.908	1331.060
	1	recruit	LF	737.260	2187.486	87.207	31.780	1.340	746.797
	2	juvenile	LF	838.913	2355.272	88.848	36.162	1.365	849.765
	3	recruit	LF	658.507	2202.339	98.967	28.385	1.521	667.025
	5	recruit	HF	812.380	2301.883	87.638	35.018	1.346	822.888
	6	juvenile	HF	858.514	2148.184	72.223	37.007	1.110	869.619
	8	juvenile	LF	784.663	2365.961	95.855	33.823	1.473	794.813
	9	recruit	HF	1177.385	1854.568	39.251	50.752	0.603	1192.615
	10	juvenile	HF	1329.657	1950.132	38.430	57.316	0.590	1346.857
	12	adult	LF	986.449	2256.310	69.343	42.521	1.065	999.209
	13	control		796.378	2384.750	95.951	34.328	1.474	806.679
	14			846.323	2306.007	84.424	36.481	1.297	857.271
	15			621.749	2269.548	111.313	26.801	1.710	629.792
pH		Technical		2067.286	2482.102	40.769	88.076	0.627	2094.649
				2073.729	2489.837	40.896	88.351	0.629	2101.178
				2067.793	2482.710	40.779	88.098	0.627	2095.163
	4	adult	LF	2854.396	2472.682	28.778	123.156	0.442	2891.202
	7	adult	HF	2311.199	2497.418	36.256	99.719	0.557	2341.001
	11	adult	HF	2754.249	2486.892	30.168	118.835	0.463	2789.763
	1	recruit	LF	2271.067	2387.173	33.711	97.987	0.518	2300.351
	2	juvenile	LF	1109.371	2453.187	72.883	47.865	1.119	1123.676
	3	recruit	LF	1749.405	2435.253	45.545	75.480	0.699	1771.962
	5	recruit	HF	1863.780	2489.134	44.662	80.415	0.686	1887.812
	6	juvenile	HF	1814.353	2468.172	45.110	78.282	0.693	1837.748
	8	juvenile	LF	1731.438	2415.798	45.285	74.704	0.695	1753.763
	9	recruit	HF	3059.240	2324.168	23.723	131.994	0.364	3098.687
	10	juvenile	HF	3251.743	2337.600	22.577	140.299	0.347	3293.672
	12	adult	LF	2252.759	2389.840	34.061	97.197	0.523	2281.807
	13	control		1657.220	2421.222	47.526	71.502	0.730	1678.589
	14			1526.315	2463.192	53.406	65.854	0.820	1545.995
	15			1384.878	2438.178	57.671	59.752	0.886	1402.735
temperature		Technical		615.841	2054.123	110.868	23.338	1.724	626.328
				647.224	2158.799	116.518	24.527	1.811	658.245
				640.675	2136.957	115.339	24.279	1.793	651.585
	1	recruit	LF	616.493	2237.356	130.113	23.515	2.021	626.844
	2	juvenile	LF	561.002	2127.022	129.228	21.399	2.008	570.422
	3	adult	LF	709.654	2202.181	109.506	27.069	1.701	721.570
	4	control		674.811	2172.648	112.092	25.740	1.741	686.142
	5	recruit	HF	723.169	2198.095	107.061	27.585	1.663	735.311
	6	juvenile	HF	787.621	2213.730	99.703	30.043	1.549	800.846
	7	juvenile	LF	768.045	2244.882	105.143	29.296	1.633	780.941
	8	control		680.026	2179.376	111.922	25.939	1.739	691.444
	9	recruit	HF	722.033	2209.856	108.380	27.541	1.684	734.156
	10	juvenile	HF	768.555	2175.113	98.643	29.316	1.532	781.460
	11	adult	HF	903.497	2211.737	86.760	34.463	1.348	918.667
	12	control		714.085	2190.570	107.682	27.238	1.673	726.075
combined		Technical		1948.110	2371.179	46.798	73.783	0.727	1981.283
				1878.016	2285.862	45.114	71.128	0.701	1909.995
				1842.219	2242.294	44.254	69.773	0.688	1873.589
	1	recruit	LF	1908.913	2414.333	49.023	72.781	0.761	1940.956
	2	juvenile	LF	1877.549	2407.697	49.568	71.585	0.770	1909.064
	3	adult	LF	1741.689	2426.506	54.273	66.405	0.843	1770.924
	4	recruit	LF	2133.175	2432.411	44.528	81.332	0.692	2168.982
	5	recruit	HF	2212.978	2371.308	40.793	84.374	0.634	2250.124
	6	juvenile	HF	2155.605	2469.336	45.413	82.187	0.705	2191.788
	7	adult	HF	2353.072	2320.845	36.749	89.716	0.571	2392.569
	8	juvenile	LF	2131.937	2353.884	41.724	81.284	0.648	2167.722
	9	recruit	HF	2107.286	2380.861	43.185	80.345	0.671	2142.657
	10	juvenile	HF	2453.872	2442.658	39.036	93.559	0.606	2495.062
	11	adult	HF	2347.582	2407.861	39.649	89.506	0.616	2386.988
	12	adult	LF	2431.871	2415.191	38.508	92.720	0.598	2472.691
	13	control		1155.203	2424.763	81.709	44.044	1.269	1174.593
	14			2140.244	2440.473	44.676	81.601	0.694	2176.169
	15			1981.107	2420.578	47.481	75.534	0.737	2014.361

Table C9: Hourly and daily rates for changes in the measured values in the coral chambers during the incubations with the ambient treatment. Δ-values are those corrected for values measured in the technical tanks before the incubations. The TA values marked in red were due to technical problems with the titrators.

Coral ID	Life stage	ΔO2 (µmol/d/cm^{-2})	ΔTA - control (µmol/h)	ΔNOx/h - control	ΔPhosphat (µmol/h) - control	ΔAmmonium (µmol/h) - control	ΔAmmonium (µmol/cm^2/d) - control	O/N	µmol CaCO3 d-1 cm-2	Δ Ω_{arg} - control	$\Delta pH_{(NBS)}$ - control
1,3,5	recruit	1.628	-0.37	-0.036	-0.001	0.003	0.098	17	6.18	-0.15	-0.003
13,15,17	juvenile	0.895	-0.32	-0.042	-0.003	0.002	0.015	59	1.67	-0.13	-0.027
7,9,11	recruit	1.572	-0.30	0.028	0.000	0.001	0.043	37	3.90	0.03	0.049
25,27,29	adult	1.584	-0.14	-0.004	0.002	0.029	0.164	10	0.48	-0.15	-0.046
2,4,6	recruit	3.328	2.36	0.036	0.000	0.003	0.095	35	-42.30	-0.15	-0.023
14,16,18	juvenile	1.943	2.47	0.027	-0.001	0.004	0.064	30	-19.29	-0.38	-0.077
26,28,30	adult	2.319	-0.11	-0.011	0.002	0.026	0.136	17	0.39	-0.44	-0.142
19,21,23	juvenile	1.463	2.56	0.008	0.000	0.005	0.108	14	-25.41	-0.02	0.004
8,10,12	recruit	3.072	-0.57	0.029	0.002	0.017	0.268	11	4.47	-0.89	-0.278
20,22,24	juvenile	2.772	-0.40	0.005	0.001	0.023	0.240	12	2.16	-0.90	-0.309
32,34,36	adult	1.597	-0.17	0.025	0.003	0.032	0.098	16	0.26	-0.43	-0.213
33.35	adult	2.240	-0.09	-0.003	0.000	0.009	0.100	22	0.57	-0.59	-0.116

Table C10: Hourly and daily rates for changes in the measured values in the coral chambers during the incubations with the pH treatment. Δ-values are those corrected for values measured in the technical tanks before the incubations.

Coral ID	Life stage	Feeding	ΔO2 (µmol/d/cm-2)	ΔTA(µmol/h) - control	ΔNOx/h	ΔPhosphat (µmol/h) - control	ΔAmmonium (µmol/h) - control	ΔAmmonium (µmol/cm-2/d)	O/N	µmol CaCO3 d-1 cm-2	Δ Ω_{arg} - control	$\Delta pH_{(NBS)}$ - control
1,3,5	recruit	LF	1.057	0.15	0.415	0.001	0.002	0.037	28	-6.67	-0.29	-0.059
13,15,17	juvenile	LF	2.091	0.42	0.317	0.005	-0.001	-0.045	-46	-11.60	0.31	0.264
7,9,11	recruit	LF	0.962	0.11	0.226	0.001	0.000	-0.005	-182	-3.98	-0.11	0.063
25,27,29	adult	LF	2.015	0.02	0.367	0.002	0.022	0.090	22	-0.74	-0.37	-0.143
2,4,6	recruit	HF	2.233	0.04	0.251	0.001	0.004	0.105	21	-4.36	-0.13	0.045
14,16,18	juvenile	HF	1.450	0.09	0.090	0.001	0.008	0.121	12	-1.29	-0.12	0.053
26,28,30	adult	HF	1.655	0.09	0.449	0.003	0.021	0.101	16	-1.26	-0.26	-0.047
19,21,23	juvenile	LF	1.527	0.07	0.332	0.001	-0.001	-0.012	-129	-4.15	-0.12	-0.036
8,10,12	recruit	HF	2.450	-0.49	0.083	0.001	0.017	0.317	8	3.89	-0.45	-0.2
20,22,24	juvenile	HF	2.039	-0.40	0.086	0.001	0.021	0.200	10	1.57	-0.47	-0.224
32,34,36	adult	HF	2.472	0.02	0.480	0.004	0.027	0.163	15	-1.44	-0.35	-0.125
31.35	adult	LF	1.886	0.02	0.261	0.001	0.018	0.149	13	-1.10	-0.29	-0.055

Table C11: Hourly and daily rates for changes in the measured values in the coral chambers during the incubations with the temperature treatment. Δ-values are those corrected for values measured in the technical tanks before the incubations. Values underlined in yellow came from corals of the health category 4 and were not used for further analysis.

Coral ID	Life stage	Feeding	ΔO2 (µmol/d/cm-2)	ΔTA(µmol/h) - control	ΔNOx/h	ΔPhosphat (µmol/h)	ΔNH4+ (µmol/h) - control	ΔNH4+ (µmol/d/cm-2)	O/N	µmol CaCO3 d-1 cm-2	Δ Ω_{arg} - control	ΔpH
1,3,7	recruit	LF	4.71	0.014	0.049	0.000	0.001	0.076	62	-2.74	0.50	0.01
13.15	juvenile	LF	5.55	0.124	0.001	-0.001	-0.001	-0.129	-43	-5.75	0.49	0.06
29	adult	LF	5.98	-0.004	0.080	0.000	0.008	0.719	8	-3.17	0.18	-0.03
4,6,	recruit	HF	6.09	-0.007	0.044	0.000	-0.004	-0.849	-7	-4.43	0.22	-0.02
14,16,18	juvenile	HF	11.33	0.035	0.044	0.002	0.010	0.585	19	-2.09	0.15	-0.04
21.23	juvenile	LF	6.12	0.013	0.039	0.000	0.004	0.391	16	-2.33	0.03	-0.07
8,10,	recruit	HF	4.24	-0.009	0.046	0.001	0.002	0.439	10	-3.28	0.12	-0.06
20,22,24	juvenile	HF	8.26	0.012	0.046	0.002	0.007	0.591	14	-2.07	0.22	-0.02
32	adult	HF	14.61	-0.007	0.041	0.001	0.013	0.384	38	-0.32	0.17	-0.04

Table C12: Hourly and daily rates for changes in the measured values in the coral chambers during the incubations with the combined treatment. Δ-values are those corrected for values measured in the technical tanks before the incubations. Values underlined in yellow came from corals of the health category 4 and were not used for further analysis.

Coral ID	Life stage	Feeding	ΔO2 (µmol/d/cm^{-2})	ΔTA(µmol/h) - control	ΔNOx/h - control	ΔPhosphat (µmol/h)	ΔAmmonium (µmol/h) - control	ΔAmmonium (µmol/cm^{-2}/d)	O/N	µmol CaCO3 d-1 cm-2	Δ Ωarg - control	ΔpH
3,7	recruit	LF	2.588	-0.05	-0.03	0.001	0.004	0.273	9	2.95	-0.14	0.066
15.17	juvenile	LF	2.267	0.02	-0.01	0.000	0.004	0.106	21	-0.04	-0.13	0.072
29	adult	LF	3.189	0.08	-0.04	-0.001	0.002	0.046	70	-0.33	-0.06	0.108
9,11	recruit	LF	3.973	-0.08	0.05	0.002	0.001	0.119	34	1.46	-0.21	0.021
4,6	recruit	HF	4.861	-0.07	-0.01	0.000	0.004	0.341	14	3.66	-0.27	-0.006
14,16,18	juvenile	HF	2.153	0.02	-0.05	0.001	0.003	0.061	35	0.37	-0.19	0.023
26	adult	HF	5.210	-0.05	0.02	0.001	0.004	0.193	27	0.76	-0.33	-0.042
19,21,23	juvenile	LF	1.958	-0.09	0.02	0.001	0.005	0.109	18	0.80	-0.25	0.007
8,10,12	recruit	HF	4.011	-0.03	0.02	0.001	0.004	0.220	18	0.45	-0.23	0.017
20,22,24	juvenile	HF	1.999	-0.05	0.00	0.004	0.013	0.230	9	0.51	-0.29	-0.038
36	adult	HF	2.753	-0.01	-0.01	0.001	0.008	0.170	16	0.26	-0.28	-0.025
35	adult	LF	2.519	0.00	-0.02	0.001	0.008	0.140	18	0.18	-0.30	-0.039

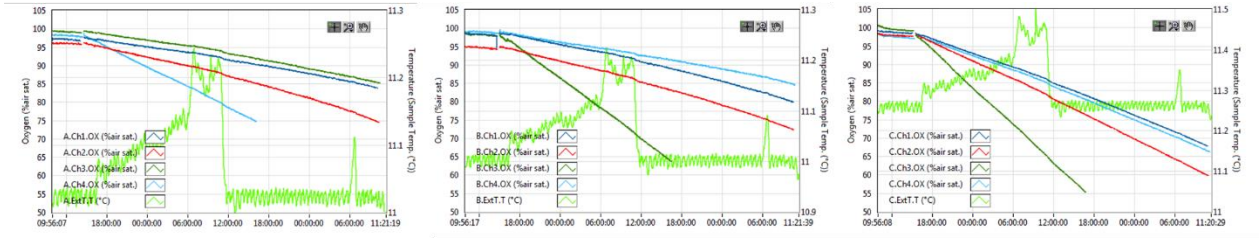


Figure C1: Oxygen saturation in % and temperature in °C measured by the Firesting® during the incubations with the corals from the ambient treatment. The temperature rise was due to a lid meant to keep out the light when people came into the room to work on the experiment. The removal of the lid can be seen in the sharp drop in temperature.

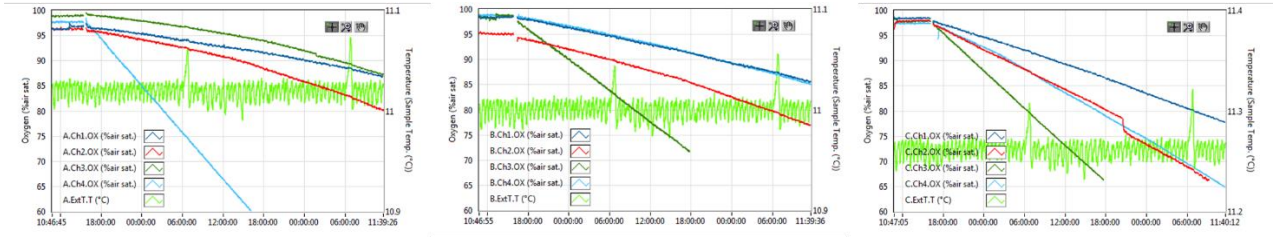


Figure C2: Oxygen saturation in % and temperature in °C measured by the Firesting® during the incubations with the corals from the pH treatment.

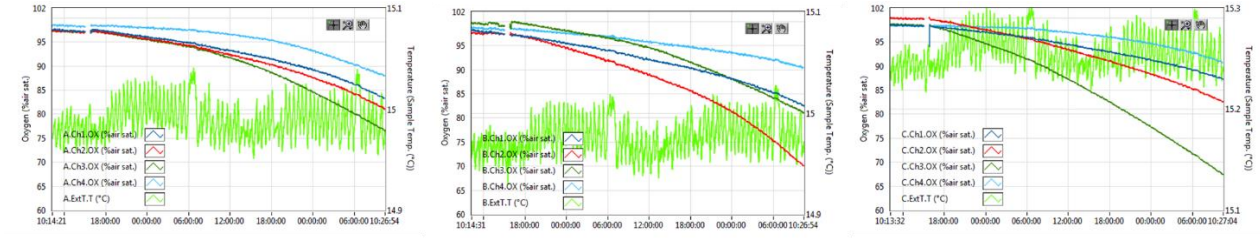


Figure C3: Oxygen saturation in % and temperature in °C measured by the Firesting® during the incubations with the corals from the temperature treatment. The light blue line is from the control chambers showing an exponential decrease after about 24 hours.

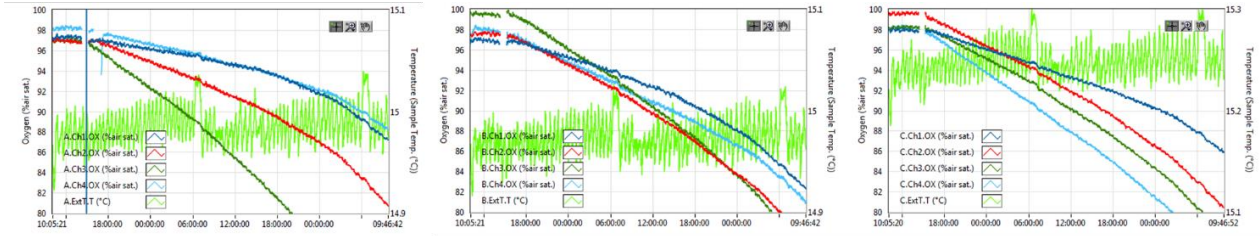


Figure C4: Oxygen saturation in % and temperature in °C measured by the Firesting® during the incubations with the corals from the combined treatment

Supplementary D: Post-hoc tests

Long time experiment

Table D1: Tukey's HSD testing for significant differences in tissue growth rates in % between the treatments. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Treatment	Df	*t*-ratio	*p*-value
Ambient vs pH	120	0.374	0.982
Ambient vs Temperature	120	10.937	< 0.0001***
Ambient vs Combined	120	7.270	< 0.0001***
pH vs Temperature	120	10.562	< 0.0001***
pH vs Combined	120	6.895	< 0.0001***
Temperature vs Combined	120	-3.667	0.0021

Table D2: Tukey's HSD testing for significant differences in tissue growth rates in % between the life stages across all treatments. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Life stage	Df	*t*-ratio	*p*-value
Recruit vs Juvenile	120	0.617	0.811
Recruit vs Adult	120	6.960	< 0.0001***
Juvenile vs Adult	120	6.343	< 0.0001***

Table D3: Tukey's HSD testing for significant differences in tissue growth rates in % between the feeding groups within the treatments. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Feeding group	Treatment	Df	*t*-ratio	*p*-value
HF vs LF	Ambient	120	3.658	0.009**
	pH	120	3.459	0.017*
	Temperature	120	-0.151	0.999
	Combined	120	0.496	0.999

Table D4: Tukey's HSD testing for significant differences in tissue growth rates in % between the life stages within the treatments. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Life stage	Treatment	Df	*t*-ratio	*p*-value
Recruit vs juvenile	Ambient	120	0.737	0.999
	pH	120	2.605	0.289
	Temperature	120	-0.139	1.000
	Combined	120	-1.969	0.713
Recruit vs adult	Ambient	120	5.149	0.0001***
	pH	120	5.873	< 0.0001***
	Temperature	120	0.963	0.998
	Combined	120	1.935	0.735
Juvenile vs adult	Ambient	120	4.412	0.0013**
	pH	120	3.268	0.06
	Temperature	120	1.102	0.994
	Combined	120	3.904	0.008**

Test incubations

Table D5: Tukey's HSD testing for significant differences between the different feeding incubations with the test corals. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

#nauplii	Df	*t*-ratio	*p*-value
30 vs 250	40	- 7.223	< 0.0001***
30 vs 252	40	- 6.609	< 0.0001***
30 vs 323	40	- 2.530	0.104
30 vs 404	40	4.589	0.0004***
250 vs 252	40	0.507	0.986
250 vs 323	40	3.870	0.003**
250 vs 404	40	2.173	0.211
252 vs 323	40	3.363	0.014*
252 vs 404	40	1.666	0.466
323 vs 404	40	- 1.697	0.471

Table D6: Tukey's HSD (Respiration, ammonium excretion and O:N) and Wilcoxon rank-sum test testing for significant differences between the measured variables during the incubations with the test corals. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Measured variable	Test incubations	Df	*t*-ratio	*p*-value
Respiration	24 h vs 48 h	21	-0.606	0.819
	24 h vs 48 h with ambient water	21	-5.328	0.0001***
	48 h vs 48 h with ambient water	21	-4.772	0.0003***
Ammonium excretion	24 h vs 48 h	21	2.511	0.051
	24 h vs 48 h with ambient water	21	5.371	0.0001***
	48 h vs 48 h with ambient water	21	2.860	0.0244*
O:N	24 h vs 48 h	19	-2.112	0.114
	24 h vs 48 h with ambient water	19	-5.764	< 0.0001***
	48 h vs 48 h with ambient water	19	-3.809	0.0032**
Calcification	24 h vs 48 h			0.29
	24 h vs 48 h with ambient water			0.03*
	48 h vs 48 h with ambient water			0.03*

Incubations to determine the energetic turnover – feeding

Table D7: Tukey's HSD testing for significant differences in feeding rates between the different tentacle extension rates observed at the end of the feeding incubations. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Feeding group	Extension rate (%)	*p*-value
Low feeding	< 25 vs 25 – 75	0.416
	< 25 vs > 75	0.08
	25 - 75 vs > 75	0.007**
High feeding	< 25 vs 25 – 75	0.299
	< 25 vs > 75	0.299
	25 - 75 vs > 75	0.929

Table D8: Tukey's HSD testing for significant differences in the calculated weekly nauplii-derived POM-uptake between treatments. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Treatments	Df	*t*-ratio	*p*-value
Ambient vs pH	81	-2.337	0.098
Ambient vs Temperature	81	-6.432	< 0.0001***
Ambient vs Combined	81	-3.096	0.014*
pH vs Temperature	81	-4.780	< 0.0001***
pH vs Combined	81	-1.172	0.646
Temperature vs Combined	81	3.331	0.007**

Table D9: Tukey's HSD testing for significant differences in the calculated weekly nauplii-derived POM-uptake between the life stages across all treatments. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Life stage	Df	*t*-ratio	*p*-value
Recruit vs Juvenile	92	4.332	0.0001***
Recruit vs Adult	92	6.447	< 0.0001***
Juvenile vs Adult	92	3.081	0.0079**

Incubations to determine the energetic turnover – Calcification and respiration

Table D10: Tukey's HSD testing for significant differences in the calcification and respiration rates between the treatments. Significant p-values are marked with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks.

Measured variable	Treatments	Df	*t*-ratio	*p*-value
Calcification	Ambient vs pH	33	4.275	0.001**
	Ambient vs Temperature	33	4.112	0.001**
	Ambient vs Combined	33	1.075	0.707
	pH vs Temperature	33	0.391	0.979
	pH vs Combined	33	-3.252	0.013*
	Temperature vs Combined	33	-3.199	0.015*
Respiration	Ambient vs pH	36	0.528	0.952
	Ambient vs Temperature	36	-10.069	< 0.0001***
	Ambient vs Combined	36	-2.173	0.15
	pH vs Temperature	36	-10.522	< 0.0001***
	pH vs Combined	36	-2.676	0.052
	Temperature vs Combined	36	7.832	< 0.0001***

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Statement of independence

I hereby confirm that this thesis was written independently by myself without the use of any sources beyond those cited, and all passages and ideas taken from other sources are cited accordingly.