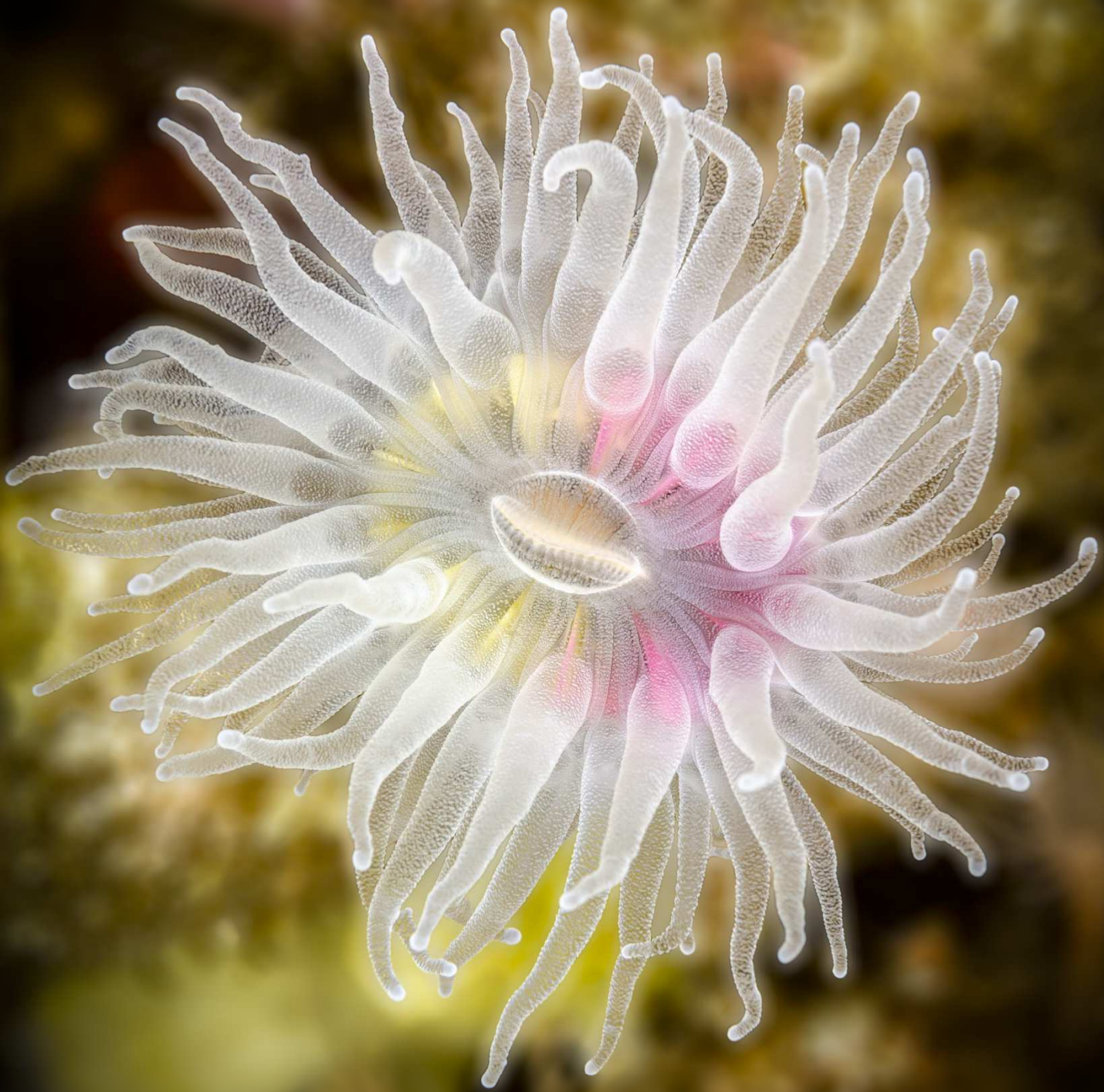
Cold-water corals in a changing ocean: Effects on their physiological performance



Dissertation

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Summary

Cold-water corals (CWCs) are abundant worldwide, with their distribution mainly determined by physico-chemical factors and food availability. Despite predominantly occurring in deep waters, CWC habitats are also affected by the impacts of global climate change, such as ocean acidification and warming as well as reduced primary productivity and oxygen concentration. Several previous studies have already investigated the effects of environmental changes on different CWCs species, but mainly focused on laboratory experiments under controlled conditions of a single parameter and the study of adult corals. To date, there is limited information on the effects of environmental changes on different life stages of CWCs, the combined effect of multiple factors, the impact of variable rather than constant conditions and the importance of food availability for the resilience of CWCs to environmental changes.

Therefore, this thesis aimed to better understand the physiological response of CWCs to changes in their environment. In both aquarium and *in situ* experiments, I examined how CWCs cope with changes in single and several combined factors under stable and variable environmental conditions, taking into account the response of different life stages and the influence of differences in food availability.

For this purpose, I have investigated the short- and long-term physiological response of three life stages of the CWC *Caryophyllia huinayensis* to different conditions of aragonite saturation (Ω_{arag}), temperature and feeding in an aquarium experiment, all as individual factors as well as their interactions (**manuscript 1**). Aragonite undersaturation did not affect the corals, but elevated temperature and reduced feeding showed a clear negative effect. Juvenile and adult corals responded differently to temperature changes and reduced food supply as calcification rates of early juveniles were most affected, while adult corals showed highest mortality rates. The clear feeding effect and the delayed response of corals after more than three months under constant treatment conditions underline the need for long-term experiments and the inclusion of food supply as an important factor.

However, CWCs are not exposed to stable environmental conditions in their natural habitat, as a year-long *in situ* experiment in Comau Fjord in northern Patagonia (Chile) showed (**manuscript 2**). We took advantage of the ubiquitous occurrence of the CWC *Desmophyllum dianthus* in this fjord and transplanted corals between spatially close habitats with contrasting physico-chemical conditions to investigate its ability to acclimatise to changing environmental conditions. This reciprocal transplantation experiment revealed the fast acclimatisation potential of most investigated traits of *D. dianthus* to a new environment, as calcification and respiration rates were clearly determined by the environment, demonstrating a high phenotypic plasticity. Unexpectedly, corals at greater depth (300 m) had higher calcification rates than corals in shallow waters (20 m), despite aragonite undersaturation in deep waters. I was able to show that natural environmental variability is inversely correlated with CWC

calcification and therefore, stable environmental conditions in deep waters of the fjord are beneficial for the corals.

Food availability and energy reserves are assumed to be important parameters for the ability of CWCs to cope with environmental changes, but little is known so far about their *in situ* food sources. Therefore, we investigated the *in situ* biochemical composition, including fatty acid composition and lipid classes, and trophic ecology of *D. dianthus* in more detail on a spatial (**manuscripts 3 and 4**) and seasonal scale (**manuscript 4**) in Comau Fjord to determine which biotic and abiotic factors influence it the most and how energy reserves can be related to coral calcification. Energy reserves strongly correlated with calcification as deep corals had a higher amount of total energy reserves and storage lipids, indicating that deep corals receive more food. Examination of fatty acid trophic markers (FATM) in conjunction with differences in lipid classes revealed differences of the zooplankton community the corals are feeding on in the two water depths. In addition, the energy reserves of novel deep corals (transplanted from shallow into deep waters) also increased rapidly, underscoring the findings of **manuscript 2** on the rapid acclimatisation potential of *D. dianthus*.

Overall, this thesis improves our understanding how environmental changes affect CWC physiology and biochemical composition by considering different CWC life stages, the interaction of multiple environmental factors, natural environmental variability and potential differences in food availability. This thesis highlights for the first time the relevance of differential effects across CWC life stages when studying the impact of environmental changes. I show that early life stages may represent an important bottleneck for the resilience of CWC populations. Since I was able to show that CWC calcification is affected by environmental variability, future studies should consider both natural fluctuations in environmental parameters and the interactive effects of multiple environmental parameters to gain a more realistic understanding of the *in situ* response of CWCs in a future changing ocean. The composition of fatty acids and lipid classes, as well as the inclusion of reduced food supply as another parameter in the multi driver experiment, provided a better understanding of the importance of food availability and composition for the resilience of CWCs to current and future environmental changes. In addition, the *in situ* biochemical composition of CWCs gave new insights into their natural diet and the relationship between energy reserves and calcification.

Zusammenfassung

Kaltwasserkorallen kommen weltweit vor, wobei hauptsächlich physikalisch-chemische Faktoren und die Nahrungsverfügbarkeit ihre Verbreitung bestimmen. Obwohl sie hauptsächlich in großen Wassertiefen vorkommen, sind Kaltwasserkorallen auch von den Auswirkungen des globalen Klimawandels betroffen, wie z. B. der Versauerung und Erwärmung der Ozeane, sowie verringerter Primärproduktion und Sauerstoffkonzentration. Mehrere Studien haben die Auswirkungen von Umweltveränderungen auf verschiedene Arten von Kaltwasserkorallen untersucht, jedoch lag deren Schwerpunkt auf Laborexperimenten unter kontrollierten Bedingungen eines einzelnen Parameters und der Untersuchung erwachsener Korallen. Bisher wissen wir jedoch nur wenig über die Auswirkungen von Umweltveränderungen auf verschiedene Lebensstadien von Kaltwasserkorallen, den wechselseitigen Effekt mehrerer Umweltparameter, die Auswirkungen variabler statt konstanter Bedingungen und die Bedeutung der Nahrungsverfügbarkeit für die Widerstandsfähigkeit von Kaltwasserkorallen gegenüber sich verändernden Umweltbedingungen.

Daher ist das Ziel dieser Arbeit, die physiologische Reaktion von Kaltwasserkorallen auf Veränderungen in ihrer Umwelt besser zu verstehen. Sowohl in Aquarien- als auch in Feldexperimenten habe ich untersucht, wie Kaltwasserkorallen mit Veränderungen einzelner und mehrerer Faktoren unter stabilen und variablen Umweltbedingungen zurechtkommen, wobei ich die Reaktion verschiedener Lebensstadien und den Einfluss von Unterschieden in der Nahrungsverfügbarkeit berücksichtigt habe.

Zu diesem Zweck habe ich in einem Aquarienexperiment die kurz- und langfristige physiologische Reaktion von drei Lebensstadien der Kaltwasserkorallenart *Caryophyllia huinayensis* auf unterschiedliche Aragonitsättigungen (Ω_{arag}), Temperaturen und Fütterungsbedingungen untersucht, sowohl die einzelner Faktoren als auch deren Interaktion (**Manuskript 1**). Eine Untersättigung mit Aragonit wirkt sich nicht auf die Korallen aus, während eine erhöhte Temperatur und eine reduzierte Fütterung einen deutlichen negativen Effekt hervorrufen. Juvenile und adulte Korallen reagierten unterschiedlich auf Temperaturveränderungen und ein reduziertes Nahrungsangebot, da die Wachstumsraten der jüngsten Korallen am stärksten betroffen waren, während adulte Korallen die höchste Sterblichkeitsrate aufwiesen. Die deutliche Auswirkung der Fütterung und die verzögerte Reaktion der Korallen auf die Behandlungsbedingungen nach mehr als drei Monaten unterstreichen die Notwendigkeit von Langzeitversuchen und die Einbeziehung des Nahrungsangebots als zusätzlichen wichtigen Faktor.

Kaltwasserkorallen sind in ihrem natürlichen Lebensraum jedoch keinen stabilen Umweltbedingungen ausgesetzt, wie ein einjähriges Feldexperiment im Comau Fjord in Nordpatagonien (Chile) zeigt (**Manuskript 2**). Dabei haben wir die weite Verbreitung der

Kaltwasserkoralle *Desmophyllum dianthus* in diesem Fjord ausgenutzt und Korallen zwischen nahe beieinander liegenden Lebensräumen mit jedoch unterschiedlichen physikalisch-chemische Bedingungen verpflanzt, um das Anpassungspotential der Korallen an sich verändernde Umweltbedingungen zu untersuchen. Dieses Kreuztransplantationsexperiment zeigt das schnelle Anpassungspotential der meisten untersuchten Merkmale von *D. dianthus* an eine neue Umgebung. Da die Wachstums- und Respirationsraten der Korallen eindeutig von der Umgebung bestimmt wurden, beweist das eine hohe phänotypische Plastizität. Unerwarteterweise wuchsen die Korallen in größerer Tiefe (300 m) schneller als die Korallen im Flachwasser (20 m), trotz der Aragonituntersättigung in größeren Wassertiefen. Ich konnte zeigen, dass Umweltvariabilität negativ mit dem Wachstum der CWC korreliert ist und daher stabile Umweltbedingungen in größeren Wassertiefen vorteilhaft für die Korallen sind.

Nahrungsverfügbarkeit und Energiereserven sind potentiell wichtige Parameter für die Fähigkeit von Kaltwasserkorallen sind, mit Umweltveränderungen zurechtzukommen, aber bisher ist nur wenig über ihre natürlichen Nahrungsquellen bekannt. Daher haben wir die natürliche biochemische Zusammensetzung, einschließlich der Fettsäurezusammensetzung und der Lipidklassen, sowie die trophische Ökologie von *D. dianthus* im Comau Fjord auf räumlicher (**Manuskript 3 und 4**) und saisonaler Ebene (**Manuskript 4**) genauer untersucht, um herauszufinden, welche biotischen und abiotischen Faktoren am meisten Einfluss auf Kaltwasserkorallen haben und wie die Energiereserven mit dem Wachstum der Korallen in Verbindung stehen. Die Energiereserven korrelieren eindeutig mit dem Wachstum, da Korallen in 300 m Tiefe eine größere Menge an Energiereserven und Speicherlipiden aufweisen. Das deutet darauf hin, dass Korallen in der Tiefe mehr Nahrung zur Verfügung haben, was es ihnen ermöglicht einen gesunden Phänotyp auszubilden. Die Untersuchung der fettsäuretrophischen Marker (FATM) in Verbindung mit Unterschieden in den Lipidklassen haben Aufschluss über mögliche Unterschiede in der Zooplanktongemeinschaft, von der sich die Korallen in den beiden Wassertiefen ernähren, gegeben. Zudem haben die Energiereserven der neuen Korallen in 300 m Tiefe, die aus 20 m transplantiert wurden, ebenfalls schnell zugenommen, was die Erkenntnisse aus **Manuskript 2** zu dem schnellen Akklimatisierungspotenzial von *D. dianthus* unterstreicht.

Insgesamt trägt diese Arbeit zu einem besseren Verständnis der Auswirkungen von Umweltveränderungen auf die Physiologie von Kaltwasserkorallen und ihrer biochemische Zusammensetzung bei, indem verschiedene Lebensstadien von Kaltwasserkorallen, die Interaktion mehrerer Umweltfaktoren, die natürliche Umweltvariabilität und potentielle Unterschiede in der Nahrungsverfügbarkeit berücksichtigt werden. Zum ersten Mal wird in dieser Arbeit deutlich, wie wichtig die verschiedenen Lebensstadien in der Analyse unterschiedlicher Auswirkungen von sich verändernden Umweltbedingungen sind. Die frühen Lebensstadien können einen wichtigen Engpass für die Widerstandsfähigkeit von Korallenpopulationen darstellen. Da ich zeigen konnte, dass Umweltvariabilität das Wachstum von Kaltwasserkorallen beeinflusst, sollten zukünftige Studien die natürliche Schwankungen von Umweltparametern sowie die wechselseitigen Auswirkungen mehrerer

Umweltparameter berücksichtigen, um ein realistischeres Verständnis der Reaktion von Kaltwasserkorallen auf zukünftige Veränderungen zu erhalten. Die Zusammensetzung der Fettsäure- und Lipidklassen sowie die Einbeziehung des reduzierten Nahrungsangebots als ein weiterer Parameter in das multifaktorielle Experiment, ermöglichten ein besseres Verständnis der Bedeutung der Nahrungsverfügbarkeit und -zusammensetzung für die Widerstandsfähigkeit von Kaltwasserkorallen gegenüber aktuellen und zukünftigen Umweltveränderungen. Darüber hinaus gab die natürliche biochemische Zusammensetzung der Korallen neue Einblicke in ihre natürliche Ernährung und den Zusammenhang zwischen Energiereserven und Wachstum der Korallen.

1

Introduction

Cold-water corals in their natural environment

Cold-water corals (CWCs) belong to the phylum Cnidaria and include stony corals (Scleractinia), soft corals and sea pens (Octocorallia), black corals (Antipatharia), gold corals (Zoanthidea) and hydrocorals (Stylasteridae). CWC ecosystems can be found across the globe in fjords, along continental shelves and on submarine seamounts in tropical to polar oceans and in shallow to deep waters (Freiwald et al., 2004; Roberts et al., 2009). Many CWC species are globally distributed with highest abundances in water depths between 200-1,000 m (Roberts et al., 2009), but can be found down to 4,000 m at low latitudes (Roberts et al., 2006). However, at high latitudes, CWCs also occur in shallow waters up to 7 m depth in fjord environments in New Zealand (Parker et al., 1997), Scandinavia (Wisshak et al., 2005; Guihen et al., 2012; Brooke & Järnegren, 2013) as well as North (Waller et al., 2014) and South America (Försterra & Häussermann, 2003). This phenomenon, when deep-dwelling organisms emerge locally from their deep habitat and also occur in shallow environments, is called “deep-water emergence” (Häussermann et al., 2021). Although more CWC species than tropical coral species exist, relatively little is still known about CWCs, as accessing and studying them in their natural environment is logistically challenging (Freiwald et al., 2004; Roberts et al., 2009). Only over the last two decades, CWC communities have been studied more intensely due to the development and advancement of remotely operated vehicles (ROVs), which facilitated the investigation and sampling of deep sea organisms (Freiwald et al., 2004; Roberts et al., 2005; Roberts et al., 2009).

CWCs of the order Scleractinia are characterised by a calcium carbonate ($CaCO_3$) skeleton, which in most cases consists of aragonite, one polymorph of $CaCO_3$. Some scleractinian species occur as solitary polyps (e.g. *Desmophyllum dianthus*), whereas other species form colonies (e.g. *Lophelia pertusa*, *Madrepora oculata*) and in particular the last are known for building complex three-dimensional frameworks comparable to tropical corals reefs. Therefore, CWCs provide habitat and nursery ground for many benthos and fish species, making them important ecosystem engineers and biodiversity hotspots in the deep sea (Freiwald et al., 2004; Roberts et al., 2009; Baillon et al., 2012).

The distribution of CWCs is defined by several abiotic factors, such as seawater temperature, salinity, oxygen concentration and carbonate chemistry (e.g. Guinotte et al., 2006; Davies et al., 2008; Dullo et al., 2008; Tittensor et al., 2010; Davies & Guinotte, 2011; Findlay et al., 2014; Flögel et al., 2014; Georgian et al., 2014a; Thresher et al., 2011; Morato et al., 2020). Yet, most research has focused almost exclusively on the habitats of *L. pertusa* (syn. *Desmophyllum pertusum*; Addamo et al., 2016). Many CWC species are globally distributed as they can tolerate a wide range of hydrographic and biogeochemical conditions (Juva et al., 2020), such as temperature and salinity (Dullo et al., 2008; Flögel et al., 2014; Georgian et al., 2016a) as well as oxygen concentrations (Dullo et al., 2008). In addition, high current speeds are an important factor for the occurrence of CWCs (Mienis et al., 2007, 2014), since tidal currents and internal waves entail several beneficial consequences: enhanced food supply to the sessile suspension feeders (White et al., 2005; Thiem et al., 2006; Duineveld et al., 2007; Davies et al., 2009; Juva et al., 2020), removal of waste products and reduced sedimentation (Roberts et al., 2006, 2009; Davies et al., 2008). Furthermore, the availability of hard substrate is crucial for the settlement of coral larvae (Davies et al., 2008; Georgian et al., 2014a).

Plenty of habitat suitability models described the environmental parameters in CWC habitats in detail over the past two decades. The environment in the natural deep sea habitats of CWCs has been considered rather stable for a long time, but recent research has shown that CWCs are also subject to diurnal as well as seasonal and annual fluctuations of environmental parameters and that discrete measurements are insufficient to monitor the environmental conditions in CWC habitats. For example, *L. pertusa* occurs in several regions with large diurnal temperature fluctuations (Wisshak et al., 2005; Mienis et al., 2007, 2014; Brooke et al., 2013; Juva et al., 2021). However, only few *in situ* studies so far investigated the physiological response of CWCs in relation to the environmental conditions in their natural habitat (e.g. Brooke et al., 2013; Rodolfo-Metalpa et al., 2015; Maier et al., 2020; Rossbach et al., 2021) due to the difficulty to assess CWC habitats. Consequently, we are still lacking an understanding of how natural environmental conditions, including environmental variability, influence the physiological performance of CWCs as most of our knowledge comes from laboratory studies, conducted at constant treatment conditions to eliminate variability in the physiological response. However, environmental fluctuations affect the physiological response of organisms (Bernhardt et al., 2018, 2020; Kroeker et al., 2020; Marshall et al., 2021)

and will increase in the future, as e.g. extreme temperature events known as marine heat waves are predicted to occur more frequently (Frölicher et al., 2018; Oliver et al., 2018, 2019). Therefore, it has previously been suggested to take environmental variability into account when investigating organism responses (Wahl et al., 2016; Bates et al., 2018; Ziegler et al., 2021), including CWCs (Gugliotti et al., 2019; Gómez et al., 2022), to environmental changes to better mimic their natural environment and obtain a more realistic response of the organisms. Therefore, the physiological measurements of CWCs need to be better linked to *in situ* environmental investigations in future studies, which should also consider natural fluctuations of environmental parameters. CWCs in shallow waters already exposed to natural environmental fluctuations provide an ideal opportunity to study whether such an environment is beneficial for CWCs to adapt to future environmental conditions, as has already been shown for tropical corals exposed to natural temperature fluctuations (Laprise & Dodson, 1994; Palumbi et al., 2014; Schoepf et al., 2015; Safaie et al., 2018).

Cold-water corals under climate change

CWCs are affected by several environmental changes on global and regional scales, including ocean acidification and global warming. Due to anthropogenic emissions of carbon dioxide (CO_2) since the beginning of the industrialisation and the CO_2 uptake by the oceans, the concentration of hydrogen ions (H^+) increases, and the pH decreases as a consequence (Caldeira & Wickett, 2005; Orr et al., 2005). Simultaneously, the concentration of carbonate ions (CO_3^{2-}) and the saturation state (Ω) of $CaCO_3$ also decrease (Feely et al., 2004; Caldeira & Wickett, 2005; Orr et al., 2005). Therefore, reduced CO_3^{2-} concentration and aragonite undersaturation ($\Omega_{arag} < 1$) may lead to the dissolution of $CaCO_3$ skeletons of calcifying organisms, such as CWCs (Hennige et al., 2015, 2020). The solubility of CO_2 is higher in cold and deep waters, which constitute the main habitat of CWCs. As this leads to a shoaling of the aragonite saturation horizon (ASH; Feely et al., 2004; Orr et al., 2005; Guinotte et al., 2006; Doney et al., 2009), about 70 % of CWCs are predicted to experience $\Omega_{arag} < 1$ by 2100 (Guinotte et al., 2006).

Therefore, CWCs were long considered especially vulnerable to ocean acidification (Guinotte et al., 2006; Turley et al., 2007; Guinotte & Fabry, 2008). Some previous studies found a negative response of several CWC species to reduced seawater pH, such as reduced calcification (Maier et al., 2009, 2016; Movilla et al., 2014a; Georgian et al., 2016b; Büscher et al., 2017; Gómez et al., 2018; Martínez-Dios et al., 2020). However, the general consensus now is that living CWCs are more resilient than previously thought (Maier et al., 2012, 2013a; Form & Riebesell, 2012; Carreiro-Silva et al., 2014; Hennige et al., 2014, 2015; Movilla et al., 2014b; Rodolfo-Metalpa et al., 2015; Gori et al., 2016), whereas $\Omega_{arag} < 1$ leads to dissolution of bare skeletal parts that are not covered with tissue (Hennige et al., 2015, 2020). CWCs even thrive at naturally low pH conditions in some regions, including aragonite undersaturation (Thresher et al., 2011; Fillinger & Richter, 2013; Jantzen et al., 2013; Baco et al., 2017). In order

to counteract low seawater pH, corals are able to up-regulate genes for the calcification process (Carreiro-Silva et al., 2014) and the internal pH in their calcifying fluid (pH_{cf}; Anagnostou et al., 2012; McCulloch et al., 2012a, 2012b; Wall et al., 2015), but this may be an energetically costly process (McCulloch et al., 2012a, 2012b).

Anthropogenic CO_2 emissions not only caused global warming of the atmosphere, but also heat absorption by the oceans and consequently, increased sea surface temperatures (IPCC, 2014). However, warmer water masses also penetrate into the deep sea (Levitus et al., 2000; Barnett et al., 2005; Mora et al., 2013; Sweetman et al., 2017), where warming may have major implications for the distribution, physiological performance and survival of benthic organisms (Hillebrand et al., 2017; Sweetman et al., 2017), including CWCs (Dodds et al., 2007; Brooke et al., 2013; Lunden et al., 2014; Gori et al., 2016; Dorey et al., 2020; Reynaud et al., 2021). Previous studies indicate that warming increases the metabolic rate of CWCs (Dodds et al., 2007; Gori et al., 2014a; Naumann et al., 2014; Dorey et al., 2020), which can be an indication of metabolic stress. Yet, our limited knowledge about CWCs' thermal tolerance so far complicates the interpretation of the results. In addition, information about the interaction of acidification and warming is still scarce. Yet, these insights are essential since CWCs will experience a combination of both factors in the future, which may lead to synergistic, additive or antagonistic responses (Kroeker et al., 2017). Previous multi-driver experiments found no effect of simultaneous changes of temperature and pH on calcification rates of CWCs (Hennige et al., 2015; Gori et al., 2016; Büscher et al., 2017), but the response depended on the investigated traits (Gori et al., 2016) and is likely also influenced by the nutritional status of the corals.

The ability of organisms to cope with rapid environmental changes due to climate change depends on their phenotypic plasticity in response to the environment (acclimatisation) or their evolutionary adaptation potential due to genetic changes (Somero, 2010; Hoffmann & Sgró, 2011; van Oppen et al., 2015). *In situ* reciprocal transplantation experiments with tropical corals revealed both plasticity (Rocker et al., 2019a) and local adaptation (Kenkel & Matz, 2016) of the observed traits in response to changing environmental conditions. Previous studies with CWCs found potential for local adaptation (Georgian et al., 2016b) and a limiting long-term adaptation potential to ocean acidification depending on the genotype (Kurman et al., 2017). However, the acclimatisation and adaptation potential of CWCs is largely unknown as long-term laboratory experiments, common garden experiments and *in situ* reciprocal transplantation studies along environmental gradients are still scarce.

Relevance of food availability for cold-water corals

In contrast to tropical corals that are in symbiosis with photosynthetic algae (zooxanthellae), CWCs are azooxanthellate and completely rely on heterotrophy. Therefore, they are not restricted to the photic zone. However, as sessile suspension feeders, they are dependent on food supply from the surface ocean and from currents. Food availability in CWC habitats is

related to primary productivity in surface waters as particulate organic matter (POM) from the photic zone is sinking to deeper water depths (Kiriakoulakis et al., 2004; White et al., 2005; Thiem et al., 2006; Duineveld et al., 2007; Carlier et al., 2009; Davies et al., 2009). CWCs are opportunistic feeders and feed on a range of food sources such as dissolved organic matter (DOM), bacteria and algae (Sherwood et al., 2008; Gori et al., 2014b; Mueller et al., 2014; van Oevelen et al., 2016; Rakka et al., 2020), but laboratory studies indicate that zooplankton is their most important diet that can fully sustain their metabolic needs (Naumann et al., 2011, 2015; Höfer et al., 2018; Rakka et al., 2020, 2021a; Maier et al., 2021). Even though these studies did not observe the diet and prey uptake *in situ*, lipid and stable isotope analyses also indicate that zooplankton is an important *in situ* food source for CWCs (Kiriakoulakis et al., 2005; Carlier et al., 2009; Mayr et al., 2011). Although some laboratory studies used natural zooplankton (Höfer et al., 2018; Maier et al., 2021), Maier et al. (2021) showed that it is not sufficient to maintain the corals' scope for growth without additional krill.

Additional feeding may providing enough energy for the corals to thrive under adverse environmental conditions and thereby counteract potential negative effects of ocean acidification (Thresher et al., 2011; Georgian et al., 2016b; Maier et al., 2016; Baco et al., 2017; Büscher et al., 2017; Gómez et al., 2018; Martínez-Dios et al., 2020), warming (Büscher et al., 2017; Hebbeln et al., 2020) and decreasing oxygen concentrations (Hanz et al., 2019; Hebbeln et al., 2020). However, as phytoplankton productivity is projected to decrease in the future due to enhanced stratification, reduced mixed layer depth, and circulation as a result of climate change (Steinacher et al., 2010; Mora et al., 2013; Sweetman et al., 2017; Seifert et al., 2020), this will likely also reduce the food availability in CWC habitats by reducing the particle flux to the deep sea (Jones et al., 2014). Some CWC species are well adapted to temporal variations in food availability and tolerate low feeding conditions for periods of several months (Larsson et al., 2013; Baussant et al., 2017; Maier et al., 2019). However, extended periods of reduced food availability or complete food deprivation affect their physiological performance (Naumann et al., 2011; Larsson et al., 2013; van Oevelen et al., 2016; Baussant et al., 2017; Büscher et al., 2017; Martínez-Dios et al., 2020) and distribution (Davies et al., 2008; Morato et al., 2020) and can further exacerbate any negative effects of other environmental factors. To date, the interactive effects of simultaneous changes in food availability, acidification and warming on CWCs are unknown.

Just like sufficient nutrition, energy reserves may be essential for the resistance of corals to environmental changes (Anthony et al., 2009; Maier et al., 2013b; Hennige et al., 2014), especially during periods of low food availability. Lipids account for the largest part of the energy reserves of corals (Harland et al., 1993; Leuzinger et al., 2003; Imbs, 2013; Schoepf et al., 2013) and provide almost twice as much energy as proteins and carbohydrates (Gnaiger & Bitterlich, 1984). Lipids and their fatty acids (FA) are essential for organisms to form cell membranes (phospholipids and sterols; Oku et al., 2003; Imbs et al., 2010), but they are also used for short- and long-term energy storage (wax esters and triacylglycerols; Harland et al., 1993). Therefore, the total energy content and especially the lipid content and composition

can provide important insights into the nutritional and health status of corals (e.g. Schoepf et al., 2013; Rocker et al., 2017, 2019b). For instance, fatty acids are used as natural biomarkers, called fatty acid trophic markers (FATM), as they are often organism specific and therefore, reflect the dietary input (Graeve et al., 1997; Dalsgaard et al., 2003; Budge et al., 2006). Since knowledge about the *in situ* feeding conditions and prey ingestion by CWCs is still scarce, lipid biomarkers can advance our understanding of their natural food sources (Dodds et al., 2009; Duineveld et al., 2012; Naumann et al., 2015). Energy reserves of tropical corals can vary seasonally because corals have to divide their available energy between different physiological processes (Leuzinger et al., 2003, 2012) and due to seasonal changes of environmental parameters (e.g. Ben-David-Zaslow & Benayahu, 1999; Oku et al., 2003; Hinrichs et al., 2013; Imbs & Dang, 2021). However, little is known about the natural variations of energy reserves of CWCs and the potential environmental drivers. Previous studies found only small seasonal fluctuations of the energy reserves of *L. pertusa* (Dodds et al., 2009; Maier et al., 2020), which were mainly related to energy investment in reproduction (Maier et al., 2020). To advance our understanding of CWC trophic ecology and the important environmental drivers, we require further *in situ* studies on the composition of total energy reserves and lipids in relation to zooplankton availability and other environmental factors. In addition, we need to directly compare the biochemical composition of CWCs to coral physiology to better understand its importance for the resilience of CWCs to future environmental changes.

Early life stages of cold-water corals

The life cycle of corals is divided into a mobile planula larvae phase and a sessile benthic polyp phase (Randall et al., 2020). Corals are either broadcast spawners, where the adult corals release the gametes into the water column for external fertilization and larval development, or brooders with internal fertilization and development of the planula larvae that will be released into the water column (Randall et al., 2020). Whereas most tropical scleractinians are hermaphroditic broadcast spawners (Randall et al., 2020), developing both eggs and sperm, most CWCs are gonochoric as they have separate sexes, and only few hermaphroditic species of the genus *Caryophyllia* were found so far (Waller et al., 2005). However, the life cycle and reproductive strategies are only known of few CWC species so far (Waller et al., 2002, 2005; Waller & Tyler, 2005; Flint et al., 2007; Waller & Feehan, 2013; Larsson et al., 2014; Rakka et al., 2017, 2021b; Heran et al., submitted). Most scleractinian CWCs, including the most commonly studied colony-forming species *L. pertusa*, *Madrepora oculata* and the solitary *D. dianthus*, are known to be gonochoric, broadcast spawners (e.g. Waller & Tyler, 2005; Waller et al., 2005; Brooke & Järnegren, 2013; Feehan et al., 2019), whereas three solitary species of the genus *Flabellum* (Waller, 2005) and *Caryophyllia huinayensis* (Heran et al., submitted) are internal brooders. After fertilization, a planktonic (feeding on phytoplankton), lecithotrophic (feeding on yolk reserves) planula larvae or benthic crawling larvae develops (Strömberg &

Larsson, 2017; Randall et al., 2020), which settles and metamorphoses into a recruit that precipitates a $CaCO_3$ skeleton and develops into a reproducing adult coral.

The reproductive process of CWCs may be affected by changing environmental conditions and anthropogenic disturbances as first studies indicate (Järnegren et al., 2017; Johnstone et al., 2021). However, little is known so far about the effect of environmental changes on different CWC life stages in general, since most previous studies were conducted with adult corals. As the development of early life stages is essential for the survival of the whole population, studying their response to environmental changes is crucial. In general, early life stages will probably be more vulnerable than adult organisms (Kurihara, 2008; Kroeker et al., 2010; Byrne & Przeslawski, 2013). For instance, the calcification of small CWC polyps is more negatively affected by reduced pH than of adult CWCs (Maier et al., 2009; Movilla et al., 2014a; Martínez-Dios et al., 2020). This is in accordance with findings for early life stages of tropical corals, which are more sensitive to warming and acidification (e.g. Albright, 2011; Foster et al., 2015; Jiang et al., 2018; Bahr et al., 2020). However, important information on the individual and interactive effects of a number of other environmental parameters on early CWC life stages is still missing, but essential to better predict the resilience of whole CWC populations to future environmental changes.

Research questions and hypotheses

This thesis aims to improve our understanding of the effect of environmental changes on the physiological performance of CWCs. In both aquarium and *in situ* experiments, I investigate how the CWC species *Desmophyllum dianthus* and *Caryophyllia huinayensis* cope with environmental changes under stable and fluctuating conditions to overcome the current limitations in the literature. The thesis addresses the following research questions and hypotheses:

(1) How do different life stages of cold-water corals react to extreme environmental conditions?

Hypothesis: Early life stages of cold-water corals are less resistant to environmental extremes than adult corals.

Environmental changes likely affect early life stages of organisms more than adult organisms (Kurihara, 2008; Kroeker et al., 2010; Byrne & Przeslawski, 2013). First observations show that small, young CWC polyps are less resilient towards reduced pH conditions (Maier et al., 2009; Movilla et al., 2014a; Martínez-Dios et al., 2020), whereas adult CWCs are more resilient to environmental changes due to their lower calcification rates (Maier et al., 2009, 2013a; Movilla et al., 2014a, 2014b; Martínez-Dios et al., 2020) and presumably higher energy reserves. **Manuscript 1** provides important new insights into the physiological response of different life stages of CWCs to extreme environmental conditions and adds a new perspective on the CWC species *C. huinayensis* as well as our understanding of CWC resilience.

(2) How do cold-water corals react to simultaneous changes of multiple environmental factors?

Hypothesis: Cold-water corals are negatively affected by simultaneous changes of multiple environmental factors.

Most previous studies showed that CWCs can cope with changes in a single factor until their tolerance limit is reached. Although a combination of elevated temperature and reduced pH did not lead to a reduction of calcification rates of CWCs in previous studies (Hennige et al., 2015; Gori et al., 2016; Büscher et al., 2017), other traits may be negatively affected (Gori et al., 2016). This thesis investigates the physiological response of two CWC species to contrasting and extreme environmental conditions. The single and interactive effects of multiple environmental factors are investigated under controlled conditions in an aquarium experiment (**manuscript 1**), while *in situ* contrasting conditions along horizontal and vertical gradients in Comau Fjord, Chile, serve as a natural laboratory (**manuscript 2**).

(3) How do cold-water corals cope with short- and long-term exposure to extreme current and future environmental conditions? Do they have the potential to acclimatise to environmental changes?

Hypothesis: Cold-water corals are able to withstand extreme environmental conditions in the short term, but are negatively affected by long-term exposure.

Previous comparative studies on the short- and long-term response of CWCs to changing environmental conditions show contradictory results (Form & Riebesell, 2012; Kurman et al., 2017). However, high energy reserves such as storage lipids may enable tropical corals to resist extreme environmental conditions for a short period of time without negative impacts on their physiology (Anthony et al., 2009), which is also suggested for CWCs (Maier et al., 2013b; Hennige et al., 2014). In **manuscript 1**, I investigate the short- and long-term effects of single and multiple environmental parameters on the physiological performance of *C. huinayensis* in an aquarium experiment with controlled environmental conditions. In addition, changes in the physiological response (**manuscript 2**) and energy reserves (**manuscript 4**) of *D. dianthus* are studied over one year after transplantation to novel contrasting environmental conditions in an *in situ* experiment in Comau Fjord, which allows to study their phenotypic plasticity and ability to cope with such changes.

(4) How much do environmental conditions fluctuate in the natural habitat of cold-water corals, especially at shallow sites where they have emerged from the deep? How does natural environmental variability affect the physiological performance of cold-water corals?

Hypothesis: Enhanced environmental variability reduces the physiological performance of cold-water corals.

Recent studies showed that CWCs experience more fluctuations of environmental factors in their deep sea environment than previously thought (Wisshak et al., 2005; Mienis et al., 2007, 2014; Brooke et al., 2013; Juva et al., 2021). Yet, most CWC communities are adapted to rather stable conditions and higher environmental variability will therefore negatively affect them. In contrast, CWCs in shallow habitats are likely to be more resilient to environmental fluctuations in their natural environment. The environmental conditions at two water depth in the natural habitat of *D. dianthus* in Comau Fjord are measured in **manuscript 2** on a seasonal basis over a period of one year. This provides the opportunity to link environmental variability with CWC calcification and investigate the ability of *D. dianthus* to cope with such conditions in its natural habitat.

(5) How variable is the *in situ* biochemical composition of CWCs and which factors influence it most? How much do the energy reserves influence the physiological performance of corals?

Hypothesis: Energy reserves have a significant impact on the physiological performance of CWCs.

Energy reserves provide information about the nutritional and health status of corals (e.g. Schoepf et al., 2013; Rocker et al., 2017, 2019b) and may be especially important for their resilience to environmental changes (Anthony et al., 2009; Maier et al., 2013b; Hennige et al., 2014). However, little is known about natural variations in the biochemical composition of CWCs, the underlying factors and their effects on the physiology of CWCs. Therefore, I investigate the spatial (**manuscripts 3 and 4**) and temporal (**manuscript 4**) variation of energy reserves as well as the fatty acid and lipid composition of *D. dianthus* in its natural habitat in Comau Fjord in response to the natural zooplankton availability (as investigated by Garcia-Herrera et al., 2022), environmental conditions and in relation to coral physiology. In addition, I use the corals' biochemical composition to infer their nutritional conditions (**manuscripts 3 and 4**).

(6) How does reduced food availability affect the ability of cold-water corals to cope with environmental changes?

Hypothesis: Reduced food availability negatively affects the physiological performance of cold-water corals and in turn their ability to cope with environmental changes.

CWCs can cope with low food availability and complete food deprivation for up to several months (Larsson et al., 2013; Baussant et al., 2017; Maier et al., 2019). However, reduced food uptake will likely reduce their energy reserves in the long term and thereby reduce their physiological performance (Naumann et al., 2011; Larsson et al., 2013; van Oevelen et al., 2016; Baussant et al., 2017; Büscher et al., 2017; Martínez-Dios et al., 2020) and consequently their resistance to other environmental changes. In **manuscript 1**, I investigate the role of food availability in combination with temperature and Ω_{arag} changes on the physiological performance and survival of *C. huinayensis*. Furthermore, the results of the *in situ* experiment in **manuscripts 2-4** are discussed in the context of recent investigations of the zooplankton abundance and composition in Comau Fjord by Garcia-Herrera et al. (2022), and how transplantation between potentially contrasting feeding regimes reflects the coral biochemical composition (**manuscript 4**).

Manuscript outline

Manuscript 1: Ontogenetic differences in the response of the cold-water coral *Caryophyllia huinayensis* to ocean acidification, warming and food availability

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Manuscript ready to be submitted

Author contributions: K.K.B., M.W., G.M.S.G., C.H., G.N. and G.S. designed the experiment and J.L. collected the corals. K.K.B., E.L. and C.N. carried out the experiment and K.K.B., J.N. and C.N. conducted the measurements. K.K.B., M.W. and J.N. analysed and interpreted the data. K.K.B. and M.W. conducted the statistical analysis and prepared the figures. K.K.B., M.W. and C.R. wrote the first draft and all authors edited the manuscript.

Manuscript 2: Environmental stability and phenotypic plasticity benefit the cold-water coral *Desmophyllum dianthus* in an acidified fjord

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Author contributions: G.M.S.G., J.L. and C.R. designed the study. J.L., V.H., G.F. and H.E.G. contributed background information and helped with the field work. J.L. and G.F. collected the corals. V.H. and J.P.E. provided background data. K.K.B. and G.M.S.G. conducted the measurements. K.K.B., M.W. and G.M.S.G. analysed and interpreted the data. M.W. and K.K.B. conducted the statistical analysis and prepared the figures. K.K.B., M.W. and C.R. wrote the first draft and all authors edited the manuscript.

Manuscript 3: Lipid biomarkers reveal trophic relationships and energetic trade-offs in contrasting phenotypes of the cold-water coral *Desmophyllum dianthus* in Comau Fjord, Chile

Marlene Wall, **Kristina K. Beck**, Nur Garcia-Herrera, Gertraud M. Schmidt-Grieb, Jürgen Laudien, Juan Höfer, Günter Försterra, Christoph Held, Gernot Nehrke, Matthias Woll, Martin Graeve, Claudio Richter

Manuscript under review at *Functional Ecology*

Author contributions: G.M.S.G., J.L. and C.R. designed the study. J.L., G.F. and G.M.S.G. contributed background information and collected the corals. M.Wall, M.Woll and K.K.B. conducted the coral preparation and lipid measurements. K.K.B. and G.M.S.G. contributed physiological background data. M.Wall and M. Woll analysed the raw data. M.Wall and M.G. interpreted the data. M.Wall conducted the statistical analysis. Together with K.K.B., M.Wall prepared the figures. M.Wall and C.R. wrote the first draft of the paper. All authors contributed to the final discussion and edited the manuscript.

Manuscript 4: Seasonal energy reserves of the cold-water coral *Desmophyllum dianthus* from Comau fjord, Chile

Kristina K. Beck, Gertraud M. Schmidt-Grieb, Antonia S. Kayser, Janine Wendels, Alexandra Kler Lago, Stefanie Meyer, Matthias Woll, Martin Graeve, Jürgen Laudien, Claudio Richter, Marlene Wall

Manuscript in preparation

Author contributions: G.M.S.G., J.L. and C.R. designed the study. J.L. and G.M.S.G. led the collection of corals. A.S.K., J.W., A.K.L., M.Woll, K.K.B., M.Wall and S.M. prepared the coral samples and conducted the measurements. K.K.B. and G.M.S.G. contributed physiological background data. K.K.B., M.Wall, M.Woll and M.G. analysed the data. K.K.B. and M.Wall interpreted the data, conducted the statistical analysis and prepared the figures. K.K.B. and M.Wall wrote the first draft and all authors edited the manuscript.

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Manuscript 1:

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

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Abstract

Cold-water corals (CWCs) have been considered vulnerable to a changing ocean, but there is growing evidence that they can cope with ocean acidification and/or warming to some degree. While most experiments to date have addressed the short-term effects of single stressors on adult CWCs, little is known about the long-term, interactive and differential effects of aragonite undersaturation and elevated temperature on different life stages. Therefore, we conducted a six months aquarium experiment to investigate the responses of survival, somatic growth, calcification and respiration of early juveniles, late juveniles and adults of the CWC *Caryophyllia huinayensis* to a wide range of aragonite saturation (0.8 and 2.5), temperature (11 and 15 °C) and food availability (8 and 87 µg C L^{-1}) that characterise their natural habitat in Comau Fjord, Chile. Differences between life stages were evident in all investigated traits. Resource limitation generally lowered the health status, somatic growth and calcification rates, but the magnitude of the change differed between life stages. Calcification rates declined more in early life stages than in adult corals, while the latter had the highest mortality rate. While acidification alone did not affect the corals, elevated temperature clearly pushed them beyond their physiological limits, both as single and interactive factor and irrespective of the feeding regime. Importantly, we observed a three months delay in response to elevated temperature and reduced feeding, presumably because sufficient energy reserves were still available, suggesting that short-term experiments may overestimate coral resilience. Our findings underscore the importance of interactive effects and the need to consider potential ontogenetic differences when addressing CWC responses to climate change at adequate temporal scales.

Introduction

Many cold-water coral (CWC) species have a wide geographical range, mainly between 200-1,000 m depth (Freiwald et al., 2004; Roberts et al., 2006, 2009). However, in fjord environments at high latitudes, CWCs also occur as shallow as 7 m (Försterra & Häussermann, 2003; Wisshak et al., 2005; Guihen et al., 2012; Brooke & Järnegren, 2013). Their calcium carbonate skeletons form three-dimensional frameworks, which support complex and diverse ecosystems (Freiwald et al., 2004). The distribution of CWCs is determined by several abiotic and biotic factors, such as seawater carbonate chemistry, temperature, salinity, oxygen concentration, current velocity and the availability of food and hard substrate (e.g. Davies et al., 2008; Flögel et al., 2014; Georgian et al., 2014, 2016a; Juva et al., 2020). However, CWCs are threatened by several ongoing environmental changes.

Ocean acidification has long been considered the most severe threat for CWCs (Roberts et al., 2006), as rising atmospheric carbon dioxide (CO_2) causes seawater carbonate ion concentrations to decrease (Orr et al., 2005; Guinotte et al., 2006), which reduces coral calcification (Kleypas et al., 1999). Surface ocean pH has already declined by 0.1 units since

pre-industrial times (Orr et al., 2005) and may decrease further by 0.3-0.4 units until 2100 (Caldeira & Wickett, 2005), with similar changes predicted for the deep sea (Gehlen et al., 2014; Sweetman et al., 2017). The higher solubility of CO_2 in cold and deep waters leads to lower seawater pH and aragonite saturation (Ω_{arag}) in natural habitats of CWCs (Feely et al., 2004; Orr et al., 2005; Guinotte et al., 2006; Doney et al., 2009), potentially reducing calcification (e.g. Maier et al., 2009; Movilla et al., 2014a; Georgian et al., 2016b; Büscher et al., 2017; Gómez et al., 2018; Martínez-Dios et al., 2020) and enhancing skeletal dissolution (Hennige et al., 2015). Due to the rise of the aragonite saturation horizon (ASH), about 70 % of CWCs are predicted to occur at aragonite undersaturation ($\Omega_{arag} < 1$) by 2100 (Guinotte et al., 2006).

Some CWCs already occur at $\Omega_{arag} \leq 1$ in the Gulf of Mexico (Lunden et al., 2013; Georgian et al., 2016a), SW Australia (Thresher et al., 2011) and in Chilean fjords (Fillinger & Richter, 2013; Jantzen et al., 2013). Previous studies showed that CWCs are able to maintain their calcification (e.g. Hennige et al., 2014; Rodolfo-Metalpa et al., 2015; Gori et al., 2016) and respiration rates (e.g. Maier et al., 2013a, 2016; Carreiro-Silva et al., 2014) over large pCO_2 ranges and even at $\Omega_{arag} < 1$ (e.g. Maier et al., 2009; Form & Riebesell, 2012; Hennige et al., 2015). However, the duration of exposure to low pH may influence their physiological response (Form and Riebesell, 2012; Kurman et al., 2017). CWCs up-regulate important genes for the calcification process (Carreiro-Silva et al., 2014), up-regulate pH in their calcifying fluid (McCulloch et al., 2012a, 2102b; Wall et al., 2015) and likely use lipid reserves (Hennige et al., 2014) to maintain these physiological processes under low pH. However, pH up-regulation is an energy consuming process (McCulloch et al., 2012a, 2102b) and enough energy reserves must be available for the mobilisation of lipid reserves.

Temperature is one of the most important environmental drivers of CWC distribution (Davies et al., 2008; Flögel et al., 2014; Morato et al., 2020), affecting main physiological processes (Dodds et al., 2007; Naumann et al., 2014; Gori et al., 2016; Dorey et al., 2020). To date, surface water temperatures have already increased by 0.6-0.9 °C since pre-industrial times (IPCC, 2014) and are projected to increase further by 1.2-2.6 °C until 2100 (Mora et al., 2013). In the deep sea, temperatures are predicted to increase by 0.2-1 °C (Mora et al., 2013; Sweetman et al., 2017). However, CWCs appear to live below their thermal optimum (Naumann et al., 2013, 2014; Gori et al., 2014; Dorey et al., 2020), so warming may pose less of a threat than acidification.

Food availability is a key parameter for the physiological performance of CWCs (Naumann et al., 2011; Larsson et al., 2013; Baussant et al., 2017) and their ability to cope with environmental changes (Maier et al., 2016; Büscher et al., 2017; Gómez et al., 2018; Hanz et al., 2019; Martínez-Dios et al., 2020). If enough food is available, their physiological performance (i.e. calcification and respiration) correlates positively with food availability (Naumann et al., 2011; Larsson et al., 2013; van Oevelen et al., 2016; Martínez-Dios et al., 2020). However, reduced food supply often has a delayed effect and may only become visible

after several months (Maier et al., 2016; Büscher et al., 2017; Martínez-Dios et al., 2020), presumably after energy reserves are depleted. As calcification is an energy-demanding process (Allemand et al., 2004, 2011; McCulloch et al., 2012a, 2102b), food availability may have an important impact on the resilience and adaptability of CWCs to environmental changes. CWCs are opportunistic feeders, using a variety of food sources (Gori et al., 2014; Mueller et al., 2014; van Oevelen et al., 2016), but only zooplankton and euphausiids provide sufficient energy to sustain their metabolism (e.g. Naumann et al., 2011; Höfer et al., 2018; Rakka et al., 2020; Maier et al., 2021). Primary productivity in surface waters (Steinacher et al., 2010; Mora et al., 2013; Sweetman et al., 2017; Seifert et al., 2020) and consequently, particle flux to deep waters (Jones et al., 2014) is expected to decline in the future. Therefore, food availability for CWCs will likely also decrease and it is unknown if sufficient energy will be available for CWCs to counteract potential negative effects of ocean acidification and warming.

So far, limited information is available on the interactive effects of ocean acidification and warming on CWCs. Most previous studies investigated the effect of a single stressor and multi-driver studies are still scarce. While CWCs seem to be tolerant to future changes in either temperature, aragonite saturation or productivity, the combination of factors may reveal so far unexpected interactive negative effects (Büscher et al., 2017). Multiple stressor experiments are therefore important to explore if one stressor may enhance, reduce or even reverse the effect of another (Kroeker et al., 2017). The first studies that examined the combined effects of warming and acidification found reduced (Gori et al., 2016) or constant (Hennige et al., 2015) respiration rates of *Desmophyllum dianthus*, but no effect on calcification rates of *D. dianthus* and *L. pertusa* (Hennige et al., 2015; Gori et al., 2016; Büscher et al., 2017).

Most studies to date have focused on adult CWCs and little is known about the response of early life stages to future environmental conditions. Even if adult corals are able to cope with environmental changes, the resilience of early life stages is a bottleneck for survival. Previous studies suggest that early life stages are particularly sensitive to pH and temperature changes (Kurihara, 2008; Kroeker et al., 2010; Albright, 2011; Byrne & Przeslawski, 2013). Low pH led to reduced calcification rates (e.g. Albright et al., 2008, 2010; Albright & Langdon, 2011; Foster et al., 2015, Jiang et al., 2018) and skeletal deformations (Cohen et al., 2009; Foster et al., 2016) in coral recruits. Elevated temperature increased calcification rates (Jiang et al., 2018) and reduced tolerance to extreme temperature events (Bahr et al., 2020). However, the response to combined stressors showed inconclusive results (e.g. Anlauf et al., 2011; Foster et al., 2015; Jiang et al., 2018). Calcification of small polyps of *L. pertusa* and *D. dianthus* was more affected by low pH than in larger polyps (Maier et al., 2009; Movilla et al., 2014a; Martínez-Dios et al., 2020). However, the effects of other environmental parameters such as temperature and food supply on early CWC life stages have not yet been studied, let alone the effects of multiple combined environmental factors.

The aim of the present study is therefore to investigate the response of different CWC life stages to the single and interactive effects of key environmental factors. In a long-term aquarium experiment (six months) with a fully crossed factorial design, three life stages of the solitary CWC *Caryophyllia huinayensis* were exposed to a combination of aragonite over- ($\Omega_{arag} > 1$) and undersaturation ($\Omega_{arag} < 1$), two temperatures (11 °C and 15 °C) and two feeding regimes (low and high). We examined the survival, calcification and respiration rates after one, three and six months to identify temporal changes in their response and potential energetic trade-offs. As organisms' responses to environmental changes are often context-specific, the treatments are based on the natural environmental conditions experienced by corals in their natural habitat in Comau Fjord, Chile, and also represent potential future scenarios.

Material and methods

Study species and coral sampling

The solitary CWC *Caryophyllia huinayensis* occurs in Comau Fjord (Northern Patagonia, Chile) between 11 and 265 m depth (max. depth due to sampling limit) and on the continental slope down to > 800 m, but is most abundant in the euphotic zone between 20-45 m (Cairns et al., 2005). In their natural environment, corals are mostly subject to aragonite oversaturation, while aragonite undersaturation may occur in deep waters and at the fjord head, covering a pH range of 7.4-8.0 (Fillinger & Richter, 2013; Jantzen et al., 2013a; Beck et al., 2022). Water temperature ranges between 11-16 °C with highest values in shallow waters, which are also characterised by short-term fluctuations (Beck et al., 2022). Zooplankton biomass in the whole water column is about four times higher in summer than in winter and decreases with water depth (Garcia-Herrera et al., 2022). To date, no study has investigated the physiological performance of *C. huinayensis*, neither under its natural environmental conditions nor with regard to expected future changes. Treatment conditions were selected to cover both natural conditions and future predictions (see Supplementary Methods).

In 2014 and 2015, specimens of *C. huinayensis* were collected and transported to the culturing aquarium facility at the Alfred Wegener institute (AWI, Germany), where they were successfully cultured in artificial seawater (Dupla Marin Premium Reef Salt, Germany; water exchange of 30 % per week). Before the start of the experiment, corals were maintained at a temperature of 12.2 ± 0.9 °C, a pH of 8.0 ± 0.1 and a salinity of 31.9 ± 0.5, reflecting mean annual *in situ* conditions (Laudien et al., 2021; Beck et al., 2022). However, the carbonate chemistry of the artificial seawater differs from natural seawater because the values for total alkalinity (TA) and dissolved inorganic carbon (DIC; Table 1) are 17-26 % and 17-32 % higher, respectively, than in Comau Fjord (Rossbach et al., 2021; Beck et al., 2022). Although the increased TA values facilitate coral calcification, aragonite undersaturation was achieved for the experiment despite the increased TA and DIC values. Juvenile corals were fed with freshly hatched *Artemia persimilis* nauplii (Aquakultur Genzel GmbH, Freiberg am Neckar, Germany)

three times per week and adults were additionally fed with thawed juvenile krill *Euphausia pacifica* (Zierfischfutterhandel Norbert Erdmann e.K., Ritterhude, Germany) once a week.

The corals have reproduced successfully in the aquarium facility since 2014, which provided the opportunity to investigate the response of different life stages of the same population to environmental changes. The life cycle of *C. huinayensis* has recently been studied (Heran et al., submitted) and accordingly, the corals were divided into three different ontogenetic stages depending on their calyx diameter and tissue covered surface area (see Supplementary Methods for details). Corals with a calyx diameter of 10.0 ± 2.0 mm were considered adults, while smaller corals were divided into early (calyx diameter: 3.0 ± 0.5 mm) and late (calyx diameter: 4.5 ± 0.8 mm) juveniles. Four weeks before the start of the experiment (September 2020), a total of 144 specimens were selected (48 early juveniles, 48 late juveniles, 48 adults) and glued on labelled polyethylene screws using Preis Easy Glue Underwater (Preis Aquaristik KG, Bayerfeld, Germany). All individuals were weighed the day after fixation (see below). To enable structural and geochemical analyses of the skeletons, which will be presented in a separate study, corals were stained with 50 mg L^{-1} fluorescent Calcein for 16-17 hours.

Experimental design and setup

Experimental design: The experiment was run for six months from October 2020 until April 2021 in a dark, thermostatically controlled room. The experimental design was a three-factor design with a combination of two scenarios of Ω_{arag}, temperature and food availability. Each of the two environmental factors (temperature and Ω_{arag}) was examined alone and in combination in a total of four aquarium systems with the following main treatment conditions: 1) ambient: aragonite oversaturation ($\Omega_{arag} > 1$, pH_T 8.0) and ambient temperature (11 °C), 2) Ω: aragonite undersaturation ($\Omega_{arag} < 1$, pH_T 7.5) and ambient temperature (11 °C), 3) temperature: aragonite oversaturation ($\Omega_{arag} > 1$, pH_T 8.0) and elevated temperature (15 °C) and 4) combined: aragonite undersaturation ($\Omega_{arag} < 1$, pH_T 7.5) and elevated temperature (15 °C). Each treatment was carried out in a total of four experimental aquaria (35 L) that were subdivided into two feeding regimes (low and high). Each experimental aquarium contained three corals per life stage (Supplementary Figure 1; see Supplementary Methods).

Experimental setup: All experimental aquaria of one system were connected to one large basin (80 L; Supplementary Figure 1) with a water flow of 5-10 L min^{-1}. A small pump in each experimental aquarium ensured constant water circulation. The same artificial seawater (Dupla Marin Premium Reef Salt, Dohse Aquaristik GmbH & Co. KG, Gelsdorf, Germany) as in the culturing facility was used to ensure rapid acclimation of the corals. The water was changed regularly with approx. 25 L in each recirculating system per week (10 % of total water volume). To achieve target conditions, the Ω_{arag} was lowered by injecting CO_2, controlled by a digital control system (iks aquastar, iks ComputerSysteme GmbH, Karlsbad, Germany) connected to pH sensors calibrated once a week with pH buffers 7 and 9 (VWR International, Radnor, USA). The iks pH sensors were cross-referenced with an additional pH meter (WTW

pH 3310, Xylem Analytics, New York, USA), which was calibrated to the total scale with TRIS-HCl buffer. The water temperature was also controlled by the iks system with a heater submerged in the basin. In addition, water parameters were monitored regularly using the iks system (temperature and pH), additional sensors (pH, oxygen and salinity) and temperature loggers. Furthermore, we took water samples for analyses of total alkalinity (TA) and nutrients (ammonium, nitrate, nitrite, phosphate, silicate) once every week (see Supplementary Methods). During the experiment, treatment conditions were constant with a mean ambient temperature of 11.2 ± 0.1 °C and an elevated temperature of 15.1 ± 0.1 °C (Table 1, Supplementary Figure 2). The Ω_{arag} was 2.4 ± 0.2 and 2.7 ± 0.1 under ambient conditions (pH_T: 8.06 ± 0.03 and 8.05 ± 0.02) and 0.8 ± 0.1 and 0.9 ± 0.1 in the low Ω_{arag} treatments (pH_T: 7.54 ± 0.04 and 7.50 ± 0.04; Table 1, Supplementary Figure 2).

Table 1: Water parameters of four treatments over the duration of the experiment (six months). Temperature, salinity, oxygen and pH on the total scale (pH_T) were measured daily during the experiment and total alkalinity (TA) was measured weekly. Dissolved inorganic carbon (DIC), pCO_2 and aragonite saturation state (Ω_{arag}) were calculated from TA and pH_T with the Excel programme CO2SYS (Pierrot et al., 2006). All values are stated as mean ± standard deviation (SD).

Treatment	Salinity	Oxygen (mg/L)	Temperature (°C)	pH_T	TA ($\mu mol\ kg^{-1}$)	DIC ($\mu mol\ kg^{-1}$)	pCO_2	HCO_3^- ($\mu mol\ kg^{-1}$)	CO_3^{2-} ($\mu mol\ kg^{-1}$)	CO_2 ($\mu mol\ kg^{-1}$)	Ω_{arag}
ambient	31.6 ± 0.2	8.94 ± 0.09	11.2 ± 0.1	8.06 ± 0.03	2730 ± 79	2532 ± 75	476 ± 36	2353 ± 71	158 ± 11	20 ± 2	2.4 ± 0.2
Ω	31.5 ± 0.1	8.93 ± 0.10	11.2 ± 0.1	7.54 ± 0.04	2719 ± 64	2719 ± 63	1725 ± 160	2591 ± 60	53 ± 5	74 ± 7	0.8 ± 0.1
temperature	31.6 ± 0.1	8.37 ± 0.23	15.0 ± 0.1	8.05 ± 0.02	2648 ± 34	2427 ± 29	473 ± 23	2238 ± 26	172 ± 8	18 ± 1	2.7 ± 0.1
combined	31.6 ± 0.2	8.33 ± 0.23	15.1 ± 0.1	7.50 ± 0.04	2671 ± 48	2666 ± 50	1902 ± 186	2538 ± 47	56 ± 5	72 ± 7	0.9 ± 0.1

Experimental feeding conditions: We used *A. persimilis* nauplii as food source and aimed for low (LF) and high (HF) food supply. A short-term pilot study was carried out to identify the ratio between high and low food concentrations (12:1; see Supplementary Methods), corroborating the approx. 10-fold difference in zooplankton supply established by Büscher et al. (2017). High food concentrations were similar to those in the culturing aquarium system (but without additional krill) and to maximum food availability in the photic zone of Comau Fjord in summer, whereas low food concentrations were similar to the minimum food availability in the aphotic zone in winter (calculated after Garcia-Herrera et al., 2022). However, *in situ* zooplankton biomass was determined from mesozooplankton and is therefore a lower estimate because larger plankton and euphausiids were not considered. Food availability was governed by concentration (nauplii per volume) and time (feeding days), with food availability being twelve times lower in the LF compared to the HF regime. Corals in the LF regime were fed once per week, while corals in the HF regime were fed three times per week. For the LF and HF regimes, a total of 0.5 g and 2 g dry *Artemia* cysts were used, respectively. After hatching, 10 mL aliquots of the well-stirred nauplii suspension were distributed into the experimental aquaria of the respective feeding regime (see Supplementary Methods). This resulted in 235 ± 63 nauplii L^{-1} for the LF and 810 ± 303 nauplii L^{-1} for the HF regime, corresponding to 940 ± 250 nauplii $coral^{-1}$ and 3240 ± 1213 nauplii $coral^{-1}$, respectively, in the experimental aquaria during each feeding period. This corresponds to effective food concentrations of 8.4 µg C L^{-1} for the LF and 86.8 µg C L^{-1} for the HF regime when considering the feeding times (see below for the determination of organic C content of *Artemia* nauplii).

Experimental timeline: The corals were acclimatised to the experimental aquaria for 20 days before the experimental conditions were changed. During the acclimatisation phase, water parameters were the same for all treatments, and all corals were fed the same amount of *A. persimilis* nauplii (2 g dry *Artemia* cysts for all corals) three times per week. The four physico-chemical treatments (including the acclimatisation period) were started consecutively over two weeks, ensuring that the physiological measurements of the treatments always took place in the same time interval after starting the experiment. Water parameters were gradually adjusted from ambient to experimental conditions over five days, with a change of 0.05 pH units and 0.5 °C every twelve hours and simultaneous changes of the feeding conditions (Supplementary Figure 3).

Physiological measurements

Coral conditions were monitored by regular photo-documentation (once a week) and an assessment of physiological performance (calcification and respiration) after one (T_1), three (T_2), and six (T_3) months (see Supplementary Methods and Results for respiration). Photo-documentation was used to assess the survival, health status and the potential for somatic maintenance or growth.

***Health status and survival*:** The lateral sides of the corals were photographed at a standardised position and illumination using a digital camera (DSC-RX10M4, Sony Group Corporation, Minato, Japan). In addition, pictures of the oral side of the corals were taken at the beginning and end of the experiment using a stereomicroscope (SteREO Discovery.V8, Carl Zeiss MicroImaging GmbH, Göttingen, Germany) connected to a SLR camera (Nikon D3200 with a microscope adapter, Minato, Japan). We used the tissue covered surface area of the corals as proxy for their health status. Based on the lateral pictures, corals were divided into six health categories (see Supplementary Figure 4) and survival rates were assessed monthly.

Somatic growth: The change in tissue covered surface area (%) between the start and end of the experiment was used to assess somatic growth. The tissue covered surface area (A) of the coral was measured with a digital calliper (reading to 0.01 mm) and calculated geometrically after Naumann et al. (2009) using the formula of a truncated cone (Gori et al., 2014, 2016; see Supplementary Methods). For normalisation of calcification and respiration rates, the surface area was determined after one, three and six months.

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

Prey capture rate: After five months, the prey capture rate was determined separately for each individual in incubations with glass vials (incubation volume: 110 mL). The vials were placed in a temperature-controlled water bath (11 °C and 15 °C) on a submergible magnetic stirring table (low speed of 180 rpm to avoid damaging the nauplii), where glass-coated magnetic stir bars kept the *Artemia* nauplii in suspension (see Supplementary Methods). Freshly hatched *A. persimilis* nauplii were counted under a stereo microscope (475002-9902, Carl Zeiss MicroImaging GmbH, Göttingen, Germany). The LF and HF corals were fed 30 and 120 nauplii, respectively, corresponding to concentrations of 0.27 nauplii mL^{-1} in the LF and 1.09 nauplii mL^{-1} in the HF regime. The prey capture rate was expressed as the number of ingested nauplii $coral^{-1}$ h^{-1}. The ash-free dry mass (AFDM) and the organic carbon (C) content of *Artemia* nauplii were determined (see Supplementary Methods). The uptake of nauplii organic matter (OM) was normalised to the surface area of the corals and expressed as mg OM cm^{-2} h^{-1}. For comparability with previous studies, the C uptake was expressed in µmol C cm^{-2} h^{-1} and µmol C g^{-1} skeletal mass h^{-1} (Supplementary Table 7).

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

Results

Health status and survival

Overall, *C. huinayensis* showed a declining health in all treatments over six months. Juvenile corals were more resilient, particularly under HF, ambient but also aragonite undersaturated conditions (dark blue bars; Figure 1). Elevated temperature had the strongest negative effect on the health status across life stages. This resulted in moribund corals and high mortality (47 %) after more than three months (yellow and red bars; Figure 1) in adult and early juvenile corals (GLM, ambient – temperature: p-value < 0.001; Supplementary Figure 6, Supplementary Tables 2 and 3). Surprisingly, the combined effect of aragonite undersaturation and elevated temperature appeared slightly less severe than elevated temperature alone and only resulted in 28 % mortality (GLM, ambient – combined: p-value = 0.051; Figure 1, Supplementary Figure 6, Supplementary Tables 2 and 3). Overall, adult corals (18 out of 48) suffered highest mortality compared to late juveniles (2 out of 48) that were the most resilient and healthiest life stage (GLM, adult – late juvenile: p-value < 0.001; Figure 1, Supplementary Figure 6, Supplementary Tables 2 and 3). Food limitation deteriorated coral health (upper panels of Figure 1) because corals in the HF regime were overall healthier with more category 1 corals (25 individuals) and lower mortality (15 % of all corals) compared LF (category 1: 18 individuals, 24 % mortality; Figure 1, Supplementary Figure 6).

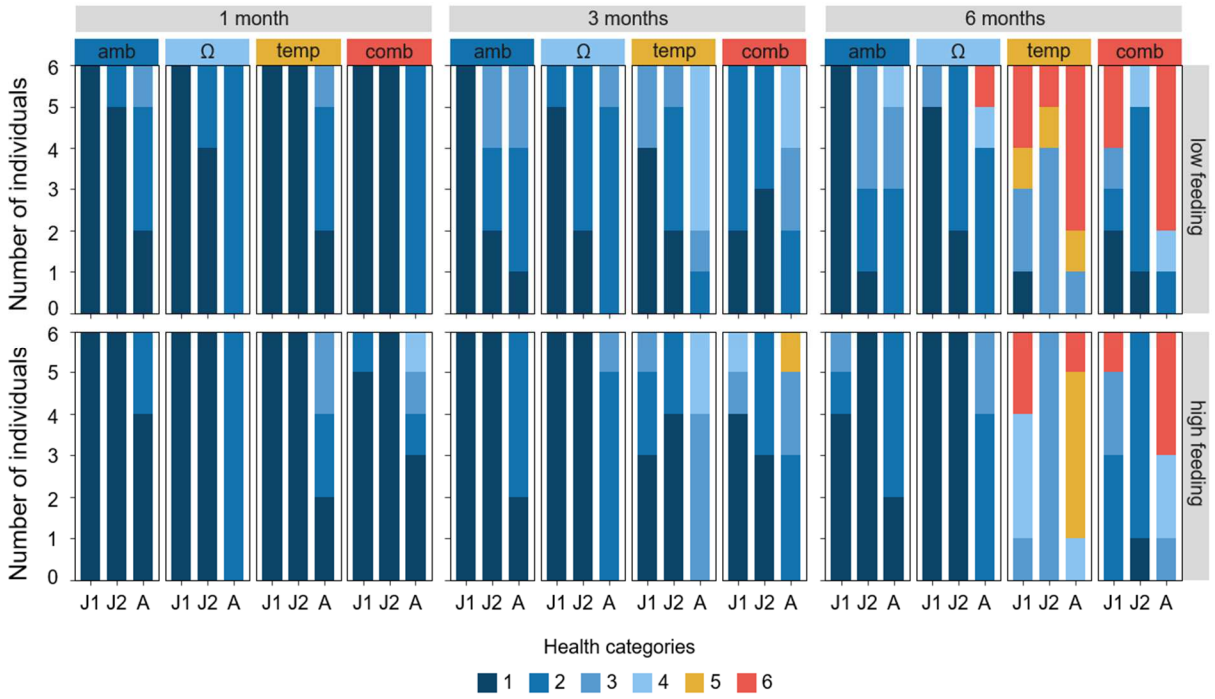

Figure 1: Health status of three life stages of *Caryophyllia huinayensis* after one, three and six months under different Ω, temperature and feeding conditions. Health status of early juveniles (Jc1), late juveniles (Jc2) and adult corals (A) under low and high feeding conditions. The four treatment conditions are: amb (dark blue) = 11 °C and $\Omega_{arag} > 1$, Ω (light blue) = 11 °C and $\Omega_{arag} < 1$, temp (yellow) = 15 °C and $\Omega_{arag} > 1$, comb (red) = 15 °C and $\Omega_{arag} < 1$. The six health categories are defined as: 1) calyx fully covered with tissue on the lateral and oral side (dark blue), 2) calyx partly covered with tissue, tissue on lateral side partly retracted (blue), 3) only oral side of calyx fully covered with tissue, lateral side not covered with tissue (blue), 4) oral side of calyx partly covered with tissue, septa largely not covered with tissue (light blue), 5) dying/recently dead coral with tissue remains in calyx (orange), 6) dead coral, bare skeleton without tissue (red).

Somatic growth

Early and late juvenile corals maintained or even increased their tissue covered surface area by an average of 50 % in the ambient and Ω treatments, with a positive response to high food availability (LMM, feeding: p-value = 0.038; Figure 2, Supplementary Tables 4-6). Adult corals, by contrast, responded with a general 40 % retraction of their tissue in these two treatments with less clear differences between feeding regimes (Figure 2). This suggests that neither feeding regimes provided enough energy to sustain somatic growth of the adult corals compared to juveniles (LMM, adult – early/late juvenile: p-value < 0.001; Figure 2, Supplementary Tables 4-6). However, all life stages significantly retracted their tissue by an average of 70 % under elevated temperature conditions (irrespective of aragonite over- or undersaturation conditions, except for late juveniles) compared to the ambient temperature treatments (LMM, ambient – temperature: p-value < 0.001; Figure 2, Supplementary Tables 4-6) and no feeding regime could compensate for this response.

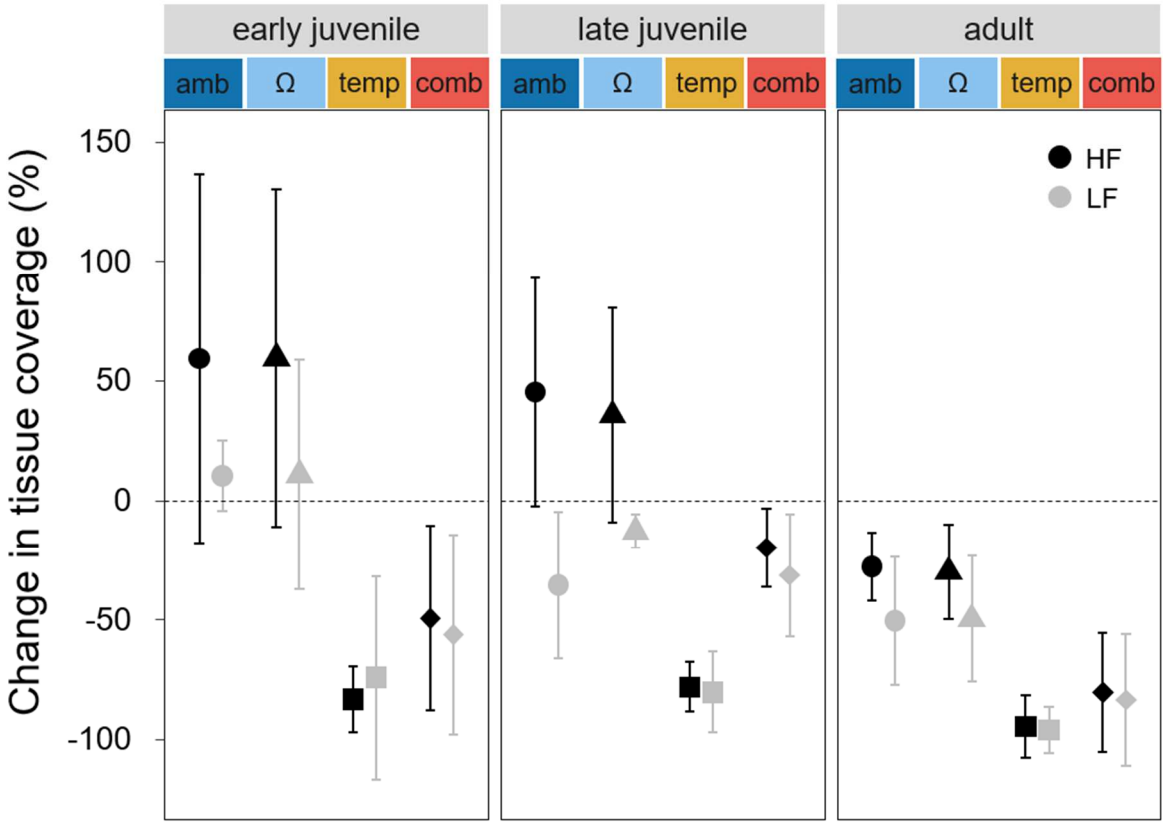

Figure 2: Somatic growth of three life stages of *Caryophyllia huinayensis* after six months under different Ω, temperature and feeding conditions. Change in tissue coverage (%) of early juveniles, late juveniles and adult corals under high (HF, black) and low (LF, grey) feeding conditions (N = 1-6). The four treatment conditions are: ambient (dark blue) = 11 °C and Ω_{arag} > 1, Ω (light blue) = 11 °C and Ω_{arag} < 1, temperature (yellow) = 15 °C and Ω_{arag} > 1, combined (red) = 15 °C and Ω_{arag} < 1. Values are stated as mean ± standard deviation.

Calcification

Aragonite undersaturation alone had no significant effect on calcification rates of all three life stages of *C. huinayensis* over six months (LMM, ambient – Ω: p-value = 1; Figure 3, Supplementary Tables 4-6). In contrast, food availability clearly affected calcification rates of corals across treatments and life stages at the end of the experiment (LMM, p-value = 0.045; Figure 3, Supplementary Tables 4-6). Under ambient conditions, calcification of early juveniles decreased by a factor of 4.4 from 0.513 ± 0.299 mg cm^{-2} d^{-1} to 0.118 ± 0.035 mg cm^{-2} d^{-1} due to food limitation after six months (Supplementary Table 4). Elevated temperature had a slightly stronger effect on calcification in this life stage with seven times lower calcification rates in the HF regime (0.073 ± 0.092 mg cm^{-2} d^{-1}, Supplementary Table 4). Food limitation further reduced calcification by a factor of 1.8 to 0.039 ± 0.122 mg cm^{-2} d^{-1} in early juveniles (Supplementary Table 4). Similar to somatic growth, calcification rates after six months differed significantly between life stages, with highest calcification in early juveniles and lowest in adult corals (LMM, p-value < 0.001; Figure 3, Supplementary Tables 4-6). Low food availability and elevated temperature as single factors had the strongest effect on all life

stages. Calcification of adult corals decreased by one fifth from 0.060 ± 0.026 mg cm^{-2} d^{-1} in the HF regime to 0.048 ± 0.030 mg cm^{-2} d^{-1} in the ambient LF regime. The effect of elevated temperature alone was variable due to the high mortality (see above) and hence, the low number of replicates (N = 1-2; Supplementary Table 4).

Throughout the experiment, a clear delay in response was apparent in the health status (Figure 1), but also in calcification (Figure 3). All life stages maintained their calcification rates irrespective of treatment and feeding conditions in the first month (Figure 3). Subsequently, calcification rates declined under LF and elevated temperatures, with significantly lower rates after three months (LMM, p-value < 0.001; Figure 3, Supplementary Tables 4-6).

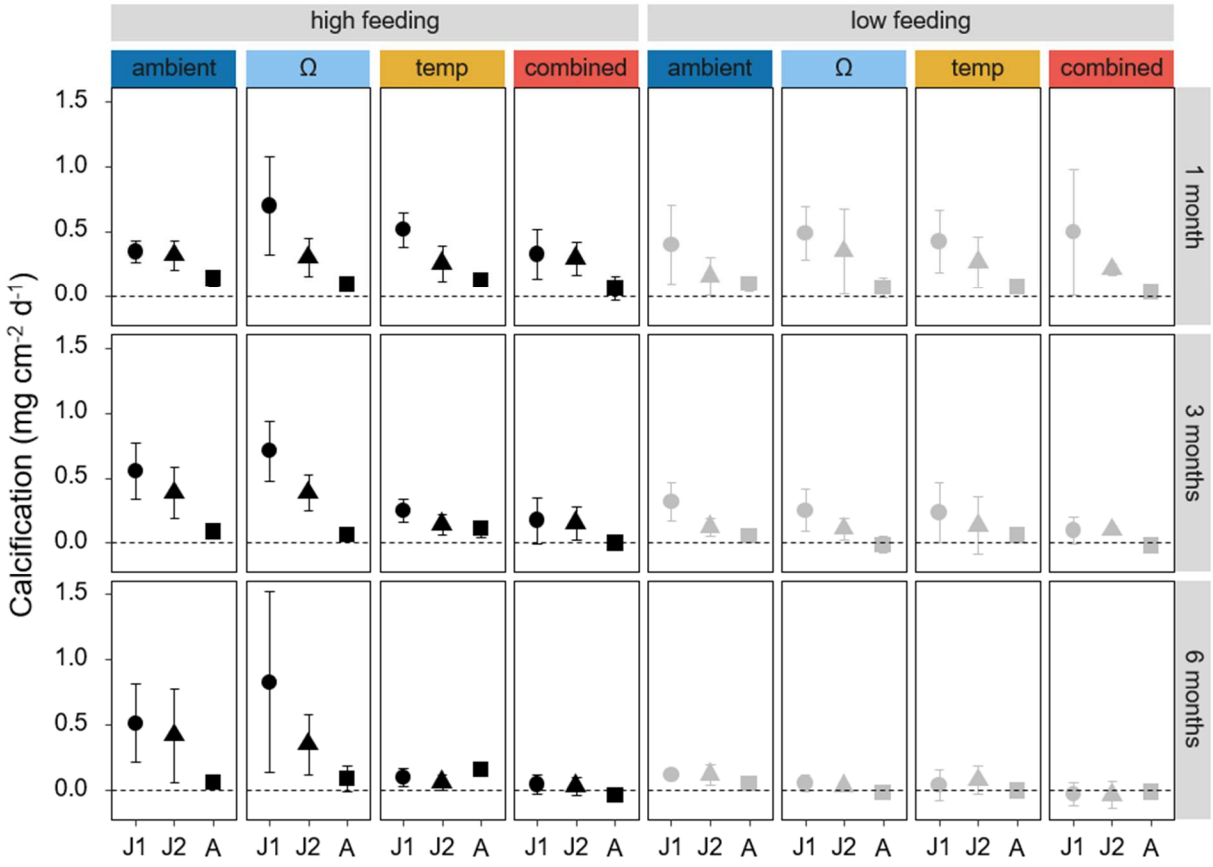

Figure 3: Calcification of three life stages of *Caryophyllia huinayensis* after one, three and six months under different Ω, temperature and feeding conditions. Calcification rate of early juveniles (J1, circle), late juveniles (J2, triangle) and adult corals (A, square) under high (black) and low (grey) feeding conditions (N = 1-6). The four treatment conditions are: ambient (dark blue) = 11 °C and Ω_{arag} > 1, Ω (light blue) = 11 °C and Ω_{arag} < 1, temperature (yellow) = 15 °C and Ω_{arag} > 1, combined (red) = 15 °C and Ω_{arag} < 1. Calcification rates are stated as mean ± standard deviation.

Prey capture rates

Prey capture rates did not differ between treatment conditions and life stages, but only between feeding regimes (LMM, p-value < 0.001; Supplementary Figure 4, Supplementary Tables 5-7), with four times higher captures rates in the HF regime (HF: 18.25 ± 10.92 nauplii coral^{-1} h^{-1}, LF: 4.39 ± 3.83 nauplii coral^{-1} h^{-1}). The same amount of captured *Artemia* nauplii resulted in significant differences in organic matter uptake between life stages (LMM, p-value < 0.001; Figure 4, Supplementary Tables 5-7). In the HF regime, early juveniles (0.259 ± 0.181 mg cm^{-2} h^{-1}) ingested 2.6 times more organic matter than late juveniles (0.100 ± 0.093 mg cm^{-2} h^{-1}) and as much as nine times more than adult corals (0.028 ± 0.019 mg cm^{-2} h^{-1}). The uptake of nauplii carbon was four times lower in the LF than the HF regime in early and late juvenile corals and even 5.6 times lower in adult corals, which is consistent with the four times higher food availability and capture rates (Supplementary Table 7). Yet, similar to the health status, corals at elevated temperatures reduced their activity over time and hardly extended their tentacles even during feeding periods (K. Beck and J. Nierste, personal observation).

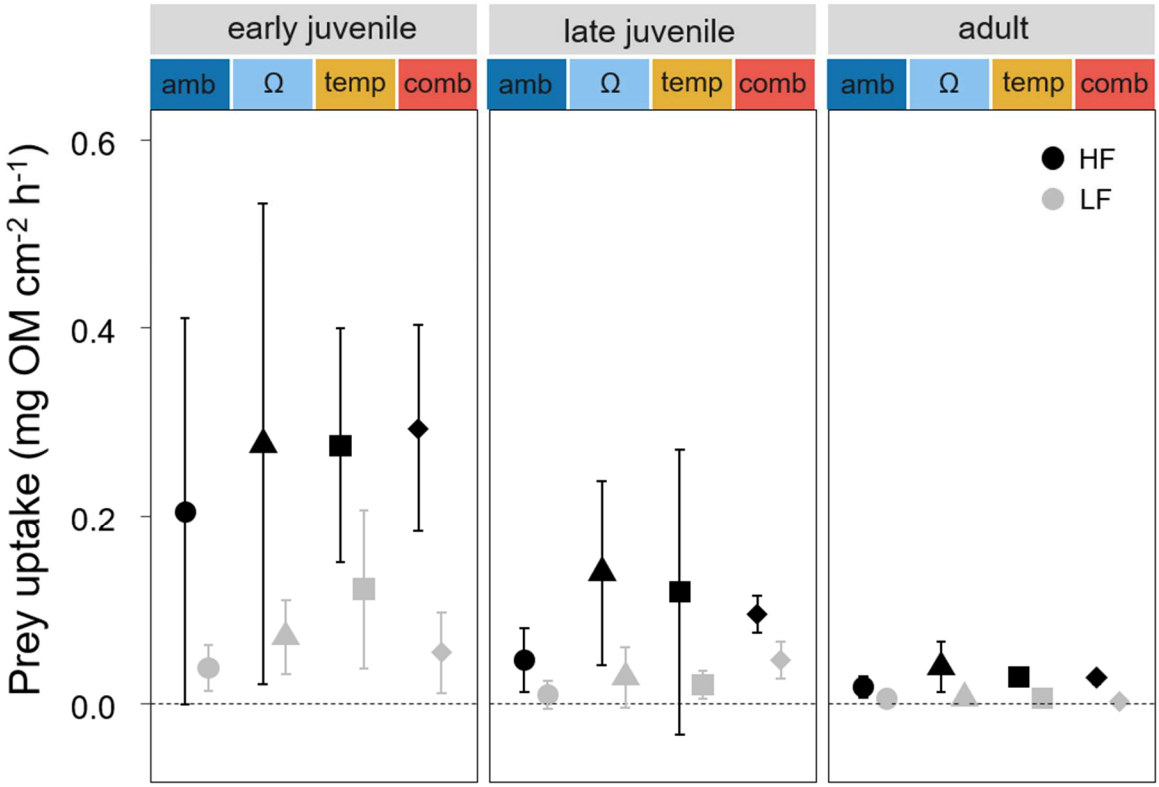

Figure 4: Prey uptake rate of three life stages of *Caryophyllia huinayensis* under different Ω, temperature and feeding conditions. Uptake of prey organic matter (OM) in early juveniles, late juveniles and adult corals under high (HF, black) and low (LF, grey) feeding conditions (N = 1-6) after five months at four different temperature and Ω conditions. Corals were fed with *Artemia* nauplii (LF: 30 nauplii; HF: 120 nauplii) to determine their prey capture rate. Note that the values correspond to uptake rates during the feeding incubations with four times higher food concentration in the HF regime, but that LF corals were fed once a week and HF corals were fed three times per week and therefore received twelve times more food. The four treatment conditions are: ambient (dark blue) = 11 °C and $\Omega_{arag} > 1$, Ω (light blue) = 11 °C and $\Omega_{arag} < 1$, temperature (yellow) = 15 °C and $\Omega_{arag} > 1$, combined (red) = 15 °C and $\Omega_{arag} < 1$. Values are stated as mean ± standard deviation.

Discussion

For the first time, this study examines the response of different CWC life stages to the single and combined effects of ocean acidification, warming and reduced food availability over the period of months. The results provide important and novel insights into trade-offs in energy allocation at different ontogenetic stages of the CWC *Caryophyllia huinayensis*. Importantly, none of the treatments showed severe short-term effects (≤ 3 months). However, reduced feeding and warming took their toll on all life stages after six months. While decreasing calcification rates mainly affected juvenile corals, mortality was highest in adult corals. Surprisingly, acidification alone showed little effect, even in combination with low food availability. In the following, we discuss the importance to consider the effects on different CWC life stages, different feeding conditions and the individual and combined effects of environmental parameters.

Response of CWC life stages

As the selective pressure and competition for space are high, early CWC life stages are characterised by faster calcification rates compared to adult corals (Maier et al., 2009, 2013b; Movilla et al., 2014a, 2014b; Martínez-Dios et al., 2020). Therefore, probably the major part of the available energy in early life stages of corals is allocated to calcification (Hughes & Jackson, 1985; Zilberberg & Edmunds, 2001) as high calcification rates are essential to reach sexual maturity quickly and establish a viable adult population. However, changing environmental conditions may negatively affect the survival and development of early life stages, which in turn has consequences for the reproductive success and maintenance of the population. Reduced pH and elevated temperature negatively affect recruits of tropical corals (e.g. Albright & Langdon, 2011; Foster et al., 2015, 2016; Jiang et al., 2018; Bahr et al., 2020). Calcification of young polyps of other CWC species was also reduced under low pH (Maier et al., 2009; Movilla et al., 2014a; Martínez-Dios et al., 2020) and the health and survival of early juveniles were negatively affected by elevated temperature and reduced food supply (Figure 1, Supplementary Figure 6). As calcification rates decreased more in early life stages than in adult corals (Figure 6), warming may delay CWC maturation in a future ocean, suggesting that early life stages may be an important bottleneck for the persistence of CWC populations.

Adult corals invest more energy into reproduction and less into the maintenance of calcification rates (Leuzinger et al., 2003, 2012). Such a decrease in calcification with age or size was also found for *C. huinayensis* (T. Heran, pers. comm.; this study) and other coral species (Goffredo et al., 2010 and references therein). In the present study, early juveniles responded with an almost twice as strong reduction in calcification under reduced feeding and elevated temperature compared to ambient conditions at the start of the experiment than adult corals (mean effect size of -0.29 ± 0.05 and -0.27 ± 0.05 compared to -0.15 ± 0.04; Figures 3 and 5). This smaller treatment effect on adult calcification rates supports the higher resilience of adult CWCs to environmental changes in terms of calcification (Maier et al., 2009; Movilla et al., 2014a; Martínez-Dios et al., 2020). However, calcification may not be the most appropriate trait to determine the sensitivity of adult corals to changing environmental conditions due to their low calcification rates (Figures 3 and 5). Adult corals showed poorer health and higher mortality than juvenile corals (Figure 1 and Supplementary Figure 6), likely because they allocate energy to traits such as reproduction, underlining their higher vulnerability to environmental changes. Our findings are at odds with the general assumption that early life stages are the most vulnerable to environmental changes (Kurihara, 2008; Kroeker et al., 2010; Albright, 2011; Byrne & Przeslawski, 2013). The treatment conditions in this study pushed the adult corals to their limits and show that later ontogenetic stages may also be very sensitive to future environmental changes.

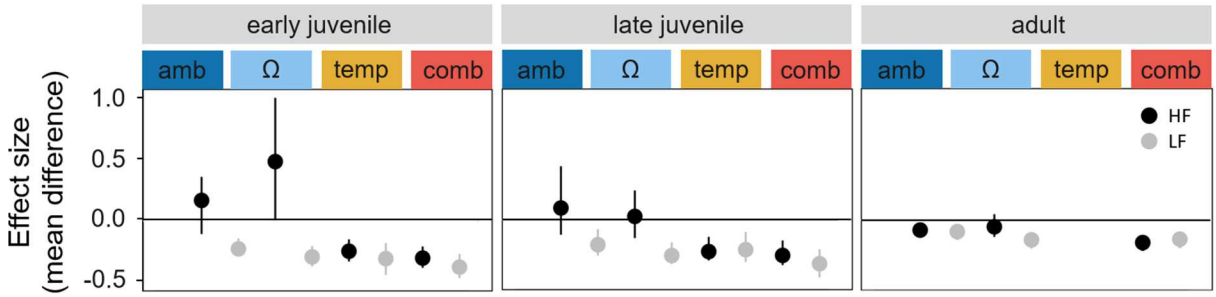

Figure 5: Effect size (mean difference) in calcification of three life stages of *Caryophyllia huinayensis* after six months under different Ω, temperature and feeding compared to initial ambient conditions. High feeding (HF) conditions are shown in black and low feeding (LF) in grey (N = 2-6). The four treatment conditions are: ambient (dark blue) = 11 °C and $\Omega_{arag} > 1$, Ω (light blue) = 11 °C and $\Omega_{arag} < 1$, temperature (yellow) = 15 °C and $\Omega_{arag} > 1$, combined (red) = 15 °C and $\Omega_{arag} < 1$.

Effect of reduced feeding

Low feeding was chosen to mimic *in situ* oligotrophic conditions in winter, considering the strong decline in zooplankton abundance and biomass in Comau Fjord (Garcia-Herrera et al., 2022), but discounting the natural zooplankton patchiness and likely occurrence of krill swarms. The conservative estimate allowed to evaluate the potential consequences of periods of resource limitations. At elevated temperature, the available energy in both feeding regimes was insufficient to maintain the long-term energy requirements of all life stages over six months. However, at ambient temperatures, a clear feeding effect emerged with higher somatic growth and calcification rates in the HF regime, although the energy requirements of adult corals were barely met.

Heterotrophic feeding and efficient use of zooplankton are critical to meet the metabolic demands of CWCs (Purser et al., 2010; Maier et al., 2016; Höfer et al., 2018). However, most feeding studies did not find an effect on calcification rates (Larsson et al., 2013; over whole experimental period in Maier et al., 2016; Baussant et al., 2017; Büscher et al., 2017) and only few reported increasing calcification at higher feeding availability (over short timescale in Maier et al., 2016; Martínez-Dios et al., 2020; this study). In the present study, a twelve times higher food supply resulted in only 3.5-4.4 or 1.3 times increase in calcification under ambient temperature in juvenile and adult corals, respectively (Figure 3 and Supplementary Table 4). This is contrary to the five times higher calcification rates of *D. dianthus* and *Madrepora oculata* due to 2.5-fold food increase (at the beginning of the experiment in Maier et al., 2016; Martínez-Dios et al., 2020). Therefore, *C. huinayensis* appears to invest more into calcification under food limitation, as has also been observed for the tropical coral *Montipora digitata* (Leuzinger et al., 2012), which however derives most of its energy from its photosymbionts (Leuzinger et al., 2012). However, a direct comparison of the feeding studies is difficult as information on the organic C uptake rates are barely provided.

Low and high feeding in previous studies differed by a factor of 2.5 (Maier et al., 2016; Martínez-Dios et al., 2020) to 10 (Büscher et al., 2017). Alternatively, food concentrations ranged between 20 to 300 % (15-fold; Larsson et al., 2013; Baussant et al., 2017), where 100 % is presumably sufficient for the corals. Maier et al. (2016) and Georgian et al. (2016b) also determined food uptake rates in addition to coral calcification. In Maier et al. (2016), mean C uptake rates of *Artemia* nauplii (0.32 and 0.78 µmol C g^{-1} skeletal dry mass h^{-1} for LF and HF, respectively) were lower than in previous studies (Purser et al., 2010: 0.75-2.31 µmol C g^{-1} skeletal dry mass h^{-1}; Tsounis et al., 2010: 73 µmol C g^{-1} skeletal dry mass h^{-1}). This may indicate that the corals were not able to consume enough food and were starving (Maier et al., 2016), but underscores the observed similar long-term calcification rate irrespective of the feeding regime. In the present study, C uptake in adult corals was within the range of Maier et al. (2016) when extrapolated to a week (Maier et al., 2016: 1.92 and 11.7 µmol C g^{-1} skeletal dry mass d^{-1} for LF and HF, respectively; Supplementary Table 7) and is insufficient to meet the metabolic demand of adult corals. However, prey capture rates were similar between life stages and unaffected by elevated temperature or acidification (Supplementary Figure 7, Supplementary Table 7). This is in accordance with findings for *D. dianthus* (Gori et al., 2015; Gómez et al., 2018) and *L. pertusa* (Maier et al., 2016; Baussant et al., 2017), but some other studies found an influence of treatment conditions (Ferrier-Pagès et al., 2010; Houlbrèque et al., 2015; Georgian et al., 2016b; Chapron et al., 2021; Gómez et al., 2022). Thus, it is essential to not only evaluate prey capture rates under ambient conditions, but also potential changes due to environmental changes.

We anticipate that the physiological performance of *C. huinayensis* will be negatively affected by reduced food availability in the future, which only became apparent after three months (Figure 3). This underscores the importance of carrying out experiments at the appropriate timescales, as CWCs appear to bypass resource limitation by fuelling their metabolism from various energy sources over longer periods of time. This resulted in delayed responses until, ultimately, the available energy was channelled into core processes limited to survival. Similar delayed responses were observed in protein and lipid concentrations of *L. pertusa* and *M. oculata* (Chapron et al., 2021) and in the survival rates of *L. pertusa* (Brooke et al., 2013) in response to elevated temperatures. Previous studies probably found no feeding effect due to unnaturally high food concentrations with *ad libitum* feeding (see also Höfer et al., 2018), which is a common drawback of laboratory studies and complicates the comparability between studies and with *in situ* conditions. This emphasises the need to experimentally determine levels of food supply for the study species before the start of experiments. Similarly, experiments should last longer than the energy reserves if meaningful interpretations are to be made about the effect of environmental factors.

In situ food availability varies seasonally, i.e. high zooplankton concentrations in spring and summer and low concentrations in autumn and winter (Maier et al., 2020; Garcia-Herrera et al., 2022). Calcification rates of CWCs are lower in autumn and winter (Maier et al., 2020; Beck et al., 2022), when CWCs potentially downregulate their metabolism (Naumann et al., 2011).

Lophelia pertusa is well adapted to naturally fluctuating feeding conditions and can withstand long periods of low food availability or even complete food deprivation (Larsson et al., 2013; Baussant et al., 2017; Maier et al., 2019) if followed by periods of increased food supply. In contrast, other CWC species such as *C. huinayensis* and *D. dianthus* are more negatively affected by prolonged low food availability and short-term starvation, as indicated by decreasing calcification rates (Naumann et al., 2011; Martínez-Dios et al., 2020; this study). Our HF regime would not allow corals to survive an average warming to 15 °C in their natural habitat in summer. However, it is difficult to compare our results to natural feeding conditions, as information on food availability in CWC habitats, the natural diet and uptake rates by CWCs are still scarce. Even though corals in the present study received similar minimum and maximum food concentrations as in their natural environment (calculated after Garcia-Herrera et al., 2022), this determination of the *in situ* food supply seems to underestimate the actual food intake. This also shows that not only zooplankton density plays an important role, but also the type of food. In Comau Fjord, the consumption of one euphausiid allows for a positive scope of growth, while naturally occurring small zooplankton cannot meet the energy requirement of *D. dianthus* (Maier et al., 2021). Therefore, the uniform diet of *Artemia* nauplii in our experiment was not sufficient for adult corals as CWCs likely feed on a range of different prey in Comau Fjord, including calanoid copepods, mysids and euphausiids (Höfer et al., 2018; Maier et al., 2021; Garcia-Herrera et al., 2022).

Effect of aragonite undersaturation

Our study shows that all life stages of *C. huinayensis* are able to withstand aragonite undersaturation at ambient temperature for six months (Figures 1-3, Supplementary Figure 6). This confirms previous findings that CWCs are able to calcify under low pH conditions (Hennige et al., 2014; Rodolfo-Metalpa et al., 2015; Gori et al., 2016), even under aragonite undersaturation (e.g. Form & Riebesell, 2012; Hennige et al., 2015). This may be due to their ability to elevate the internal pH in their calcifying fluid (pH_{cf}), especially if sufficient energy is available (Cohen & Holcomb, 2009; McCulloch et al., 2012a, 2102b), which is likely the case for juvenile corals in the HF regime. However, the slightly lower calcification rates in the LF regime at aragonite undersaturation may be a first indication that enhanced up-regulation requires energy that is not as readily available as under ambient conditions (Figure 3, Supplementary Table 4). It is therefore important to better understand the energy requirements for processes involved in calcification such as pH_{cf} up-regulation. We only measured negative calcification rates of adult corals at aragonite undersaturation, as the tissue covered surface area decreased and therefore, the unprotected skeleton was in contact with seawater (Hennige et al., 2015, 2020; Figures 2-3, Supplementary Table 4). In contrast, juvenile corals did not retract their tissue and even increased the tissue surface area (Figure 2), which protected their skeleton from dissolution. However, traits other than survival, somatic growth, calcification and respiration may be negatively affected by aragonite undersaturation due to re-allocation of energy.

Combined effects of aragonite undersaturation and elevated temperature

In contrast to aragonite undersaturation alone, the response to a combination of elevated temperature and aragonite undersaturation clearly differed between assessed traits. While calcification resembled the negative response to elevated temperature (Figure 3), both somatic growth and survival rate increased in the combined treatment (Figure 2, Supplementary Figure 6). Here, the combination clearly affected the traits antagonistically, counteracting the negative response to elevated temperature and improved the corals' health status (Figure 1). Similar mixed responses were found in multi-driver experiments ranging from additive, synergistic to antagonistic responses in *D. dianthus* (Gori et al., 2016) and *L. pertusa* (Hennige et al., 2015; Büscher et al., 2017). Calcification rates were either positively affected by elevated temperature and negatively by elevated pCO_2 (Büscher et al., 2017), negatively by temperature but not by pCO_2 (Gori et al., 2016) or not affected by any single factor (Hennige et al., 2015). However, a combination of both parameters resulted in no change in calcification (Hennige et al., 2015; Gori et al., 2016; Büscher et al., 2017), which is in contrast to the present study and may be linked to differences in nutritional status.

Effect of elevated temperature

The metabolism and health of *C. huinayensis* were more negatively affected by elevated temperature than any other factors, except for food limitation (Figures 1-3). CWCs can tolerate exposures beyond their thermal optimum for hours to days (Brooke et al., 2013; Dorey et al., 2020). The elevated temperature in the present study is only slightly higher than the maximum temperature for CWC habitats (14-15 °C; Freiwald et al., 2009; Roberts et al., 2009; Brooke et al., 2013), but a further long-term increase by 1 °C may pose critical for CWC health, as our results show. The HF density was not able to meet the higher energy demand during this period of six months (Figures 1-3, Supplementary Figure 6) and the question arises whether higher food availability could have at all compensated for the higher energy demand or whether 15 °C already represents their long-term physiological temperature limit. However, more detailed performance assays are necessary to answer this question.

While thermal performance curves (TPC) already exist for tropical corals (e.g. Rodolfo-Metalpa et al., 2015; Jurriaans & Hoogenboom, 2019, 2020; Silbiger et al., 2019; Jurriaans et al., 2021), they are still scarce for CWCs (Dorey et al., 2020; Chapron et al., 2021; Reynaud et al., 2021). However, TPC are crucial to put the physiological responses of CWCs into a broader context. A temperature increase can bring corals closer to their thermal optimum if the ambient temperature was at their lower thermal limit compared to when it has already reached their thermal optimum. We expect that 11 °C is slightly below the corals' thermal optimum that is most likely around the proposed 12-14 °C (Brooke et al., 2013; Lunden et al., 2014; Chapron et al., 2021) and beyond which performance in terms of calcification will decrease (Supplementary Figure 9; Brooke et al., 2013; Lunden et al., 2014).

Most studies to date that addressed the effect of elevated temperatures focused on two areas (North Atlantic/Gulf of Mexico: Brooke et al., 2013; Lunden et al., 2014; Hennige et al., 2015; Büscher et al., 2017; Dorey et al., 2020, and Mediterranean Sea: Naumann et al., 2013, 2014; Gori et al., 2014, 2016; Chapron et al., 2021; Reynaud et al., 2021) and studied few species (*L. pertusa*, *D. dianthus*, *M. oculata*, *D. cornigera* and *D. ramea*). Species-specific tolerance ranges became clear as *Caryophyllidae* and *Oculinidae* have lower thermal ranges (approx. 6-15 °C; e.g. Brooke et al., 2013; Naumann et al., 2014; Gori et al., 2016; Büscher et al., 2017; Chapron et al., 2021) than *Dendrophyllidae* (approx. 10-21 °C; e.g. Naumann et al., 2013; Roder et al., 2013; Gori et al., 2014; Reynaud et al., 2021). *Caryophyllidae* are more sensitive towards elevated temperatures, with mortality observed at 15-17 °C (Brooke et al., 2013; Chapron et al., 2021), supporting a critical upper thermal limit of no more than 17 °C. Elevated temperatures of 12 °C for *M. oculata* and *L. pertusa* (Naumann et al., 2014) and 17.5 °C for *D. dianthus* (Naumann et al., 2013) increased calcification rates during a period of three months, but five months at 15 °C reduced calcification in *D. dianthus* (Gori et al., 2016). At the lowest temperatures applied (6-10 °C) calcification was reduced but still positive (Naumann et al., 2014) and their lower critical thermal limit has never been assessed (see Supplementary Discussion). Critical temperatures for a species do not have to be the same across the entire distribution range either, since no mortality of *L. pertusa* from the Mediterranean Sea has been observed after six months (Naumann et al., 2013) compared to the Gulf of Mexico, where 20 % already died after seven days at 15 °C (Brooke et al., 2013).

Potentially, thermal acclimatisation also occurred in Comau Fjord, where CWCs in shallow waters are regularly exposed to elevated temperatures for short periods (Beck et al., 2022). The present study indicates that *C. huinayensis* can tolerate 15 °C for up to three months, but not for longer under resource limitation (Figure 3). Thus, the corals' nutritional condition plays a critical role for its ability to endure stressful conditions. However, it is still questionable if higher food availability close to their upper thermal limit could have sustained the corals' health or would just delay the lethal response by a few months. The strong temperature fluctuations in shallow waters of Comau Fjord are accompanied by changes in a number of parameters (e.g. oxygen, pH, salinity; Beck et al., 2022) that may further restrict their upper thermal limit (as a consequence of Jensen's inequality, see Bernhardt et al., 2018). Currently, monthly average temperatures reach approx. 13 °C in summer and autumn (Rossbach et al., 2021; Beck et al., 2022) and the projections suggest an increase of almost 1 °C for the Gulf of Ancud by 2100 (van Leeuwen et al., 2021). Although this is still below the critical temperature of 15 °C, the combination with strong natural environmental variation in summer and autumn and the expected impact on organisms (Bernhardt et al., 2018) could restrict their physiological limits.

Conclusion

Our study clearly shows that elevated temperature and decreasing food supply negatively affect the health status, somatic growth and calcification rates of all CWC life stages, albeit in different ways. While calcification is reduced in early life stages, the survival probability of adult corals decreases, both of which in turn affect the survival of the whole population. Overall, *C. huinayensis* is more sensitive to elevated temperature than aragonite undersaturation, both as a single stressor and in combination with aragonite undersaturation. As sufficient feeding is an important factor determining physiological response, CWCs may be able to tolerate short-term environmental changes if enough energy reserves are available and the conditions do not exceed their tolerance level. However, long-term exposure to 15 °C is clearly beyond the critical upper thermal limit of *C. huinayensis*. More detailed investigations of the thermal performance of CWCs and a better knowledge of the *in situ* feeding conditions are essential in the future to interpret the observed findings of laboratory experiments in the context of natural CWC habitats.

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Author contributions

K.K.B., M.W., G.M.S.G., C.H., G.N. and G.S. designed the experiment and J.L. collected the corals. K.K.B., E.L. and C.N. carried out the experiment and K.K.B., J.N. and C.N. conducted the measurements. K.K.B., M.W. and J.N. analysed and interpreted the data. K.K.B. and M.W. conducted the statistical analysis and prepared the figures. K.K.B., M.W. and C.R. wrote the first draft and all authors edited the manuscript.

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Supplementary Methods

Study species and coral sampling

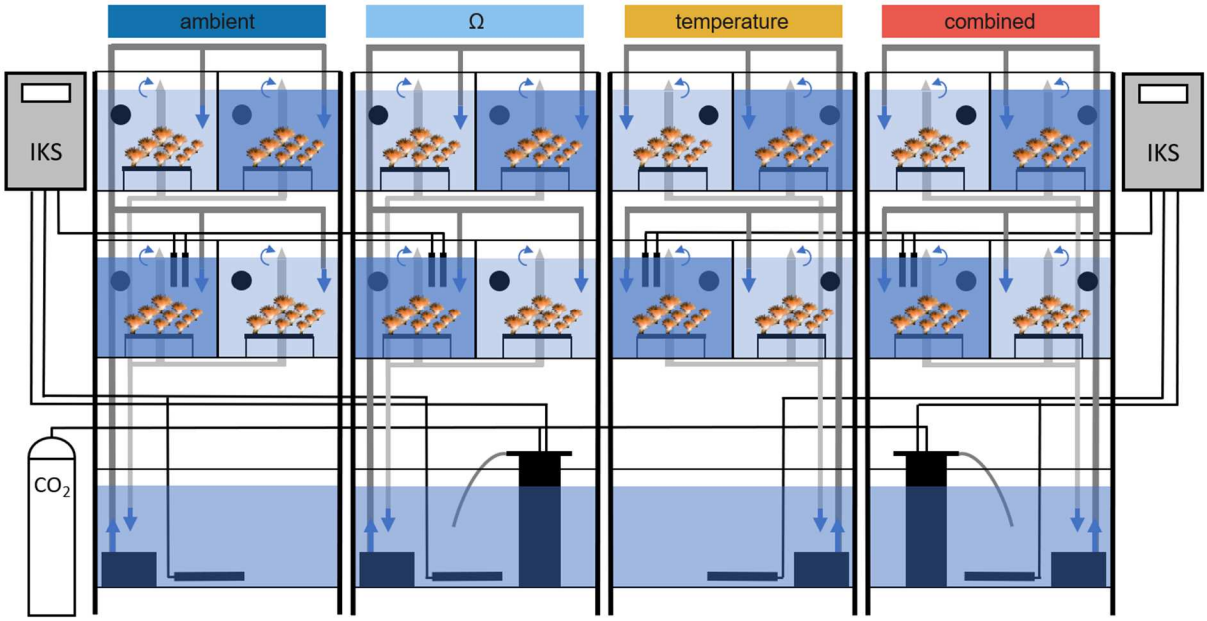
The solitary, azooxanthellate scleractinian cup coral *C. huinayensis* (Cairns et al., 2005) can be found in the wider SE Pacific region and is locally very abundant in the Chilean Fjord region, including Comau Fjord (Cairns et al., 2005; Häussermann & Försterra, 2009). In Chilean fjords, deep water emergence of CWCs is common (Försterra & Häussermann, 2003; Häussermann et al., 2021) and *C. huinayensis* occurs on steep walls and below overhangs at depths between 11-800 m (Cairns et al., 2005; Häussermann & Försterra, 2009; Häussermann et al., 2021). This CWC species occurs at densities of more than 4000 individuals m^{-2} and is often closely associated with *D. dianthus* specimens (Cairns et al., 2005). The Comau Fjord represents a strongly stratified system with a high tidal range of up to 7.5 m (Häussermann & Försterra, 2009) and thus, shallow waters of the fjord are found to be more variable with short-term temperature fluctuations that also correlate with other environmental variables like salinity (Beck et al., 2022).

A total of 69 adults of *C. huinayensis* were collected in Comau Fjord at approx. 20 m depth using SCUBA diving in 2014 and 2015. During each sampling campaign the transport to the Alfred Wegener Institute (AWI) in Bremerhaven (Germany) occurred within two days and in the laboratory, the fjord water was exchanged by culturing water over a period of two hours to allow the corals to acclimate before being transferred into the culturing aquarium system at AWI. Due to active reproduction since 2014, successive cohorts of coral offspring were added and thus enlarging the population by early life stages that later formed a new adult coral generation. The life cycle of *C. huinayensis* is characterized by a faster growth at younger age and size and *in situ* reproduction of the adult stage starts at a calyx diameter of 7.7 ± 2.0 mm, which corresponds to an approx. age of four years (T. Heran, pers. comm.).

Experimental design and setup

Experimental design: Due to the complexity of eight treatments and the available control system for temperature and Ω_{arag} conditions, it was not possible to have truly independent aquaria for each treatment. Even though this is a pseudo-replicated design (Hurlbert, 1984), the advantage was to conduct a long-term experiment with simultaneous manipulation of eight combinations of temperature, Ω_{arag} and feeding conditions.

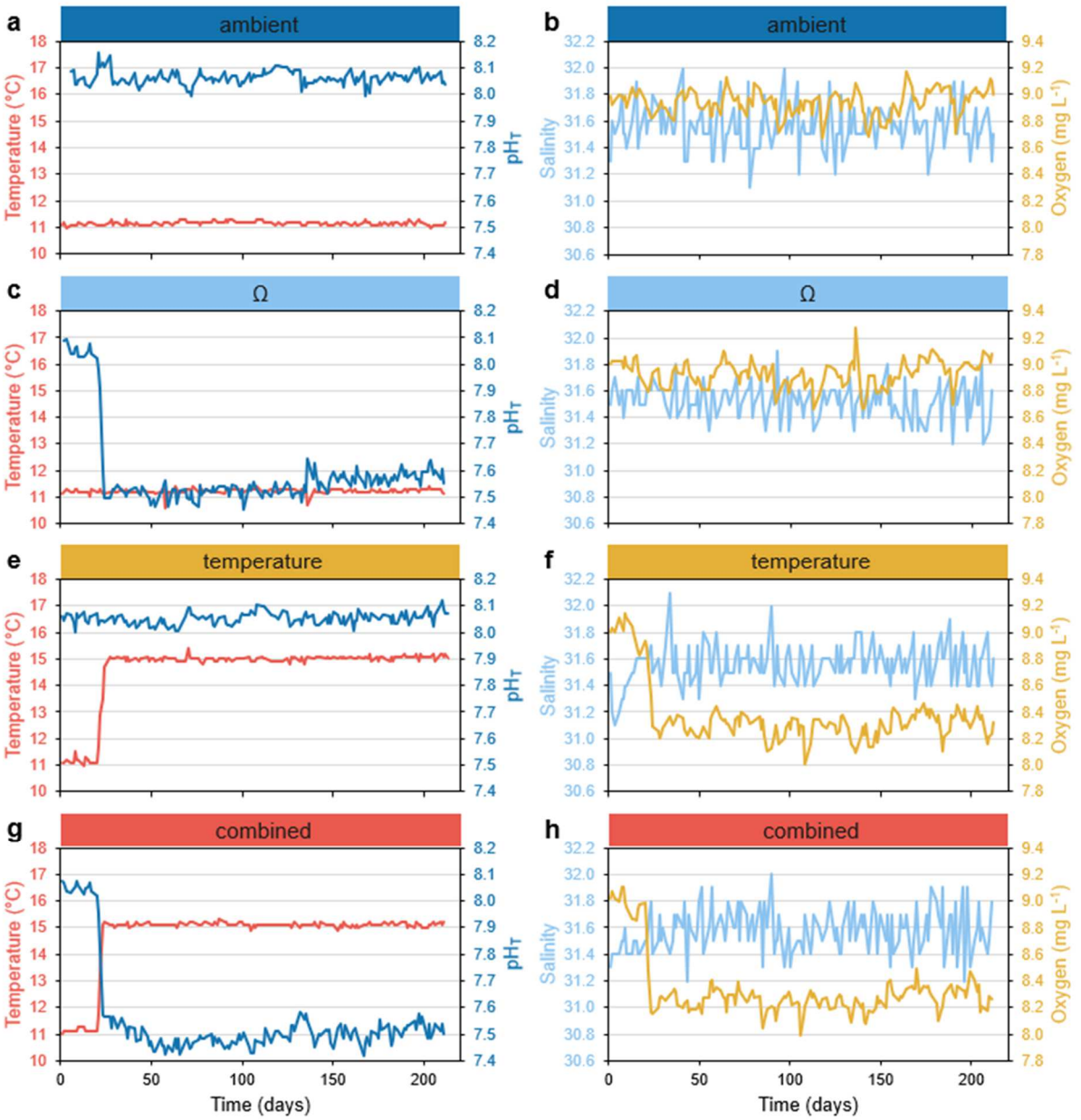
Physico-chemical treatment conditions: Aragonite saturation state manipulation was performed by bubbling pure CO_2 gas into a separate container within the basin, targeting a low pH seawater within this container. Water from this container was then injected in small amounts into the water basin of the recirculating aquarium systems to reach the desired aragonite undersaturated conditions. The supply of CO_2 gas and of low pH water into the aquarium system was manipulated with a digital control system (iks aquastar, iks ComputerSysteme GmbH, Karlsbad, Germany). The pH sensors of the aquarium systems were calibrated once a week using pH buffers 7 and 9 (VWR International, Radnor, USA).



Supplementary Figure 1: Experimental setup. Each recirculating aquarium system for the four physico-chemical treatment combinations consisted of one water basin (80 L) at the bottom and four experimental aquaria (35 L each) on top. Water flow out of the basin and into the experimental aquaria is indicated by blue arrows. Temperature and pH were controlled by computer systems (one for two aquarium systems) and measured in one of the four aquaria of each system. The basin was equipped with a heater to maintain the temperature at ambient or elevated temperature conditions and a CO_2 gas mixing device in the aquarium systems with aragonite undersaturation, where low pH water was added from a separate container in the basin. Two experimental aquaria in each aquarium system were used for the low feeding regime (light blue) and two for the high feeding regime (dark blue). Each experimental aquarium was equipped with one small water circulation pump and contained nine corals (three early juveniles, three late juveniles and three adults).

Seawater pH and temperature were recorded every 15 min. in one of the four aquaria of each system by the iks control system. In addition, HOBO TidbiT v2 water temperature data loggers (ONSET, USA) recorded the temperature in each aquarium every 15 min. Seawater pH and temperature (WTW pH 3310, Xylem Analytics, New York, USA), salinity (WTW cond 3210, Xylem Analytics, New York, USA) and oxygen concentration (YSI ProODO, YSI Incorporated, Yellow Springs, USA) were measured five times per week in one aquarium of each system. The oxygen meter was calibrated once before the start of the experiment with 100 % air saturated water. The pH sensor was calibrated once per week using pH buffers 4, 7 and 10 (WTW, Xylem Analytics, New York, USA) and pH values were corrected to total scale using TRIS-HCl buffer (Dickson, Sabine, & Christian, 2007). We took water samples for analyses of total alkalinity (TA) and nutrients (ammonium, nitrate, nitrite, phosphate, silicate) once every week. All water samples were taken as duplicates from the basin of each recirculating aquarium system. Water for TA analyses was filtered through 0.7 µm glass fibre filters (Whatman GF/F, GF Healthcare Life Sciences, Amersham, United Kingdom) into 50 mL falcon tubes without air inclusion and stored at 4 °C until analysis. TA was measured in potentiometric titrations (in duplicates, 25 mL

each) with 0.05 M hydrochloric acid (Titrisol, Merck KGaA, Darmstadt, Germany) using a TW alpha plus titration unit (SI Analytics, Xylem Analytics, New York, USA). Prior to each titration, the pH electrode of the titration unit was two-point calibrated using pH buffers 4.006 and 6.865 (WTW, Xylem Analytics, New York, USA). TA was calculated from linear Gran plots (Gran, 1952) and corrected for seawater density and our inhouse North Sea standard seawater corrected against Dickson standard seawater (batch 102). According to Hoppe et al. (2012), we calculated other parameters of the carbonate system based on TA and pH_T measurements at the respective temperature and salinity using the Excel programme CO2SYS (Pierrot et al., 2006). For the calculations, we used the dissociation constants of carbonic acid in seawater (K_1 and K_2) of Lueker et al. (2000), the dissociation constants of hydrogen sulphate of Dickson (1990) and boric acid of Uppström (1974) and pH on the total scale. Samples for nutrient measurements were filtered through 0.7 µm glass fibre filters into 15 mL falcon tubes and stored at -20 °C until analysis. Nutrients were measured in two replicate samples using a QuAAtro39 autoanalyzer with a XY-2 autosampler (Seal Analytical GmbH, Norderstedt, Germany) and the software AACE (Version 7.06).



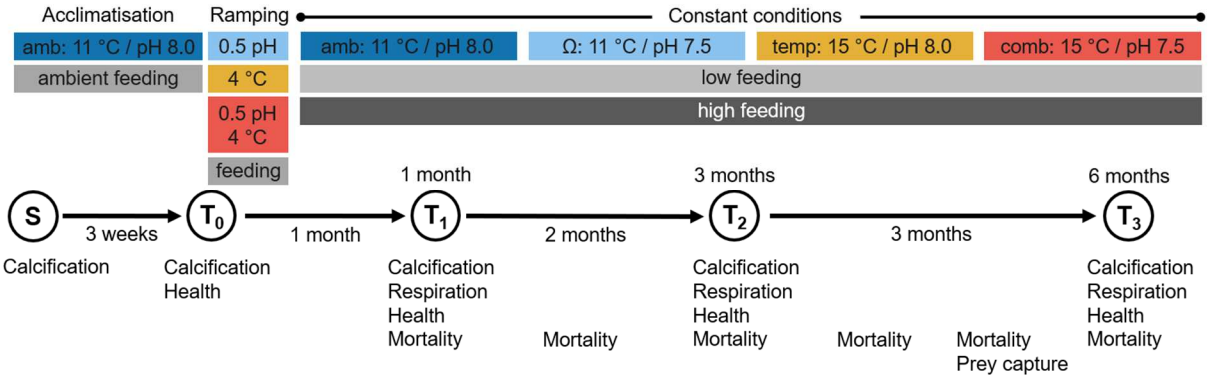
Supplementary Figure 2: Water parameters of four experimental treatments over the whole duration of the experiment (six months). Temperature, pH on the total scale (pH_T), salinity and oxygen were measured daily. The first 20 days of the graph show the acclimatisation period with low temperature (11 °C) and aragonite oversaturation ($\Omega_{arag} > 1$) for all four treatments. Temperature and pH were adjusted to treatment conditions over five days with changes of 0.05 pH units and 0.5 °C every twelve hours. The four treatments targeted the following conditions: ambient (dark blue) = 11 °C and $\Omega_{arag} > 1$, Ω (light blue) = 11 °C and $\Omega_{arag} < 1$, temperature (yellow) = 15 °C and $\Omega_{arag} > 1$, combined (red) = 15 °C and $\Omega_{arag} < 1$.

Feeding procedure of pre-experiment: The feeding procedure was established in a pilot study that aimed at developing a protocol to ensure that food was available to the corals and remained in the aquaria during the feeding period (despite the constant flow-through required to regulate pH and temperature). This short-term (one month) pilot study was conducted with early juveniles of *C. huinayensis* with four different feeding regimes. Corals were either starved or fed on one, three or five days per week with the same amount of *A. persimilis* nauplii and calcification and respiration rates were measured after one month.

Four recirculating aquarium systems were used, one aquarium per system for each of the four feeding regimes. Twelve early juveniles were used for each feeding regime with three corals in each aquarium. Different amounts of food (0.05-0.3 g dry *Artemia* cysts) were tested at the beginning of the experiment. Based on the final concentration of *Artemia* nauplii in the aquaria, the number of nauplii available for each coral in relation to the food concentration in the culturing aquarium system and the clearance rate of the corals, 0.15 g dry *Artemia* cysts were used for each feeding regime. This resulted in 124 ± 72 nauplii L^{-1} in each experimental aquarium during each feeding period and 1486 ± 859 nauplii per early juvenile coral. The *Artemia* cysts were placed in hatchery kits with seawater and constantly bubbled with air at 25 °C one to three days prior to the feeding to allow the nauplii to hatch. The solution with *Artemia* nauplii of each feeding regime was concentrated to 40 mL stock solution and then homogenizing before separating the concentrated solution in 10 mL aliquots for each aquarium, which was poured into the four aquaria of the feeding regime. During the feeding period of four hours, it was tested how much the water inflow into the aquaria could be reduced to keep the nauplii in suspension but also allow regulation of temperature and pH in the main experiment. The outflow was covered with a 100 µm net in each aquarium to prevent nauplii from being flushed out. The circulation pump in each aquarium allowed *Artemia* nauplii to stay in suspension and reduced entrapment in the mesh covering the outflow. In addition, nets were controlled regularly and cleaned from entrapped nauplii. After four hours, the water inflow was increased and nauplii flushed into the nets, which were exchanged. Additional nets over the inlet of each aquarium ensured that nauplii were not flushed into the aquaria of the other feeding regimes. The nets on the in- and outflows were cleaned and replaced every two days and after each feeding period.

Prior to each feeding, a small subsample (1 mL) of the stock solution was taken and fixed in ethanol to count the number of nauplii in the whole subsample. After this pilot study, the food concentrations for the main experiment were adjusted for the number of corals in each aquarium (three in pilot study and nine in main experiment) and the higher biomass in the main experiment (three early juveniles, three late juveniles and three adult corals in main experiment, but only three early juveniles in pilot study). The aim was to achieve half the food concentration per coral (1486 ± 859 nauplii $coral^{-1}$) of the pilot study for the LF regime (705 ± 188 nauplii $coral^{-1}$) of the main experiment and a two times higher concentration for the HF regime (2430 ± 910 nauplii $coral^{-1}$).

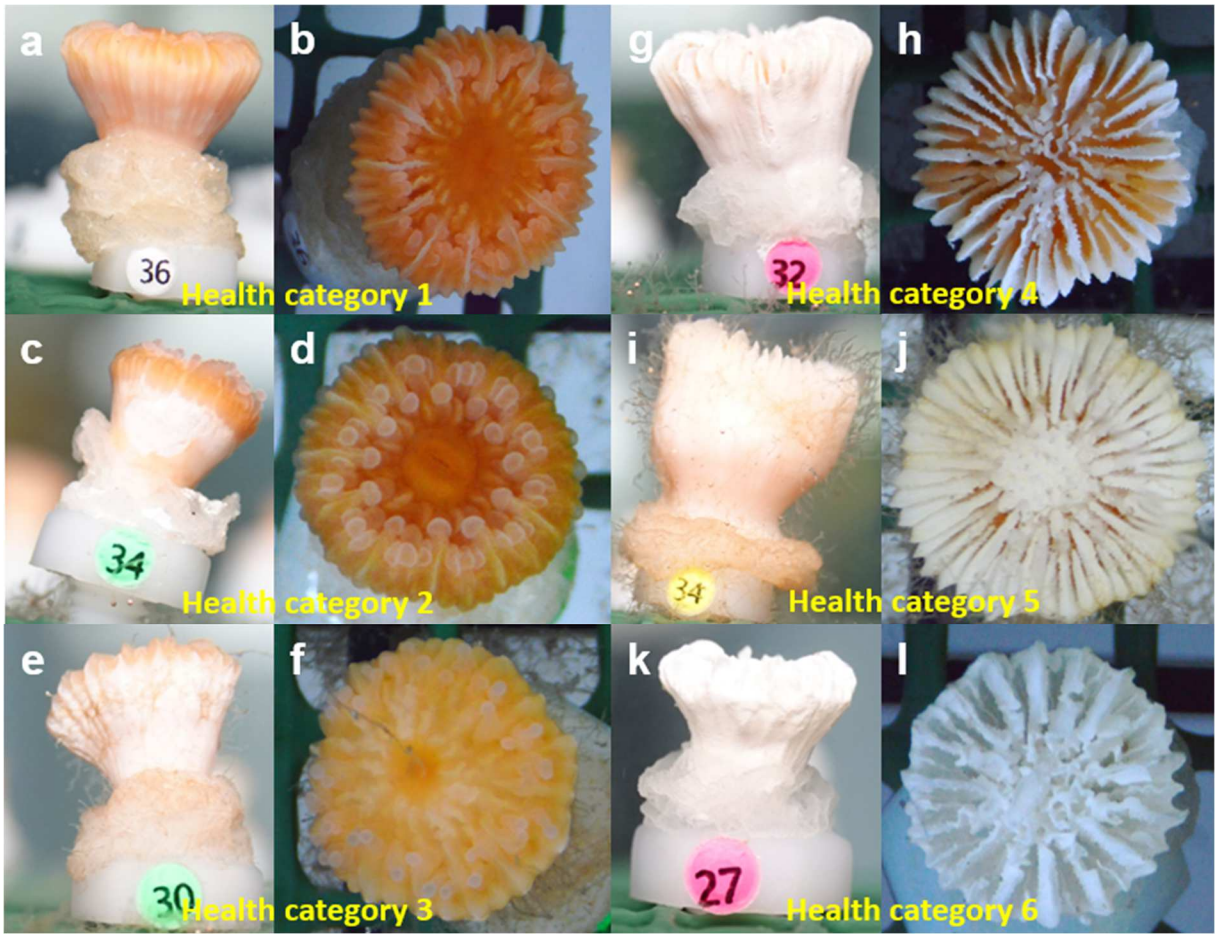
Experimental feeding conditions: The *Artemia* cysts were placed in a hatchery kit with seawater and constantly bubbled with air at 25 °C two to three days prior to the feeding to allow the nauplii to hatch. The solution with *Artemia* nauplii of each feeding regime was concentrated to 80 mL stock solution and then homogenized before separating the concentrated solution in 10 mL aliquots for each aquarium, which was poured into the eight aquaria of the feeding regime. During the feeding period of six hours, the water inflow into the aquaria was reduced but not completely stopped to maintain temperature and Ω_{arag} conditions. The outflow was covered with a 100 µm net in each aquarium to prevent nauplii from being flushed out. The circulation pump in the aquaria allowed *Artemia* nauplii to stay in suspension and reduced entrapment in the mesh covering the outflow. In addition, nets were controlled regularly and cleaned from entrapped nauplii. In the HF regime, only half of the *Artemia* solution was added to the aquaria at the beginning of the feeding period and the second half was added after three hours, otherwise the outlets were clocked with nauplii and the aquaria were overflowing due to the high amount of nauplii. After six hours, the water inflow was increased and nauplii flushed into the nets, which were exchanged. Additional nets over the inlet of each aquarium ensured that nauplii were not flushed into aquaria of the other feeding regime. The nets on the in- and outflow were cleaned and replaced every two days. Every two weeks, a small subsample (1 mL) of the stock solution was taken and fixed in ethanol prior to feeding to count the number of nauplii. The subsamples were diluted to 50 mL and the nauplii counted in 10 aliquots of 1 mL.



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

Physiological measurements

***Health status and survival*:** For the standardised photo-documentation procedure, the camera was mounted on a custom-made frame equipped with an external light source (Walimex pro LED Flat 200, Samyang Optics, Changwon, South Korea) set at 75 % intensity. The pictures of the lateral side of the corals were taken at a defined distance of 4 cm from the corals in the aquaria. Unhealthy and dead corals of categories 5 and 6 (Supplementary Figure 4) were excluded from calcification and respiration measurements.



Supplementary Figure 4: Health categories of *Caryophyllia huinayensis*. Photographs of the lateral (a, c, e, g, I, k) and oral side (b, d, f, h, j, l) of *Caryophyllia huinayensis*. Corals were divided into six health categories depending on the tissue coverage of their skeleton after one, three and six months. Health categories are defined as: 1) calyx fully covered with tissue (orange) on the lateral and oral sides (a, b), 2) calyx partly covered with tissue, tissue (orange) on lateral side partly retracted (c, d), 3) only oral side of calyx fully covered with tissue (orange), lateral side not covered with tissue (e, f), 4) oral side of calyx partly covered with tissue (orange), septa largely not covered with tissue (g, h), 5) dying/recently dead with tissue remains in calyx (I, j), 6) dead, bare skeleton without tissue (k, l). Dead corals (categories 5 and 6) were excluded from respiration and calcification measurements.

Somatic growth: For the calculation of the tissue covered surface area of the coral polyp without considering the surface areas of the individual septa, the following equations were used:

$$A\ (cm^2) = \pi \times [R^2 + s \times (r + R)]$$

where *R* and *r* are the oral and aboral radius of the polyp, respectively, and *s* is the slant height of the calyx calculated from the measured outer height:

$$s = \sqrt{(R - r)^2 + h^2}$$

where *h* is the mean height of the tissue covered surface area of the polyp.

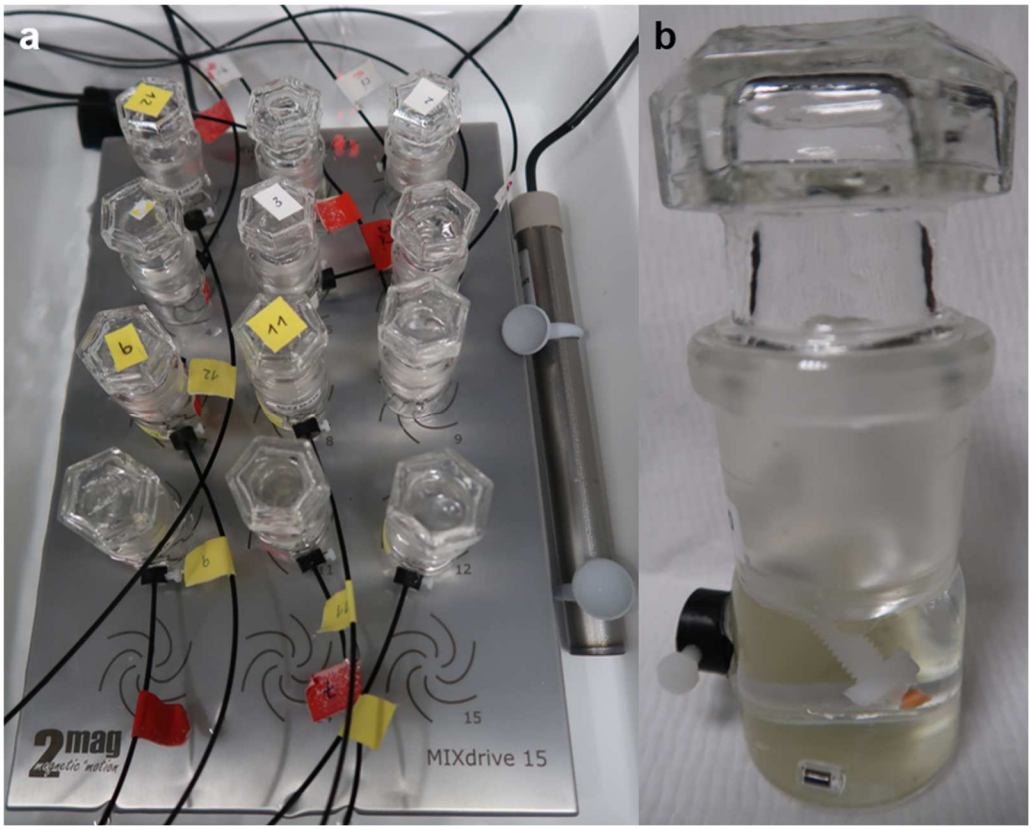
***Respiration*:** Respiration rates were measured in closed-cell incubations using wide-mouth glass vials with glass stopper lids customized for our purpose and adjusted to 25 mL (for late juveniles and adults) and 15 mL (for early juveniles; Eydam, Kiel, Germany; Supplementary Figure 5b). The glass stopper lid was equipped with a small nut that allowed to fix the individual coral screws. Incubation vials were completely submerged in a temperature-controlled water bath (11 °C and 15 °C) on a submergible magnetic stirring table (170 rpm) and glass coated magnetic stir bars were placed inside the vials to ensure homogeneous water movement (Supplementary Figure 5a). Corals and screws were carefully cleaned with a soft tooth brush before respiration measurements to remove any attached organisms on the screws and bare skeleton.

For the measurements, we used a fibre optic oxygen meter system (FSO2-4 and FSPRO-4, PyroScience GmbH, Aachen, Germany) with contactless optical fibre oxygen sensors (SPFIB-BARE, PyroScience GmbH, Aachen, Germany) and oxygen sensor spots inside the incubation vials (OXSP5, PyroScience GmbH, Aachen, Germany) as well as Pt100 temperature probes (TSUB21, PyroScience GmbH, Aachen, Germany). Oxygen sensors were calibrated with O_2-free (0 % O_2, sodium dithionite) and air-saturated (100 % O_2) seawater prior to the incubations. The sensors were calibrated before the start of the measurements using the respective experimental temperature conditions. Three FireSting meters with four channels each were used for the measurements which allowed to measure twelve vials simultaneously. Thus, the respiration rate of corals of the same life stage per experimental treatment at both feeding regimes was measured simultaneously. The oxygen concentration in the vials was measured in % air saturation by the software (PyroOxygenLogger Version 3.317 for FSO2-4 and PyroWorkbench Version 1.2.0.1359 for FSPRO-4) in order to have a direct control on the respiration rate and ensure that it did not decrease too much (below 60 %). The oxygen concentration in the incubation vials was logged every ten seconds using the oxygen meters and the temperature was measured every ten seconds in the water bath.

All corals of the same life stage of one treatment were incubated at the same time after the start of the experiment (± 1 day), resembling the applied shift in the start of the experimental conditions. To achieve this, the respiration procedure had to be adapted to other commonly used approaches. Instead of parallel background measurements in separate

vials, each incubation vial was filled with seawater from the respective aquarium system, closed hermetically and background measurements were conducted for each vial. After four hours, the background measurements were stopped, the corals were screwed in the lid of the incubation vials in their natural downward orientation and the oxygen measurements continued. The respiration rate of adult corals was measured over six hours, of late juveniles over twelve hours and of early juveniles over 18 hours in the dark.

The obtained raw respiration data in % were converted into mg L^{-1} using the Excel conversion file provided by PyroScience and taking the temperature and salinity during the incubations into account. The respiration rate of the corals was calculated by linear regression of the oxygen depletion using the software R (R Core Team, 2021) and a customized script including functions from the R package rMR. The slope of the respiration rates was analysed for two hours intervals for late juveniles and adults and for three hours intervals for early juveniles. Mean respiration rates were calculated over all time intervals. The script involved quality control steps and corrected for mean background respiration measured prior to the start of the incubation in each incubation vial as well as for the incubation volume (measured for each individual vial). Respiration rates (mg O_2 cm^{-2} d^{-1}) were normalised to tissue covered surface area of the corals at the time of measurement.



Supplementary Figure 5: Incubation setup for respiration measurements. A) Twelve 15 mL incubation vials fully submerged in water bath on submergible magnetic stirring table with black contactless optical fibre oxygen sensors and heating rod. B) 15 mL incubation vial (wide-mouth glass bottle with glass stopper lid) with early juvenile of *Caryophyllia huinayensis* fixed on the lid and glass coated magnetic stir bar. The black holder on the left side fixes the oxygen sensor securely on the oxygen sensor spot inside the incubation vial.

Calcification: Before the start of the experiment (T_{-1}), corals were weighted twice without as well as with screws. The skeletal density of *C. huinayensis* (2.7397 ± 0.0437 g cm^{-3}) was derived from nine specimens after Davies (1989). For this, the buoyant weight of bare *C. huinayensis* skeletons in seawater was determined three times before rinsing the skeleton with reverse osmotic water (conductivity: 18.0 MΩcm; Sartorius Arium Pro, Sartorius Corporate Administration GmbH, Göttingen, Germany) and drying them to constant mass at 60 °C for four weeks. Calcification rates were normalised to initial skeletal dry mass (% d^{-1}) and tissue covered surface area (mg cm^{-2} d^{-1}) using the following equations:

$$G\ (\%\ d^{-1}) = \frac{M_{t+1} - M_t}{M_t \times t} \times 100$$

$$G\ (mg\ CaCO_3\ cm^{-2}\ d^{-1}) = \frac{M_{t+1} - M_t}{A \times t} \times 1000$$

where M_t and M_{t+1} is the skeletal dry mass of each specimen (g) at the beginning (M_t: T_0-T_2) and the end (M_{t+1}: T_1-T_3) of each growth period, respectively, and t is the respective growth period (days).

Prey capture rate: Before the incubations, the bare skeletal part of the corals and the screws were carefully cleaned with a soft tooth brush to remove attached organisms. The corals were then screwed into nuts in the lids of the vials and incubated for one hour. Twelve incubations were carried out simultaneously (one life stage, two feeding regimes, one temperature and Ω_{arag} treatment) and incubated on the day they would be fed.

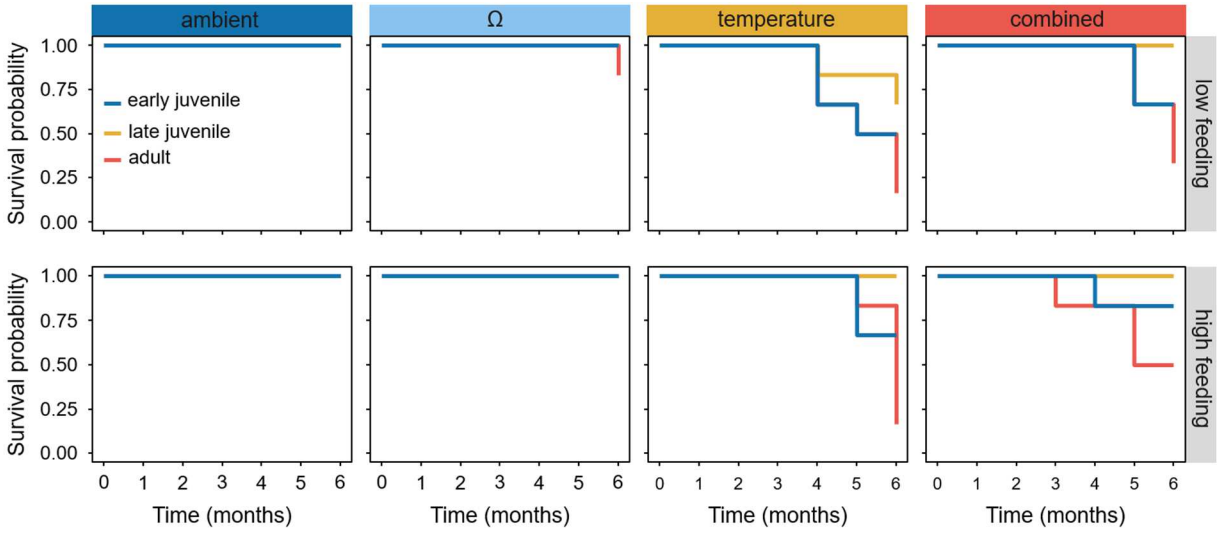
To determine the nauplii biomass, 300 two days old nauplii were counted and filtered on pre-weighed 0.7 µm glass fibre filters (Whatman GF/F, GF Healthcare Life Sciences, Amersham, United Kingdom). The filters were dried overnight at 60 °C, weighed, combusted in a muffle furnace at 500 °C for 4 hours and weighed again using an electronic fine balance (Sartorius M2P, Sartorius AG, Göttingen, Germany; precision: 0.001 mg) to determine their ash-free dry mass (AFDM; 3 ± 0.5 µg nauplii^{-1}). The uptake of the nauplii organic matter (OM) was normalised to the surface area of the corals and expressed as mg OM cm^{-2} h^{-1}. The filters with 300 nauplii were also used to determine the organic carbon (C) content of *Artemia* nauplii (0.001 mg C nauplii^{-1} or 0.083 µmol C nauplii^{-1}) using an elemental analyser Euro EA 3000 (EuroVector, HEKAtech GmbH, Wegberg, Germany) to calculate the C uptake in µmol C cm^{-2} h^{-1} and µmol C g^{-1} skeletal mass h^{-1} (Supplementary Table 7), which allows comparability with results of previous studies.

Supplementary Results

The nutrient concentrations (silicate, phosphate, nitrate, nitrite and ammonium) were similar in all four experimental treatments (Supplementary Table 1).

Supplementary Table 1: Nutrient concentrations in aquarium systems. Duplicate nutrient samples were taken one per week in each of the four recirculating aquarium systems over the six months of the experiment (N = 62-66).

Treatment	Silicate (µmol L^{-1})	Phosphate (µmol L^{-1})	Nitrate (µmol L^{-1})	Nitrite (µmol L^{-1})	Ammonium (µmol L^{-1})
ambient	5.42 ± 2.51	1.64 ± 1.51	49.40 ± 35.19	0.54 ± 0.50	1.31 ± 1.28
pH	5.79 ± 2.47	1.62 ± 1.47	52.29 ± 36.52	0.17 ± 0.11	1.15 ± 0.94
temperature	5.28 ± 2.18	1.93 ± 1.34	54.29 ± 31.46	0.22 ± 0.11	0.98 ± 0.71
combined	5.59 ± 2.81	1.54 ± 1.33	53.09 ± 39.62	0.23 ± 0.09	0.64 ± 0.42
all treatments	5.59 ± 2.81	1.68 ± 1.41	52.25 ± 35.67	0.29 ± 0.30	1.01 ± 0.92



Supplementary Figure 6: Kaplan-Meier survival plot of three life stages of *Caryophyllia huinayensis* under different Ω, temperature and feeding conditions over six months. Survival probability of early juveniles (blue), late juveniles (yellow) and adult corals (red) under low and high feeding conditions (N = 6). The four treatment conditions are: ambient (dark blue) = 11 °C and $\Omega_{arag} > 1$, Ω (light blue) = 11 °C and $\Omega_{arag} < 1$, temperature (yellow) = 15 °C and $\Omega_{arag} > 1$, combined (red) = 15 °C and $\Omega_{arag} < 1$.

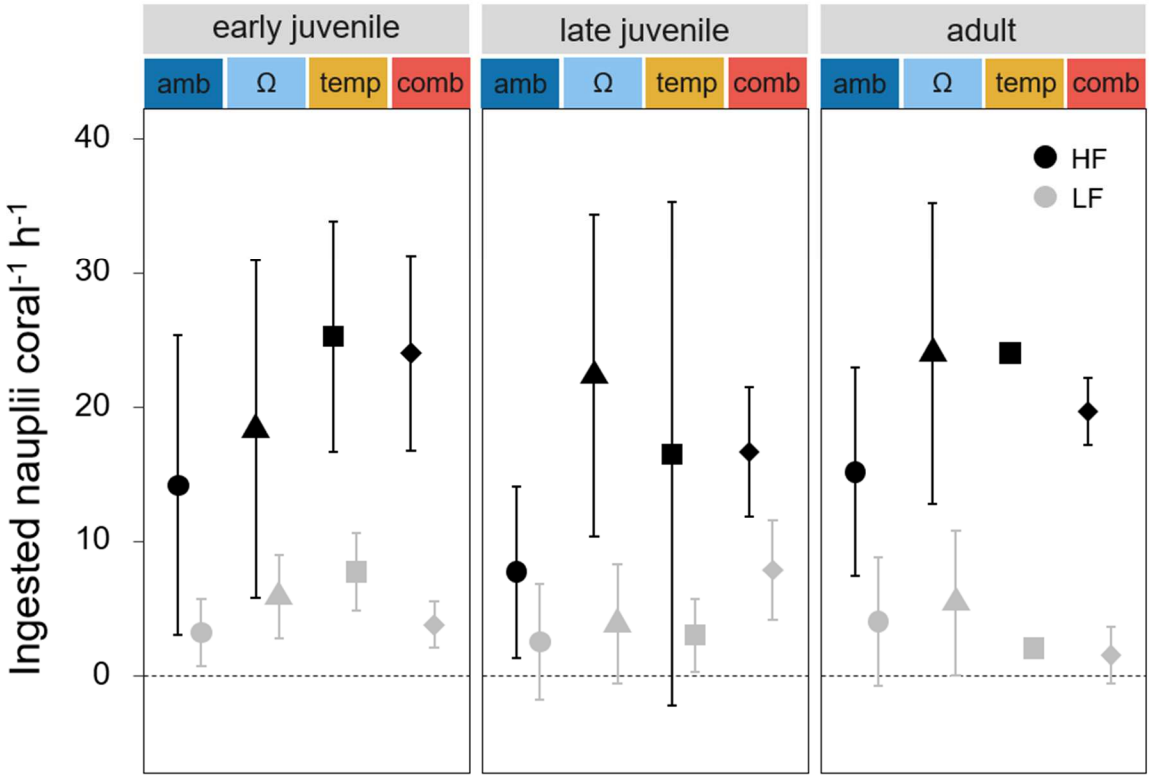
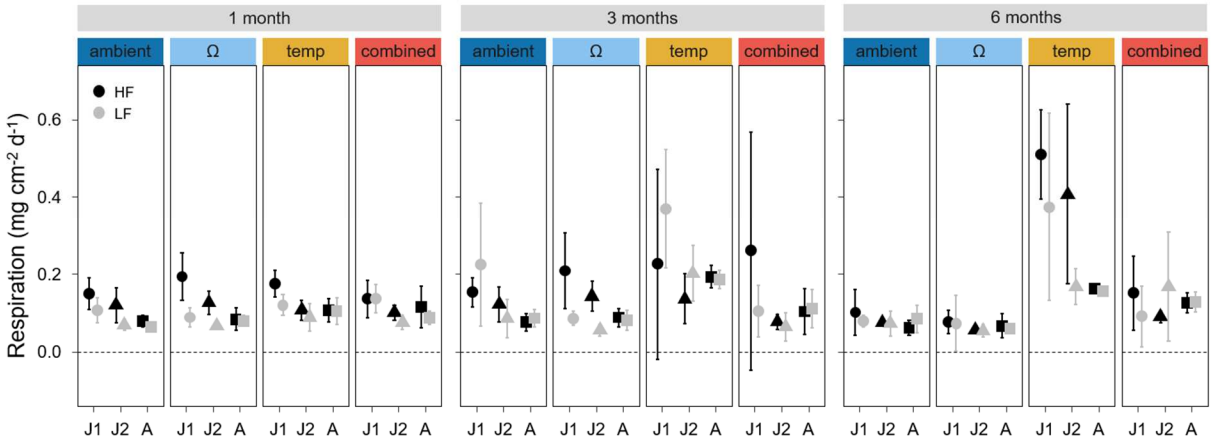


Figure 7: Feeding rates of three life stages of *Caryophyllia huinayensis* under different Ω, temperature and feeding conditions. Prey capture rates of early juveniles, late juveniles and adult corals under high (HF, black) and low (LF, grey) feeding conditions (N = 1-6) after five months at four different temperature and Ω conditions. Corals were fed with *Artemia* nauplii (LF: 30 nauplii; HF: 120 nauplii) in order to determine their prey capture rate. Note that the values correspond to uptake rates during the feeding incubations with four times higher food concentration in the HF regime, but that LF corals were fed once a week and HF corals were fed three times per week and therefore received twelve times more food. The four treatment conditions are: ambient (dark blue) = 11 °C and $\Omega_{arag} > 1$, Ω (light blue) = 11 °C and $\Omega_{arag} < 1$, temp (yellow) = 15 °C and $\Omega_{arag} > 1$, combined (red) = 15 °C and $\Omega_{arag} < 1$. Values are stated as mean ± standard deviation.

Respiration

Interestingly, respiration rates were similar between life stages and feeding regimes in the ambient and Ω treatments, but deviated in the temperature and combined treatments (Supplementary Figure 8). At elevated temperature, respiration rates increased by a factor of up to 4.8 in early juveniles (LMM, e.g. ambient-temperature: p-value < 0.001; Supplementary Figure 8, Supplementary Tables 4-6). Respiration rates also became more variable, potentially a result of reduced biomass and the lower number of surviving individuals in these treatment combinations. In contrast to one and three months, early and late juveniles reduced their respiration rates after six months under ambient conditions and at aragonite undersaturation, but not under elevated temperatures, where respiration increased compared to the early phase of the experiment (Supplementary Figure 8).



Supplementary Figure 8: Respiration rate of three life stages of *Caryophyllia huinayensis* after one, three and six months under different Ω, temperature and feeding conditions. Respiration rate of early juveniles (J1), late juveniles (J2) and adult corals (A) under high (HF, black) and low (LF, grey) feeding conditions (N = 5-6). The four treatment conditions are: ambient (dark blue) = 11 °C and $\Omega_{arag} > 1$, Ω (light blue) = 11 °C and $\Omega_{arag} < 1$, temperature (yellow) = 15 °C and $\Omega_{arag} > 1$, combined (red) = 15 °C and $\Omega_{arag} < 1$. Respiration rates are stated as mean ± standard deviation.

Supplementary Table 2: Generalized linear model for differences in survival of *Caryophyllia huinayensis*. Significant p-values are shown in bold.

Effect	DF	Deviance Residual	DF Residual	Dev	Pr(>Chi)
Survival					
treatment	3	5.389	140	17.167	**<0.001**
life stage	2	2.722	138	14.444	**<0.001**
feeding	1	0.250	137	14.194	0.120

Supplementary Table 3: Post hoc tests for generalized linear model for differences in survival of *Caryophyllia huinayensis*. Only relevant results are displayed here. Significant p-values are shown in bold.

Effect	Contrast	Estimate	Std. Error	z value	Pr(>|z|)
Survival					
treatment	combined - ambient	0.278	0.076	3.661	**0.001**
	Ω - ambient	0.028	0.076	0.366	0.983
	temperature - ambient	0.472	0.076	6.224	**<0.001**
	Ω - combined	-0.250	0.076	-3.295	**0.005**
	temperature - combined	0.194	0.076	2.563	0.051
	temperature - Ω	0.444	0.076	5.858	**<0.001**
life stage	late juvenile - adult	-0.333	0.066	-5.073	**<0.001**
	early juvenile - adult	-0.208	0.066	-3.171	**0.004**
	early juvenile - late juvenile	0.125	0.066	1.902	0.138
feeding	low - high	0.083	0.054	1.553	0.120

Supplementary Table 4: Physiological parameters of three life stages of *Caryophyllia huinayensis* at the start of the experiment and after one, three and six months under different Ω, temperature and feeding conditions. Tissue covered surface area and skeletal dry mass of corals at the beginning of the experiment. Calcification and respiration rates of early juveniles, late juveniles and adults of *C. huinayensis* were measured after one, three and six months of the aquarium experiment (N = 1-6). The four treatment conditions are: ambient = 11 °C and $\Omega_{arag} > 1$, Ω = 11 °C and $\Omega_{arag} < 1$, temperature = 15 °C and $\Omega_{arag} > 1$, combined = 15 °C and $\Omega_{arag} < 1$. The two feeding regimes with *Artemia persimilis* nauplii are: low = 8 µg C L^{-1} and high = 87 µg C L^{-1}. The tissue covered surface area at each measurement time was used as reference value for calcification rates (mg cm^{-2} d^{-1}) and respiration rates (mg cm^{-2} d^{-1}). Calcification rates were also calculated in % d^{-1} using the skeletal dry mass at the beginning of each measurement period as reference value. All values are stated as mean ± standard deviation.

Supplementary Table 4

Treatment	Feeding	Life stage	Start		1 month				
			Surface area (cm^2)	Skeletal dry mass (mg)	N	Calcification (mg cm^{-2} d^{-1})	Calcification (% d^{-1})	N	Respiration (mg O_2 cm^{-2} d^{-1})
ambient	low	early juveniles	0.26 ± 0.07	0.015 ± 0.005	6	0.399 ± 0.305	0.608 ± 0.495	6	0.106 ± 0.033
		late juveniles	0.64 ± 0.24	0.060 ± 0.026	6	0.155 ± 0.150	0.174 ± 0.176	6	0.069 ± 0.015
		adults	2.53 ± 0.61	0.461 ± 0.177	6	0.096 ± 0.060	0.066 ± 0.064	6	0.063 ± 0.013
	high	early juveniles	0.23 ± 0.06	0.013 ± 0.003	5	0.488 ± 0.356	0.481 ± 0.207	6	0.149 ± 0.041
		late juveniles	0.47 ± 0.14	0.036 ± 0.013	6	0.320 ± 0.112	0.368 ± 0.128	6	0.120 ± 0.045
		adults	2.86 ± 0.65	0.491 ± 0.198	6	0.141 ± 0.067	0.084 ± 0.047	6	0.078 ± 0.016
Ω	low	early juveniles	0.26 ± 0.05	0.019 ± 0.005	6	0.488 ± 0.208	0.586 ± 0.322	6	0.088 ± 0.024
		late juveniles	0.43 ± 0.07	0.033 ± 0.009	6	0.348 ± 0.329	0.435 ± 0.437	6	0.065 ± 0.005
		adults	2.94 ± 0.71	0.596 ± 0.161	6	0.069 ± 0.078	0.037 ± 0.048	6	0.079 ± 0.014
	high	early juveniles	0.24 ± 0.07	0.015 ± 0.005	6	0.700 ± 0.378	0.929 ± 0.494	6	0.193 ± 0.061
		late juveniles	0.52 ± 0.11	0.049 ± 0.014	6	0.301 ± 0.148	0.316 ± 0.191	6	0.125 ± 0.030
		adults	2.15 ± 0.91	0.388 ± 0.224	6	0.092 ± 0.040	0.055 ± 0.030	6	0.083 ± 0.029
temperature	low	early juveniles	0.25 ± 0.08	0.013 ± 0.006	6	0.425 ± 0.237	0.754 ± 0.426	6	0.120 ± 0.027
		late juveniles	0.55 ± 0.20	0.046 ± 0.018	6	0.263 ± 0.195	0.269 ± 0.214	6	0.089 ± 0.035
		adults	2.45 ± 1.06	0.467 ± 0.272	5	0.096 ± 0.074	0.043 ± 0.026	6	0.104 ± 0.034
	high	early juveniles	0.27 ± 0.04	0.018 ± 0.004	6	0.517 ± 0.132	0.695 ± 0.285	6	0.174 ± 0.034
		late juveniles	0.48 ± 0.09	0.042 ± 0.017	6	0.253 ± 0.136	0.280 ± 0.195	6	0.107 ± 0.026
		adults	2.45 ± 0.94	0.507 ± 0.363	6	0.125 ± 0.029	0.075 ± 0.043	6	0.105 ± 0.030
combined	low	early juveniles	0.23 ± 0.07	0.015 ± 0.005	4	0.656 ± 0.451	0.543 ± 0.558	6	0.136 ± 0.037
		late juveniles	0.48 ± 0.08	0.035 ± 0.010	6	0.210 ± 0.048	0.272 ± 0.098	6	0.075 ± 0.019
		adults	2.19 ± 0.73	0.358 ± 0.164	5	0.047 ± 0.057	0.018 ± 0.032	6	0.087 ± 0.016
	high	early juveniles	0.26 ± 0.07	0.013 ± 0.004	5	0.503 ± 0.460	0.405 ± 0.259	6	0.135 ± 0.048
		late juveniles	0.52 ± 0.08	0.041 ± 0.009	6	0.293 ± 0.132	0.338 ± 0.150	6	0.100 ± 0.019
		adults	2.36 ± 0.99	0.387 ± 0.247	6	0.062 ± 0.094	0.036 ± 0.061	6	0.115 ± 0.053

Supplementary Table 4 (continued)

Treatment	Feeding	Life stage	3 months				
			N	Calcification (mg cm^{-2} d^{-1})	Calcification (% d^{-1})	N	Respiration (mg O_2 cm^{-2} d^{-1})
ambient	low	early juveniles	6	0.318 ± 0.149	0.391 ± 0.175	6	0.095 ± 0.028
		late juveniles	6	0.123 ± 0.066	0.113 ± 0.046	6	0.085 ± 0.049
		adults	6	0.052 ± 0.035	0.022 ± 0.012	6	0.086 ± 0.023
	high	early juveniles	6	0.553 ± 0.218	0.592 ± 0.251	6	0.152 ± 0.037
		late juveniles	6	0.385 ± 0.200	0.382 ± 0.172	6	0.121 ± 0.044
		adults	6	0.089 ± 0.043	0.043 ± 0.023	6	0.076 ± 0.022
Ω	low	early juveniles	6	0.252 ± 0.163	0.250 ± 0.162	6	0.086 ± 0.018
		late juveniles	6	0.111 ± 0.084	0.115 ± 0.086	6	0.055 ± 0.015
		adults	6	-0.013 ± 0.065	0.000 ± 0.025	6	0.080 ± 0.026
	high	early juveniles	6	0.711 ± 0.231	0.692 ± 0.154	6	0.207 ± 0.096
		late juveniles	6	0.385 ± 0.136	0.342 ± 0.089	6	0.142 ± 0.039
		adults	5	0.081 ± 0.059	0.025 ± 0.018	6	0.088 ± 0.024
temperature	low	early juveniles	6	0.236 ± 0.231	0.316 ± 0.312	6	0.224 ± 0.160
		late juveniles	6	0.134 ± 0.222	0.121 ± 0.207	6	0.201 ± 0.071
		adults	6	0.058 ± 0.022	0.024 ± 0.018	6	0.185 ± 0.024
	high	early juveniles	6	0.250 ± 0.084	0.254 ± 0.077	6	0.225 ± 0.246
		late juveniles	6	0.141 ± 0.077	0.138 ± 0.084	6	0.135 ± 0.064
		adults	6	0.109 ± 0.065	0.040 ± 0.034	6	0.192 ± 0.029
combined	low	early juveniles	5	0.104 ± 0.093	0.077 ± 0.078	6	0.104 ± 0.066
		late juveniles	6	0.095 ± 0.037	0.107 ± 0.035	6	0.064 ± 0.036
		adults	6	-0.022 ± 0.040	-0.011 ± 0.017	6	0.111 ± 0.049
	high	early juveniles	4	0.245 ± 0.283	0.205 ± 0.232	6	0.261 ± 0.307
		late juveniles	6	0.152 ± 0.130	0.160 ± 0.137	6	0.076 ± 0.019
		adults	5	-0.003 ± 0.057	0.002 ± 0.019	5	0.103 ± 0.058

Supplementary Table 4 (continued)

Treatment	Feeding	Life stage	6 months					
			Surface area (cm^2)	N	Calcification ($mg\ cm^{-2}\ d^{-1}$)	Calcification ($\%\ d^{-1}$)	N	Respiration ($mg\ O_2\ cm^{-2}\ d^{-1}$)
ambient	low	early juveniles	0.28 ± 0.08	6	0.118 ± 0.035	0.127 ± 0.038	6	0.078 ± 0.015
		late juveniles	0.65 ± 0.28	5	0.118 ± 0.077	0.066 ± 0.033	6	0.072 ± 0.031
		adults	1.20 ± 0.59	6	0.048 ± 0.030	0.015 ± 0.011	6	0.084 ± 0.035
	high	early juveniles	0.36 ± 0.18	6	0.513 ± 0.299	0.566 ± 0.416	6	0.101 ± 0.059
		late juveniles	0.64 ± 0.17	6	0.418 ± 0.355	0.343 ± 0.248	6	0.074 ± 0.008
		adults	2.07 ± 0.63	6	0.060 ± 0.026	0.025 ± 0.010	6	0.062 ± 0.019
Ω	low	early juveniles	0.29 ± 0.11	5	0.053 ± 0.061	0.065 ± 0.028	6	0.072 ± 0.071
		late juveniles	0.38 ± 0.06	6	0.029 ± 0.016	0.028 ± 0.015	6	0.054 ± 0.015
		adults	1.77 ± 0.69	4	-0.020 ± 0.030	-0.004 ± 0.007	5	0.060 ± 0.012
	high	early juveniles	0.35 ± 0.10	6	0.829 ± 0.695	0.590 ± 0.471	6	0.076 ± 0.029
		late juveniles	0.69 ± 0.19	6	0.349 ± 0.235	0.259 ± 0.149	6	0.056 ± 0.006
		adults	1.49 ± 0.83	6	0.087 ± 0.101	0.037 ± 0.047	6	0.066 ± 0.031
temperature	low	early juveniles	0.08 ± 0.05	3	0.039 ± 0.122	0.060 ± 0.141	3	0.374 ± 0.243
		late juveniles	0.13 ± 0.03	4	0.077 ± 0.105	0.037 ± 0.058	4	0.167 ± 0.046
		adults	0.26	1	-0.006	-0.001	1	0.156
	high	early juveniles	0.07 ± 0.02	4	0.073 ± 0.092	0.078 ± 0.096	4	0.510 ± 0.115
		late juveniles	0.11 ± 0.07	6	0.062 ± 0.059	0.035 ± 0.017	6	0.406 ± 0.233
		adults	0.81	1	0.159	0.039	1	0.161
combined	low	early juveniles	0.14 ± 0.02	4	-0.031 ± 0.089	-0.017 ± 0.054	4	0.090 ± 0.077
		late juveniles	0.34 ± 0.16	6	-0.038 ± 0.104	-0.025 ± 0.070	6	0.167 ± 0.140
		adults	1.36 ± 0.14	2	-0.014 ± 0.035	-0.007 ± 0.016	2	0.127 ± 0.026
	high	early juveniles	0.14 ± 0.04	5	0.043 ± 0.071	0.038 ± 0.047	5	0.151 ± 0.095
		late juveniles	0.42 ± 0.12	6	0.030 ± 0.072	0.021 ± 0.056	6	0.090 ± 0.015
		adults	0.81 ± 0.26	3	-0.042 ± 0.016	-0.015 ± 0.005	3	0.125 ± 0.026

Supplementary Table 5: Linear mixed effect models for change in tissue coverage, feeding, prey capture, calcification and respiration rates of *Caryophyllia huinayensis*. Significant p-values are shown in bold.

Fixed effects	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Tissue coverage						
treatment	54969	18323	3	11	19.579	**<0.001**
life stage	128653	64327	2	414	68.737	**<0.001**
feeding	5183	5183	1	11	5.538	**0.038**
Feeding rate						
treatment	261.51	87.17	3	11.90	1.539	0.256
life stage	192.56	96.28	2	98.60	1.700	0.188
feeding	2160.30	2160.30	1	11.56	38.132	**< 0.001**
Prey uptake rate						
treatment	0.032	0.011	3	12.23	1.16	0.365
life stage	0.410	0.205	2	99.47	22.09	**< 0.001**
feeding	0.246	0.246	1	11.14	26.44	**< 0.001**
Calcification (model 1: after 6 months)						
treatment	0.287	0.096	3	11.92	2.400	0.119
life stage	1.038	0.519	2	96.36	13.018	**< 0.001**
feeding	0.204	0.204	1	11.80	5.109	**0.044**
Calcification (model 2: after 1 and 3 months)						
duration	0.472	0.472	1	136.66	24.265	**< 0.001**
Respiration (after 6 months)						
treatment	0.595	0.198	3	7.90	24.382	**< 0.001**
life stage	0.038	0.019	2	95.37	2.322	0.104
feeding	0.015	0.015	1	7.60	1.799	0.219

Supplementary Table 6: Post hoc tests for linear mixed effect models for change in tissue coverage, feeding, prey capture, calcification and respiration rates of *Caryophyllia huinayensis*. Only relevant results are displayed here. Significant p-values are shown in bold.

Fixed effects	Contrast	Estimate	SE	df	t ratio	p value
Tissue coverage						
treatment	ambient - combined	25.91	6.35	11	4.082	**0.008**
	ambient - Ω	0.73	6.35	11	0.115	0.999
	ambient - temperature	40.45	6.35	11	6.374	**<0.001**
	combined - Ω	-25.18	6.35	11	-3.967	**0.010**
	combined - temperature	14.55	6.35	11	2.292	0.159
	Ω - temperature	39.72	6.35	11	6.259	**<0.001**
life stage	adult - late juvenile	-33.69	3.61	414	-9.346	**<0.001**
	adult - early juvenile	-38.95	3.61	414	-10.805	**<0.001**
	late juvenile - early juvenile	-5.26	3.61	414	-1.459	0.312
feeding	low - high	10.60	4.49	11	2.353	**0.038**
Feeding rate						
treatment	ambient - combined	-5.12	3.15	10.54	-1.627	0.406
	ambient - Ω	-5.52	3.02	9.04	-1.830	0.321
	ambient - temperature	-5.51	3.28	12.34	-1.682	0.373
	combined - Ω	-0.40	3.15	10.60	-0.128	0.999
	combined - temperature	-0.39	3.38	13.64	-0.117	0.999
	Ω - temperature	0.01	3.28	12.38	0.002	1.000
life stage	adult - late juvenile	2.80	1.82	98.20	1.539	0.277
	adult - early juvenile	0.20	1.84	97.80	0.108	0.994
	late juvenile - early juvenile	-2.60	1.64	97.60	-1.584	0.257
feeding	low - high	13.9	2.25	10.80	6.156	**<0.001**
Prey uptake rate						
treatment	ambient - combined	-0.04	0.028	10.5	-1.273	0.598
	ambient - Ω	-0.04	0.025	7.8	-1.533	0.464
	ambient - temperature	-0.05	0.030	14.5	-1.531	0.446
	combined - Ω	0.00	0.028	10.6	-0.132	0.999
	combined - temperature	-0.01	0.032	16.9	-0.339	0.986
	Ω - temperature	-0.01	0.030	14.6	-0.234	0.995
life stage	adult - late juvenile	-0.04	0.023	99.2	-1.791	0.178
	adult - early juvenile	-0.15	0.024	98.7	-6.200	**<0.001**
	late juvenile - early juvenile	-0.10	0.021	98.3	-4.970	**<0.001**
feeding	low - high	0.10	0.020	10.2	5.095	**<0.001**

Supplementary Table 6 (continued)

Fixed effects	Contrast	Estimate	SE	df	t ratio	p value
Calcification (model 1: after 6 months)						
treatment	ambient - combined	0.24	0.117	10.6	2.090	0.217
	ambient - Ω	-0.01	0.115	10.0	-0.064	1.000
	ambient - temperature	0.19	0.120	11.7	1.580	0.426
	combined - Ω	-0.25	0.117	10.7	-2.149	0.199
	combined - temperature	-0.05	0.121	12.2	-0.452	0.968
	Ω - temperature	0.20	0.120	11.7	1.640	0.395
life stage	adult - late juvenile	-0.16	0.049	95.8	-3.261	**0.004**
	adult - early juvenile	-0.25	0.050	95.4	-5.095	**<0.001**
	late juvenile - early juvenile	-0.09	0.044	95.6	-2.116	0.092
feeding	low - high	0.19	0.084	10.9	2.259	**0.045**
Calcification (model 2: after 1 and 3 months)						
duration	1 month - 3 months	0.08	0.017	136	4.924	**<0.001**
Respiration (after 6 months)						
treatment	ambient - combined	-0.05	0.034	10.4	-1.447	0.500
	ambient - Ω	0.02	0.032	8.8	0.473	0.963
	ambient - temperature	-0.26	0.036	12.9	-7.381	**<0.001**
	combined - Ω	0.06	0.034	10.5	1.895	0.287
	combined - temperature	-0.21	0.037	14.3	-5.850	**<0.001**
	Ω - temperature	-0.28	0.036	13.0	-7.797	**<0.001**
life stage	adult - late juvenile	0.00	0.022	99.5	-0.112	0.993
	adult - early juvenile	-0.04	0.022	99.0	-1.789	0.179
	late juvenile - early juvenile	-0.04	0.020	99.2	-1.889	0.147
feeding	low - high	0.03	0.024	10.7	1.336	0.209

Supplementary Table 7: Feeding rates of three life stages of *Caryophyllia huinayensis* after five months under different Ω, temperature and feeding conditions. Number of ingested nauplii, prey uptake and C uptake rates of early juveniles, late juveniles and adults of *C. huinayensis* were measured after five months of the aquarium experiment (N = 1-6). The four treatment conditions are: ambient = 11 °C and $\Omega_{arag} > 1$, Ω = 11 °C and $\Omega_{arag} < 1$, temperature = 15 °C and $\Omega_{arag} > 1$, combined = 15 °C and $\Omega_{arag} < 1$. The two feeding regimes with *Artemia persimilis* nauplii are: low = 8 µg C L^{-1} and high = 87 µg C L^{-1}. The number of ingested nauplii is stated per coral and hour (nauplii $coral^{-1}$ h^{-1}). The tissue covered surface area was used as reference value for the number of ingested nauplii and uptake of prey organic matter (mg OM cm^{-2} d^{-1}). C uptake rates per hour were normalised to the coral surface area (µmol C cm^{-2} h^{-1}) and skeletal dry mass (µmol C g^{-1} h^{-1}). They were also extrapolated to one week, considering the different feeding times and food concentrations of both feeding regimes, and expressed per day. All values are stated as mean ± standard deviation.

Supplementary Table 7

Treatment	Feeding	Life stage	N	Ingested nauplii coral^{-1} h^{-1}	Prey uptake (mg OM cm^{-2} h^{-1})	C uptake (µmol C cm^{-2} h^{-1})	C uptake (µmol C cm^{-2} d^{-1})	C uptake (µmol C g^{-1} h^{-1})	C uptake (µmol C g^{-1} d^{-1})
ambient	low	early juveniles	6	3.17 ± 2.48	0.038 ± 0.025	1.04 ± 0.68	0.89 ± 0.58	9.08 ± 5.67	7.78 ± 4.86
		late juveniles	5	2.50 ± 4.32	0.009 ± 0.015	0.25 ± 0.42	0.21 ± 0.36	0.85 ± 1.23	0.73 ± 1.05
		adults	6	4.00 ± 4.73	0.005 ± 0.006	0.14 ± 0.18	0.12 ± 0.15	0.66 ± 0.79	0.56 ± 0.67
	high	early juveniles	6	14.17 ± 11.18	0.205 ± 0.205	5.68 ± 5.69	14.61 ± 14.64	33.95 ± 33.36	87.30 ± 90.92
		late juveniles	6	7.67 ± 6.38	0.046 ± 0.034	1.29 ± 0.94	3.31 ± 2.43	9.65 ± 9.23	24.81 ± 23.72
		adults	6	15.17 ± 7.78	0.018 ± 0.011	0.49 ± 0.31	1.27 ± 0.80	2.96 ± 2.22	7.60 ± 5.70
Ω	low	early juveniles	5	5.83 ± 3.06	0.071 ± 0.039	1.97 ± 1.09	1.69 ± 0.94	12.98 ± 6.17	11.12 ± 5.29
		late juveniles	6	3.83 ± 4.45	0.028 ± 0.032	0.78 ± 0.90	0.67 ± 0.77	7.54 ± 9.77	6.46 ± 8.37
		adults	4	5.40 ± 5.37	0.006 ± 0.007	0.17 ± 0.20	0.15 ± 0.17	0.84 ± 0.81	0.72 ± 0.70
	high	early juveniles	6	18.33 ± 12.61	0.276 ± 0.256	7.67 ± 7.11	19.72 ± 18.28	37.40 ± 30.22	96.18 ± 77.72
		late juveniles	6	22.33 ± 12.04	0.139 ± 0.098	3.86 ± 2.71	9.93 ± 6.98	23.21 ± 12.25	59.69 ± 31.49
		adults	6	24.00 ± 11.21	0.039 ± 0.027	1.08 ± 0.75	2.77 ± 1.92	6.27 ± 5.28	16.13 ± 13.58
temperature	low	early juveniles	3	7.67 ± 2.89	0.122 ± 0.084	3.38 ± 2.34	2.90 ± 2.00	36.84 ± 24.80	31.58 ± 21.26
		late juveniles	4	3.00 ± 2.71	0.020 ± 0.015	0.56 ± 0.42	0.48 ± 0.36	4.25 ± 3.22	3.64 ± 2.76
		adults	1	2.00	0.006	0.15	0.13	1.06	0.91
	high	early juveniles	4	25.25 ± 8.58	0.274 ± 0.125	7.62 ± 3.46	19.60 ± 8.89	61.48 ± 23.28	158.08 ± 59.86
		late juveniles	6	16.50 ± 18.77	0.119 ± 0.152	3.29 ± 4.21	8.47 ± 10.83	32.59 ± 49.24	83.80 ± 126.63
		adults	1	24.00	0.028	0.78	2.02	4.66	12.00
combined	low	early juveniles	4	3.75 ± 1.71	0.054 ± 0.043	1.51 ± 1.19	1.29 ± 1.02	12.34 ± 8.31	10.58 ± 7.13
		late juveniles	5	7.80 ± 3.70	0.046 ± 0.020	1.27 ± 0.55	1.09 ± 0.47	13.51 ± 4.99	11.58 ± 4.28
		adults	2	1.50 ± 2.12	0.002 ± 0.003	0.05 ± 0.07	0.05 ± 0.06	0.40 ± 0.57	0.34 ± 0.49
	high	early juveniles	5	24.00 ± 7.25	0.293 ± 0.110	8.14 ± 3.05	20.93 ± 7.83	68.27 ± 15.56	175.56 ± 40.01
		late juveniles	6	16.67 ± 4.80	0.095 ± 0.020	2.65 ± 0.55	6.81 ± 1.41	24.72 ± 4.60	63.57 ± 11.84
		adults	3	19.67 ±2.52	0.028 ± 0.007	0.77 ± 0.18	1.97 ± 0.47	4.54 ± 1.19	11.68 ± 3.06

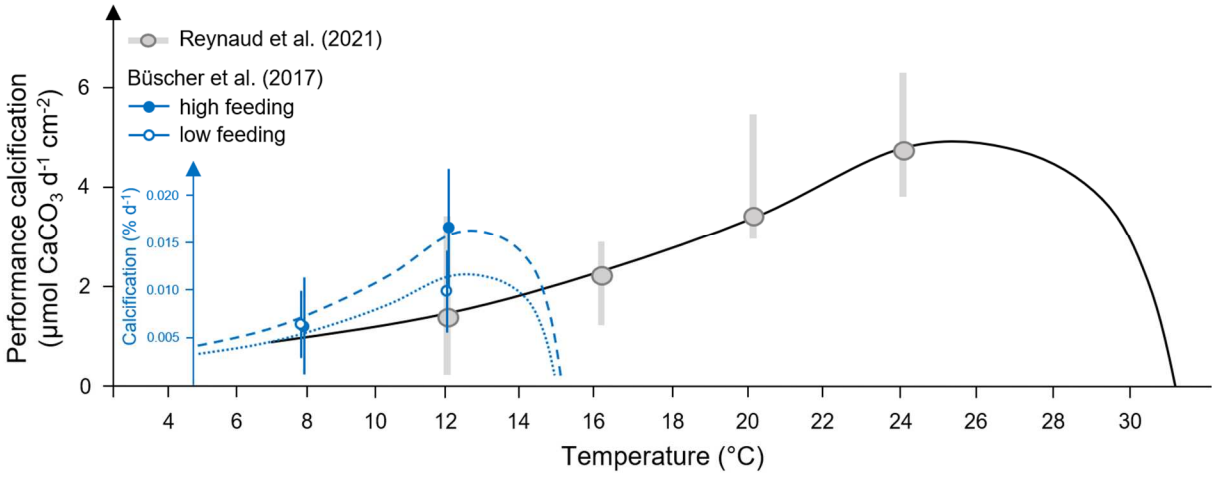
Supplementary Discussion

Metabolic depression: The decreasing respiration rates of juvenile corals under ambient temperature may indicate that they downregulated their metabolism over the course of the experiment (Supplementary Figure 8). While the respiration rates differed between the two feeding regimes at the beginning of the experiment, they were reduced to a similarly low level at the end. Even though this trend is small and the corals still received enough energy to maintain their calcification, this may indicate a depression and change of their metabolism. Reduced respiration rates of *L. pertusa* were also observed after long-term starvation periods of six months, which indicates a downregulation of its metabolism under resource limitation (Larsson et al., 2013; Baussant et al., 2017). This can either mean that less energy was available at the end of the present experiment or that the available energy was invested into other processes instead.

Highest respiration rates of *C. huinayensis* at 15 °C provide evidence for an increased metabolic activity at elevated temperature, which affects the energy budget of the corals, as has been shown for *L. pertusa* (Dodds et al., 2007; Dorey et al., 2020; Gómez et al., 2022), however on much shorter timescales of a few days. Due to the low number of replicates at the end of the experiment and the decrease in tissue covered surface area, the respiration rates are variable, but nevertheless these high respiration rates suggest a sensitivity and inability to compensate for a long-term temperature change to 15 °C (Dodds et al., 2007).

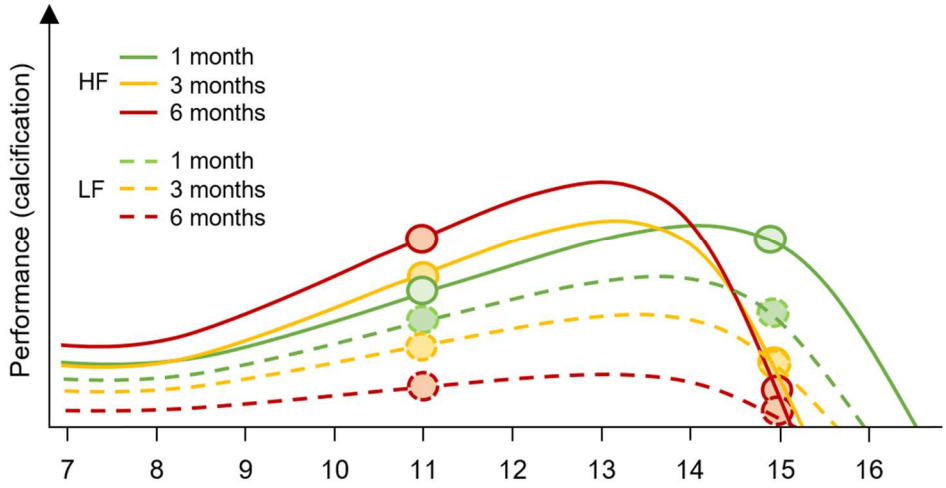
Lower thermal limits and no detectable feeding effect: A number of studies (Larsson et al., 2013; Baussant et al., 2017; Büscher et al., 2017) observed no effect of different feeding regimes on calcification rates of *L. pertusa*, which is a bit unexpected. One aspect that we already discussed in the main text may be that corals aim for a certain calcification rate, and once this is reached, no more energy is channelled into calcification. Another explanation could be that feeding studies did not allow corals to efficiently extract the provided food (e.g. by not keeping food particles in suspension or due to active predator avoidance by the prey). Under such conditions, the actual differences in capture rates at the different densities are diminished and thus, could not fuel the corals metabolism to the same extent as the administered food density. However, the metabolic rates reflect the increase in food uptake to some degree in the mentioned studies. Furthermore, additional feeding resulted in increased (though not significantly different) calcification rates at elevated temperatures (Büscher et al., 2017). Here, thermal performance curves (TPC) could provide further insights and show how they shift under different food levels. The most comprehensive thermal performance to date was evaluated for *Dendrophyllia ramea* (Reynaud et al., 2021). We fitted a thermal performance curve to their data (at the higher temperature ranges we approximated the shape based on typical TPC due to missing data), used the TPC shape to fit it to the thermal optimum range described for *L. pertusa* (12-14 °C; Brooke et al., 2013) and further modulated the performance range to simulate different food densities (Supplementary Figure 9). The obtained performance at 8 and 12 °C as well as low and high

food densities resembles the response observed in Büscher et al. (2017) with no discernible differences in calcification rate at 8 °C but elevated rates and differences between feeding regimes at 12 °C. Since the other studies (Larsson et al., 2013; Baussant et al., 2017) used similarly low temperatures (7.5 °C) close to the critical lower temperature, the same effect as in Büscher et al. (2017) may account for similar calcification rates despite different food concentrations. The feeding levels in previous studies may have been too low, which is why, together with the generally high variability of calcification rates, no measurable effect was detected. This does not mean an effect would emerge once we increase the number of individuals studied and the difference between treatment conditions. However, we want to stress the critical importance of TPC to better understand observed responses. We provide a potential explanation, nevertheless, actual performance assays with CWCs are needed to confirm our hypothesis with an additional more detailed assessment of the upper critical thermal limit of different CWC species.



Supplementary Figure 9: Thermal performance curves for cold-water corals. Based on the thermal performance study of Reynaud et al. (2021) with *Dendrophyllia ramea* over a period of two years (grey points reflect median calcification rates in µmol $CaCO_3$ cm^{-2} d^{-1} and light grey boxes the observed interquartile range), we fitted a typical performance curve (black line, (Sinclair et al., 2016). Further, we used the shape of this curve to fit it to the thermal optimum range of *L. pertusa* (12-14 °C; Brooke et al., 2013) and simulated two different feeding regimes (dashed blue line: high feeding, dotted blue line: low feeding). Blue filled and open points represent the measured calcification rates (mean ± SD in % d^{-1}, blue y-axis) of *L. pertusa* under two different feeding regimes (high and low feeding, respectively) at 8 °C and 12 °C (Büscher et al., 2017).

We fitted a similar curve as derived from Reynaud et al. (2021) to our measured calcification rates of early juvenile corals at ambient and elevated temperature (at aragonite oversaturation; Supplementary Figure 10) and compared the curve for the two different feeding regimes after one, three and six months. This reflects the ability of the corals of the HF regime to sustain calcification at ambient temperatures but only in the short-term at elevated temperatures (Supplementary Figure 10). It also suggests that *C. huinayensis* can even sustain short-term temperatures beyond 16 °C, but this is still very speculative until actual performance assays tested this hypothesis.



Supplementary Figure 10: Hypothetical thermal performance curve for *Caryophyllia huinayensis* and their temporal changes at two different feeding regimes. Solid lines are the thermal performance curves for high (HF) and dashed lines for the low (LF) feeding regime. The colours indicate their temporal changes after one (green), three (yellow) and six (red) months.

3

Manuscript 2:

Environmental stability and phenotypic plasticity benefit the cold-water coral *Desmophyllum dianthus* in an acidified fjord

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Key words: calcification, growth, respiration, reciprocal transplantation, temperature variability, acclimatization

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Abstract

The stratified Chilean Comau Fjord sustains a dense population of the cold-water coral (CWC) *Desmophyllum dianthus* in aragonite supersaturated shallow and aragonite undersaturated deep water. This provides a rare opportunity to evaluate trade-offs of CWC physiological performance in response to physico-chemical drivers and their variability. Here, we combined year-long reciprocal transplantation experiments along natural oceanographic gradients with an *in situ* assessment of CWC calcification and respiration. Following transplantation, corals acclimated fast to the novel environment with no discernible difference between native and novel (i.e. cross-transplanted) corals, demonstrating high phenotypic plasticity. Surprisingly, corals exposed to lowest aragonite saturation (Ω_{arag} < 1) and temperature (T < 12.0 °C), but stable environmental conditions, at the deep station grew fastest. We found an inverse relationship between calcification rates and environmental variability and propose to consider the high frequency fluctuations of abiotic and biotic factors to better predict the future of CWCs in a changing ocean.

Introduction

Scleractinian cold-water corals (CWCs) are important ecosystem engineers providing a three-dimensional habitat in cold and deep waters comparable to the complexity of shallow tropical coral reefs. CWCs sustain high levels of biodiversity and provide important nursery grounds for numerous benthic and fish species (Roberts et al., 2009; Baillon et al., 2012; Försterra et al., 2017). The distribution of CWCs is controlled i.a. by seawater carbonate chemistry, temperature, salinity, oxygen concentration, food availability and substrate topography (Wisshak et al., 2005; Roberts et al., 2009; Davies et al., 2011; Thresher et al., 2011; Lunden et al., 2013; Flögel et al., 2014; Georgian et al., 2016a; Försterra et al., 2017; Hanz et al., 2019). Like tropical corals, CWCs cope with environmental variability through adaptive mechanisms, which makes them particularly vulnerable to rapid anthropogenic changes, especially ocean warming, acidification (Guinotte et al., 2006; Hoegh-Guldberg et al., 2007) and deoxygenation (Försterra et al., 2014; Hanz et al., 2019; Hebbeln et al., 2020).

The physiological response of CWCs to changing temperature, pH and aragonite saturation (Ω_{arag}) has so far been mainly investigated in laboratory studies under controlled conditions (Hennige et al., 2015; Georgian et al., 2016b; Gori et al., 2016; Büscher et al., 2017; Kurman et al., 2017; Martínez-Dios et al., 2020). However, laboratory studies are usually conducted under constant conditions and do not consider the variability of environmental conditions that corals experience in their natural habitat. Some previous studies investigated the physiology of CWCs *in situ* (Jantzen et al., 2013a; Büscher et al., 2019; Rossbach et al., 2021), but only few studies considered the seasonal differences in biotic and abiotic parameters or the small-scale environmental heterogeneities in the habitat of CWCs (Rodolfo-Metalpa et al., 2015; Maier et al., 2020). The few available *in situ* measurements show that temperature, salinity, oxygen and pH vary seasonally and even daily in response to tides, internal waves and advection

(Mienis et al., 2007, 2014; Findlay et al., 2013; Georgian et al., 2016a; Juva et al., 2021), suggesting that the environment of CWCs is far less uniform than previously assumed. However, the lack of *in situ* data limits our ability to assess the extent and ability of CWCs to cope with fluctuating environmental conditions. The physiological response of marine organisms to variable conditions may differ from their response to constant environmental conditions, as has been shown for phytoplankton and mussels (Bernhardt et al., 2018; Morash et al., 2018; Marshall et al., 2021). This suggests that the physiological response of CWCs (Jantzen et al., 2013a; Rodolfo-Metalpa et al., 2015) and other organisms (Morash et al., 2018; Marshall et al., 2021) in laboratory experiments acclimated to stable environmental conditions may not match their physiological performance in natural, varying environments. Organisms from an environment with greater variability may have enhanced tolerance to changing environmental conditions (Rivest et al., 2017). Therefore, we need to improve our understanding of the impact of natural environmental variability on the resilience of corals. Several tropical coral species have already been shown to be more resistant to heat stress and less susceptible to bleaching in thermally variable environments (Oliver & Palumbi, 2011; Palumbi et al., 2014; Schoepf et al., 2015; Rivest et al., 2017). On the other hand, corals from more stable environments may be less resistant to climate change if the corals have adapted to their natural habitat (Kenkel et al., 2015). Thus, it is similarly important to know whether populations are adapted to local conditions and if this also determines their response to future changes.

In order to assess the resilience of CWCs to future climate changes, it is important to first understand their physiological performance under present day *in situ* conditions and environmental variability. Therefore, long-term studies of oceanographic conditions *in situ* are paramount to assess natural environmental variability. Species living under different environmental conditions enable us to study their acclimatization and adaptation potential and ability to deal with natural variability. Acclimatization is the ability of an organism to change its physiological performance in response to changes in environmental conditions without genetic changes (phenotypic plasticity). By contrast, adaptation represents changes in the genome in response to environmental conditions over multiple generations through natural selection (van Oppen et al., 2015). A good opportunity to study the response and acclimatization potential of corals to changing environmental conditions *in situ* are reciprocal transplantation experiments (Hereford, 2009; Sanford & Kelly, 2011). A transplantation experiment can show either (1) adaptation if the organism's performance depends on its origin and is not influenced by the environment, (2) local adaptation if the organism's performance depends on both origin and environmental conditions, or (3) acclimatization if the organism's performance depends on the environment, regardless of its origin (Hereford, 2009; Sanford & Kelly, 2011; Rocker et al., 2019). Reciprocal transplantation experiments often show local adaptation of organisms, but sometimes native organisms at the site of origin are not better adapted than organisms that were transplanted from different environments (Hereford, 2009; Sanford & Kelly, 2011). Several studies transplanted tropical corals from their

natural habitats to stations with contrasting abiotic conditions (Kenkel et al., 2015; Rocker et al., 2019; Tamir et al., 2020), but only two reciprocal transplantation experiments with CWCs have been conducted so far (Chapron et al., 2020; Rossbach et al., 2021).

The aim of this study was to investigate the physiological performance and acclimatization potential of CWCs to changing *in situ* environmental conditions. Therefore, we conducted a year-long reciprocal transplantation experiment with the CWC *Desmophyllum dianthus* in Comau Fjord (northern Chilean Patagonia, Figure 1a) in order to distinguish between long-term adaptation and short-term acclimatization to the local environment. We took advantage of the occurrence of *D. dianthus* in contrasting environments in the stratified Comau Fjord, with low salinity, high pH and oxygen concentrations in surface waters and marine conditions, but low pH and oxygen levels in deeper waters (Silva, 2008; Häussermann & Försterra, 2009; Fillinger & Richter, 2013; Jantzen et al., 2013b; Garcia-Herrera et al., 2022). Corals were collected at opposing ends of horizontal and vertical environmental gradients (head vs. mouth and shallow vs. deep; Addamo et al., 2021) and reciprocally transplanted in order to study their physiological responses to contrasting environmental conditions (Figure 1b). The vertical gradient persists with the strong environmental differences described (Fillinger & Richter, 2013; Jantzen et al., 2013b; Addamo et al., 2021), whereas the horizontal gradient is strongest in the productive summer season, but influenced by mixing in autumn and winter (Supplementary Table 1, Supplementary Figure 3). Over a one-year period, coral physiological traits were evaluated every three to four months focusing on calcification, respiration and tissue composition. In addition, tissue coverage was measured at the beginning and end of the experiment. We aimed to better understand the drivers of acclimatization and adaptation to local environmental parameters by: 1) characterising differences in environmental parameters in the natural habitat of *D. dianthus*, 2) measuring coral physiological parameters along environmental gradients and between seasons, and 3) correlating environmental conditions with *D. dianthus* calcification. Here we show that *D. dianthus* benefits from stable environmental conditions in deep waters of the fjord and is able to acclimatise quickly to a new environment after transplantation.

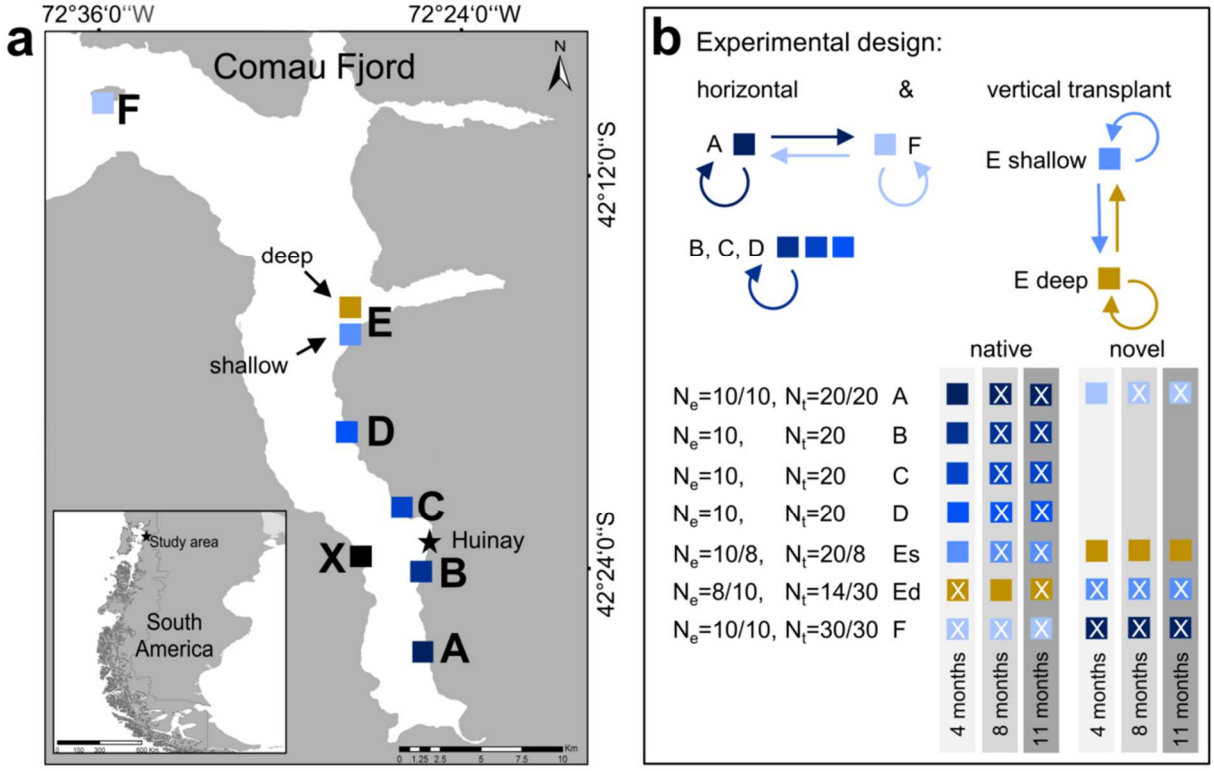

Figure 1: Experimental design and coral sampling scheme. a) Coral sampling stations in Comau Fjord, Chile: six stations at 20 m water depth (A-F shallow, blue colours) and one station at 300 m water depth (E deep, yellow). The research station in Huinay is located between station B and C (star). The CTD was deployed at 25 m water depth at the station X. b) The experimental design includes vertical and horizontal reciprocal transplantation of novel (i.e. cross-transplanted) corals between the shallow stations A and F as well as between shallow (E shallow: Es) and deep (E deep: Ed), where colours indicate the station of origin. Corals collected at stations B, C and D were only returned to their respective native station. One subset of corals (experimental corals) was used repeatedly for calcification and respiration measurements over the entire experimental period (i.e. after four, eight and eleven months; number of individuals N_e: 8-10 biologically independent samples per station and sampling time point). A second subset of corals (tissue corals) was sampled for biomass analysis after four, eight and eleven months (N_t: 6-10 biologically independent samples per station and sampling time point; see Supplementary Methods and Results). The tissue corals were initially sampled for the same time points as experimental corals, but due to logistical problems could only be obtained for the time points and stations marked with an X.

Material and Methods

Study site and organisms

Comau Fjord in the northern part of Chilean Patagonia has a total length of about 45 km, a width of 2-8.5 km and a maximum depth of almost 500 m near the mouth (Häussermann et al., 2012). It is characterized by a high tidal range of up to 7.5 m (Häussermann & Försterra, 2009). Throughout the Chilean fjord region, high precipitation and glacial melt lead to substantial freshwater runoff, causing strong stratification with a superficial low salinity surface water layer down to 7-15 m depth and a marine subsurface layer below (Häussermann & Försterra, 2009; Fillinger & Richter, 2013; Garcia-Herrera et al., 2022). As a result of high inputs of terrigenous organic material and its subsequent degradation at depth, the marine layer is low in oxygen (as low as 40-50 % saturation) and pH (<7.7; Silva, 2008; Garcia-Herrera et al., 2022).

In Comau Fjord, the cosmopolitan, azooxanthellate CWC species *Desmophyllum dianthus*, typically a deep-sea species, is found at exceptionally shallow depths of up to 15 m (Försterra et al., 2005; Häussermann & Försterra, 2009). It is the most abundant coral species in the Chilean fjord region, with densities of more than 1500 specimens m^{-2} below 25 m depth and provides habitat for a diverse benthic community (Försterra et al., 2005; Häussermann & Försterra, 2007; Försterra et al., 2017). *Desmophyllum dianthus* is a pseudo-colonial species with aclonal individuals that can grow on top of each other (Försterra et al., 2005), but tend to be solitary in shallow waters of the fjord. In Comau Fjord, *D. dianthus* mainly grows under overhangs, the underside of rocks and on the steep fjord walls with the calyx oriented downward (Försterra & Häussermann, 2003; Cairns et al., 2005; Försterra et al., 2005), presumably to prevent negative effects of high sedimentation rates in this region. The distribution of *D. dianthus* across a wide range of environmental conditions provides a rare opportunity to study the response of CWCs to contrasting conditions.

Environmental data

At each coral station (Figure 1a), water temperature was recorded (Tidbit v2 logger, ONSET computers, Bourne, USA; 0.2°C resolution; attached to one of the coral plates) in 15 min intervals over the whole study period (September 2016 – August 2017). Salinity was measured with a CTD (SBE 19 plus, V2 SeaCAT profiler, Sea-Bird Scientific, Bellevue, USA; internal sensors: temperature, conductivity, pressure; external sensor: oxygen sensor SBE 43, Sea-Bird Scientific, Bellevue, USA) once during each season (January, May and August 2017). In addition to the coral stations, temperature and salinity were also measured every 30 min. with a CTD (AML plus X, AML Oceanographic, Dartmouth, Canada; internal sensors: conductivity and temperature, CT-Xchange; pressure, Xchange p.x) at 25 m depth at station X (Figure 1a) between September 2016 and August 2017. Discrete water samples for total alkalinity (TA), dissolved inorganic carbon (DIC), and nutrient concentrations (phosphate, nitrate, silicate) were taken once per season at the coral stations with a Niskin bottle close to the experimental

corals (max. distance 2 m). Samples for TA (50 ml) were filtered through glass microfiber filters (GF/F, 0.7 µm pore size; Whatman, GF Healthcare Life Sciences, Amersham, United Kingdom) and kept at 4 °C until analysis within latest seven days. TA was determined in four replicate Gran titrations with 0.01 M HCl using a TW alpha plus titrator (SI Analytics, Xylem Analytics, New York, USA) and corrected for Dickson standard seawater (batch 102). Samples for DIC measurements (4.5 ml) were sterile filtered through polycarbonate membrane filters (0.2 µm pore size) and poisoned with 2 µl saturated $HgCl_2$ before storing them at 4 °C until analysis. DIC was determined in two replicate samples each measured twice using a QuAAtro39 AutoAnalyser with a XY-2 autosampler (Seal Analytical GmbH, Norderstedt, Germany) and the software AACE (version 7.09). $NaHCO_3$ standards were measured for calibration and to correct the measurements for the methodological drift and samples were corrected with Dickson seawater (batch 161). Nutrient samples (50 ml) were sterile filtered through glass microfibre filters (GF/F, 0.2 µm pore size; Whatman, GF Healthcare Life Sciences, Amersham, United Kingdom) and immediately frozen (-20 °C) until analyses at the Pontificia Universidad Católica de Valparaíso with an autoanalyzer (Technicon AutoAnalyzer, Seal Analytical Inc., Wisconsin, USA) after Atlas et al. (1971). Seawater carbonate chemistry parameters (pH, pCO_2, Ω_{arag}, carbonate ion concentrations [CO_3^{2-}]) were calculated from the measured TA, DIC and nutrient concentrations at the experimental water temperature, salinity and pressure using the program CO2SYS (Pierrot et al., 2006) with the dissociation constants for carbonic acid in seawater (K_1 and K_2) of Lueker et al. (2000), for hydrogen sulphate of Dickson (1990) and for boric acid of Uppström (1974) and pH on the total scale.

Experimental design

This field study combined an environmental assessment with coral physiological investigations, including both continuous and discrete measurements. A total of six shallow sampling stations were selected at approx. 20 m water depth, all located on the steep eastern walls of Comau Fjord, spanning a spatial gradient from the mouth to the head of the fjord (Figure 1a). In addition to the shallow stations, a deep station at E was established at about 300 m depth (Figure 1a), coinciding with the vertical pH minimum (Fillinger & Richter, 2013; Jantzen et al., 2013b). The *in situ* physiological assessment of *D. dianthus* was initiated in September 2016 and included a year-long investigation of corals at all seven stations and a reciprocal transplantation experiment between four stations. At regular intervals (every three to four months), the same coral specimens were collected for measurements of their key metabolic responses in terms of calcification and respiration rates (Figure 1b).

In shallow waters of Comau Fjord, corals were collected by scientific SCUBA divers who carefully chiselled the corals from the fjord wall. Corals were collected in ambient water in 1 L closed plastic containers to avoid a potential osmotic shock in the low salinity surface layer while ascending. Care was taken not to expose them to light during transportation on the boat to the research station. The divers drilled holes into the bare rock using a pneumatic drill-hammer (Atlas Copco DKR 36; bit: 10 mm, Atlas Copco, Nacka, Stockholm, Sweden) and

inserted and securely fixed plastic holders with stainless-steel bolt anchors (FAZ II 10/30 A4, Fischerwerke GmbH & Co. KG, Waldachtal, Germany) on the fjord wall at the shallow stations to re-install the corals in their natural downward orientation (Figure 2a). The corals were fixed with polyamide screws on special plastic plates (two to three plates per station, max. 34 corals on each plate; Figure 2) that were mounted on these holders. The natural density of *D. dianthus* in the fjord was taken into account for the spacing of corals on the plates. However, the spacing on the plates might have been slightly larger than in their natural habitat to facilitate handling and avoid damaging the corals. These plates allowed to re-collect (as well as re-install) subsamples of the corals during each season without disturbing the remaining corals on the other plates. The plates with the corals fitted into black watertight Peli cases (Pelican Products Inc., Torrance, USA) filled with seawater (volume: 80 L) in which they were transported underwater and which protected the corals from the low salinity surface layer as well as from daylight exposure during transport on the boat to the laboratory facilities at the research station. Corals at the deep station were sampled at 280-290 m depth using a remotely operated vehicle (Commander 2, Mariscope Ingeniería, Puerto Montt, Chile; modified with manipulator arms and high-resolution camera) with a wire frame and a bag attached to scrape the corals from the wall and collect them in a 2 m long bag that allowed to insulate the corals on their way through the low salinity surface layer. We do not expect that the corals were differently affected by the two collection techniques, especially given the short sampling period compared to the long experimental period in the field. The few corals that were damaged during collection were not used for the transplantation experiment. On the boat, corals were transferred to a cool box (volume: 120 L) filled with seawater for transportation to the research station. At the deep station, the two coral plates were first installed at the holders of a metal rack at 20 m water depth by scientific SCUBA divers transported in the Peli case. The metal rack was attached to a pulley and subsequently lowered down to 300 m (Figure 2b and c). For the re-collection of corals at the deep station, the metal rack with the coral plates was pulled up until 20 m water depth, where the coral plates were removed by divers and transferred into Peli cases for transportation. After the measurements, coral plates were re-installed according to the installation procedure described.

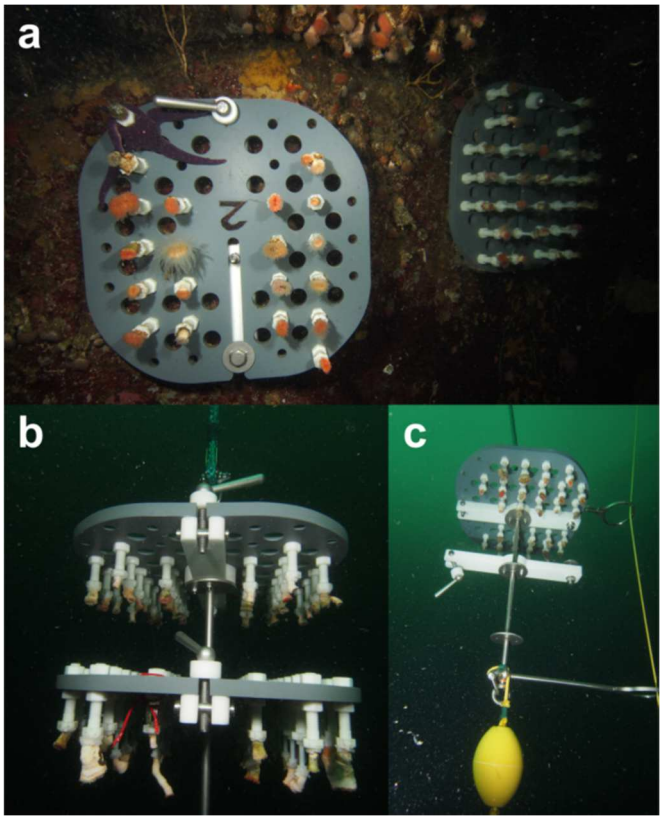

Figure 2: *Desmophyllum dianthus* on coral plates and mooring. a) Corals glued on white polyamide screws, which are fixed on grey plastic plates. The plates were fixed on a white plastic holder that was installed on the rock of a coral bank. b) and c) Corals on grey plastic plates fixed on metal rack of mooring. The metal rack was lowered on a pulley (yellow line, b) until the yellow stopper buoy reached the anchored stone at 300 m water depth.

Following the initial collection, all corals were maintained in 20-30 L flow-through aquaria filled with natural seawater pumped from 20 m water depth in front of the research station. The phenotypes of *D. dianthus* differed between the source populations in shallow and deep waters of the fjord. Some shallow corals (mainly at stations B, C and Es) were not fully covered with tissue and infested with endolithic photoautotrophic organisms (Försterra et al., 2005; Försterra & Häussermann, 2008), whereas corals at 300 m depth were often completely covered with tissue and therefore showed less signs of infestation (Supplementary Figure 6). In the laboratory, the bare skeletal parts were removed as far as possible using a submerged grinding disc attached to a rotary tool (Dremel 4000, Dremel, Breda, The Netherlands) following Rossbach et al. (2021) in order to reduce the skeletal parts of shallow corals affected by bioerosion (Försterra et al., 2005; Försterra & Häussermann, 2008). Care was taken not to damage the coral tissue inside the coelenteron. Afterwards, corals were glued on individually labelled polyamide screws (Toolcraft AG, Georgensgmünd, Germany) using underwater easy glue (Preis Aquaristik KG, Bayerfeld, Germany). Once corals were fixed, handling was only done by touching the screws to prevent any disturbance by direct contact with the corals. Maximum time for maintenance in the laboratory facilities was three weeks before the corals were returned into the fjord. Right before the first re-installation, the corals were stained with

50 mg l^{-1} Calcein for 16-19 h in order to mark the beginning of the experiment in the skeleton for further skeletal analyses that are not part of this study. Corals were either re-installed at their collection station (native) or cross-transplanted between stations (novel) where we expect the strongest differences in environmental conditions (Figure 1), i.e. stations A vs. F (head vs. mouth; horizontal gradient) and stations Es vs. Ed (shallow vs. deep; vertical gradient).

Coral physiology

In order to investigate the physiological conditions of the corals as well as seasonal adjustments along the two environmental gradients (horizontal and vertical), a total of 392 corals were collected. Corals from each station were divided in two different sets of corals for the following purposes: A) a subset was used to monitor their seasonal changes and repeatedly measure their response to changes in their natural environment (experimental corals), and B) another subset was collected seasonally to measure their biomass (tissue corals; see Supplementary Methods). The experimental corals were used to assess seasonal physiological adjustments by repeatedly measuring their response to changes in their natural environment. While experimental corals were returned into the field, the tissue corals were directly processed for further analysis.

Ten *D. dianthus* individuals were collected at each of the six shallow stations and eight individuals at the deep station in September 2016 and fixed on screws (see above). For cross-transplantation, another ten corals were sampled at the shallow stations A, F and Es and eight corals at the deep station Ed. This gives a total of 68 native corals along the environmental gradient and at depth and 38 novel corals at shallow and deep stations (experimental corals). Overall, only individuals of similar size were sampled in order to reduce the size bias in calcification rates (oral diameter: 18.10 ± 4.47 mm).

Calcification and respiration rates were determined seasonally after four, eight and eleven months in austral summer (January 2017), autumn (May 2017) and winter (August 2017), respectively, using the same experimental corals for each station. For this purpose, corals were transported to the research station, unscrewed from the plates and carefully cleaned with a soft tooth brush to remove attached fouling organisms on the screws and bare skeleton. Corals were in the laboratory for a maximum of seven days before re-exposure.

Respiration rates were determined through closed-cell incubations immediately after re-collection of the corals without acclimatisation to laboratory conditions. The corals were screwed into the lid of 800 ml Schott vials filled to the brim with 100 µm filtered seawater (in order to remove larger plankton organisms and particles) and vials were closed hermetically. Two Schott vials without corals were used as seawater controls to measure background plankton oxygen consumption. Magnetic stir bars were put into all vials to provide water circulation. The vials were placed in a temperature-controlled water bath (temperature: 12.75 ± 1.44 °C, salinity: 32.1 ± 0.3) on a multi-position magnetic stirrer (MIX 15, 2mag AG, München Germany; stirring rate: 170 rpm). Due to logistical reasons, the temperature of the

water bath was controlled by a temperature-controlled room and small temperature differences (< 0.5 °C) between shallow stations were not taken into account as they are within the error of the thermostat. We also did not take into account the larger temperature differences between shallow and deep (up to 2 °C in summer and autumn) as we preferred to use uniform temperatures that deviate from *in situ* temperatures for reasons of standardisation and due to logistical reasons. Therefore, respiration measurements were conducted at standardised conditions, approximately representing water temperatures of shallow stations at the end of each season and seasonally increasing from 11.76 ± 1.63 °C in austral winter, 12.19 ± 0.63 °C in autumn and 14.16 ± 0.43 °C in summer (with more variable temperature conditions in winter as the temperature control system was not working well). This resulted in a seasonally standardised assessment of metabolic rates, which is not related to *in situ* temperature. Due to this standardisation and because we do not know the temperature performance curves of *D. dianthus*, the temperature change between *in situ* and incubation temperature can lead to either an under- or overestimation of the respiration rates of deep corals. Nevertheless, it allows a direct comparison of the metabolic potential of corals between stations. Corals were incubated for 6 hours in the dark. Oxygen (HQ40D multimeter with LDO-101 sensor, Hach Lange GmbH, Düsseldorf, Deutschland), pH (WTW pH 3310, Xylem Analytics, New York, USA) and salinity (WTW cond 3110, Xylem Analytics, New York, USA) were measured prior to the incubation. The oxygen probe was calibrated using 100 % air-saturated water and the pH sensor was calibrated using pH buffers 4, 7 and 10 (WTW, Xylem Analytics, New York, USA) prior to measurements. Oxygen consumption (ΔO_2) was derived from the difference in O_2 concentration of the seawater at the beginning and end of the incubations after the background plankton respiration measured in the control vials was subtracted. Respiration rates were normalised to the tissue covered surface area of the corals (see below) and expressed as daily rates (µmol cm^{-2} d^{-1}). However, respiration rates were only measured once at the end of each season and unlike calcification rates, they do not represent the performance of the corals over the entire season.

Initial coral mass (with and without screws and glue) was determined in September 2016 using the buoyant weighing technique (Jokiel et al., 1978). Subsequently, calcification rates were assessed seasonally by measuring buoyant weight one day after re-collection and respiration measurements of the corals. For each coral individual, the buoyant weight was determined with a precision balance (Sartorius CPA 225D-OCE, Sartorius AG, Göttingen, Germany; precision: 0.01 mg) mounted on a platform above a small aquarium filled with seawater from the fjord. Corals were weighed in a metal weighing basket attached to the underfloor unit of the balance and after allowing the corals to acclimate for 15 min. to the water temperature and salinity in the small aquarium. Water temperature (ama-digit ad 15^{th}, Amarell GmbH & Co. KG, Kreuzwertheim, Germany) and salinity (WTW cond 3110, Xylem Analytics, New York, USA) were recorded for the subsequent calculation of seawater density and skeletal dry mass after Jokiel et al. (1978).

Skeletal aragonite density for *D. dianthus* (2.793 ± 0.026 g cm^{-3}) was derived from nine experimental corals from stations A and F with overlapping density values after Davies (1989) with some slight modifications. For this purpose, the coral tissue was separated from the skeleton using an airbrush (Starter Class set, Revell GmbH, Bünde, Germany) connected to pressurised air at 5 bar and afterwards, bare skeletons were bleached in a 6% sodium hypochlorite solution for 48 hours, changing the solution once after 24 hours. The corals were split lengthwise and one half of the skeleton of each specimen was used for measurements of the skeletal density. The buoyant weight of the skeleton in seawater was determined three times before rinsing the skeleton with reverse osmotic water (conductivity: 18.0 MΩcm; Sartorius arium pro, Sartorius AG, Göttingen, Germany) and drying to constant mass at 60°C for about three weeks.

Seasonal calcification rates were calculated as the difference between skeletal dry mass at the beginning and end of austral summer (September 2016 – January 2017), autumn (January 2017 – May 2017) and winter (May 2017 – August 2017) per tissue covered coral surface area (see below) and expressed per day (mg cm^{-2} d^{-1}) using the following equation:

$$G\ (\mathrm{mg\ CaCO_3\ cm^{-2}d^{-1}}) = \frac{(M_{t+1}-M_t)\times 1000}{A_{coral}\times t}$$

where M_t and M_{t+1} are the skeletal dry mass (g) of the specimen at the beginning and the end of each growth period, t is the exposure time in days (d) and A_{coral} is the tissue covered surface area of the coral (cm^2, see below). For comparability, calcification rates were additionally normalised to the initial skeletal dry mass at the beginning of each growth period after Orejas et al. (2011) and expressed in % d^{-1} (Supplementary Data 2 and Supplementary Figure 8). This comparison shows that it does not make much difference which reference variable is used (at least if the influence of the bare skeleton that is not covered with tissue is reduced as in the present study).

The tissue covered surface area of the experimental corals was used as reference variable for calcification (mg cm^{-2} d^{-1}) and respiration rates (µmol cm^{-2} d^{-1}). The outer tissue covered surface area of all experimental corals was measured at the end of the field study (August 2017) using a digital calliper (reading to 0.01 mm). A detailed description of the surface area measurements with a calliper can be found in the Supplementary Methods (Supplementary Figures 1 and 2). In brief, a modulated formula for a truncated cone following the geometric approximation "Advanced Geometry" by Naumann et al. (2009) was used to calculate the inner and outer surface area of the calyx based on the trumpet shape of *D. dianthus*. For this, the shape of the coral was approximated to a cup and the surface areas of the individual septa were not considered. In addition, the surface area of native and novel corals at station Ed was calculated at the end of each sampling period (January, May and August 2017) using scaled pictures of the corals with the software ImageJ (version 1.52) as the surface areas of the corals at the deep station increased largely during the year of this study (Supplementary Figures 6 and 7). Therefore, the change in tissue covered surface area was considered for the calculation of calcification and respiration rates of the deep corals. Based on the scaled images, the tissue

covered surface area of the corals at shallow stations changed only slightly and not substantially (Supplementary Figure 7). Therefore, the more accurate measurements at the end of the experiment were used for every sampling period for the shallow corals. This difference in surface area determination between shallow and deep corals did not have an essential effect on the calcification results as shown by the comparison with the calcification data normalised to the skeletal dry mass (Supplementary Figure 8). The change in tissue covered surface area of the shallow corals over the experimental time was small and the calcification rate at the beginning of the study was therefore only slightly underestimated by using the slightly larger surface area in August. In contrast, the tissue covered surface area of the deep corals was determined retrospectively in each season to minimise the larger error, as the calcification rates in January and May would otherwise have been underestimated.

Statistics and reproducibility

All statistical analyses were performed using the software R (version 4.1.0; R Core Team, 2021). As calcification and respiration data were not normally distributed (Shapiro-Wilk test), we used a linear mixed effect model (LMM; *lmer*) to examine the relationship between the response variables calcification and respiration with depth, season, station and transplantation using the R package *lme4*. For this, season, station and station*transplant were considered as fixed factors and coral specimens as random factor for a repeated measures design. One model was only run with the native corals of the shallow stations to identify changes along the horizontal gradient and between seasons. For a second model, only data of native and novel corals from stations A, F, Es and Ed were used to identify differences between native and novel corals and between depths. Post-hoc comparisons of significant effects were tested using the *lsmeans* function of the package *lsmeans*.

Long-term temperature records for each station were used to quantify the mean temperature variability for the entire year and the different seasons. To do so, temperature data were decomposed into diurnal temperature anomaly values and mean seasonal or annual variability was used as a measure of station-specific environmental variability proxy for other co-varying environmental factors such as seawater pH_T, Ω_{arag}, salinity and oxygen concentration. We used the linear model function (*lm*) in R for a multifactorial analysis to test for relationships between calcification and these environmental parameters. Mean seasonal temperature variability, temperature, pH_T, Ω_{arag}, salinity and oxygen concentration were used as fixed factors and model selection was performed using the Akaike information criterion (AIC), which was calculated using the R package *AICcmodavg*. We used AIC to go through all models from single environmental to multiple factors without inclusion of interactions. We used a linear regression approach here because we expected to be in a range of all environmental variables where calcification is approximately linearly related. We tested for normality of residuals with the Kolmogorov-Smirnov test. Model residuals were plotted and assessed for normal distribution and homoscedasticity using the *ols_test_normality* function of the R package *olsrr*.

Results

Environmental variability

The water temperature at 20 m water depth in Comau Fjord shows a mean annual temperature of 12.5 ± 0.9 °C with high frequency fluctuations at all stations (Figure 3a, Supplementary Table 1). Highest variability was found in austral summer and autumn with daily temperature fluctuations of up to 3.7 °C and maximum temperature of 16.6 °C (Figure 3a, Supplementary Table 1). CTD data from station X showed that temperature and salinity co-varied strongly throughout the year (Supplementary Figure 4). Temperature and salinity fluctuations were correlated, but the direction and strength differed with season, changing from a positive relationship from spring until autumn to a negative one in winter (Supplementary Figure 4). Salinity regularly fluctuated between 31.5 and 32.5 but occasionally also reached below 30 in winter. In contrast, water temperatures at 300 m water depth were lower and showed much less variability throughout the year with a mean temperature of 11.4 ± 0.2 °C (Figure 3a, Supplementary Table 1). In deep waters of Comau Fjord, water temperatures increased only slightly and fluctuated more in austral winter. However, in austral winter, water temperatures were higher at 300 m compared to 20 m water depth due to surface cooling and convective mixing of the upper water column. The salinity was higher at the deep station compared to all shallow stations, whereas the oxygen concentration, pH_T and Ω_{arag} were lower at 300 m compared to 20 m water depth but followed the same seasonal pattern (Figure 3b-e, Supplementary Figure 5, Supplementary Table 1).

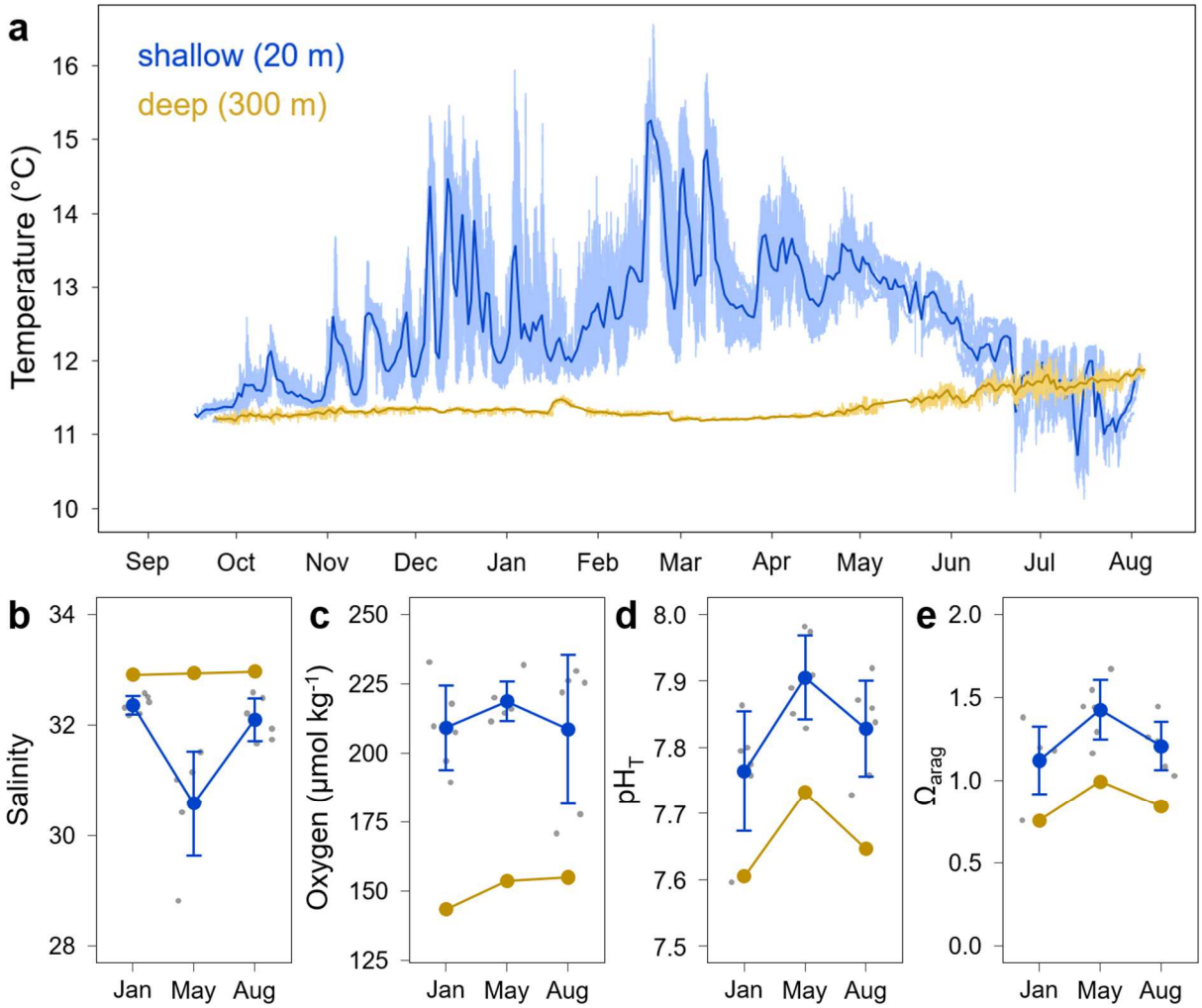

Figure 3: Seasonal environmental conditions in shallow and deep waters of Comau Fjord, Chile. a) Mean water temperature at all shallow stations at 20 m water depth (A-F, blue) and at the deep station at 300 m water depth (Ed, yellow) between September 2016 and August 2017. The light blue shaded area is the raw temperature of all six shallow stations and the yellow shaded area is the raw temperature of the deep station. The blue and yellow lines are the daily mean temperature data for all shallow stations and the deep station, respectively. b) Salinity and c) oxygen from CTD, d) seawater pH_T and e) aragonite saturation (Ω_{arag}) calculated from TA and DIC in austral summer (January), autumn (May) and winter (August). b-e) Mean ± standard deviation for all shallow stations at 20 m water depth (A-F, N = 6 independent samples) are shown in blue and conditions at the deep station at 300 m water depth (Ed, N = 1) in yellow (data points in grey).

Calcification and respiration rates of native and novel corals

Calcification and respiration rates of both native and novel (cross-transplanted) corals of *D. dianthus* were significantly higher at 300 m compared to 20 m depth (LMM; Es-Ed: p-value < 0.001, Figure 4a and b, Supplementary Tables 2-4). In shallow waters along the fjord, calcification rates were higher at the mouth of the fjord compared to the head (LMM; A-F: p-value < 0.001; Figure 4a, Supplementary Tables 2-4) and differed between seasons with lower calcification rates in austral winter (August) compared to austral summer (January) and

autumn (May; LMM; Jan-Aug and May-Aug: p-value < 0.001, Figure 4a, Supplementary Tables 2-4). Respiration rates at shallow stations were also higher at the mouth of the fjord (LMM; A-F: p-value = 0.011; Figure 4a, Supplementary Tables 2-4), but highest at station C (LMM; e.g. A-C: p-value < 0.001; Figure 4a, Supplementary Tables 2-4), and also differed between seasons with higher respiration rates in austral summer compared to autumn and winter (LMM; e.g. Jan-May: p-value = 0.007 and Jan-Aug: p-value = 0.038; Figure 4a, Supplementary Tables 2-4).

Novel corals at the shallow stations and the deep station adjusted their calcification rates to the novel environmental conditions of the respective station (LMM; transplant: p-value = 0.257, Figure 4a, Supplementary Tables 2-4). However, both native and novel corals at the deep station changed their morphology throughout the experiment and had trumpet-shaped calyxes at the end of the experiment (Supplementary Figure 4b). Novel deep corals transplanted from shallow waters were also able to expand their tissue surface area and biomass to a similar extent as the native deep corals (Supplementary Figures 6, 7 and 10). Transplantation of corals between stations had also no effect on respiration rates as novel corals at all four stations showed the same respiration rates as native corals at the same station (LMM; transplant: p-value = 0.562 Figure 4b, Supplementary Tables 2-4). Therefore, novel corals acclimatised fast to novel environmental conditions after transplantation in shallow and deep waters and showed the same physiological response as the native corals at the respective stations.

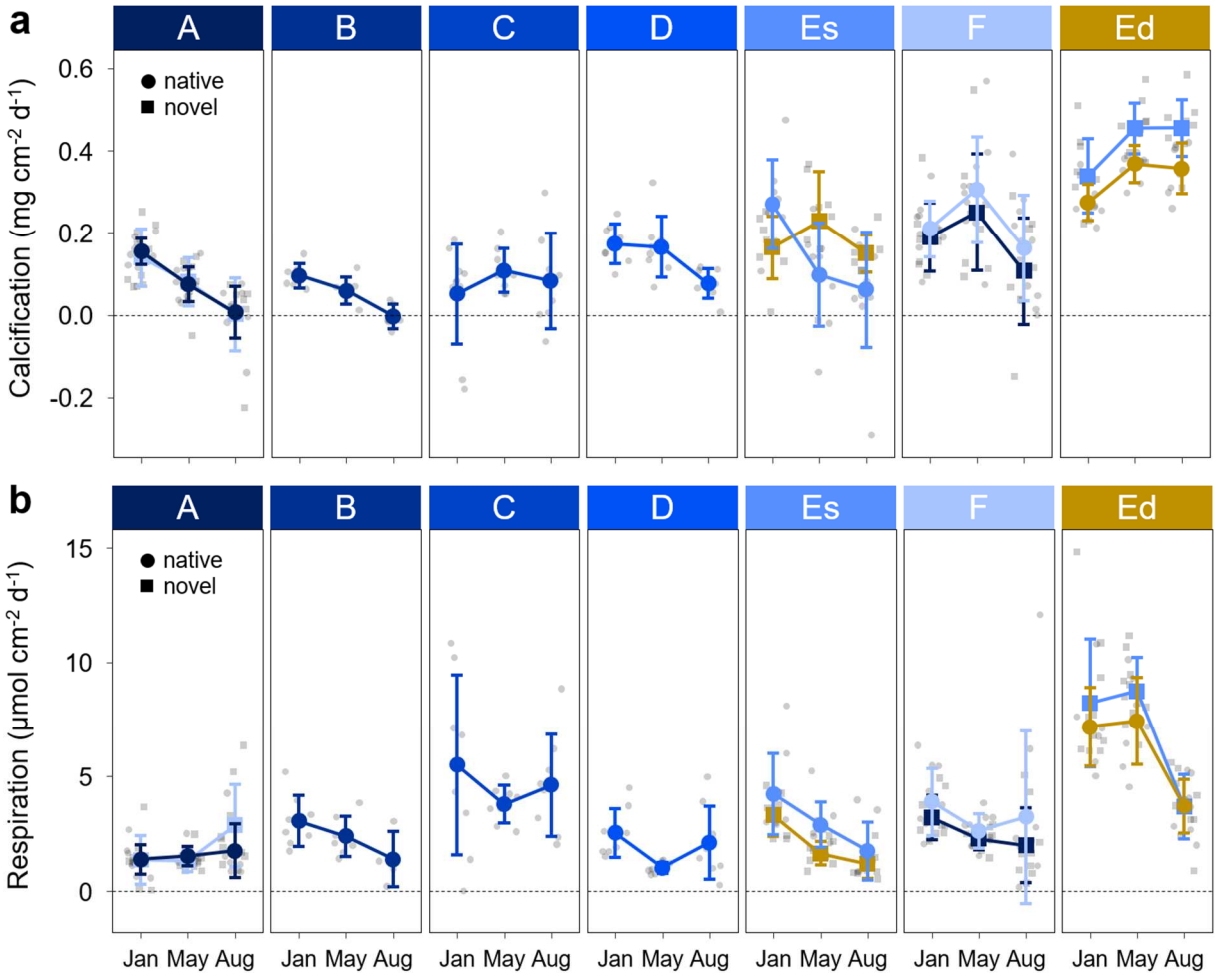

Figure 4: Seasonal physiological parameters of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. a) Calcification and b) respiration rates of *D. dianthus* (mean ± standard deviation) at six stations at 20 m water depth along the fjord from head to mouth (A-F) are shown in blue and at one station at 300 m water depth (Ed) in yellow (data points in grey). Native corals (circles) were re-installed at the same station after collection in September 2016 and novel corals (squares) were cross-transplanted between the shallow stations at the head (A) and the mouth of the fjord (F) and between shallow (Es) and deep (Ed). Calcification and respiration rates were measured after four, eight and eleven months (January, May and August 2017) using the same individuals in each season (N= 4-10 independent samples) and standardized to the tissue covered surface area of the corals at the beginning of the respective growth period. Respiration rates were measured at a standardised temperature of 12.75 ± 1.44 °C, representing water temperatures of shallow stations at the end of each season (January: 14.16 ± 0.43 °C, May: 12.19 ± 0.63 °C, August: 11.76 ± 1.63 °C) and not at *in situ* temperatures of each station.

The calcification rates of *D. dianthus* correlated with the mean annual and seasonal pH_T and Ω_{arag} in Comau Fjord at the different stations (Supplementary Figure 9a-d). However, calcification rates were highest in undersaturated conditions. Therefore, we performed a model selection with all environmental parameters including pH_T, Ω_{arag}, mean seasonal temperature, mean seasonal temperature variability, salinity and oxygen concentration. This multivariate analysis showed that mean seasonal temperature and mean seasonal temperature variability were the two most important factors explaining 55 % of the calcification data (adjusted R^2 = 0.555, Figure 5). Temperature variability was negatively related with calcification rates of *D. dianthus* in Comau Fjord as calcification rates were highest at the deep station with lowest temperature variability.

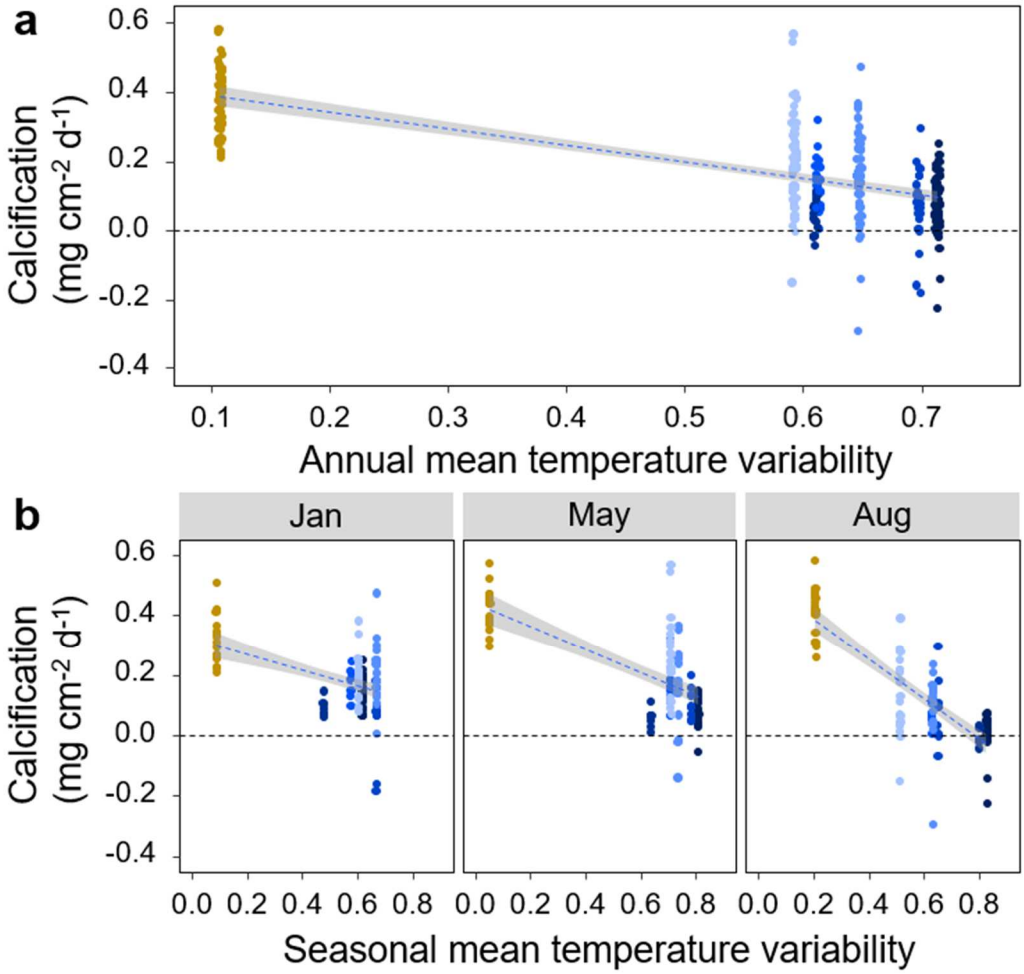

Figure 5: Relationship of calcification rates of *Desmophyllum dianthus* and mean temperature variability at sampling stations in Comau Fjord, Chile. a) Combined data of all three seasons (N = 19-57 independent samples) and b) seasonal comparison of calcification rates with mean temperature variability (N = 6-20 independent samples). Calcification rates of *D. dianthus* at six stations at 20 m water depth along the fjord (A-F) are shown in blue and at one station at 300 m water depth (Ed) in yellow. Calcification rates of native and novel corals were measured after four, eight and eleven months (January, May and August 2017) using the same individuals in each season. Note that native and novel corals at each station are combined in this graph. Adjusted R^2 = 0.555.

Discussion

This horizontal and vertical reciprocal transplantation experiment with CWCs assessed the seasonal physiological performance of the CWC *Desmophyllum dianthus* between two spatially close but strongly contrasting environments. Corals were transplanted between an aragonite saturated, thermally variable shallow environment and an aragonite undersaturated, thermally stable deep environment in Comau Fjord, Chile. Unexpectedly, we found fastest growing *D. dianthus* in deep waters characterised by aragonite undersaturation, but also stable environmental conditions. Following transplantation, *D. dianthus* showed a remarkably fast acclimatisation to the novel environment with no discernible differences between native and novel corals despite different environmental conditions at their original location. This underscores the ability of *D. dianthus* to accommodate a broad range of habitats and may help explain the great success of this cosmopolitan CWC species.

The low pH and aragonite undersaturation did not reduce the physiological performance of *D. dianthus* (Supplementary Figure 9a-d), explaining the so far enigmatic occurrence of dense coral banks in deep waters of Comau Fjord (Fillinger & Richter, 2013). CWC reefs in other areas (e.g. Gulf of Mexico, SW Australia) dominated by *L. pertusa* have also been found close to or below the aragonite saturation horizon (Thresher et al., 2011; Lunden et al., 2013; Georgian et al., 2016a). However, *D. dianthus* occurs at lower Ω_{arag}, pH, TA and DIC values than previously reported for CWC habitats in the NE Atlantic Ocean and Mediterranean Sea (Findlay et al., 2014; Flögel et al., 2014). In austral summer (January), the pH and aragonite saturation in shallow waters of the head of the fjord were as low as in deep waters at station Ed, presumably due to increased run-off and decomposition of terrestrial organic matter, showing that the observed differences in calcification rates are not related to differences in aragonite saturation (Supplementary Figure 9a-d). As we found specimens with highest calcification rates at highest DIC values in Comau Fjord, this does not support the hypothesis that the occurrence of healthy CWC reefs is prevented by high DIC (Flögel et al., 2014). While breakage and dissolution of bare coral skeletons occurs under aragonite undersaturation (Hennige et al., 2015, 2020), there is growing evidence that carbonate chemistry is not as important for live CWCs as has long been thought. Several laboratory and field studies have confirmed the capability of CWCs to calcify and survive at aragonite undersaturated conditions (Hennige et al., 2015; Rodolfo-Metalpa et al., 2015). Even though it was not statistically significant, a similar trend of highest calcification rates under aragonite undersaturation was also found in a long-term laboratory experiment with *L. pertusa* (Form & Riebesell, 2012), which is explained by the overall good physiological conditions of the corals due to regular feeding. However, the fact that CWCs are able to maintain calcification despite low pH *in situ* and in laboratory experiments does not explain why the individuals of *D. dianthus* with an almost twice as high calcification rate are found at 300 m depth in Comau Fjord.

As elevated temperatures coincide with elevated metabolic rates (Naumann et al., 2014; Gori et al., 2016; Dorey et al., 2020), we expected to find higher CWC calcification rates at

shallow stations, where the mean seasonal temperature was up to 1.9 °C higher than at 300 m depth. However, environmental variability can modulate performance (Klepac & Barshis, 2020; Schoepf et al., 2021) and may lead to reduced performance in shallow waters as highest temperature fluctuations at the head of the fjord coincide with the lowest coral calcification along the horizontal gradient (Figures 4 and 5). The macrotidal environment of Comau Fjord features tidal ranges of up to 7.5 m (Häussermann & Försterra, 2009) and associated temperature and salinity fluctuations in shallow waters with daily swings of more than 3 °C and short temperature peaks beyond 16 °C in summer (Figure 3a, Supplementary Figure 4). Similar short-term temperature fluctuations were also measured by Rossbach et al. (2021) in Comau Fjord, in neighbouring Reloncaví Fjord (Montero et al., 2011) and in other deep CWC habitats (Mienis et al., 2007, 2014; Guihen et al., 2012; Brooke et al., 2013). Thus, even in CWC habitats that have long been regarded as stable environments, short-term variabilities are ubiquitous and of ecological importance in macrotidal environments. They affect not only temperature and salinity (Wisshak et al., 2005; Mienis et al., 2007, 2014; Davies et al., 2010; Georgian et al., 2016a), but also oxygen concentration (Wisshak et al., 2005; White et al., 2012; Lunden et al., 2014; Guihen et al., 2018), pH_T and nutrients (Findlay et al., 2013). As all conservative oceanographic parameters co-vary with temperature and potentially affect the physiological performance of corals, we used temperature as a proxy for environmental variability in this study.

So far, no studies addressed the ability of CWCs to cope with short-term environmental fluctuations. Data are accumulating on the range of environmental conditions in the natural habitats of CWCs that exhibit high frequency fluctuations (Thresher et al., 2011; Findlay et al., 2013; Lunden et al., 2013; Georgian et al., 2016a; Juva et al., 2021), underscoring the dynamics that CWCs can be exposed to in their natural habitat, as well as the temporal and spatial range relevant to them. However, we often miss corresponding data on the physiological performance of corals. Only few studies investigated the short-term effect of elevated temperatures on CWCs (Brooke et al., 2013; Dorey et al., 2020). Temperatures of up to 15 °C, that may be comparable to daily temperature fluctuations in their natural habitat, lead to increased metabolic activity (Dorey et al., 2020). In long-term studies under constant conditions, the effect of elevated temperatures on the physiological performance of different CWC species varies and differs between locations (Dorey et al., 2020) as well as species (Naumann et al., 2013, 2014), ranging from a positive effect on calcification to no effect or even a negative response (Table 1). Similar variable results are found for the effect of pH with differences between locations (Georgian et al., 2016b), species (Movilla et al., 2014a) as well as short- and long-term exposure (Form & Riebesell, 2012; Kurman et al., 2017). Reduced pH either reduces calcification rates of CWCs, has no effect on their calcification or even slightly enhances long-term calcification rates of CWCs (Table 1; Form & Riebesell, 2012). CWCs in regions with large oxygen variability (White et al., 2012; Guihen et al., 2018) are able to tolerate low oxygen concentrations (Hanz et al., 2019; Hebbeln et al., 2020), but only for a short period of time under experimental conditions (Dodds et al., 2007; Lunden et al., 2014).

However, studies investigating the effect of environmental factors other than temperature and pH as well as experiments with multi-factorial design with CWC are still scarce (except for Hennige et al., 2015; Gori et al., 2016 and Büscher et al., 2017). Similarly, most studies used constant conditions and neglected naturally occurring strong and short-term fluctuations relevant to individual organisms (Gunderson et al., 2016; Wahl et al., 2016). However, this may hamper our understanding of the physiological performance of organisms, contribute to observed response heterogeneity and limit our predictions for the future of the ocean (Bates et al., 2018; Vargas et al., 2022). As extreme events are expected to increase in the future (Frölicher et al., 2018; Oliver et al., 2018), higher environmental variability may expose CWCs to more stressful conditions.

Table 1: Effect of elevated temperature and reduced pH/elevated pCO_2 on calcification rates of cold-water corals. Duration of exposure: short-term < 3 months and long-term ≥ 3 months. The species used in the studies are *L. pertusa* = *Lophelia pertusa*, *M. oculata* = *Madrepora oculata*, *D. dianthus* = *Desmophyllum dianthus, D. cornigera* = *Dendrophyllia cornigera*, *D. ramea* = *Dendrophyllia ramea* and *C. smithii* = *Caryophyllia smithii, S. variabilis = Solenosmilia variabilis.*

Effect	Duration	Region	Species and references
Elevated temperature			
positive	short-term	Mediterranean Sea	*D. cornigera* (Reynaud et al., 2021), *D. ramea* (Reynaud et al., 2021)
	long-term	Mediterranean Sea	*L. pertusa* (Naumann et al., 2014), *M. oculata* (Naumann et al., 2014), *D. cornigera* (Naumann et al., 2013; Gori et al., 2014)
		NE Atlantic Ocean	*L. pertusa* (Büscher et al., 2017)
none	long-term	Mediterranean Sea	*L. pertusa* (Chapron et al., 2021), *M. oculata* (Chapron et al., 2021), *D. dianthus* (Naumann et al., 2013)
		NE Atlantic Ocean	*L. pertusa* (Hennige et al., 2015)
negative	long-term	Mediterranean Sea	*D. dianthus* (Gori et al., 2016), *D. cornigera* (Reynaud et al., 2021), *D. ramea* (Reynaud et al., 2021)

Table 1 (continued)

Effect	Duration	Region	Species and references
Reduced pH / elevated pCO_2			
none	short-term	Mediterranean Sea	*L. pertusa* (Maier et al., 2013), *M. oculata* (Maier et al., 2012, 2013), *D. dianthus* (Rodolfo-Metalpa et al., 2015)
		NE Atlantic Ocean	*L. pertusa* (Hennige et al., 2014; Georgian et al., 2016b)
		Gulf of Mexico	*L. pertusa* (Kurman et al., 2017)
	long-term	Mediterranean Sea	*L. pertusa* (Maier et al., 2013; Movilla et al., 2014b), *M. oculata* (Maier et al., 2013; Movilla et al., 2014b), *D. dianthus* (Rodolfo-Metalpa et al., 2015; Gori et al., 2016), *D. cornigera* (Movilla et al., 2014a; Rodolfo-Metalpa et al., 2015), *C. smithii* (Rodolfo-Metalpa et al., 2015)
		NE Atlantic Ocean	*L. pertusa* (Form & Riebesell, 2012; Hennige et al., 2015), *D. dianthus* (Carreiro-Silva et al., 2014)
		SW Pacific Ocean	*S. variabilis* (Gammon et al., 2018)
negative	short-term	Mediterranean Sea	*M. oculata* (Maier et al., 2016)
		NE Atlantic Ocean	*L. pertusa* (Maier et al., 2009; Form & Riebesell, 2012)
		NE Pacific Ocean	*L. pertusa* (Gómez et al., 2018)
		Gulf of Mexico	*L. pertusa* (Lunden et al., 2014; Georgian et al., 2016b)
	long-term	Mediterranean Sea	*D. dianthus* (Movilla et al., 2014a)
		NE Atlantic Ocean	*L. pertusa* (Büscher et al., 2017)
		SE Pacific Ocean	*D. dianthus* (Martínez-Dios et al., 2020)
		Gulf of Mexico	*L. pertusa* (Kurman et al., 2017)

There is a growing body of literature addressing environmental sensing techniques with high temporal resolution and highlighting the ubiquity of environmental variability at numerous temporal and spatial scales as well as at remote locations (Helmuth et al., 2002, 2010). All emphasise their physiological relevance and initial experiments demonstrate their ecological significance and ability to influence organism responses (Kern et al., 2015; Kroeker et al., 2020; Ziegler et al., 2021). Several studies on tropical corals revealed that environmental variability can improve their physiological performance and render them more stress tolerant (Palumbi et al., 2014; Schoepf et al., 2015; Bay & Palumbi, 2017; Safaie et al., 2018, but see also Klepac & Barshis, 2020; Schoepf et al., 2021). However, our study clearly indicates that this may not be the case for CWCs as environmental variability negatively correlates with coral calcification (Figure 5). It indicates that high environmental variability entails energetic costs

in *D. dianthus*, compromising calcification in shallow waters, whereas deep corals may need less energy to compensate for stress. However, it still needs to be elucidated in more detail whether environmental fluctuations have a direct or only indirect effect on corals, e.g. by influencing their food availability.

Due to high environmental variability in shallow waters of Comau Fjord, corals are likely to feed less during periods of elevated temperatures, as suggested by the low prey capture rates of *Lophelia pertusa* and *Madrepora oculata* in laboratory experiments at higher temperatures (17 °C; Chapron et al., 2021), which are probably a consequence of lower polyp activities. Fluctuating physico-chemical conditions may also alter zooplankton communities both in abundance and composition (Laprise & Dodson, 1994; Wells et al., 2021). For instance, changes in salinity may result in the reduction in coastal zooplankton as osmotic stress can be lethal for some zooplankton groups (Wells et al., 2021). In deep waters (300 m) of Comau Fjord, zooplankton abundance and biomass are low throughout the year and show only low diel variations (Garcia-Herrera et al., 2022). At shallower depths (0-200m), abundance and biomass are often an order of magnitude higher and strongly affected by diel vertical migration (Garcia-Herrera et al., 2022), supporting a higher food availability for shallow corals. Unlike calcification rates, which integrate over months, respiration rates were determined over hours and are thus not entirely comparable. However, they provide insights into the current metabolic potential of the corals and indicate a generally elevated metabolic activity in deep corals (supported by higher calcification rates and biomass; Figure 4a, Supplementary Results, Supplementary Figure 10), possibly fuelled by higher food intake (Naumann et al., 2011; Maier et al., 2021, but also see Supplementary Discussion for temperature effects on respiration rates of deep corals). While the higher food availability appears to contradict the zooplankton data, it has to be taken into account that other factors (e.g. swarming behaviour, zooplankton aggregations near walls, micronekton, etc.) may play an important role in the food supply to CWCs. Similarly, factors such as competition for food from a diverse benthic community, particularly found in shallow waters, may further deplete the available abundant zooplankton community. It is also plausible that recurrent disturbances caused by high frequency environmental fluctuations as well as mobile benthic organisms influence the behaviour of the corals, e.g. by inducing the retraction of their tentacles and thus a polyp inactivity (Chapron et al., 2021), which limits their feeding time. Another important aspect is the energy density as well as energy gain from different zooplankton groups.

A laboratory study by Maier et al. (2021) clearly indicates that prey size is important. With a diet of small fjord zooplankton, *D. dianthus* requires a minimum of 700 individuals per day to balance metabolic needs, while the addition of one euphausiid provides a positive scope for growth (Maier et al., 2021). Euphausiids are known to form dense swarms in Chilean fjords (Antezana, 1999; Palma & Silva, 2004), but data from the immediate vicinity of the corals are missing. Euphausiids are underrepresented in the study by Garcia-Herrera et al. (2022) as they are active swimmers capable of escaping plankton nets at low tow speeds. Mysids account for up to 70 % of the zooplankton volume and abundance in deep waters of Comau Fjord in all

seasons and may provide a reliable food source for deep corals throughout the year (Garcia-Herrera et al., 2022) with potentially similar energy gain as derived from euphausiids (Höfer et al., 2018; Maier et al., 2021). Thus, a difference in zooplankton composition may compensate for a large difference in zooplankton abundance between depths, and together with other drivers (high frequency fluctuations, competition, behavioural adaptation), contribute to differences in energy gain.

The present study shows a remarkable phenotypic plasticity of *D. dianthus* after transplantation, underscoring its potential to acclimatise to local environmental conditions in Comau Fjord (Figure 4). Seasonal calcification data show that novel corals acclimatised quickly in less than four months without any subsequent change throughout the remainder of the study. Population genetic data support the lack of local adaptation with gene flow along both the horizontal and vertical axes of the fjord (Addamo et al., 2021). Similar results of local acclimatisation have been shown for calcification rates of the gorgonian coral *Antillogorgia bipinnata* (Calixto-Botía & Sánchez, 2017) and several tropical coral species (Barott et al., 2021; Baumann et al., 2021) after reciprocal transplantation. The morphological change of the native and novel deep corals on the pulley in the water column is also a sign of acclimatisation to the environmental conditions in deep waters. However, we cannot say to what extent biological factors (e.g. supposedly lower predation) or environmental factors (e.g. stronger currents) may also have played a role compared to the corals on the fjord wall. For example, it was observed that *L. pertusa* colonies grow in different shapes depending on the hydrodynamic conditions (De Clippele et al., 2018). However, some reciprocal transplantation experiments clearly revealed local adaptation (Kenkel et al., 2015; Kenkel & Matz, 2016) or a combination of local adaptation and phenotypic plasticity depending on the investigated traits (Palumbi et al., 2014; Bay & Palumbi, 2017; Rocker et al., 2019). The main traits measured in the present study (calcification and respiration) show a clear acclimatisation of *D. dianthus* to novel environmental conditions but other traits may also provide insights into potential local adaptation. The low tissue coverage of many shallow corals (mainly at stations B, C and Es) indicates that these corals have a reduced scope for somatic growth (Supplementary Figures 6,7 and 10). In addition, the low tissue cover is associated with a higher infestation with endolithic photoautotrophic organisms (Supplementary Figure 6; Försterra et al., 2005; Försterra & Häussermann, 2008; Hassenrück et al., 2013) which negatively affects their septal linear extension rates (Hassenrück et al., 2013). This may be an additional stressor for shallow corals and contribute to potentially reduced linear extension rates (Hassenrück et al., 2013) as the defence against infesting organisms and maintenance of the skeletal integrity requires an increased energy expenditure. However, this likely did not affect deep corals to the same extent, which were completely covered with tissue and therefore protected throughout the duration of the experiment. Deep corals transplanted to shallow were able to maintain their tissue covered surface area without tissue retraction (Supplementary Figures 6 and 7). Whether this is a real local adaptation or a delayed response, potentially caused by the availability of enhanced energy reserves, needs to be elucidated.

The large tissue covered surface area of native deep corals and the tissue surface area expansion of novel deep corals also protected the coral skeletons from dissolution at aragonite undersaturation. As the buoyant weighing method measures net calcification (growth minus dissolution), the higher calcification rates in deep waters may therefore be partly due to lower dissolution rates. Novel corals at the deep station invested considerably more energy into somatic growth compared to native deep corals. Altogether, deep corals not only have 1.7-fold higher respiration and 2.3-fold higher calcification rates than shallow corals, but they also have a higher scope for somatic growth and invest 6.7-times more into the build-up of tissue biomass (Supplementary Results, Supplementary Figure 10) and presumably also into energy reserves. This means that firstly, there may be more energy available at the deep station and secondly, energy may be channelled differently as additional energy is used to build-up biomass rather than for calcification. In contrast, somatic growth is clearly sacrificed at the shallow stations, maybe to maintain reproductive output (Leuzinger et al., 2012). As reproduction requires substantial energy (Maier et al., 2020), low tissue coverage and calcification rates of shallow corals could potentially indicate an energetic trade-off. In addition, decreasing calcification rates may not or not solely be linked to decreased seasonal temperatures, but indicate that more energy is channelled into reproduction than into other traits as *D. dianthus* is actively reproducing in shallow waters of this fjord in austral winter (Feehan et al., 2019). The results of the present study indicate that deep corals generally have more energy available and are potentially also more fecund as proposed by Feehan et al. (2019), but nothing is known about their reproductive cycle so far. Therefore, future studies on coral energetics should also include the reproductive cycle, in order to better understand the interplay of traits and potential consequences for the corals as well as the whole population.

While somatic growth provides hints towards local adaptation, it warrants further investigations of other traits when studying the acclimatization potential of CWCs to a new environment. Some previous studies on tropical corals revealed these possible different trait responses (Bay & Palumbi, 2017; Rocker et al., 2019). For instance, the biochemical signature together with gene expression (Rocker et al., 2019) could provide more detailed insights. Additional studies are also necessary to identify if somatic growth of deep corals in shallow will be reduced after a longer period of time and whether calcification and respiration rates continue to show local acclimatisation. Temporal effects are known from tropical studies, where some traits may acclimatize faster than others. For instance, *Porites astreoides* showed higher calcification rates and energy reserves in the natural environment (local adaptation) but only after twelve months of the experiment and not yet after six months (Kenkel et al., 2015).

The physiological performance of *D. dianthus* in Comau Fjord demonstrates strong phenotypic plasticity of this cosmopolitan CWC. While somatic growth indicates local adaptation, calcification and respiration are clearly driven by the environment. Unexpectedly, highest calcification rates were found in deep waters of the fjord with aragonite

undersaturated conditions. Although depth-related differences in food availability and bioerosion could not be accounted for, our results indicate that environmental variability plays a stronger role than aragonite saturation in governing CWC calcification in this macrotidal system, where shallow corals are exposed to stronger environmental fluctuations. High fluctuations in other regions may thus be one reason that limits the ability of CWCs to emerge from the deep and conquer shallow environments. However, this warrants further investigations into the relative role of individual parameters and their ability to limit the physiological performance of CWCs. It is important to consider environmental variability in CWC habitats in future physiological studies when investigating their potential vulnerability to changing environments, rather than assuming constant conditions. While we now have a better idea of the environmental conditions in the natural habitats of CWCs, important information on the physiological performance of corals is still missing. Such data are crucial to better understand the well-being of corals and their response to future changes, as environmental variability (especially temperature, salinity and pH) is likely to increase in the future, exposing CWCs to more stressful conditions.

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Author contributions

G.M.S.G., J.L. and C.R. designed the study. J.L., V.H., G.F. and H.E.G. contributed background information and helped with the field work. J.L. and G.F. collected the corals. V.H. and J.P.E. provided background data. K.K.B. and G.M.S.G. conducted the measurements. K.K.B., M.W. and G.M.S.G. analysed and interpreted the data. M.W. and K.K.B. conducted the statistical analysis and prepared the figures. K.K.B., M.W. and C.R. wrote the first draft and all authors edited the manuscript.

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Supplementary Methods

Coral physiology

The tissue covered surface area of the experimental corals was used as reference variable for calcification (mg cm^{-2} d^{-1}) and respiration rates (µmol cm^{-2} d^{-1}). The outer surface area of the coral skeletons was measured at the end of the field study (August 2017) using a digital calliper (reading to 0.01 mm). A modulated formula for a truncated cone after the geometric approximation "Advanced Geometry" by Naumann et al. (2009) was used to calculate the surface area based on the trumpet shape of *D. dianthus*. For this, the shape of the coral was approximated to a cup, the surface areas of the individual septa were not considered.

The surface area of *D. dianthus* has previously been measured as the outer surface area of the coral polyp, including its oral side (Gori et al., 2014, 2016). A conceptual problem with this approach is the cup shape of *D. dianthus* as the oral side of the calyx is not tissue covered but the tissue coats the skeleton on the inside of the calyx. A more straightforward approach is to consider all parts of the coral tissue that are in direct contact with the skeleton, assuming that these contribute to calcification and respiration of the polyp. This includes the tissue covered areas on the outside (but excluding the oral side of the polyp; A_o) and inside (tissue covered surface area of the coelenteron; A_i) of the calyx. For this purpose, the inner and outer tissue covered surface areas of 30 *D. dianthus* specimen were measured with a digital calliper and surface area I (outer and oral part of the polyp; Gori et al., 2014, 2016) and surface area II (inner and outer surface areas of the calyx excluding the oral side of the polyp) were calculated and correlated (Supplementary Figure 1, regression line: Surface area II = 1.319 x Surface area I, R^2 = 0.996, n = 30). In case of the surface area I (A), the following formula was applied:

$$A\ (cm^2) = \pi \times [R_o^2 + s_o \times (r_o + R_o)]$$

where R_o and r_o are the outer oral and aboral radius (half diameter D_o and d_o) of the polyp, respectively, and s_o is the outer slant height calculated from

$$s_o = \sqrt{(R_o - r_o)^2 + h_o^2}$$

where h_o is the mean height of the outer tissue covered surface area of the polyp (Supplementary Figure 2a). The surface area II (A_i and A_o) were calculated as:

$$A_i\ (cm^2) = \pi \times [r_i^2 \times s_i \times (r_i + R_i)]$$

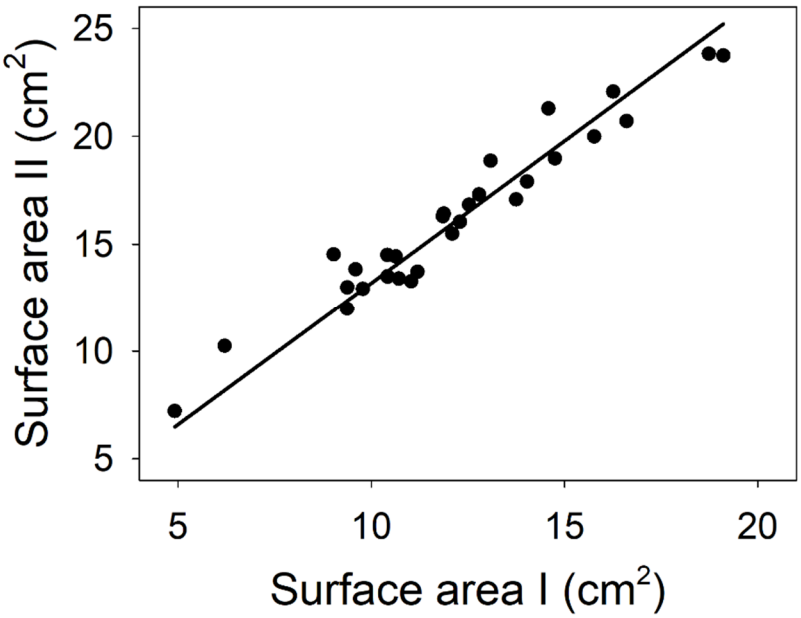
where R_i and r_i are the oral and aboral radius (half diameter D_i and d_i) of the inner tissue-coated surface area of the calyx (coelenteron), respectively, and s_i is the inner slant height of the calyx (calculated from the measured inner height h_i, Supplementary Figure 2b); and

$$A_o\ (cm^2) = \pi \times [s_o \times (r_o + R_o)]$$

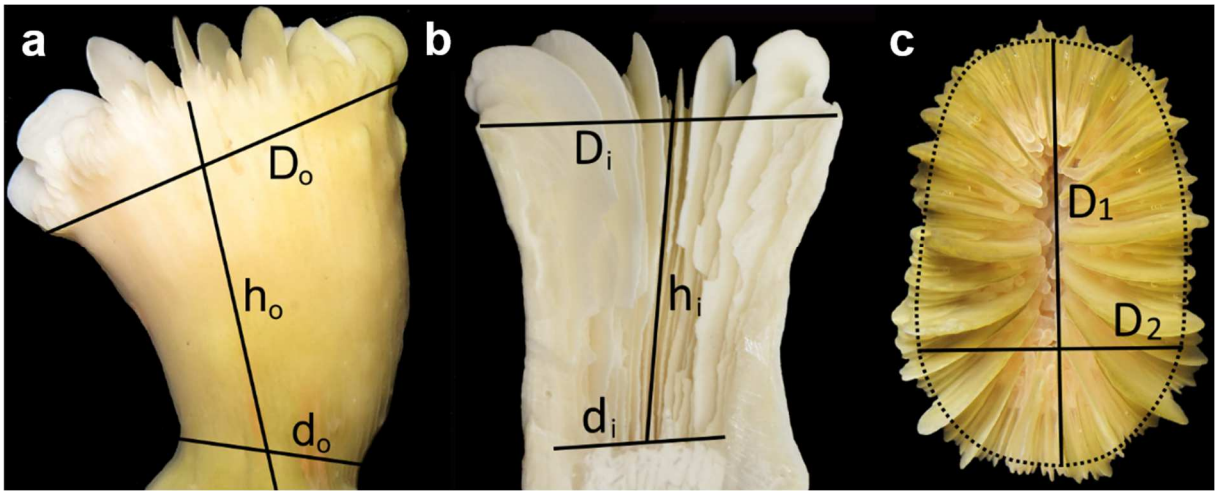
where R_o and r_o are the oral and aboral radius of the outer tissue covered surface area of the calyx, respectively, and s_o is the outer slant height of the calyx (calculated from the measured outer height h_o, Supplementary Figure 2a). Due to the elliptical shape of the calyx of

D. dianthus, the inner and outer diameters of the oral and aboral side of the polyp were each measured twice and the mean diameter was used to calculate the oral and aboral radius for both surface areas (I and II), respectively (Supplementary Figure 2c).

Using this correlation of surface areas I and II (Surface area II = 1.319 × Surface area I), the tissue covered surface area II can be calculated from outer measurements of the polyp (surface area I).



Supplementary Figure 1: Surface area measurements of *Desmophyllum dianthus*. Scatter plot showing the linear regression of the surface areas of I) the outer surface area of the coral polyp (including the oral side of the polyp) and II) the inner (tissue coated surface area of the coelenteron) and outer (excluding the oral side of the polyp) tissue covered surface area of the calyx (regression line: Surface area II = 1.319 × Surface area I, R^2 = 0.996, n = 30). Black dots represent individual specimens.



Supplementary Figure 2: Measurements of the tissue covered surface area of *Desmophyllum dianthus*. Measurements of the a) outer surface area, b) inner surface area, and c) diameters at the oral side. Dashed line = outer edge of calyx wall (excluding septa), D = oral diameter, d = aboral diameter, h = height, X_i = inner diameter/height, X_o = outer diameter/height.

In order to determine if the tissue covered surface area of an individual varied over the duration of the experiment and whether the surface area measurements of the shallow corals at the end of the experiment (August 2017) were representative for the whole duration of the experiment, scaled pictures of the same side of each individual from September 2016 and August 2017 were used and analysed using the software ImageJ. The extent of the tissue along the calyx was measured from the oral to the aboral edge of the tissue at three points on this image and then averaged. The tissue length and the ability to extend or retract the tissue is also an important parameter for changes in coral tissue biomass.

In addition to the experimental corals, 30 individuals of *D. dianthus* were collected at each of the shallow stations and eight individuals at the deep station in September 2016 and prepared as described in the main text by fixing them on screws. For cross-transplantation, another 30 corals were sampled at the shallow stations A, F and Es and eight corals at Ed. This gives a total of 188 native corals along the horizontal gradient and at depth and 98 novel corals at shallow and deep stations (tissue corals). The size of tissue corals (oral diameter: 14.96 ± 3.94 mm) was representative for the population.

At the end of each season (January, May and August 2017), ten native corals were collected at each of the shallow stations. In addition, ten novel corals were collected at stations A, F and Ed. Only in austral summer (January), eight native corals were collected at station Ed and eight novel corals at station Es. After collection, corals were transported to the research station, where they were unscrewed from the plates and maintained in flow-through aquaria for a maximum of four days before being removed from the screws, snap-frozen in liquid nitrogen, transported to the Alfred Wegener Institute (AWI) within liquid nitrogen containers (dry shipper) and stored at -80 °C until processing. Unfortunately, most frozen coral samples collected in austral summer (except for native and novel corals from stations Ed

and F) were lost by malfunction of one of the freezers, so that we had to discard the thawed samples from tissue analyses.

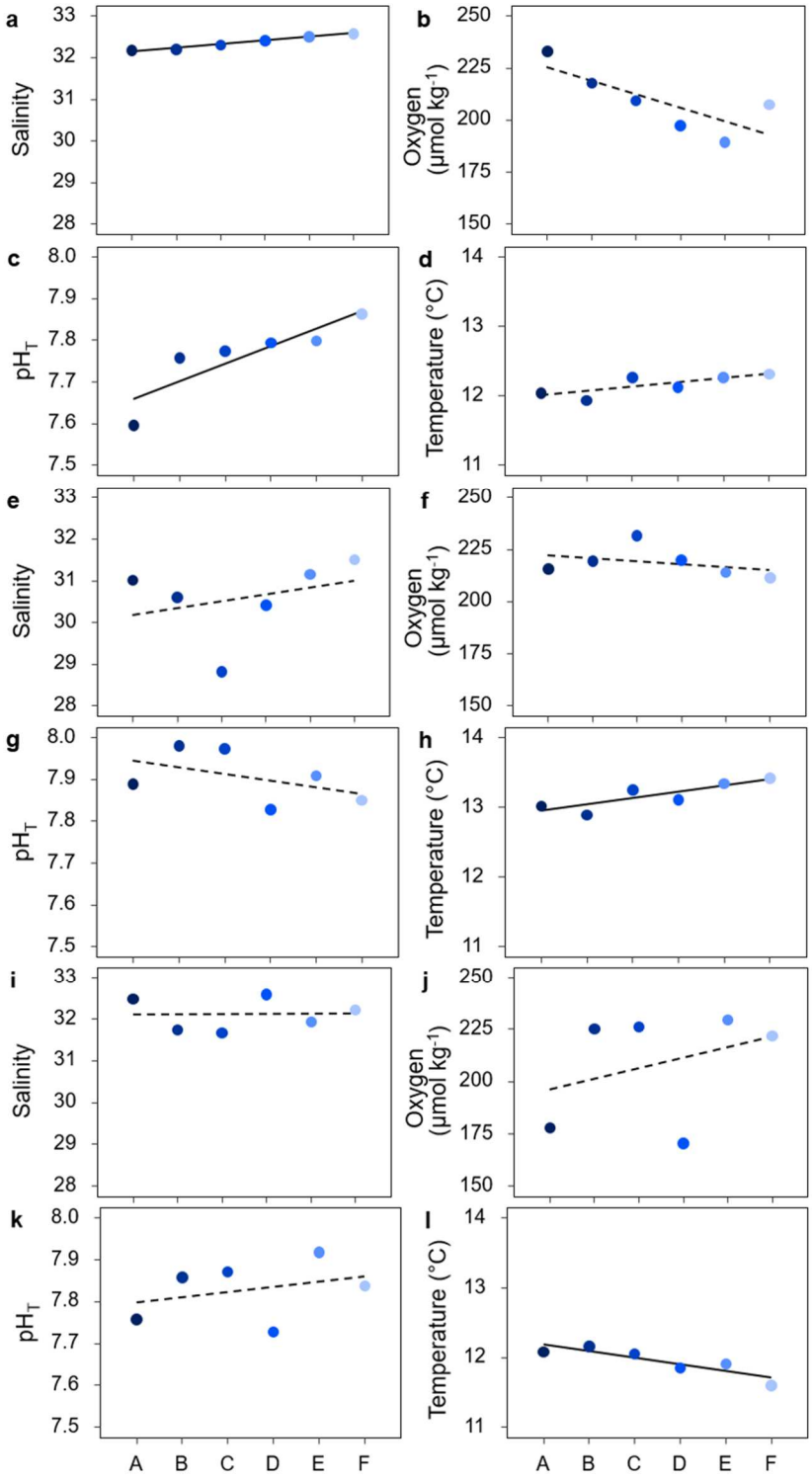
Frozen tissue corals from station Ed were cut in half using a diamond-tipped saw (FKS/E, Proxxon S.A., Wecker, Luxemburg) in a -30 °C cold room to prevent the tissue from thawing during treatment. Only one half of each coral specimen of station Ed was used for biomass determination, while whole corals were used from all shallow stations. The tissue was separated from the skeleton working on ice and using an airbrush (Starter Class set, Revell GmbH, Bünde, Germany) connected to pressurised air at 5 bar and the tissue slurry was homogenized using an Ultra Turrax (T18 basic, IKA GmbH & Co. KG, Staufen, Germany). A subsample (1 mL) of the tissue slurry was taken on a pre-combusted (4 hours at 500°C) and pre-weighed filter (GF/C; Whatman, GF Healthcare Life Sciences, Amersham, United Kingdom) for the determination of tissue biomass (dry mass). The filter with the tissue sample was dried to constant mass (24 hours at 60 °C) and weighed again using an electronic fine balance (Sartorius M2P, Sartorius AG, Göttingen, Germany; precision: 0.001 mg).

The surface area covered by tissue of the frozen tissue corals was measured using a digital calliper (as described above) prior to the separation of the tissue from the skeleton and used as reference variable for the biomass data (mg cm^{-2}).

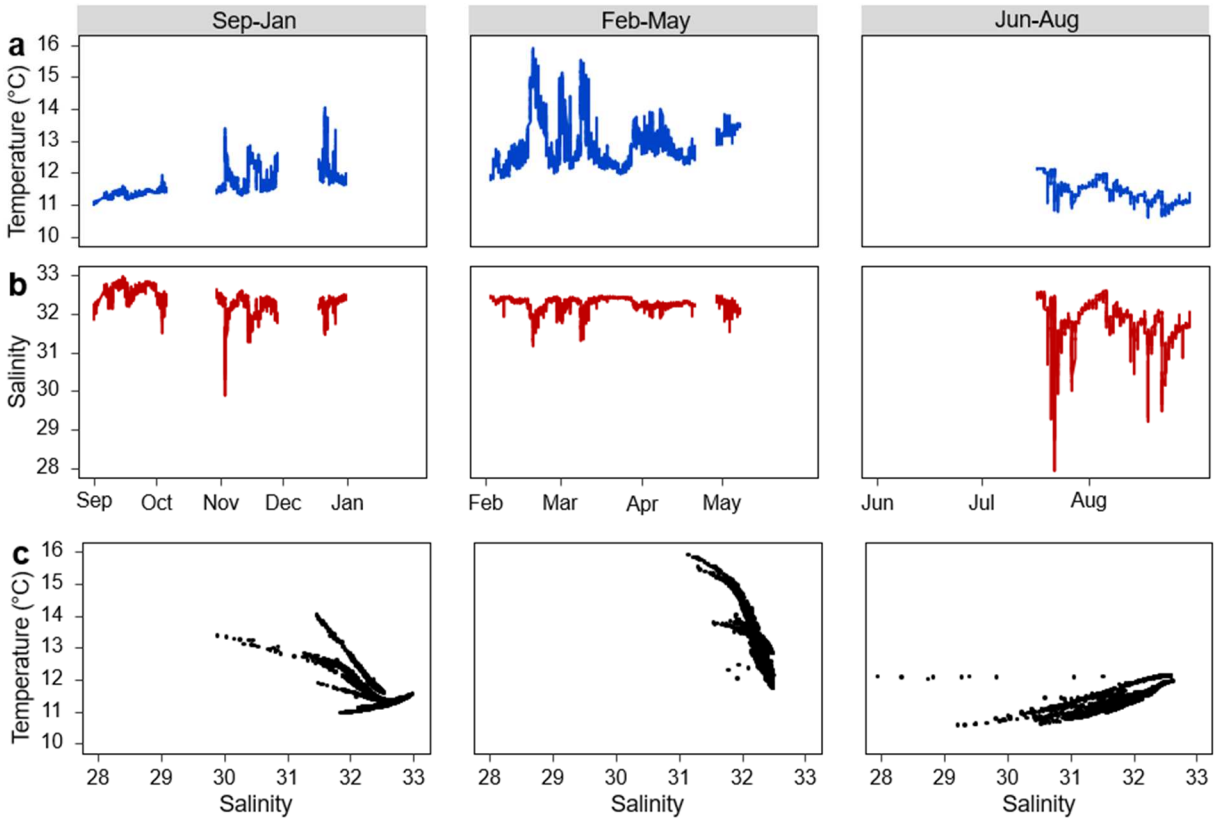
Supplementary Results

Supplementary Table 1: Overview of seasonal environmental conditions and carbonate chemistry in Comau Fjord, Chile. Environmental conditions at six coral stations at 20 m water depth along the fjord from head to mouth (A-F) and at one station at 300 m water depth (Ed). Water depth of coral stations is given relative to Mean Lower Low Water. Salinity and oxygen concentrations were measured with a CTD. Water samples were collected at coral stations and analysed for total alkalinity (TA) and dissolved inorganic carbon (DIC) and carbonate chemistry was calculated from TA and DIC using CO2SYS (Pierrot et al., 2006). Temperature was measured using TidbiT temperature loggers over a period of three to four months for each season. Temperature values are given as mean ± standard deviation. Temperature and salinity measurements at station X were conducted with a CTD and are given as mean ± standard deviation.

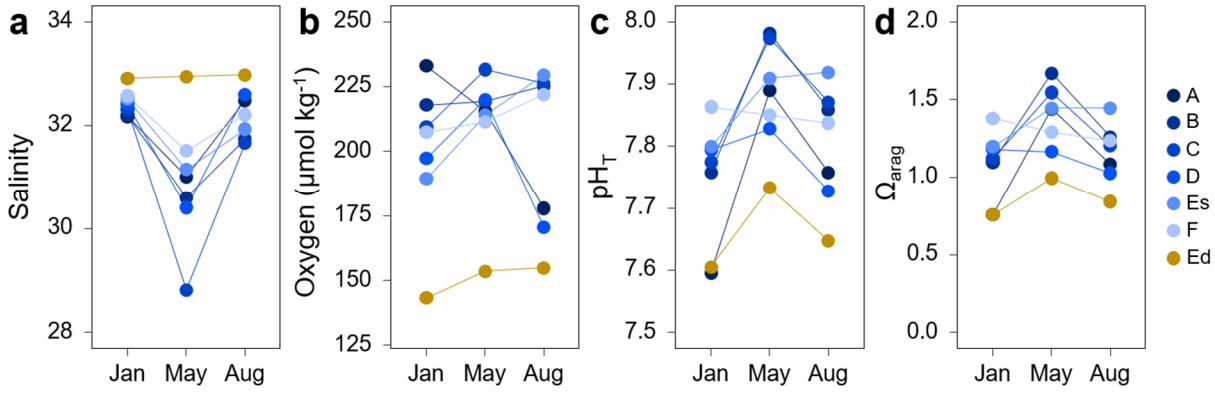
Station	Latitude	Longitude	Depth (m)	Salinity	Temp (°C)	TA ($\mu mol\ kg^{-1}$)	DIC ($\mu mol\ kg^{-1}$)	pH_T	pCO_2 (μatm)	HCO_3^- ($\mu mol\ kg^{-1}$)	CO_3^{2-} ($\mu mol\ kg^{-1}$)	CO_2 ($\mu mol\ kg^{-1}$)	Ω_{arag}	Oxygen ($\mu mol\ kg^{-1}$)
January 2017														
A	-42°26'38.64"	-72°25'08.46"	19.98	32.17	12.04 ± 0.78	2107	2078	7.595	1160	1981	49.20	47.66	0.75	233
B	-42°24'00.83''	-72°25'10.49''	20.59	32.20	11.93 ± 0.63	2164	2087	7.758	799	1983	71.52	32.83	1.10	218
C	-42°22'15.28''	-72°25'51.18''	20.14	32.31	12.26 ± 0.86	2141	2060	7.774	758	1956	73.14	31.22	1.12	209
D	-42°19'55.20"	-72°27'39.60"	19.77	32.41	12.12 ± 0.78	2174	2086	7.794	731	1979	77.05	30.31	1.18	197
Es	-42°16'45.06"	-72°27'31.26"	18.76	32.51	12.26 ± 0.85	2171	2084	7.799	722	1976	78.10	29.88	1.20	189
F	-42°09'46.20"	-72°35'47.28"	16.72	32.57	12.31 ± 0.84	2181	2069	7.863	616	1954	90.07	25.39	1.38	207
Ed	-42°16'09.34"	-72°27'34.02"	~300	32.91	11.31 ± 0.06	2194	2164	7.605	1137	2064	51.96	48.23	0.76	143
X	-42°23'14.14"	-72°27'39.74"	~25	32.36 ± 0.32	11.65 ± 0.45	-	-	-	-	-	-	-	-	-
May 2017														
A	-42°26'38.64"	-72°25'08.46"	19.98	31.01	13.02 ± 0.86	2134	2015	7.889	571	1899	93.21	23.01	1.44	216
B	-42°24'00.83''	-72°25'10.49''	20.59	30.60	12.89 ± 0.74	2088	1942	7.981	442	1816	108.07	17.98	1.67	219
C	-42°22'15.28''	-72°25'51.18''	20.14	28.82	13.25 ± 0.81	2090	1959	7.973	459	1840	99.68	19.25	1.54	232
D	-42°19'55.20"	-72°27'39.60"	19.77	30.41	13.11 ± 0.73	2032	1942	7.828	637	1840	75.35	26.23	1.16	220
Es	-42°16'45.06"	-72°27'31.26"	18.76	31.15	13.34 ± 0.70	2103	1982	7.909	535	1866	93.79	21.93	1.44	214
F	-42°09'46.20"	-72°35'47.28"	16.72	31.51	13.42 ± 0.60	2117	2015	7.850	623	1905	83.94	25.62	1.29	211
Ed	-42°16'09.34"	-72°27'34.02"	~300	32.94	11.26 ± 0.06	2188	2117	7.733	623	2014	68.28	35.00	0.99	154
X	-42°23'14.14"	-72°27'39.74"	~25	32.28 ± 0.17	12.88 ± 0.74	-	-	-	-	-	-	-	-	-
August 2017														
A	-42°26'38.64"	-72°25'08.46"	19.98	32.48	12.08 ± 0.62	2175	2099	7.758	800	1995	70.70	33.45	1.08	178
B	-42°24'00.83''	-72°25'10.49''	20.59	31.74	12.16 ± 0.57	2134	2034	7.859	610	1926	82.18	26.26	1.26	225
C	-42°22'15.28''	-72°25'51.18''	20.14	31.66	12.05 ± 0.62	1992	1893	7.871	552	1791	78.43	23.76	1.20	226
D	-42°19'55.20"	-72°27'39.60"	19.77	32.59	11.85 ± 0.51	2182	2115	7.728	865	2012	67.07	36.00	1.03	170
Es	-42°16'45.06"	-72°27'31.26"	18.76	31.93	11.91 ± 0.61	2152	2031	7.918	529	1914	94.31	22.68	1.44	230
F	-42°09'46.20"	-72°35'47.28"	16.72	32.21	11.60 ± 0.48	2155	2059	7.837	649	1951	80.75	27.68	1.24	222
Ed	-42°16'09.34"	-72°27'34.02"	~300	32.97	11.64 ± 0.14	2176	2129	7.647	1020	2029	57.53	42.51	0.84	155
X	-42°23'14.14"	-72°27'39.74"	~25	31.78 ± 0.51	11.42 ± 0.34	-	-	-	-	-	-	-	-	-



Supplementary Figure 3: Seasonal horizontal gradients at 20 m depth of Comau Fjord, Chile. Water parameters at six coral stations at 20 m water depth along the fjord from head to mouth (A-F, colours correspond to Fig. 1) in austral summer (January, a-d), autumn (May, e-h) and winter (August, i-l). Salinity and oxygen concentration were measured once during each season with a CTD. Total pH (pH_T) was calculated from water samples once during each season and calculated from total alkalinity (TA) and dissolved inorganic carbon (DIC) using CO2SYS(Pierrot et al., 2006). Temperature was measured every 15 min. over a period of three to four months for each season using TidbiT temperature loggers and the mean temperature was plotted. Regression lines with significant p-values ($p < 0.05$) are plotted as solid lines, non-significant results are plotted as dotted lines.



Supplementary Figure 4: Seasonal water temperature and salinity of Comau Fjord, Chile. a) Water temperature (blue) and b) salinity (red) were measured with a CTD installed at 25 m depth at station X between September 2016 and August 2017. c) Correlation between temperature and salinity.



Supplementary Figure 5: Seasonal environmental conditions at shallow and deep coral stations in Comau Fjord, Chile. a) Salinity and b) oxygen from CTD, c) seawater pH_T and d) aragonite saturation (Ω_{arag}) calculated from TA and DIC in austral summer (January), autumn (May) and winter (August). Single data points for all shallow stations at 20 m water depth (A-F) are shown in blue and conditions at the deep station at 300 m water depth (Ed) in yellow.

Supplementary Table 2: Seasonal physiological parameters of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. Calcification rates, respiration rates and biomass content of *D. dianthus* (mean ± standard deviation) at six stations at 20 m water depth along the fjord from head to mouth (A-F) and at one station at 300 m water depth (Ed). Native corals were re-installed at the same station after collection in September 2016 and novel corals were cross-transplanted between the shallow stations at the head (A) and the mouth of the fjord (F), and between shallow (Es) and deep (Ed). Calcification and respiration rates were measured after four, eight and eleven months (January, May and August 2017) using the same individuals (experimental corals) in each season (N= 4-10). The tissue biomass was determined from tissue corals that were collected during each season (N = 6-10). Note that biomass data could not be obtained for all stations and seasons due to logistical problems. The tissue covered surface area was used as reference values for calcification rates (mg cm^{-2} d^{-1}) and respiration rates (µmol cm^{-2} d^{-1}) and for the tissue biomass (mg cm^{-2}). Calcification rates were also calculated in % d^{-1} using the skeletal dry mass as reference value.

Supplementary Table 2

Station	N	Surface area (cm^2)	Skeletal dry mass (g)	Calcification (mg cm^{-2} d^{-1})	Calcification (% d^{-1})	N	Respiration (µmol cm^{-2} d^{-1})	N	Biomass (mg cm^{-2})
January 2017									
A (native)	9	17.27 ± 4.71	5.49 ± 2.91	0.15 ± 0.03	0.07 ± 0.04	9	1.38 ± 0.64	-	-
A (novel)	10	12.54 ± 4.92	3.20 ± 1.70	0.14 ± 0.07	0.07 ± 0.05	9	1.35 ± 1.06	-	-
B	7	8.35 ± 2.74	3.05 ± 0.97	0.09 ± 0.03	0.03 ± 0.02	8	3.05 ± 1.12	-	-
C	10	6.76 ± 1.39	2.47 ± 0.73	0.05 ± 0.12	0.02 ± 0.04	8	5.50 ± 3.93	-	-
D	8	15.57 ± 3.21	2.68 ± 0.94	0.17 ± 0.05	0.13 ± 0.05	8	2.53 ± 1.08	-	-
Es (native)	8	13.60 ± 4.63	4.97 ± 2.99	0.27 ± 0.11	0.11 ± 0.05	9	4.23 ± 1.76	-	-
Es (novel)	8	26.38 ± 10.91	5.66 ± 3.89	0.16 ± 0.08	0.11 ± 0.07	8	3.31 ± 0.92	-	-
F (native)	10	16.22 ± 2.96	3.26 ± 1.38	0.21 ± 0.07	0.15 ± 0.11	10	3.89 ± 1.47	8	10.29 ± 3.68
F (novel)	9	17.07 ± 4.20	4.03 ± 1.50	0.19 ± 0.08	0.10 ± 0.04	9	3.20 ± 0.98	10	8.74 ± 2.47
Ed (native)	8	24.76 ± 8.62	4.88 ± 2.20	0.27 ± 0.04	0.19 ± 0.07	8	7.17 ± 1.71	8	50.89 ± 26.30
Ed (novel)	10	18.00 ± 6.02	5.20 ± 2.81	0.34 ± 0.09	0.17 ± 0.10	10	8.21 ± 2.79	10	78.14 ± 41.55
May 2017									
A (native)	9	17.27 ± 4.71	5.65 ± 2.88	0.07 ± 0.04	0.03 ± 0.03	8	1.51 ± 0.43	10	6.38 ± 2.71
A (novel)	9	12.54 ± 4.92	3.45 ± 1.78	0.08 ± 0.06	0.03 ± 0.03	9	1.38 ± 0.49	10	7.30 ± 4.43
B	7	8.35 ± 2.74	3.11 ± 0.96	0.06 ± 0.03	0.02 ± 0.01	7	2.38 ± 0.87	9	11.89 ± 3.38
C	8	6.76 ± 1.39	2.49 ± 0.71	0.11 ± 0.05	0.03 ± 0.02	8	3.79 ± 0.81	9	16.01 ± 4.39
D	8	15.57 ± 3.21	3.00 ± 0.95	0.17 ± 0.07	0.11 ± 0.07	8	1.01 ± 0.24	10	7.69 ± 2.87
Es (native)	8	13.60 ± 4.63	5.88 ± 3.52	0.10 ± 0.12	0.04 ± 0.05	9	2.89 ± 1.00	7	9.27 ± 2.65
Es (novel)	8	26.38 ± 10.91	6.32 ± 4.04	0.23 ± 0.12	0.13 ± 0.12	8	1.64 ± 0.51	-	-
F (native)	10	16.22 ± 2.96	3.83 ± 1.36	0.31 ± 0.13	0.18 ± 0.12	9	2.63 ± 0.75	9	8.47 ± 1.45
F (novel)	9	17.07 ± 4.20	4.57 ± 1.84	0.25 ± 0.14	0.11 ± 0.06	8	2.27 ± 0.49	10	8.70 ± 1.81
Ed (native)	10	33.48 ± 9.00	6.13 ± 2.44	0.37 ± 0.04	0.29 ± 0.12	8	7.41 ± 1.90	-	-
Ed (novel)	10	26.50 ± 5.41	6.42 ± 2.89	0.45 ± 0.06	0.28 ± 0.13	10	8.74 ± 1.48	10	83.58 ± 44.34
August 2017									
A (native)	9	17.27 ± 4.71	5.66 ± 2.86	0.01 ± 0.06	0.01 ± 0.02	9	1.74 ± 1.18	10	7.59 ± 3.12
A (novel)	9	12.54 ± 4.92	3.32 ± 1.73	0.00 ± 0.09	0.00 ± 0.03	9	3.07 ± 1.78	10	7.27 ± 2.07
B	6	8.35 ± 2.74	3.05 ± 1.03	0.00 ± 0.03	0.00 ± 0.01	4	1.38 ± 1.21	7	8.39 ± 3.75
C	8	6.76 ± 1.39	2.54 ± 0.71	0.08 ± 0.12	0.03 ± 0.04	8	4.62 ± 2.22	9	18.46 ± 6.04
D	8	15.57 ± 3.21	3.09 ± 0.97	0.08 ± 0.04	0.04 ± 0.02	8	2.12 ± 1.59	10	6.78 ± 1.96
Es (native)	10	13.60 ± 4.63	5.87 ± 3.32	0.06 ± 0.14	0.02 ± 0.04	8	1.74 ± 1.26	10	7.78 ± 1.66
Es (novel)	7	26.38 ± 10.91	7.19 ± 4.09	0.15 ± 0.05	0.07 ± 0.03	7	1.19 ± 0.65	-	-
F (native)	10	16.22 ± 2.96	4.01 ± 1.32	0.16 ± 0.13	0.08 ± 0.07	9	3.23 ± 3.76	10	9.86 ± 2.80
F (novel)	9	17.07 ± 4.20	4.71 ± 1.92	0.11 ± 0.13	0.04 ± 0.06	9	1.99 ± 1.63	10	6.37 ± 1.99
Ed (native)	8	41.61 ± 9.52	7.33 ± 2.64	0.36 ± 0.06	0.27 ± 0.11	8	3.69 ± 1.16	6	28.59 ± 7.22
Ed (novel)	10	35.97 ± 7.47	7.74 ± 3.04	0.46 ± 0.07	0.29 ± 0.10	10	3.69 ± 1.41	10	72.73 ± 19.42

Supplementary Table 3: Linear mixed effect models for calcification and respiration rates of *Desmophyllum dianthus*. Only relevant results are displayed here. Significant p-values are shown in bold.

Fixed effects	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Calcification (model 1: shallow stations)						
season	0.254	0.127	2	96.308	19.800	**<0.001**
station	0.233	0.047	5	43.578	7.257	**<0.001**
Calcification (model 2: stations A, F, Es, Ed)						
station	1.401	0.467	3	64.601	51.073	**<0.001**
transplant	0.012	0.012	1	64.664	1.307	0.257
station*transplant	0.069	0.023	3	64.601	2.512	0.066
Respiration (model 1: shallow stations)						
season	32.414	16.207	2	96.108	5.489	**0.006**
station	143.820	28.764	5	44.210	9.742	**<0.001**
Respiration (model 2: stations A, F, Es, Ed)						
station	712.12	237.375	3	202	65.207	**<0.001**
transplant	1.23	1.227	1	202	0.337	0.562
station*transplant	26.82	8.941	3	202	2.456	0.064

Supplementary Table 4: Post hoc tests for calcification and respiration rates of *Desmophyllum dianthus*. Only relevant results are displayed here. Significant p-values are shown in bold.

Fixed effects	Contrast	Estimate	SE	df	t ratio	p-value
Calcification (model 1: shallow stations)						
season	Jan-Aug	-0.095	0.016	100.9	-5.972	**<0.001**
	May-Aug	-0.076	0.016	99.5	-4.710	**<0.001**
	Jan-May	0.020	0.016	99.1	1.238	0.434
station	A-B	0.029	0.037	46.1	0.777	0.970
	A-C	0.010	0.035	47.6	0.295	1.000
	A-D	-0.600	0.036	45.1	-1.687	0.547
	A-Es	-0.065	0.035	47.6	-1.887	0.422
	A-F	-0.148	0.034	45.1	-4.400	**<0.001**
	B-C	-0.019	0.037	48.4	-0.504	0.996
	B-D	-0.089	0.038	46.1	-2.330	0.203
	B-Es	-0.094	0.037	48.4	-2.529	0.136
	B-F	-0.177	0.036	46.2	-4.866	**<0.001**
	C-D	-0.070	0.036	47.5	-1.976	0.371
	C-Es	-0.075	0.034	50.4	-2.185	0.263
	C-F	-0.159	0.034	47.8	-4.711	**<0.001**
	D-Es	-0.005	0.036	47.5	-0.141	1.000
	D-F	-0.088	0.035	45.1	-2.534	0.136
	Es-F	-0.083	0.034	47.8	-2.472	0.153
Calcification (model 2: stations A, F, Es, Ed)						
station	A-F	-0.127	0.024	64.2	-5.209	**<0.001**
	Es-Ed	0.217	0.025	65.9	8.533	**<0.001**
station*transplant	A (native) - A (novel)	0.002	0.035	65.1	0.052	1.000
	F (native) - F (novel)	0.044	0.034	63.4	1.291	0.899
	Es (native) - Es (novel)	-0.043	0.037	68.4	-1.173	0.937
	Ed (native) - Ed (novel)	-0.084	0.035	63.4	-2.366	0.276

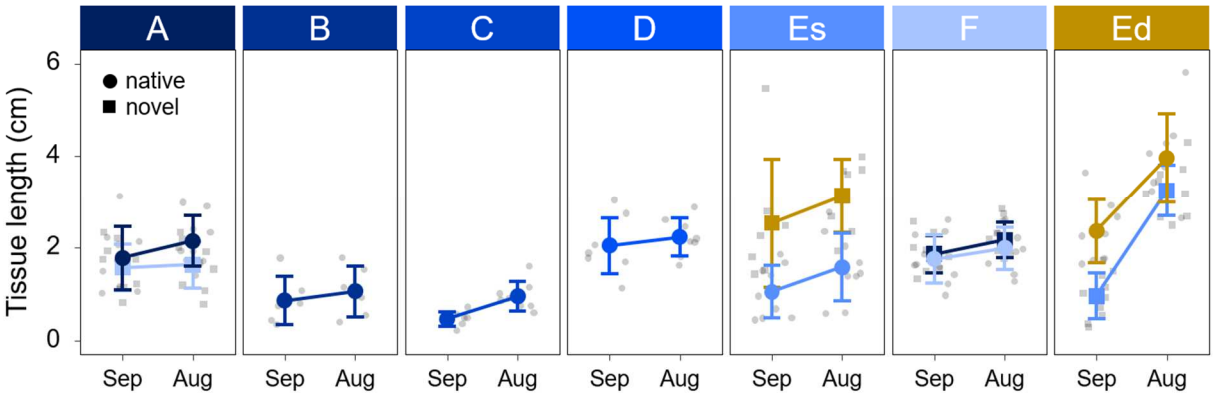
Supplementary Table 4 (continued)

Fixed effects	Contrast	Estimate	SE	df	t ratio	p-value
Respiration (model 1: shallow stations)						
season	Jan-Aug	-0.872	0.350	99.1	-2.494	**0.038**
	May-Aug	0.190	0.355	98.5	0.537	0.853
	Jan-May	1.063	0.343	96.0	3.102	**0.007**
station	A-B	-0.850	0.537	49.6	-1.583	0.613
	A-C	-3.107	0.502	44.5	-6.186	**<0.001**
	A-D	-0.354	0.502	41.9	-0.705	0.980
	A-Es	-1.468	0.492	45.4	-2.983	**0.049**
	A-F	-1.714	0.483	44.0	-3.549	**0.011**
	B-C	-2.258	0.546	50.8	-4.136	**0.002**
	B-D	0.495	0.546	48.2	0.908	0.943
	B-Es	-0.619	0.536	51.8	-1.155	0.856
	B-F	-0.865	0.528	50.7	-1.638	0.578
	C-D	2.753	0.512	43.2	5.375	**<0.001**
	C-Es	1.639	0.502	46.9	3.263	**0.024**
	C-F	1.393	0.493	45.5	2.822	0.072
	D-Es	-1.114	0.502	44.1	-2.218	0.250
	D-F	-1.360	0.494	42.7	-2.756	0.085
	Es-F	-0.246	0.483	46.5	-0.510	0.996
Respiration (model 2: stations: A, F, Es, Ed)						
station	A-F	-1.187	0.369	64.8	-3.215	**0.011**
	Es-Ed	3.945	0.378	63.5	10.435	**<0.001**
station*transplant	A (native) - A (novel)	-0.296	0.525	64.8	-0.565	0.999
	F (native) - F (novel)	0.777	0.520	64.7	1.495	0.808
	Es (native) - Es (novel)	0.919	0.547	66.8	1.680	0.700
	Ed (native) - Ed (novel)	-0.786	0.523	60.1	-1.504	0.802

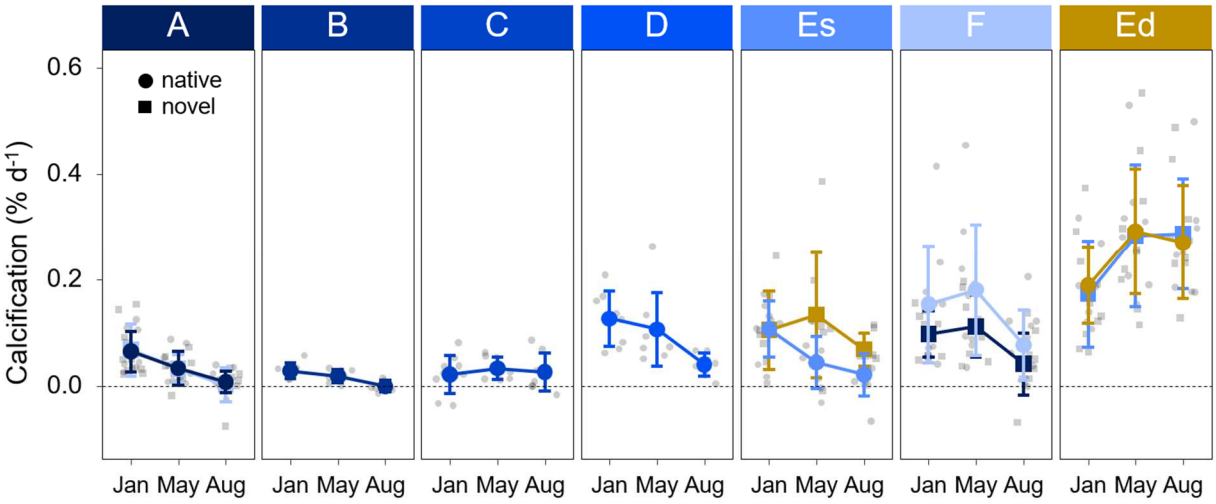

a
origin
A shallow (20 m)
F shallow (20 m)
native
treatment
novel
AsCe2
AsCe4
AsCe6
AsCe8
AsCe10
FsCe2
FsCe4
FsCe9
FsCe10
FsCe8
AsTe1
AsTe2
AsTe4
AsTe7
AsTe10
FsTe2
FsTe4
FsTe5
FsTe5
FsTe10


b
origin
E shallow (20 m)
E deep (300 m)
native
treatment
novel
EsCe1
EsCe3
EsCe4
EsCe7
EsCe8
EdCe1
EdCe3
EdCe6
EdCe7
EdCe8
EsTe2
EsTe8
EsTe4
EsTe3
EsTe9
EdTe1
EdTe4
EdTe5
EdTe7
EdTe8

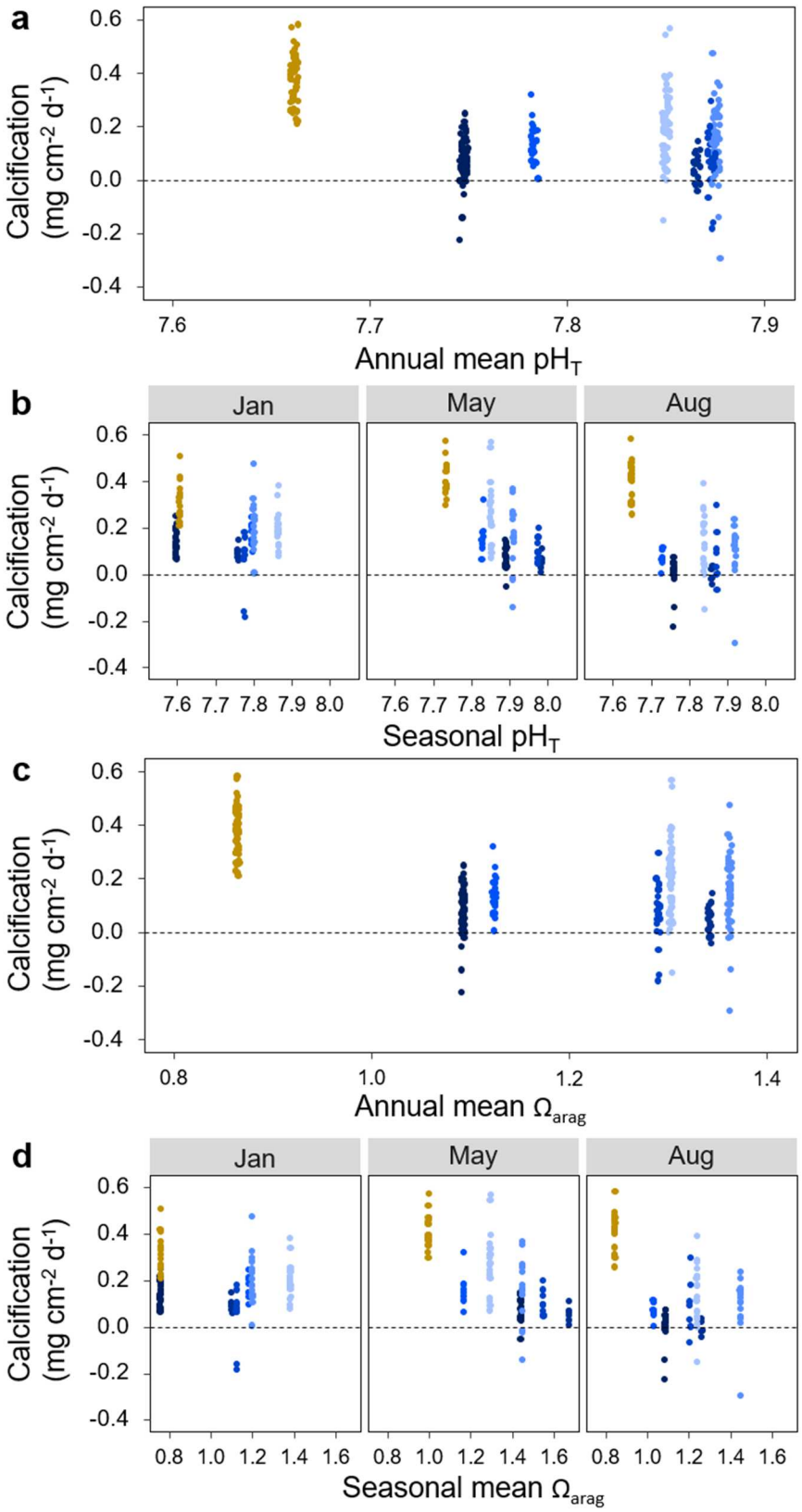
Supplementary Figure 6: Pictures of experimental individuals of *Desmophyllum dianthus* throughout the reciprocal transplantation experiment. Pictures of 5 of the 8-10 native and novel corals from each reciprocal transplantation station at a) shallow (20 m depth; station A: fjord head, station F: fjord mouth) and b) between shallow (20 m; station Es) and deep (300 m depth; station Ed) are displayed at the four sampling dates: September 2016, January, May and August 2017. Background colour indicates the station of origin, e.g. the background colour of the novel corals at station Es is the colour of the deep station. The labels of the corals indicate: 1) station of origin (A, E, F), 2) depth of origin (s = shallow, d = deep), 3) native (C) or novel (T), 4) experimental coral (e) and 5) replicate number. Note the expansion of tissue area of the novel corals at station Ed.

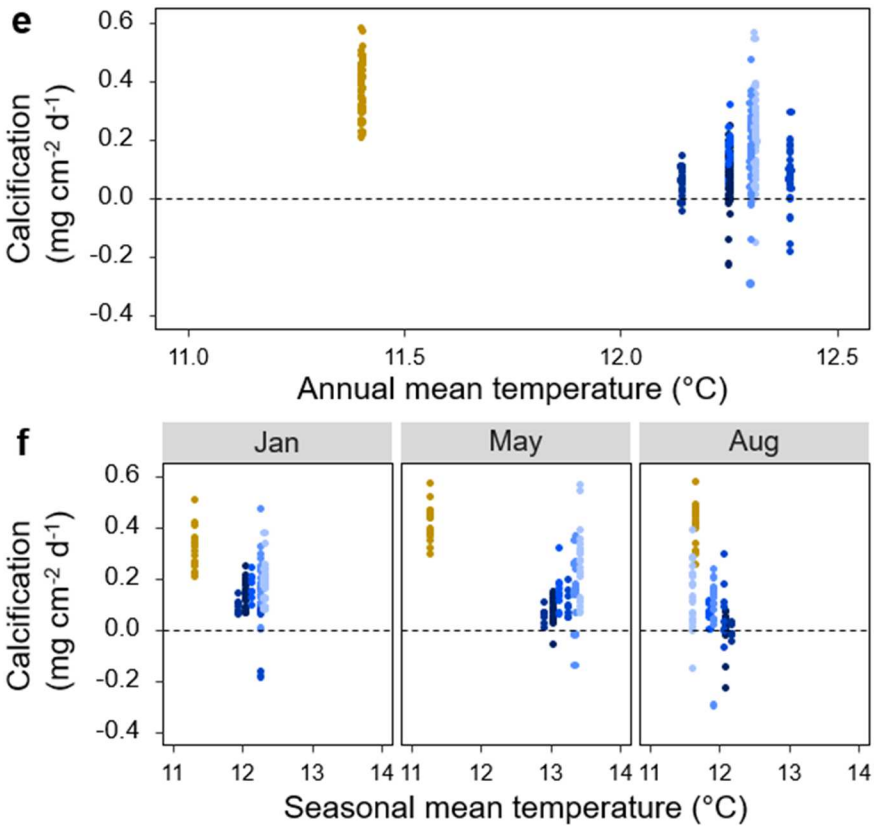


Supplementary Figure 7: Seasonal tissue coverage of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. The length of the tissue covered calyx of *D. dianthus* (mean ± standard deviation) at six stations at 20 m water depth along the fjord from head to mouth (A-F) is shown in blue and at one station at 300 m water depth (Ed) in yellow (data points in grey). Native corals (circles) were re-installed at the same station after collection in September 2016 and novel corals (squares) were cross-transplanted between the shallow stations at the head (A) and the mouth of the fjord (F) and between shallow (Es) and deep (Ed). Tissue length was measured at the beginning (September 2017) and end (August 2017) of the reciprocal transplantation experiment using the same individuals in each season (N = 6-10 independent samples). Note: As the tissue covered surface area changed only slightly at the shallow stations between September 2016 and August 2017, the surface area measurements carried out with a digital calliper at the end of the experiment (August 2017) were used as variable of reference for all sampling dates (January, May and August 2017). As the tissue covered surface area of native and novel corals at station Ed increased largely over time, the surface area of the corals at Ed was measured for each sampling date using scaled pictures of the corals.



Supplementary Figure 8: Calcification rates of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. Calcification rates of *D. dianthus* (mean ± standard deviation) at six stations at 20 m water depth along the fjord from head to mouth (A-F) are shown in blue and at one station at 300 m water depth (Ed) in yellow (data points in grey). Native corals (circles) were re-installed at the same station after collection in September 2016 and novel corals (squares) were cross-transplanted between the shallow stations at the head (A) and the mouth of the fjord (F) and between shallow (Es) and deep (Ed). Calcification rates were measured after four, eight and eleven months (January, May and August 2017) using the same individuals in each season (N= 6-10 independent samples) and are standardized to the skeletal dry mass of the corals at the beginning of the respective growth period.

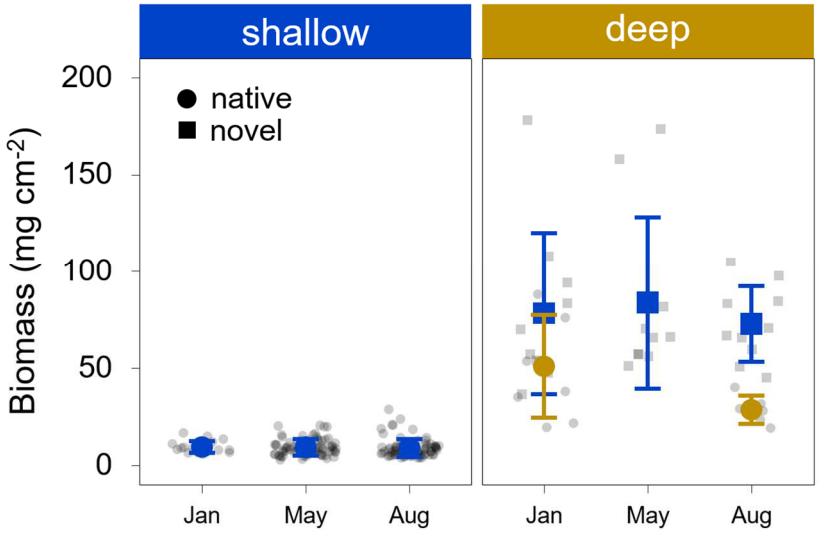

a
Calcification (mg cm-2 d-1)
0.6
0.4
0.2
0.0
-0.2
-0.4
7.6
7.7
7.8
7.9
Annual mean pHT
b
Jan
May
Aug
Calcification (mg cm-2 d-1)
7.6 7.7 7.8 7.9 8.0
Seasonal pHT
c
Calcification (mg cm-2 d-1)
0.8
1.0
1.2
1.4
Annual mean Ωarag
d
Jan
May
Aug
Calcification (mg cm-2 d-1)
0.8 1.0 1.2 1.4 1.6
Seasonal mean Ωarag



Supplementary Figure 9: Relationship between calcification rates of *Desmophyllum dianthus*, seawater pH, aragonite saturation and temperature at sampling stations in Comau Fjord, Chile. Combined calcification data of all three seasons (N = 19-57 independent samples) plotted against a) annual mean seawater pH_T, b) seasonal pH_T, c) annual mean aragonite saturation (Ω_{arag}), d) seasonal Ω_{arag}, e) annual mean temperature and f) seasonal mean temperature. Calcification rates of *D. dianthus* at six stations at 20 m water depth along the fjord (A-F) are shown in blue and calcification rates at one station at 300 m water depth (Ed) in yellow. Calcification rates of native and novel corals were measured after four, eight and eleven months (January, May and August 2017) using the same individuals in each season. Note that native and novel corals at each station are combined in this graph.

Biomass

In general, the tissue biomass of native and novel corals at 300 m depth was higher than that of all corals at 20 m water depth (p-value < 0.001, Supplementary Figures 10, Supplementary Table 2). Transplantation of corals from 20 m to 300 m water depth had a significant effect on the tissue biomass of novel corals. Not only was the biomass of novel corals at 300 m depth higher than the biomass of native corals at this station (p-value < 0.001, Supplementary Figures 10, Supplementary Table 2), but the corals were also able to expand the tissue covered surface area (Supplementary Figures 6 and 7).



Supplementary Figure 10: Seasonal tissue biomass of native and novel *Desmophyllum dianthus* of Comau Fjord, Chile. Tissue biomass of *D. dianthus* (mean ± standard deviation) at all six shallow stations (20 m depth, A-F) is shown in blue and at one deep station (300 m depth, Ed) in yellow, with native corals shown as circles and novel corals shown as squares. Note that there are no novel corals at the shallow stations. Corals were sampled after four, eight and eleven months (January, May and August 2017) to determine their tissue biomass (N = 6-76 independent samples).

Supplementary Discussion

The respiration rates of deep corals are also influenced by the higher incubation temperatures compared to the *in situ* temperature at the deep station. Due to the standardisation of respiration measurements for comparability and because we do not know the temperature performance curves of *D. dianthus*, we can only speculate if the change in temperature led to an under- or overestimation of the respiration rates of deep corals. As we expect the deep corals to have higher mitochondria density and activity (based on increased calcification rates, higher biomass as well as expected enhanced nutrition), this should result in elevated respiration rates under similar temperatures. Thus, by using the same temperatures, we gain insights into the metabolic potential rather than the exact *in situ* respiration rate. In addition, the effect of a 2 °C temperature change from 11.8 °C in winter to 14.2 °C in summer is evident in the native shallow corals at station Es, where the respiration rate increases from 1.7 µmol cm^{-2} d^{-1} in winter to a maximum of 4.2 µmol cm^{-2} d^{-1} in summer. This suggests that an increase of about 3°C (from 11.3 °C *in situ* to 14.2 °C in incubations in summer) could lead to a respiration rate of approx. 5 µmol cm^{-2} d^{-1} but not to 8 µmol cm^{-2} d^{-1} as measured for the deep corals in summer. The generally twice as high metabolic rate of deep corals over the seasons is therefore rather an indication of a changed metabolism in deep corals.

4

Manuscript 3:

Lipid biomarkers reveal trophic relationships and energetic trade-offs in contrasting phenotypes of the cold-water coral *Desmophyllum dianthus* in Comau Fjord, Chile

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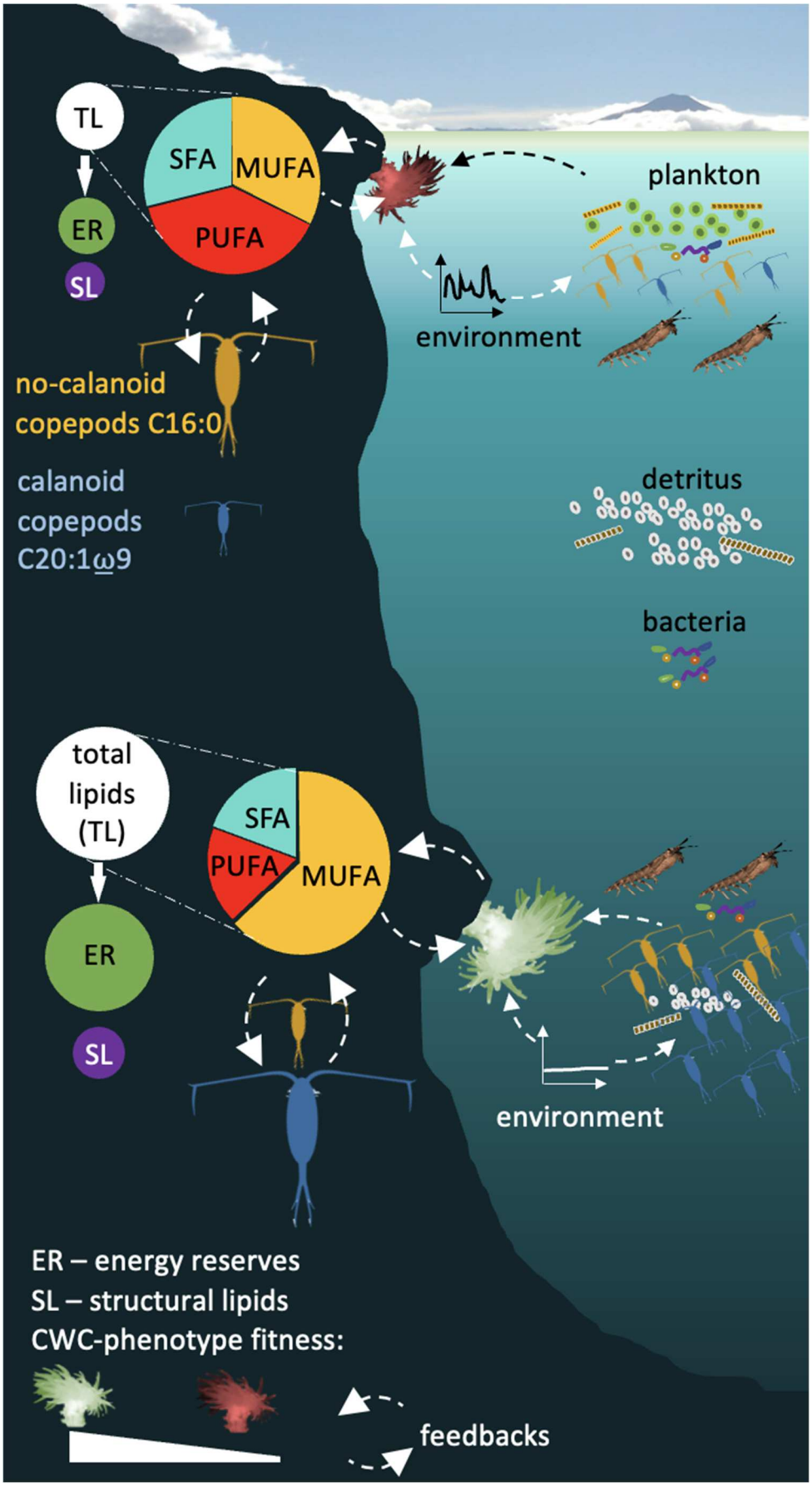
[#] These authors jointly supervised this work

Key words: cold-water coral, *Desmophyllum dianthus*, lipid biomarker, trophic ecology, essential fatty acids, physiological requirements

Manuscript under review at *Functional Ecology*

Graphical abstract



Abstract

Cold-water corals (CWCs) are considered wide-ranging opportunistic filter feeders, but little is known on their actual food *in situ*. To tackle this limitation, fatty acid trophic markers (FATM) have been employed to gain dietary insights. Yet, these *in situ* studies have not been combined with physiological investigations to understand how physiological limitations modulate the coral biochemistry. Here, we studied *Desmophyllum dianthus* in its natural habitat in Comau Fjord (Northern Patagonia, Chile) to assess the trophic ecology of this pan-globally distributed CWC in response to differing physico-chemical (variable vs. stable) and ecological drivers (food availability). Contrasting coral phenotypes were collected from shallow (20 m) and deep (300 m) sites with high calcification rates, biomass and energy reserves in 300 m water depth. We analysed the corals' fatty acid composition to evaluate the utility of FATM profiles to gain dietary insights and assess how physiological trade-offs potentially modulate the corals' FATM composition. We find that 20:1(n-9) zooplankton markers dominate the deep site, while 20:5(n-3) and 22:6(n-3) diatom and flagellate markers, respectively, are more prominent in shallow waters. The zooplankton diet supports higher energy stores in deep corals, in spite of measured lower zooplankton availability. Interestingly, essential FA concentrations are conserved across sites and likely reflect required levels for coral functioning and survival. While deep corals can easily meet these requirements, shallow-water corals appear to need more energy to maintain vital levels in their variable environment, potentially causing intrinsic re-allocations of energy and enrichment in certain essential markers (20:5(n-3), 22:6(n-3)). Our analysis highlights the biological and ecological insights that can be gained from FATM profiles in CWCs, but also cautions the reliability of FATM as diet tracers under limiting environmental conditions.

Introduction

Cold-water corals (CWCs) are important foundation species in all deep and dark ocean waters (Freiwald & Roberts, 2005; Roberts et al., 2006), where they create complex habitats that sustain a high biodiversity of up to 900 species (Rogers, 1999), including many commercially important fish species (Fosså et al., 2002; Buhl-Mortensen & Mortensen, 2004; Roberts et al., 2006). Their remoteness and depth have hampered early discovery and exploration, but advances in underwater technology providing submersible and remotely operated vehicles (ROV) has allowed much progress over the last decades (Freiwald et al., 2009). The combination of CWC distribution data, physicochemical characteristics (temperature, salinity, oxygen, turbulence) and modelling now allow to predict suitable CWC habitats (Davies et al., 2008; Davies & Guinotte, 2011; Morato et al., 2020). In addition, both *ex situ* (e.g. Georgian et al., 2016; Maier et al., 2016; Büscher et al., 2017) as well as *in situ* (e.g. Jantzen et al., 2013; Lartaud et al., 2017; Büscher et al., 2019; Chapron et al., 2020; Rossbach et al., 2021) manipulative experiments enable us to identify the drivers governing their health and vulnerability to human pressure as well as climate change and thus, their occurrence as well

as distribution today and in the future. Among the biological drivers, productivity and the supply of particulate organic carbon are considered important (e.g. Davies et al., 2008; Davies & Guinotte, 2011; Morato et al., 2020), but not consistently linked to habitat suitability (see discussion in Davies & Guinotte, 2011). Field observations underpin such variable modelling results and CWC reefs can be found in areas of variable (both high and low) surface productivity and thus, food availability (e.g. Cau et al., 2017; Dodds et al., 2009; Gori et al., 2018; Hebbeln et al., 2020). This indicates the corals' broad tolerance towards a range of nutritional conditions as well as their ability to take up various food sources (Naumann et al., 2011; Mueller et al., 2014; Höfer et al., 2018; Maier et al., 2019).

The availability of food, however, affects the corals' physiological performance, like their metabolic rate and growth (Naumann et al., 2011; Larsson et al., 2013; Maier et al., 2021) and it was shown that higher food availability can compensate for otherwise limiting conditions (e.g. Georgian et al., 2016; Maier et al., 2016; Büscher et al., 2017; Martínez-Alarcón et al., 2019). While CWCs may be quite tolerant and resilient to projected future changes in temperature and aragonite saturation state alone (e.g. Hennige et al., 2015; Büscher et al., 2017; Dorey et al., 2020; but also see e.g. Maier et al., 2009; Georgian et al., 2016; Gori et al., 2016), combined changes in physico-chemical conditions and food availability have been shown to compromise the calcification rates of CWCs (Hennige et al., 2015; Büscher et al., 2019). Corals are suspension-feeding omnivores gaining their metabolic energy from a variety of food particles ranging from microbes to phyto- and zooplankton (Duineveld et al., 2004; Mueller et al., 2014; Höfer et al., 2018; Maier et al., 2019; Rakka et al., 2021), where the zooplankton and krill appear to provide a key energy source to sustain their metabolic needs (Naumann et al., 2011; Maier et al., 2019, 2021). Thus, the relative availability of food along the plankton size spectrum *in situ* may be crucial to CWCs' response to future changes in their environment. However, still little is known about CWCs' feeding ecology in the field and the role of food on coral *in situ* performance.

Lipids, which constitute up to 40% of the corals' biomass (Harland et al., 1993) and their fatty acids, are promising biochemical markers providing insights into the corals' nutritional status, ecology and health (e.g. Dalsgaard et al., 2003; Imbs & Yakovleva, 2012; Rocker et al., 2019; Kim et al., 2021). Lipids provide more metabolic energy per gram than any other tissue compound like proteins or carbohydrates (Bureau et al., 2002) and represent a diverse group of large biological molecules (Joseph, 1979; Imbs et al., 2019). Dietary lipid is required by animals for the provision of metabolic energy, generated as ATP through the oxidative metabolism of fatty acids, and for the production of polar lipids, i.e. phospholipids and sphingolipids, necessary for the formation of cell membranes. This dual role is reflected in the compartmentalization of body lipid into adipose tissue, composed mainly of wax esters and/or triacylglycerols, and cell membrane lipid composed mainly of polar lipids and cholesterol (Sargent et al., 1993). Their balance is critical for the corals' stress resistance (Yamashiro et al., 2005; Imbs & Yakovleva, 2012). Lipids and their fatty acids (FAs) are involved in the majority of biochemical and physiological processes in organisms (Tocher, 2003; Russo, 2009).

The analysis of FA and fatty alcohols (FAlc) composition - so called fatty acid trophic markers (FATM) - has been widely used to trace the main food sources in marine organisms (e.g. Graeve et al., 1997; Dalsgaard et al., 2003; Budge et al., 2006). The lipid content as well as lipid class composition, together with the FATM profiles of marine organisms provide insight into the biochemical and ecological conditions of their surroundings (Bergé & Barnathan, 2005). Similarly, specific fatty acid ratios (e.g. DHA/EPA, n-3 PUFA/n-6 PUFA) serve as useful tracers of nutritional conditions (Graeve et al., 1997; Dalsgaard et al., 2003; Budge et al., 2006). At the same time, many PUFAs are essential for coral functioning and health and their biosynthetic pathways together with the organism's ability to modify FATM marker signal should be considered as this can modify the pure dietary FATM signal (Rocker et al., 2019; Galloway & Budge, 2020; Kim et al., 2021). Biosynthetic pathways are clearly described for phyto- and zooplankton and these pathways underscore their FATM profiles as well as their ability of trophic upgrading (i.e. the modification of essential dietary precursor PUFAs like 18:3n-3 (ALA - alpha linolenic acid) to essential LC PUFAs like EPA; a schematic biosynthesis pathway are depicted in Supplementary Figure 1). *De novo* synthesis of long-chain PUFAs, however, is linked to the unique possession of specific desaturase enzymes (Δ12, Δ15; Kabeya et al., 2020). These are key enzymes in primary producers that synthesize LC PUFA precursors, but these enzymes are lacking in higher trophic levels, e.g. fishes. Recently, evidence is accumulating that also intermediate consumers and invertebrate groups, including tropical corals, do possess such enzymes (Kabeya et al., 2018; Monroig & Kabeya, 2018). A matter of fact that needs to be considered in future FATM studies.

In CWCs, FATM analyses, together with the study of the corals' isotopic composition, could identify the corals *in situ* main food sources, distinguish between phytoplankton- (Duineveld et al., 2004, 2012; Kiriakoulakis et al., 2005) and zooplankton-dominated diets (Kiriakoulakis et al., 2005; Carlier et al., 2009; Dodds et al., 2009) at low and high supply levels (Dodds et al., 2009; Gori et al., 2018). Thus, biomarkers can provide a powerful tool to identify potential differences in prey composition. Since corals are omnivorous (Duineveld et al., 2004; Carlier et al., 2009; Höfer et al., 2018) and not actively select their prey (Höfer et al., 2018) but consume what is provided, CWCs represent an ideal system to infer nutritional condition and trophic ecology from FATM signal (Dodds et al., 2009; Duineveld et al., 2012; Naumann et al., 2015; Gori et al., 2018). It has to be borne in mind, however, that physiological responses to unfavourable conditions (e.g. like eutrophication in tropical corals; Rocker et al., 2019; Kim et al., 2021) may affect the trophic transfer or modification of biomarkers and potentially distort the diet signal (Galloway & Budge, 2020). While in tropical corals first studies addressed the potential changes in biosynthetic pathways under optimal and suboptimal conditions and identified putative FA indicators for coral health (Rocker et al., 2019; Kim et al., 2021), similar investigations for CWCs are still missing.

Here we investigated the suitability of biomarkers to assess dietary composition and health in CWC from contrasting habitats, using *Desmophyllum dianthus* in its natural Comau Fjord environment as our model species. We analysed the FATM signal in *D. dianthus*

individuals sampled along strong environmental gradients (both horizontal and vertical), and analysed the results against the background of concomitant data on coral physiology (Beck et al., 2022) and zooplankton composition (Garcia-Herrera et al., 2022). This allowed us to assess the FATM signal links to the available diet and possible shifts due to coral physiology influencing the FATM composition. Ultimately, how contrasting CWC phenotypes modulate their lipid composition provides a first baseline on potential physiological constraints on FA biosynthesis pathways in CWCs, and an important step forward to advance this line of research in these deep-sea foundation species.

Material and methods

Site and collection

The study was conducted in the Comau Fjord, Northern Patagonia, Chile (Figure 1), one of the few places worldwide where CWC emerged from the deep and inhabited shallow waters (Häussermann et al., 2021). Thus, local populations of *D. dianthus* are found within the same region in very contrasting environments, between deep and shallow, but also between fjord head and mouth (Beck et al., 2022). To represent the horizontal and vertical environmental gradients, corals were collected at 20 m at three stations (A, E, F) along the horizontal in the fjord, and at two depth (20 m and 280-290 m) at station (E), midway along the horizontal transect. At each sampling location, six *D. dianthus* individuals were collected in September 2016 (06.09.-22.09.) by SCUBA divers (shallow sites) and ROV (deep site, Commander 2, Mariscope Ingeniería, Puerto Montt, Chile; modified with manipulator arms and high-resolution camera). The collection of deep-water specimens required the ROV to be equipped with a wire frame and a water-tight bag attached to scrape the corals from the wall. The detached corals were secured in the bag, sealed and brought to the surface avoiding sample contact with the brackish surface layer.

Environmental and physiological background data

The physico-chemical environmental conditions during the sampling period were characterized along the entire fjord by CTD vertical profiles ranging from the surface to the bottom of the fjord. These CTD casts were conducted between 07.09-12.09.2016 at a total of seven stations in the centre of the fjord (Figure 1, yellow triangles). The CTD (SBE 19plus V2 SeaCAT profiler CTD, Sea-Bird Scientific, USA) was equipped with oxygen (SBE 43 dissolved oxygen, Sea-Bird Scientific, USA) and pH sensors (SBE 18 pH, Sea-Bird Scientific, USA).

Coral calcification, respiration and biomass were assessed subsequently to the coral sampling in a separate year-long *in situ* experiment. Corals were collected at the four sites and prepared for re-installation and re-collected seasonally after 4, 8 and 11 months to assess their performance. In brief, growth was measured through the buoyant weight technique (Jokiel et al., 1978) and respiration through closed-cell incubations. Further, separate corals were

prepared and collected at the same seasonal time scales, snap frozen and the coral tissue biomass determined. The procedure and seasonally resolved responses are presented in Beck et al. (2022). Here, we averaged all seasonal data to obtain a site-specific representation of coral performance. In addition, scaled pictures of the lateral side of the corals were taken in September 2016 after collection to show visual differences of the corals between sites.

Coral sample processing and FATM analysis

After collection, corals were transported to the Huinay field station and maintained in the flow-through aquaria system (for approx. 3-14 days). Corals were then snap-frozen in liquid nitrogen and maintained at -80 °C until further processing. In the laboratory, corals were crushed and ground to a relatively fine and homogeneous powder in a liquid nitrogen cooled stainless steel mortar. Subsequently, the total ground material was weighed (ranging from 970-8250 mg per coral individual) and subsampled for downstream analyses (i.e. ash free dry weight (AFDW) determination and fatty acid analysis) as follows: Approximately 300 mg per sample were used to determine ash free dry weight (approx. 10 % of the whole sample) and a minimum of 700 mg per sample (700-6600 mg, approx. 80 % of the whole animal) for lipid concentration and fatty acid composition analyses. The remaining material (approx. 10 %) was snap frozen and returned to -80 °C. Ash free dry weight was determined by transferring the subsample to a pre-combusted aluminium weighing pan and dried to constant dry weight for approx. 24 hours in an oven at 60 °C. Subsequently, the sample was weighed and combusted at 450 °C for 6 hours. Ash free dry weight was used to normalise the quantitative lipid and fatty acid composition analyses by extrapolating measurement to the total crushed coral sample and standardised to the organic fraction of the samples.

The lipid sub-sample was freeze-dried for approx. 24 hours and total lipid extracted in dichloromethan:methanol (DCM:MeOH, 2:1 per volume), modified after Folch et al. (1957). Aqueous KCl solution was added prior to centrifugation for phase separation. The extracted total lipid mass was determined gravimetrically and expressed as normalised to AFDW. As an internal standard, tricosanoic acid methyl ester (23:0) was added to each sample (1 µg μl^{-1} in n-Hexan). Transesterification of the lipid extracts was performed with 3 % sulfuric acid in methanol for 4 hours at 80 °C under nitrogen atmosphere. A gas chromatograph (HP 6890 N, Agilent Technologies, Inc) was used to determine the fatty acid methyl esters and fatty alcohols (Kattner & Fricke, 1986; Graeve et al., 1997). Individual fatty acids (FA) and fatty alcohol compounds (FAlc) were identified by their retention time and compared to known standards. Unknown peaks with less than one percentage contribution were excluded and the remaining chromatograms were evaluated using the Clarity Chromatography Software from DataApex. Total lipid mass per individual was derived by GC-FA/FAlc content from the measurements. Individual FA and FAlc compounds were calculated as relative percentage based on the total FA or FAlc concentration and also normalised to AFDW.

Data analyses and statistics

Analyses were performed using RStudio 1.3.1073 with R version 4.0.2 (R Core Team, 2020; RStudio Team, 2020). Site-specific differences in both FA and FAlc percentage composition were visualized using heatmaps with hierarchical clustering of both samples and FA/FAlc (package *ComplexHeatmap*, v2.6.2, Gu et al., 2016) and characterized by ordination analyses based on weighted log-ratio analysis (LRA) using the package *easyCODA* (Greenacre, 2018). Log-ratio analyses were performed on the total FA as well as total FAlc marker sets. Within LRA biplots loading vectors were limited to the major contributing markers following the procedure described in *easyCODA* or Greenacre (2018) and Graeve & Greenace (2020). Here we also summed markers for bacteria-specific origin: i15:0, ai15:0, i17:0 and 18:1(n-7) (Meziane & Tsuchiya, 2000; Boschker & Middelburg, 2002; Brett et al., 2006) to identify their diet contribution. In addition, the sum of FA and FAlc groups (SFA - saturated fatty acids/alcohols, MUFA - mono-unsaturated fatty acids/alcohols and PUFA - poly-unsaturated fatty acids) were derived as both relative and absolute concentration and in addition, ratios of putative FA trophic marker (e.g. 18:1n9 / 18:1n7, DHA / EPA) as well as putative health indicators (e.g. EPA / ARA, PUFAn3 / PUFAn6; Rocker et al., 2019; Kim et al., 2021) were calculated from the FATM signal. One-factorial ANOVA (normal and equal variance), Welch One-Way test (violation of equal variance) or Kruskal-Wallis test (violation of both equal variance and normality) were performed on total lipid composition, FA or FAlc classes, important dietary compounds/ratios (i.e. 20:1(n-9), trophic marker ratio: 18:1(n-9) / 18:1(n-7)) as well as essential FAs or health markers (e.g. EPA, DPA) to identify site-specific differences. Pairwise tests were used (with Tukey or Bonferroni correction) to reveal post hoc differences between individual sites. Fatty acid class composition differences between sites were tested with PERMANOVA in the R package *vegan*.

Plots of the CTD data were performed with Ocean Data View (Schlitzer, 2021). In the along-fjord profiles (Figure 1B), the colour scales were adapted to highlight the structure of the entire water column. Site-specific profiles were derived from the CTD profiles closest to each station and depth related average values obtained from these profiles per depth (shallow: 20-30 m and deep: 280-300 m to cover the maximum diurnal range for the region).

Results

Environmental background: The sampling period marks the end of the austral winter, characterized by a strong temperature inversion near the surface due to atmospheric cooling (Figure 1B and C). Winter mixing of the upper water column was evident in all parameters measured, showing deep mixing (down to 120 m) of oxygen- and pH-rich surface water in the outer two stations, eroding the suboxic and low-pH subsurface (30-80 m) layer of below the persisting pycnocline in the inner parts of the fjord, where mixing remained shallower than 30 m. Below 200 m, we found uniform conditions with only small vertical or lateral gradients. Shallow corals thrive at the lower edge of the halocline under slightly lower salinity (32.49 ± 0.104 95 %-CI) compared to deep corals (33.15 ± 0.0002 95 %-CI, Supplementary Figure 2).

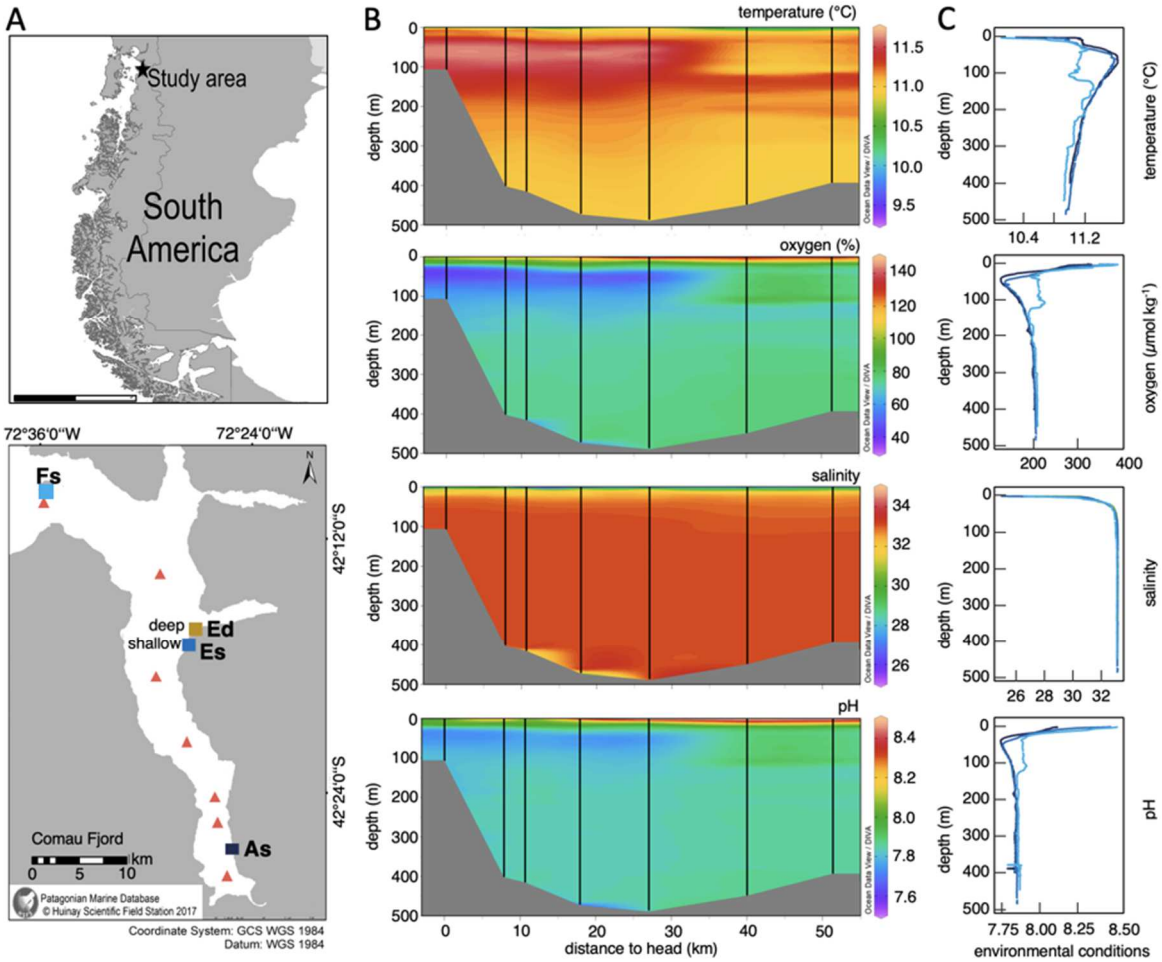


Figure 1: Sample sites and conditions. A) Study area is located in South America (upper panel) in the Fjord Comau in Northern Patagonia, Chile (lower panel). Shallow (20 m) coral sampling sites are denoted with light to dark blue squares (stations A, E, F), the deep site (280-290 m) in E is denoted in dark yellow. Oceanographic stations along the fjord are marked with red triangles. B) Cross sections of temperature (°C), oxygen saturation (%), salinity and pH from fjord head to mouth and deep to shallow are provided. Sampling stations (triangles in A) are shown by vertical black lines. C) Vertical profiles of temperature, oxygen saturation, salinity and pH at the sampling stations (A, E, F) are shown. Line colours correspond to the blue colour hues in (A).

Coral phenotypes and its relative biochemical composition: *Desmophyllum dianthus* expressed different coral phenotypes between shallow and deep sites in Comau Fjord that differed visually, metabolically as well as biochemically (Figure 2A-D). Corals with highest calcification rates can be found at the deep site and within the shallow sites we found a clear gradient of coral growth from the head towards the fjord mouth (Figure 2B). Biochemically, shallow water corals from all sites were very similar and have almost equal proportion of SFA, MUFA and PUFA (30.04 ± 1.22 %, 29.50 ± 1.43 %, 40.33 ± 1.54 %, respectively), compared to the significantly different deep corals with a specific fatty acid group composition (PERMANOVA df = 3, F = 112.81, p-value < 0.001, Figure 2C). Deep coral fatty acids were dominated by MUFA (60.75 ± 1.62 %) with lower but equal parts of PUFA and SFA (18.81 ± 0.99 %, 20.44 ± 0.71 %, respectively). Deep corals stood out with a significantly higher total lipids content (4-fold increase, Welch-test, df = 3, F = 4.09, p-value = 0.038) and content of fatty alcohols (One-Way ANOVA, df = 3, F = 103.95, p-value < 0.001, 33.8 ± 4.0 % compared to 10 ± 2.8 % across all shallow sites, Figure 2C and D).

Fatty acid trophic marker composition: A total of 44 FA and 8 FAlc markers were determined with very characteristic and different compositions at the two depths. The main FAs differentiating among depth were a long LRA dim 1, which explained 79.1 % of the observed variance and in particular involved the FAs 20:1(n-9) and 22:1(n-11), as well as essential FAs like 20:5(n-3) and 22:5(n-3) (Figure 3A). Thus, the clear distinction between deep and shallow phenotypes is mirrored also in the FA and FAlc composition (Supplementary Figure 3, Supplementary Table 1), indicating pronounced dietary differences between deep and shallow corals.

The trophic marker ratio 18:1(n-9)) : 18:1(n-7) > 3, (Figure 4A, Graeve & Greenacre, 2020) is slightly higher at the deep site, indicating a higher trophic level, i.e. more carnivorous diet. Phytoplankton markers, by contrast, are higher in shallow water corals (e.g. 20:5(n-3) and 22:5(n-3) with 14-12 % and 4.5-3.8 % in shallow water compared to 7 and 2.5 % in deep, respectively; Figure 3A, Supplementary Figure 3), indicating a more herbivorous diet. The shallow corals' FATM profiles (Figure 3A) showed a stronger contribution of diatom markers (20:5(n-3), EPA) compared to dinoflagellates markers (22:5(n-3), DHA) across sites (Figures 3A and 4B). However, EPA and DHA are also major compounds of the membranes and other algal markers are less distinct (e.g. 16:1(n-7) or 18:4(n-3) with 4.12 ± 0.84 and 0.87 ± 0.25 in shallow compared to 6.53 ± 0.61 and 0.57 ± 0.09 in deep, respectively). In addition, the contribution of bacterial markers to the individuals' biochemical composition is higher in shallow corals (marginally significant, F = 2.798, p = 0.067), but in general its overall contribution to the trophic structure was negligible.

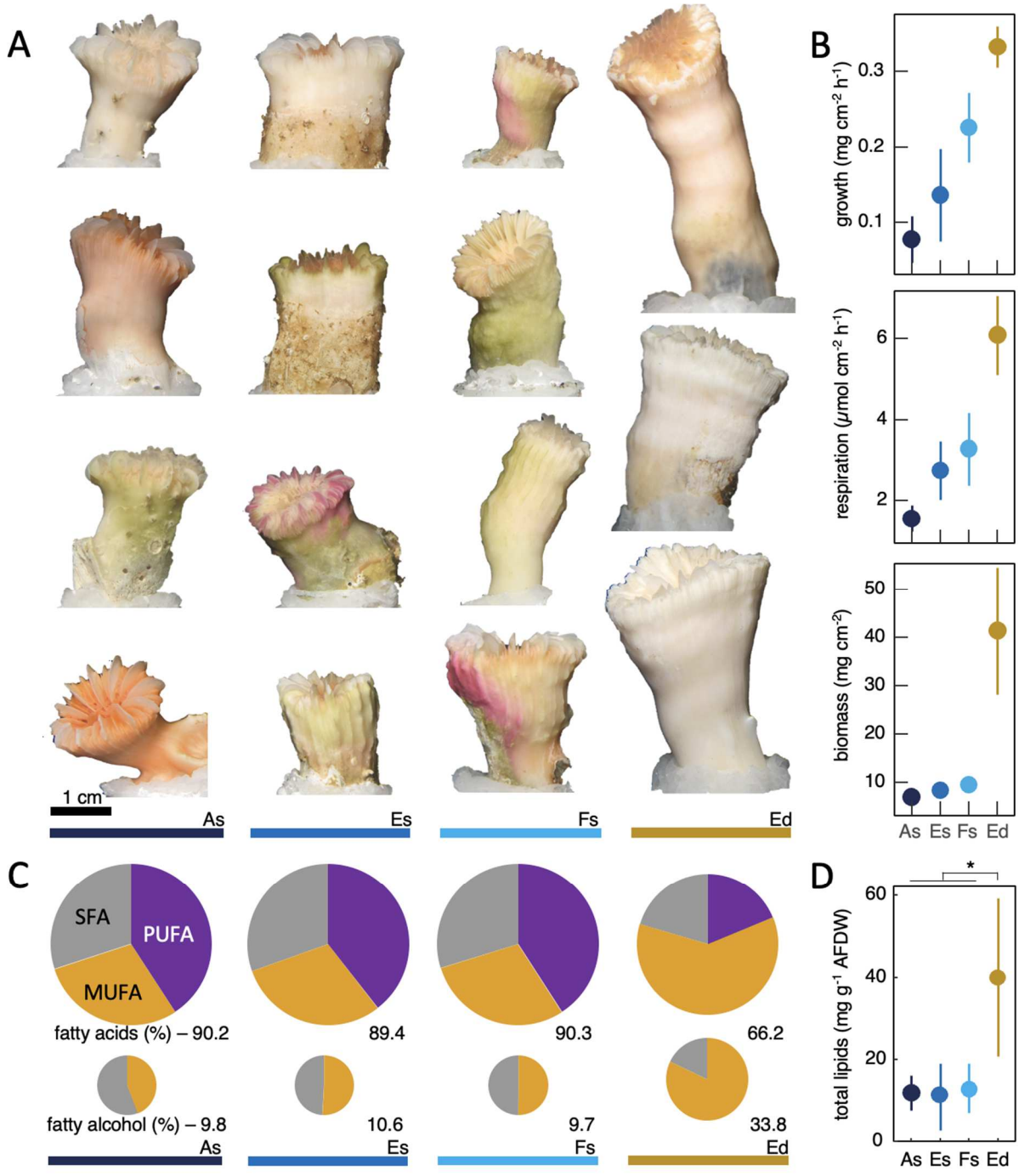


Figure 2: Coral phenotype and lipid composition across sites. A) Coral phenotypes at the shallow sites (first three columns; sites are depicted by dark blue, blue and light blue colour bars) and the deep site (dark yellow horizontal bar). B) Coral traits across sites in terms of growth, respiration and biomass are provided and assessed during September 2016 to August 2017 (Beck et al., 2022). C) Coral fatty acid trophic marker (FATM) composition is depicted in terms of fatty acids and fatty alcohols (upper and lower panel, respectively; circle diameters reflect percentage of fatty acids and fatty alcohols of total lipids at the given sites) and pie charts further indicate their specific composition (SFA: saturated fatty acid/alcohols, grey; MUFA: monounsaturated fatty acids/alcohols, orange; PUFA: polyunsaturated fatty acids, violet). D) The corals' total lipid content across sites. Shallow sites are indicated by As, Es, Fs (coloured in dark blue, blue and light blue, respectively) and the deep site by Ed (coloured in dark yellow). Data are mean ± 95 %-confidence intervals.

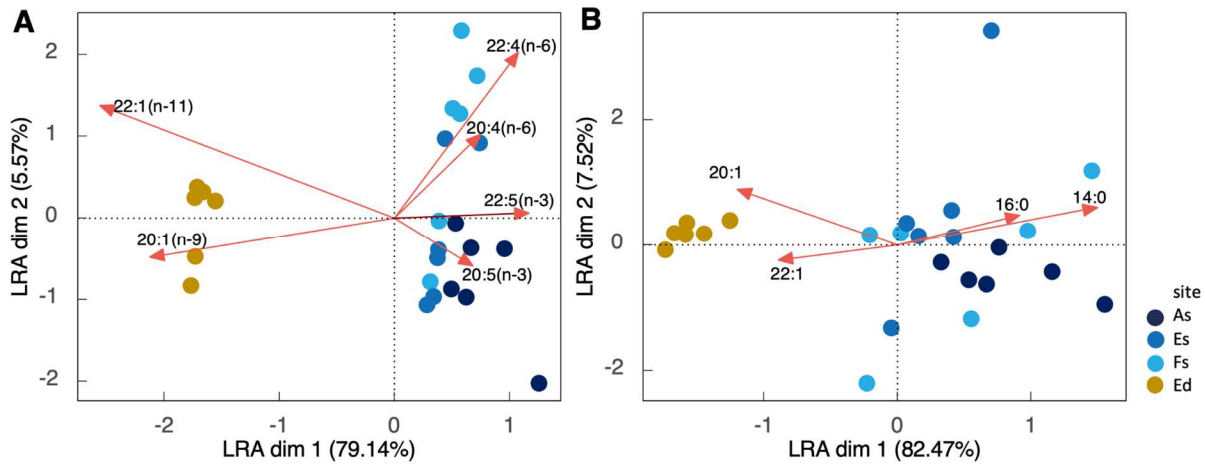


Figure 3: Log-ratio analysis (LRA) of the relative fatty acid trophic marker composition of *Desmophyllum dianthus*. Biplot of LRA of 44 fatty acids (FA, in A) and 8 fatty alcohol (Falc, in B) in specimens (circles) from four different sites. The LRA dimension 1 and 2 are differentiated by depth and by within shallow variance, respectively. Only markers (FA, Falc) that contribute highly to the separation of the samples are shown in red.

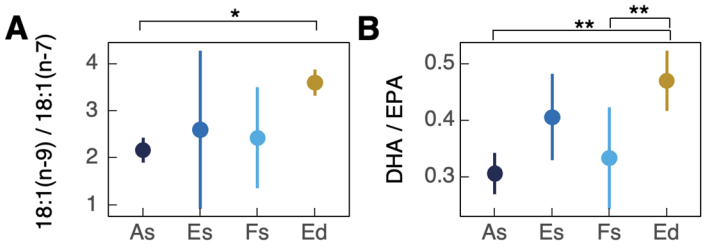


Figure 4: Fatty acid trophic marker ratios. Ratio of specific markers across sites provide insights into trophic position A) 18:1(n-9) / 18:1(n-7) or trophic network composition B) DHA / EPA (DHA: docosahexaenoic acid 22:6(n-3), EPA: eicosapentaenoic acid 20:5(n-3)). Data are mean ± 95 %-confidence intervals. Shallow sites are indicated by As, Es, Fs and coloured in dark blue, blue and light blue, respectively, and the deep site by Ed and coloured in dark yellow. Significant differences are denoted by * ($p \leq 0.05$), ** ($p \leq 0.01$).

Absolute fatty acid composition, essential fatty acids and potential mobilization and modification of fatty acids: The higher lipid content but lower proportion of PUFA and SFA in deep corals result in very similar total PUFA (One-Way ANOVA df = 3, F = 1.621, p-value = 0.216, 4.38-7.60 mg g^{-1} AFDW) and SFA concentrations (Welch-test, df = 3, F = 2.468, p-value = 0.119, 3.56-8.24 mg g^{-1} AFDW) across all sites. By contrast, the MUFA content differed significantly with an almost 7-fold change between deep and shallow sites (Kruskal-Wallis test, df = 3, X^2 = 12.96, p-value = 0.005, 3.57 ± 0.95 vs. 24.16 ± 11.43 mg g^{-1} AFDW; Figure 5A-C), dominated by increases in 20:1 and 22:1 fatty acids in deep corals (Figure 3A). Similar clear differences were found in the wax ester content (Kruskal-Wallis test, df = 3, X^2 = 12.98, p-value = 0.005) as well as the storage-to-structural-compound ratio (SFA+MUFA vs. PUFA) that is 2.9-fold enriched in deep corals (One-Way ANOVA, F = 221.6, p-value < 0.001, Figure 5D and E).

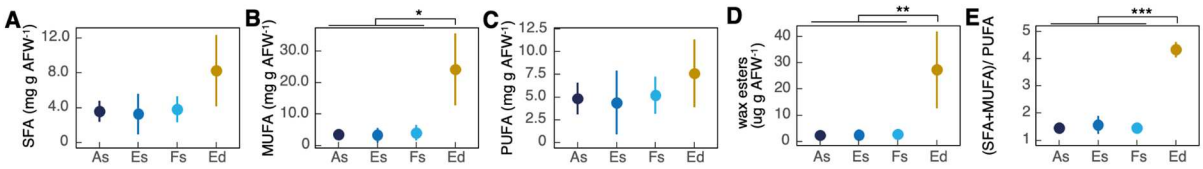


Figure 5: Coral fatty acid group concentrations and energy reserves. A-D) Absolute fatty acid group concentrations (SFA: saturated fatty acid; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids) and wax ester content across sites. E) Fatty acid class ratios reflect the storage capacity ((SFA+MUFA)/PUFA) and are depicted across sites. Shallow sites are indicated by As, Es, Fs and coloured in dark blue, blue and light blue, respectively and the deep site by Ed and coloured in dark yellow. Data are mean ± 95 %-confidence intervals.

Fatty acid analysis indicated that SFA markers like palmitic acid (PA, 16:0) and stearic acid (SA, 18:0) together with oleic acid (OleA 18:1(n-9)) were enriched in absolute concentration in deep corals, though not all significantly differ between shallow and deep sites (Figure 6; PA: Kruskal-Wallis test p-value = 0.057, X^2 = 7.533, SA: One-Way ANOVA, p-value = 0.090, F = 2.488, OleA: p-value = 0.001, F = 7.867). Oleic acid forms one important substrate for n-3 and n-6 PUFA synthesis pathways and their intermediates linoleic acid (LA, 18:2(n-6)) as well as alpha linoleic acid (ALA, 18:3(n-3)) were reduced in shallow corals (p-value = 0.002, F = 6.932 and p-value = 0.066, X^2 = 7.193, respectively). While most PUFAs were elevated in deep corals, some essential PUFAs were remarkably similar and non-significantly different concentrations across sites (Figure 6; arachidonic acid ARA, 20:4(n-6): p-value = 0.29, F = 1.338, Adrenic acid AdA 22:4(n-6): p = 0.115, X^2 = 5.927, EPA 20:5(n-3): p-value = 0.453, F = 0.912, docosapentaenoic acid DPA 22:5(n-3): p = 0.879, F = 0.224). Putative health indicators (e.g. EPA / ARA, PUFA(n-3)/PUFA(n-6)), were also very similar across sites (Supplementary Figure 4).

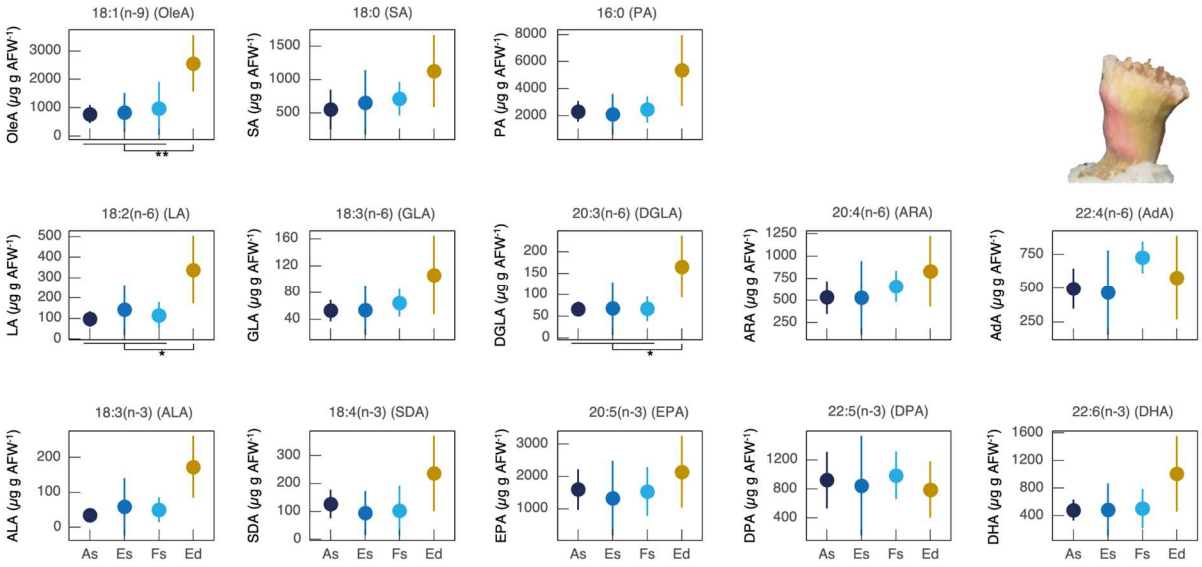


Figure 6: Fatty acid concentration through potential biosynthetic pathways. Schematic fatty acid synthesis pathways are provided in the supplementary material (Supplementary Figure 1) and some saturated, monounsaturated and in particular polyunsaturated fatty acids are provided for the different sites (As, Es, Fs and Ed). Shallow sites are indicated by As, Es, Fs and coloured in dark blue, blue and light blue, respectively, and the deep site by Ed and coloured in dark yellow. For the fatty acids acronyms are used: OleA: oleic acid, SA: stearic acid, PA: palmitic acid, LA: linoleic acid , GLA: gamma-linoleic acid, DGLA: dihomo-gamma-linoleic acid, ARA: arachidonic acid, AdA: adrenic acid, ALA: alpha linoleic acid, SDA: stearidonic acid, EPA: eicosapentaenoic acid, DPA: docosapentaenoic acid, DHA: docosahexaenoic acid. Significant differences are denoted by * ($p \leq 0.05$), ** ($p \leq 0.01$). Data are mean ± 95 %-confidence intervals.

Discussion

Fatty acid trophic markers in deep and shallow *D. dianthus* clearly distinguish between a deep lipid-rich phenotype and a leaner phenotype in shallow, despite expectedly more challenging conditions like year-round aragonite undersaturation and lower temperature (Fillinger & Richter, 2013; Jantzen et al., 2013). Our findings suggest that food is sufficient for the build-up of energy reserves (e.g. wax esters) in deep corals, in line with their higher calcification rates (Beck et al., 2022) and this may be linked to a more carnivorous diet. Shallow water corals do not possess the ability to accumulate much energy reserves, underpinning their lower calcification rates (Beck et al., 2022) and potentially subsisting on a more vegetarian diet. This is in conflict, however, with measured higher zooplankton quantity in shallow waters (Garcia-Herrera et al., 2022). To resolve this paradox, we link coral physiological performance with FATM data and provide hypotheses explaining the contradictory observations in the context of physico-chemical parameters and resource availability.

Trophic network inferences

The Comau Fjord and other Chilean fjords are productive environments sustaining high zooplankton stocks (Palma & Silva, 2004; González et al., 2010; Garcia-Herrera et al., 2022). Zooplankton composition and biomass vary over wide temporal (seasonal, tidal, diel) and spatial (horizontal and vertical) scales (Palma & Silva, 2004; Hamame & Antezana, 2010; Garcia-Herrera et al., 2022), resulting in contrasting nutritional environments to their coral predators. We thus expect moderate horizontal differences in trophic networks between head and mouth, and large differences between shallow and deep waters that should be reflected in the corals' FATM signal. Overall, the *D. dianthus'* rich biochemical composition supports their omnivore feeding behaviour (Gori et al., 2018; Höfer et al., 2018), similar to other deep-sea corals (Orejas et al., 2001; Rakka et al., 2021). It also clearly indicates differences in prey community between deep and shallow sites, but not along the head-mouth axis of the fjord (Supplementary Figure 3). Along the same isobath, the FATM signals cluster together but we do see a stronger spread as well as variation within this cluster even within the same site (Supplementary Figure 3, Figure 3A-C). This rather points towards stronger spatial gradients within sites in shallow waters (Supplementary Figure 3) and it may reflect local microenvironments of similar trophic niche across sites with less clear differentiation of the plankton community along the fjord.

As observed for other CWCs (Naumann et al., 2015; Gori et al., 2018; van Oevelen et al., 2018), bacterial markers appear in *D. dianthus'* fatty acids profile, however, their contribution to the corals' diet is negligible with a slightly larger relative contribution in shallow waters (Supplementary Figure 3). Phytoplankton and phytodetritus may serve as potential food sources for deep sea corals (Orejas et al., 2001, 2016; Maier et al., 2019) and could thus, directly account for these specific markers. Inputs are visible through a higher proportion of algal related markers (EPA, DHA and slightly for 18:4(n-3)), especially in shallow corals

(Supplementary Figure 3, Figure 3A; Harwood & Russell, 1984; Dalsgaard et al., 2003) and the ratio DHA/EPA indicates a diatom signal prevailed over dinoflagellate (Petersen et al., 1987; Auel et al., 2002; Falk- Scott et al., 2002) at both depths (Figure 3A). This also coincides with a predominant pattern of diatom-zooplankton succession in the plankton communities of Chilean fjords (González et al., 2010; Montero et al., 2017), which is reflected in the corals' FATM signal. However, we also need to consider the importance of EPA and DHA as major membrane constituents that will be discussed in more detail below.

From an energetic perspective, bacteria, phytoplankton and phytodetritus are insufficient to sustain the corals' metabolic needs compared to a zooplankton-based diet (Naumann et al., 2011; Maier et al., 2019, 2021; Rakka et al., 2021). Phytoplankton markers are ambiguous, indicating either direct uptake of phytoplankton, or the uptake of herbivorous zooplankton containing accumulated phytoplankton markers. Other FAs, like 14:0, 16:0, 18:0, are also major structural elements in copepods (Boissonnot et al., 2019) and together with EPA also indicate herbivore copepods. Between depths, however, they differ in relative abundance (Figure 3A and B, Supplementary Figure 3). The 16:0 fatty alcohol in particular is dominant in shallow corals (Figure 3B) and such short-chained fatty alcohols (similar to FAlc 14:0) are found to be more prevalent in small or non-calanoid species (e.g. cyclopoid copepods; Sargent & Falk-Petersen, 1988; Kattner et al., 2003; Lischka & Hagen, 2007). As non-calanoid copepods (e.g. Cyclopoida) and small calanoid copepods (e.g. Paracalanus, Clausocalanus) are abundant in the shallow water layers of Comau Fjord (Garcia-Herrera et al., 2021), they may have contributed to the observed shallow water phytoplankton FATM signal in the corals.

The biomarkers 20:1 and 22:1 (both the FA and FAlc) clearly differ between deep and shallow corals. They are enriched in coral tissue of deep waters and only found in a reduced proportion in shallow corals (Figure 3A and B). These markers are mainly synthesized *de novo* by calanoid copepods (Sargent & Whittle, 1981; Dalsgaard et al., 2003), in particular by the family Calanidae (Hagen & Auel, 2001). While calanoid copepods occur in almost similar biomass across all depths in winter and spring (around the time of sampling), compositional differences exist. For instance, Calanidae are more prevalent in deeper sites, while Metrinidae occur at shallower water layers. Yet, they have shown diurnal migration patterns and may still contribute to the diet in both depths (Garcia-Herrera et al., 2022). The low concentration of LC MUFA in shallow corals, however, may result from these two different dominating families. It has been shown that they have distinct FATM signals in other regions with *Calanus* spp. accumulating 20:1(n-9) and 22:1(n-11) FA and FAlc as major end products compared to *Metridia* spp. with 14:0 and 16:0 FAlc as well as 16:1(n-7) and 18:1(n-9) FA as major end products (Hagen & Auel, 2001). This suggests that even though both groups of zooplankton migrate across several water layers (though at different extent), the family Calanidae dominates the deep corals' diet while contributing little to the shallow corals' nutrition.

The trophic marker ratio 18:1n-9/18:1n-7, indicating a higher trophic level in the zooplankton community (Graeve et al., 1997; Legeżyńska et al., 2012), suggests a higher

contribution of carnivorous zooplankton to the deep corals' diet (Figure 4). This may indicate that the algal markers found in shallow corals arose from a consumption of herbivorous zooplankton, not by direct phytoplankton uptake. Similarly, the deep corals' rich calanoid signal may not necessarily derive from direct consumption alone. Biomarkers also accumulate at the higher trophic level (Dalsgaard et al., 2003) and it is, thus, possible that they actually prey on larger zooplankton species that feed on calanoid copepods (Kobari et al., 2021). For instance, mysids and Euchaetidae are abundant in the deep fjord region and can represent an important food source for deep corals (Garcia-Herrera et al., 2021). Euchaetidae are large carnivorous copepods consuming smaller calanoid copepods (Yen, 1985), which could have accounted in part to the calanoid signal. While mysids are in general omnivores (Siegfried & Kopache, 1980; Grossnickle, 1982), adults may become more carnivorous (Fulton, 1982) and potentially also prey on calanoid copepods (Crescenti, 1997; Díaz-Astudillo et al., 2017).

Overall, we do see clear differences across depths in the corals' FATM signals that can be linked to available zooplankton data and support the dominance of certain zooplankton groups (e.g. Calanidae vs. Metridae; Garcia-Herrera et al., 2021). Based on markers for trophic position we can speculate whether some markers derive from direct consumption or through accumulation along the food chain but this requires more detailed food web analyses. So far, we compared the relative FATM signal without considering absolute values, the clear differences in the corals' energetic status and physiological performance observed across sites. It is also possible that FATM profiles are differently modulated by the organisms in concert with the ecological settings and this may further distort the trophic network signal. Subsequently, we will discuss what we can learn from the lipid data in terms of zooplankton biomass availability across depths and potential consequences that may arise for the corals' FATM signal.

Energy availability in the fjord

In Comau Fjord, the zooplankton biomass and abundance vary across depths with highest abundances and biomasses in the upper 50 m of the water column (Garcia-Herrera et al., 2022). Thus, shallow water corals should thrive in a land of plenty compared to deep water corals. Yet, this is neither reflected in the directly measured coral traits (Beck et al., 2022; data summarised in Figure 2), nor in the biochemical signature of the corals. Deep corals have first and foremost approx. 4-fold higher lipid content in addition to an elevated ratio of energy storage (SFA+MUFA) to structural (PUFA) FAs as well as 3.4-fold higher wax ester content. Both highlight a thicker coral tissue with high energy storage capacity reflected by the wax ester content in deep corals. There are a number of potential explanations for this food paradox that are not mutually exclusive. It may be possible that a) shallow corals grow in denser banks along with other suspension and filter feeders compared to deep corals, hence experiencing greater competition due to interdependence of competition for space and food (Buss, 1979), b) shallow corals are exposed to other environmental drivers, not considered in this study, that inflict an energetic burden, c) major differences in plankton biomass and

composition exist between the central water column and the plankton close to the steep walls harbouring the corals (e.g. wall effects) and/or d) plankton communities represent different food qualities for corals.

In the Chilean fjords, CWCs emerged from the deep and conquered the shallows, inaccessible for CWCs in most other regions (8 m; Försterra et al., 2005; Häussermann et al., 2021). Emergence may be associated with *D. dianthus*' strong phenotypic plasticity and ability to acclimate to very contrasting conditions (Häussermann et al., 2021; Beck et al., 2022), but may come at a cost and may only be possible in rather plankton-rich environments (reviewed in Häussermann et al., 2021), such as the Comau Fjord (Garcia-Herrera et al., 2021). Recent studies suggest that *D. dianthus* in the shallow environments experiences stronger environmental variability and conditions potentially more stressful for corals (Beck et al., 2022). Together with pressures from infestations of their skeleton by microscopic endolithic photo-autotrophs (like *Ostreobium queckettii* or the cyanobacterium *Plectonema terebrans;* Försterra et al., 2005; Försterra & Häussermann, 2008; Hassenrück et al., 2013) and other epi- and endolithic organisms (Försterra et al., 2005), the emerged corals may be at their physiological limits. Ecological factors may add to this, such as competition. Coral banks in the regions are dominated by *D. dianthus* and they can be associated with other suspension or filter feeders across depths, e.g. brachiopod banks occur from shallow to deep, mussel and barnacle banks are restricted to the intertidal (Häussermann & Försterra, 2009; Betti et al., 2017) and *Acesta patagonica* co-occurs with *D. dianthus* below 60 m (Fillinger & Richter, 2013; Häussermann et al., 2013). The shallow regions, however, can be particularly diverse (Försterra et al., 2017) and CWCs co-occur with a myriad of both sessile and mobile species that decrease with depth (Försterra et al., 2005). This probably leads to competition for food and depletion of the rich plankton community in shallow waters, which may likely be reflected in the overall lower calcification rates of these corals.

Additionally, the strong environmental variability in shallow waters, in particular registered salinity fluctuations (Beck et al., 2022), may affect the plankton composition. For instance, some zooplankton groups are known for their higher salinity tolerance (e.g. Cyclopoida, with known FATM characteristics such as high 16:0 and 14:0 FAlc, 16:0 FA visible in shallow corals; Lischka & Hagen, 2007), whereas others are more sensitive (Magouz et al., 2021). This may also affect the abundance of the zooplankton (Laprise & Dodson, 1994; Wells et al., 2021) and potentially restrict certain zooplankton groups to deeper waters. However, as the available plankton data derive from integrated plankton tows across the upper 50 m of the water column (Garcia-Herrera et al., 2021), they are too coarse to elucidate small scale patterns. They can only serve as first approximations to evaluate the response of the zooplankton community to environmental variability to better understand its cascading effects on the physiological performance of corals and their FATM signal.

Zooplankton abundance and biomass diminish with increasing depth, yet the biomass per prey item increases with depth (Garcia-Herrera et al., 2021). Thus, we calculate that shallow

corals may have a 10-fold higher individual capture rate compared to deeper ones, however, this difference shrinks to a 2-fold difference when the biomass per prey is considered (Garcia-Herrera et al., 2021). This does not consider prey handling, which may be energetically unfavourable, when dealing with many small items versus few large ones (Sebens, 1982). Nor does it include differences in food quality (Dessier et al., 2018; Schaafsma et al., 2018). Certain calanoid copepods are known for their high wax ester and thus, energy content (Hagen & Auel, 2001; Dessier et al., 2018; Schaafsma et al., 2018). Additionally, even within the group of calanoid copepods energy density may differ, with up to one third lower energy content in some genera compared to others (e.g. *Calanus hegolandicus* vs. *Metridia* sp. or *Temora longicornis*; Dessier et al., 2018). The same accounts also for other taxa and strong variability in energy density within zooplankton groups (reviewed in Schaafsma et al., 2018). Thus, it may be possible that different calanoid copepod species dominating the deep and shallow corals diet (e.g. Metrinidae vs. Calanidae; Garcia-Herrera et al., 2021) have potentially very different energy content. While the FATM signal may not be affected, it has consequences for the corals and can contribute to the distinct performance observed at different depths.

Sampling bias may also account for some inconsistencies and limit a more precise FATM signal interpretation. For instance, plankton tows were performed in the centre of the fjord, but the zooplankton community may be different closer to the steep fjord walls (Greene et al., 1988; Hirche et al., 2016). Additionally, larger zooplankton and micronekton is mobile and capable of avoiding the nets (Brinton, 1962). *Euphausia vallentini* (krill) is common in Comau Fjord (Sánchez et al., 2011) however, it has not been caught efficiently by vertical plankton tows (few young stages & one adult individual; Garcia-Herrera et al., 2021). Similarly, euphausiids employ a number of unique adaptations to entrapped life in fjords and for instance, take advantage of demersal habitats where they exploit a rich and alternative food source compared to their open ocean counterparts (Hamame & Antezana, 2010). Potentially, euphausiids play a critical role in the Northern Chilean fjords (Maier et al., 2021), representing an energy-rich diet for deep corals in Comau Fjord (Maier et al., 2021) together with Euchaetidae and mysids (Garcia-Herrera et al., 2021). Certain Euphausiids can also accumulate wax esters as well as a calanoid signal (like 20:1(n-9) FAlc; Falk-Petersen et al., 2000; Hagen & Auel, 2001). Thus, a revised interpretation of the deep corals' Calanidae FATM signal (20:1(n-9) & 22:1(n-11) FA & FAlc) is possible and potentially krill can additionally account for such a signal in deeper sites.

All these mentioned aspects can contribute to the apparent resource limitation and stronger differences in energy availability than originally expected between deep and shallow waters of the Comau Fjord. While sampling biases, with underrepresented zooplankton groups, can have a direct effect on the interpretation of the FATM signals, resource limitation can also result in a modification of fatty acids and a distortion of the FATM signal. In the latter case, the FATM signal may rather be driven by the corals' metabolic needs than their diet. Subsequently, we discuss what we can learn from the physiological background data in terms

of energy allocation and finally discuss insights gained from the FATM signal regarding the corals' potential active fatty acid modifications.

Energy turn-over and trade-offs

Physiological background data support higher net energy availability for deep corals, yet they also reveal energetic trade-offs. Energy is channelled into 2.3-fold higher calcification, 5.0-fold higher tissue biomass and 3.4-fold higher energy reserves (e.g. wax esters) in deep water corals, compared to shallow corals. Energy reserves prevailed through winter in spite 2- to 3–fold lower zooplankton availability during the cold season (Garcia-Herrera et al., 2022), typical also of other CWC regions (Wiborg, 1954; Gaard, 1999; González et al., 2010). The prevalence is even more remarkable considering the reproduction of *D. dianthus* which, in spite of being energetically costly (Calow, 1979), peaks in austral winter (Feehan et al., 2019). Population genetic analyses indicated a mixed population from shallow to the deep sites within Comau Fjord and speculated about a source/sink separation and that potentially the deep corals serve as an important source of coral recruits in general (Addamo et al., 2021). This represents a likely scenario based on our data. Yet, it is also plausible that the reduced energy reserves derive from a similar or even higher investment into reproduction that deplete these reserves in shallow water. Physiological trade-offs and shifts in energy allocation are prevalent in an organism's life history and are strategic processes underpinning the success and physiological performance of organisms, especially under resource limitations (Leuzinger et al., 2012; English & Bonsall, 2019). Under severe limitations there are two possible strategies: a) invest in reproduction at the risk of death or b) invest into somatic growth to endure periods of scarcity (Stearns, 1989; Fischer et al., 2009). In a tropical coral, resource limitations lead to a substantial reduction in somatic growth, while calcification and reproduction was maintained and energy transfer increased. However, under severe resource scarcity reproduction was halted, but growth to some extent maintained in the same study (Leuzinger et al., 2012). Applied to our study, this could mean that somatic growth (in terms of reduced biomass in Figure 2B or seen in some corals with lower tissue cover in Beck et al., 2022) is sacrificed to maintain calcification and reproduction. While we do see such higher energy transfer into growth, investment into reproduction requires further investigation. However, such physiological trade-offs likely require the mobilization of energy reserves and contribute to the distortion of the FATM signal, which must be taken into account.

Fatty acids as indicators of coral health and functionality

Despite clear differences in total lipids as well as energy storage capacity (Figures 2 and 5E), the similar total PUFA concentration across sites and depths is striking (Figure 5C). It may represent the corals' dependencies on specific concentrations of essential fatty acids for their general metabolic regulation and point towards their need to maintain them across sites. Polyunsaturated FA are key molecules for metabolic regulation and support structural integrity, membrane functioning and immune system competency (Tocher, 2003; Russo,

2009; Kim et al., 2021). Under stressful conditions, invertebrates were found to metabolise SFA and MUFA, while preserving PUFA as long as possible (Schlechtriem et al., 2008; Mezek et al., 2010). Here we also find very low MUFA content in shallow corals but similar PUFA content, in line with the lower calcification rates in shallow water, the limiting conditions and need to mobilise fatty acids like MUFAs. Marked differences in absolute lipid concentration can, thus, result in an over-representation of these essential lipids in the relative FATM signal (e.g. algal markers like EPA, ARA in shallow corals; Figure 3C). In turn, it potentially also results in a lack of certain markers (e.g. LC MUFAs like Calanidae markers 20:1n-9) that were readily metabolised to fuel the organism's metabolic demands. This clearly shows the duality of some FA markers, i.e. the derivation from their diet or the modification through their catabolism (fatty acid integration "black box"; Galloway & Budge, 2020; Helenius et al., 2020; Kabeya et al., 2020).

Underlying drivers for such modified levels may be selective retention of essential FAs (Yasuda et al., 2021), trophic upgrading (Helenius et al., 2020) or *de novo* synthesis by the coral (Kabeya et al., 2018). The significantly lower linoleic acid (LA, 18:2(n-6)) and reduced ALA (18:3(n-3)) concentration may indicate their trophic upgrading into LC PUFAs (Figure 5), but it may also be possible that *D. dianthus* is capable of *de novo* synthesis following all PUFA biosynthesis steps (Figure 6) through the activity of methyl-end desaturation (Δ12, Δ15) enzymes (Kabeya et al., 2018). For example, *Lophelia pertusa* - a sibling species - is able to synthesize essential fatty acids *de novo* including PUFA(n-3) (EPA and DHA; Mueller et al., 2014). Similar observations exist for tropical corals, where the two essential PUFAs (LA and ALA) were identified (Kabeya et al., 2018). Yet, the energetic costs and the potential rate of modification (that may still be limited in animals) of this *de novo* synthesis need to be evaluated. Besides, a capability does not necessarily indicate its activity. Chronic stress, e.g. eutrophication, has been shown to actually limit the ability for lipid synthesis in tropical corals (Kim et al., 2021).

Notably, fatty acid modifications can be linked to organism physiology, and in tropical corals PUFA ratios (e.g. DHA:EPA, EPA:ARA) were employed as indicators for water quality as well as putative coral health (Rocker et al., 2019; Kim et al., 2021). In this study, we expect that the FATM signal of the deep coral phenotype more closely resembles their diet, while the limiting conditions in shallow waters warrant further investigation of the corals' fatty acid metabolism and thus potentially stronger modification of their FATM signal, especially following winter. This also adds caution to the interpretation of the FATM profiles from other CWC species, in particular from areas with distinct and in particular low background productivity (first insights and comparisons are provided in the supplementary material). Analogue to studies in tropical corals (Rocker et al., 2019; Kim et al., 2021), specific PUFA ratios may rather be used to differentiate between optimal versus suboptimal environmental conditions, but this will require more detailed experimental studies to support such application in *D. dianthus* as well as other CWC species.

Conclusion

In the past, FA profiles in CWCs helped to gain insight into their trophic ecology and the ecological setting they flourish in. Yet, none have combined *in situ* sampling with physiological investigations to understand how physiological limitations modulate the coral biochemistry in CWCs. Here FATM provides insights into the corals' potential *in situ* food sources, but we also emphasise the need for a more holistic view and better integration of physiological (metabolic rates) and ecological information (e.g. food availability and sources, physico-chemical conditions) with FATM analysis. While FATM and lipid content analyses gained a whole new perspective on corals in Comau Fjord, it also revealed numerous open questions that warrant further investigations. In this respect, the Comau Fjord represents an ideal natural laboratory that allows the design of experiments able to trace lipid metabolism and energy allocation pathways. This will provide a more precise understanding of the CWCs' ability to cope with future changing conditions in particular under contrasting productivity regimes.

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Author contributions

G.M.S.G., J.L. and C.R. designed the study. J.L., G.F. and G.M.S.G. contributed background information and collected the corals. M.Wall, M.Woll and K.K.B. conducted the coral preparation and lipid measurements. K.K.B. and G.M.S.G. contributed physiological background data. M.Wall and M. Woll analysed the raw data. M.Wall and M.G. interpreted the data. M.Wall conducted the statistical analysis. Together with K.K.B., M.Wall prepared the figures. M.Wall and C.R. wrote the first draft of the paper. All authors contributed to the final discussion and edited the manuscript.

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Supplementary Results

Supplementary Table 1: List of fatty acids (FA) and fatty alcohols (FAlc). Individual marker concentrations are given as relative abundance as well as absolute concentration per site. All values are stated as mean ± standard deviation (SD) and fatty acids as well as fatty alcohols with a relative abundance < 0.5 % were excluded from the data set.

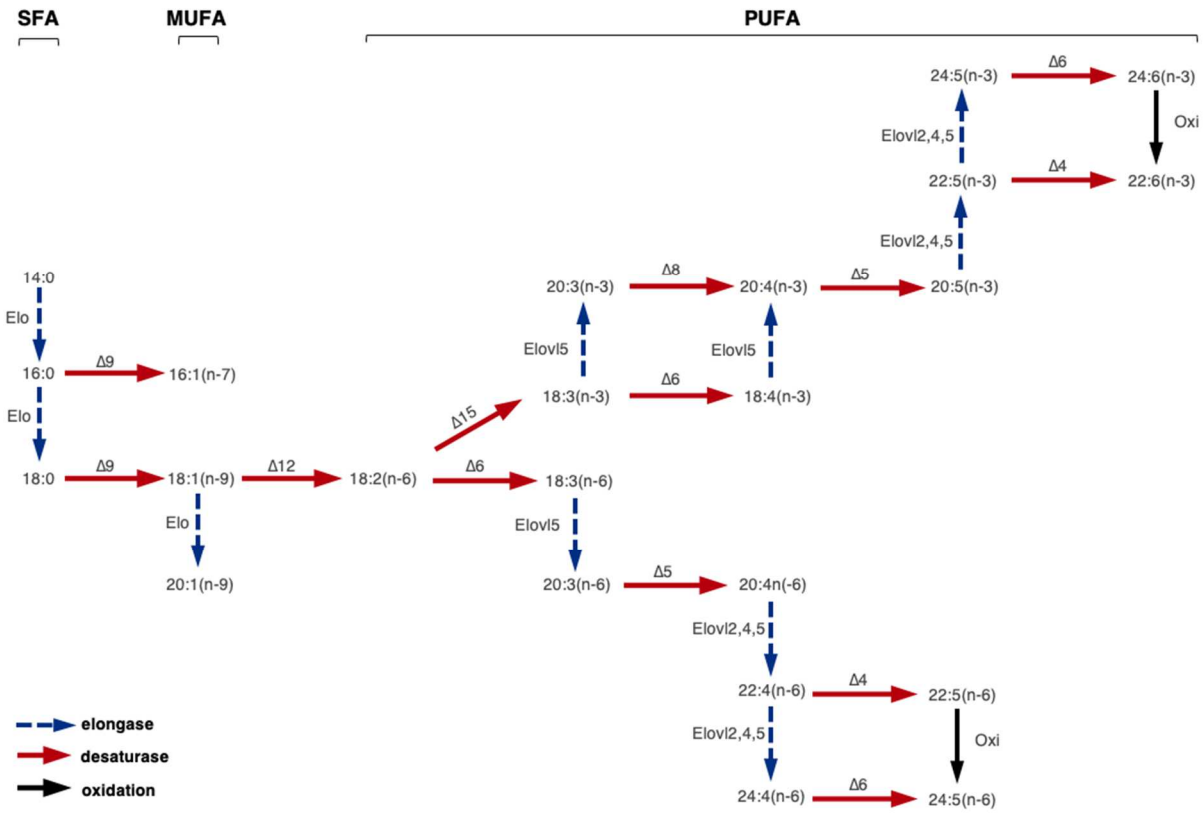
FA	Relative concentration (%)			
	As	Es	Fs	Ed
14:0	2.21 ± 0.30	2.11 ± 0.37	1.23 ± 0.26	2.82 ± 0.40
16:0	19.51 ± 1.86	19.50 ± 2.22	19.22 ± 1.24	13.30 ± 0.69
16:1(n-5)	1.06 ± 0.10	0.96 ± 0.10	0.87 ± 0.19	1.28 ± 0.13
16:1(n-7)	4.55 ± 0.49	4.22 ± 0.57	3.60 ± 1.15	6.53 ± 0.61
16:2(n-4)	0.79 ± 0.16	0.55 ± 0.14	0.52 ± 0.18	0.86 ± 0.19
16:3(n-4)	0.61 ± 0.13	0.41 ± 0.24	0.35 ± 0.11	0.21 ± 0.09
16:4(n-1)	0.71 ± 0.15	0.40 ± 0.24	0.37 ± 0.19	0.17 ± 0.05
17:0	0.57 ± 0.09	0.30 ± 0.48	0.64 ± 0.06	0
18:0	4.71 ± 1.80	5.94 ± 0.48	5.63 ± 0.42	2.83 ± 0.20
18:1(n-5)	2.94 ± 0.22	2.93 ± 0.63	2.58 ± 0.44	2.44 ± 0.30
18:1(n-7)	2.98 ± 0.24	3.02 ± 0.45	2.67 ± 0.27	1.84 ± 0.08
18:1(n-9)	6.43 ± 0.58	7.50 ± 3.75	6.56 ± 3.05	6.62 ± 0.60
18:2(n-6)	0.81 ± 0.11	1.33 ± 0.30	0.90 ± 0.35	0.84 ± 0.05
18:3(n-6)	0.45 ± 0.04	0.49 ± 0.30	0.52 ± 0.07	0.26 ± 0.05
18:4(n-3)	1.07 ± 0.22	0.82 ± 0.17	0.73 ± 0.26	0.57 ± 0.10
20:0	1.43 ± 0.06	1.47 ± 0.25	1.38 ± 0.22	0.59 ± 0.07
20:1(n-5)	1.12 ± 0.13	0.61 ± 0.71	1.22 ± 0.26	0
20:1(n-7)	2.09 ± 0.33	1.99 ± 0.13	2.24 ± 0.23	0.79 ± 0.07
20:1(n-9)	1.48 ± 0.24	1.90 ± 0.27	1.66 ± 0.24	12.85 ± 0.51
20:1(n-11)	0.24 ± 0.03	0.21 ± 0.18	0.26 ± 0.05	0.85 ± 0.03
20:2(n-6)	0.73 ± 0.25	0.59 ± 0.35	0.91 ± 0.46	0.52 ± 0.10
20:3(n-6)	0.57 ± 0.05	0.53 ± 0.27	0.53 ± 0.07	0.42 ± 0.05
20:4(n-3)	0.62 ± 0.09	0.42 ± 0.35	0.62 ± 0.23	0.77 ± 0.11
20:4(n-6)	4.49 ± 0.51	5.30 ± 1.36	5.33 ± 0.92	2.10 ± 0.49
20:5(n-3)	13.33 ± 0.89	11.59 ± 2.94	11.64 ± 1.58	5.26 ± 0.49
22:0	0.48 ± 0.27	0.23 ± 0.36	0.63 ± 0.18	0
22:1(n-7)	0.89 ± 0.36	0.76 ± 0.37	0.90 ± 0.44	0.51 ± 0.11
22:1(n-9)	1.77 ± 0.94	1.76 ± 0.78	1.60 ± 0.18	2.43 ± 0.31
22:1(n-11)	1.59 ± 0.72	2.67 ± 0.70	2.70 ± 0.27	22.26 ± 0.81
22:4(n-6)	4.24 ± 0.62	4.60 ± 1.31	6.11 ± 1.66	1.48 ± 0.41
22:5(n-3)	7.66 ± 0.80	7.41 ± 1.80	7.82 ± 0.75	1.99 ± 0.34
22:6(n-3)	4.09 ± 0.61	4.56 ± 0.79	3.78 ± 0.47	2.46 ± 0.20
24:1(n-9)	1.17 ± 0.13	1.08 ± 0.22	1.10 ± 0.19	0.81 ± 0.03
24:1(n-11)	0.64 ± 0.12	0.33 ± 0.39	0.89 ± 0.22	1.54 ± 0.42

Supplementary Table 1 (continued)

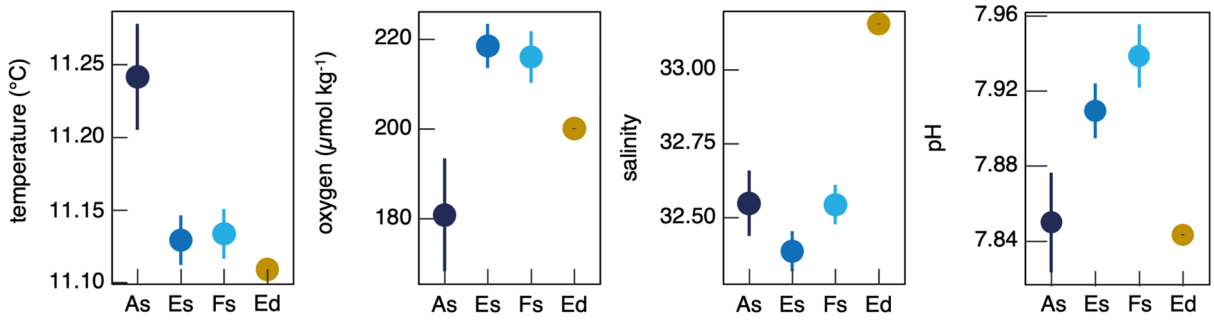
FA	Absolute concentration (µg g^{-1} AFDW)			
	As	Es	Fs	Ed
14:0	264.5 ± 101.4	215.1 ± 154.8	168.3 ± 109.8	1161.4 ± 647.2
16:0	2317.6 ± 743.8	2108.3 ± 1440.5	2453.0 ± 927.8	5349.8 ± 2491.9
16:1(n-5)	126.3 ± 45.6	105.7 ± 74.4	119.7 ± 75.1	514.0 ± 251.6
16:1(n-7)	552.5 ± 238.6	450.1 ± 335.3	509.6 ± 374.6	2634.5 ± 1254.9
16:2(n-4)	96.0 ± 46.9	64.3 ± 49.7	72.8 ± 51.9	359.9 ± 201.6
16:3(n-4)	74.4 ± 37.9	46.5 ± 32.3	48.8 ± 35.0	90.2 ± 67.5
16:4(n-1)	87.0 ± 43.4	53.7 ± 43.9	46.6 ± 26.5	70.3 ± 39.2
17:0	68.2 ± 22.9	16.1 ± 28.4	80.9 ± 24.8	0
18:0	548.8 ± 284.1	653.3 ± 458.9	712.3 ± 241.1	1124.8 ± 515.5
18:1(n-5)	350.3 ± 123.1	351.0 ± 284.5	337.2 ± 171.2	973.1 ± 444.3
18:1(n-7)	356.8 ± 130.3	324.2 ± 247.7	357.5 ± 197.8	724.1 ± 312.6
18:1(n-9)	774.6 ± 306.3	830.1 ± 661.3	978.0 ± 885.7	2560.5 ± 954.0
18:2(n-6)	96.5 ± 35.2	142.3 ± 115.3	115.0 ± 60.2	337.6 ± 157.5
18:3(n-6)	52.7 ± 15.3	53.7 ± 34.8	64.4 ± 19.5	105.9 ± 55.7
18:4(n-3)	126.8 ± 48.7	94.2 ± 75.3	102.7 ± 85.4	235.8 ± 128.5
20:0	168.4 ± 49.1	172.9 ± 137.6	174.1 ± 60.3	236.9 ± 114.7
20:1(n-5)	132.2 ± 40.1	29.6 ± 48.3	149.7 ± 40.0	0
20:1(n-7)	250.5 ± 87.7	214.6 ± 145.9	281.8 ± 89.4	315.5 ± 145.7
20:1(n-9)	177.8 ± 69.8	208.4 ± 148.6	225.0 ± 129.0	5133.8 ± 2419.5
20:1(n-11)	29.3 ± 11.3	18.2 ± 23.9	34.8 ± 20.6	340.3 ± 155.1
20:2(n-6)	83.3 ± 29.2	77.0 ± 59.5	109.6 ± 47.7	211.3 ± 109.8
20:3(n-6)	66.4 ± 16.7	68.5 ± 58.4	67.2 ± 27.1	164.9 ± 68.1
20:4(n-3)	73.7 ± 29.2	67.7 ± 66.6	88.6 ± 77.8	313.5 ± 155.3
20:4(n-6)	531.7 ± 176.0	528.5 ± 394.7	657.2 ± 170.6	828.9 ± 378.4
20:5(n-3)	1596.2 ± 596.9	1324.6 ± 1101.6	1528.9 ± 724.2	2142.5 ± 1056.9
22:0	60.1 ± 36.2	14.8 ± 28.5	79.0 ± 32.7	0
22:1(n-7)	100.1 ± 40.6	79.8 ± 63.6	111.8 ± 57.7	199.5 ± 93.2
22:1(n-9)	194.5 ± 64.4	161.3 ± 98.6	206.5 ± 88.6	955.9 ± 422.5
22:1(n-11)	201.7 ± 120.0	318.9 ± 250.7	351.2 ± 159.0	8869.2 ± 4095.2
22:4(n-6)	495.5 ± 142.8	468.0 ± 296.8	727.4 ± 112.3	577.3 ± 294.7
22:5(n-3)	921.4 ± 368.9	842.7 ± 652.9	985.8 ± 313.3	789.9 ± 369.1
22:6(n-3)	479.8 ± 146.1	486.4 ± 360.2	501.2 ± 272.2	1007.9 ± 523.5
24:1(n-9)	137.7 ± 46.0	123.9 ± 95.5	150.1 ± 91.5	322.4 ± 146.9
24:1(n-11)	74.9 ± 22.4	29.8 ± 42.9	106.4 ± 18.1	616.0 ± 366.2

Supplementary Table 1 (continued)

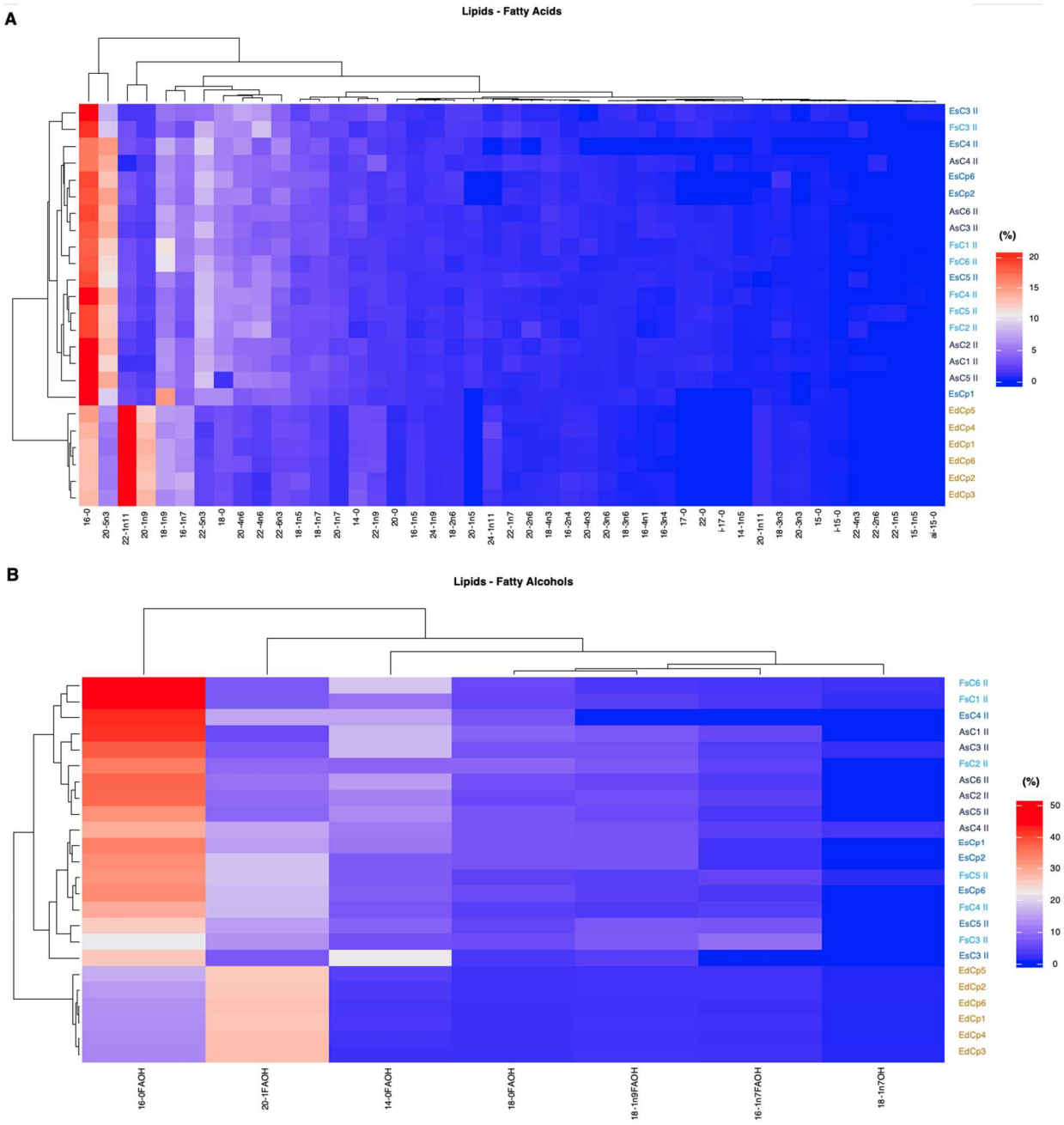
FAlc	Relative concentration (%)			
	As	Es	Fs	Ed
14:0	13.9 ± 2.72	11.67 ± 5.70	9.41 ± 4.48	2.68 ± 0.60
16:0	35.64 ± 4.52	32.12 ± 6.15	35.24 ± 10.20	13.42 ± 1.34
16:1(n-7)	3.73 ± 0.73	2.35 ± 2.38	4.54 ± 2.52	2.00 ± 0.13
18:0	6.42 ± 0.96	5.27 ± 1.45	5.29 ± 1.63	1.90 ± 0.12
18:1(n-7)	0.68 ± 1.09	0	0.77 ± 0.89	0.73 ± 0.05
18:1(n-9)	5.80 ± 0.65	4.44 ± 2.52	4.60 ± 1.92	2.18 ± 0.16
20:1	9.11 ± 3.45	14.42 ± 3.94	11.88 ± 4.98	26.42 ± 0.52
22:1	24.71 ± 5.61	29.73 ± 6.38	28.27 ± 8.27	50.68 ± 1.76
FAlc	**Absolute concentration (µg g^{-1} AFDW)**			
	As	**Es**	**Fs**	**Ed**
14:0	1711.7 ± 843.4	958.2 ± 490.0	1297.8 ± 905.9	1029.0 ± 389.2
16:0	4288.1 ± 1657.4	3457.5 ± 2542.7	4966.8 ± 3477.2	5308.9 ± 2221.1
16:1(n-7)	432.7 ± 131.0	332.3 ± 291.2	523.2 ± 175.3	801.4 ± 375.8
18:0	763.4 ± 267.0	610.3 ± 479.4	676.7 ± 301.9	755.3 ± 323.1
18:1(n-7)	82.3 ± 132.6	0	128.1 ± 158.4	293.6 ± 144.2
18:1(n-9)	687.0 ± 242.7	585.8 ± 468.5	564.2 ± 240.1	872.0 ± 407.3
20:1	1024.1 ± 290.8	1754.1 ± 1429.2	1403.0 ± 468.2	10618.8 ± 5038.8
22:1	2908.3 ± 1040.0	3209.6 ± 2205.8	3433.4 ± 1107.9	20318.2 ± 9643.1



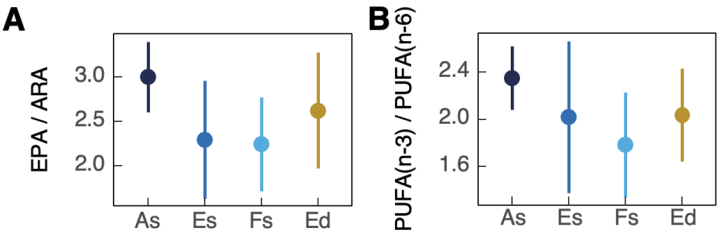
Supplementary Figure 1: Fatty acid biosynthesis pathways. Schematic fatty acid synthesis pathways provided with solid red line arrows indicate desaturase enzymes (with type specified as ΔX), blue dashed line arrows indicate elongase enzymes and black arrow represent β-oxidation involved in a potential coral biosynthesis pathway. Fatty acid groups are indicated above showing saturated (SFA), monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA). Pathways modified and adapted from Dalsgaard et al. (2003), Monroig et al. (2013), Rocker et al. (2019), Kim et al. (2021).



Supplementary Figure 2: Average environmental conditions during sampling. Site-specific average conditions (temperature, oxygen, salinity and pH) are provided per station (A, E, F) at the shallow sites (20-30 m depth range for As, Es, Fs) and the deep site (280-300 m depth range, Ed). Shallow sites are indicated by As, Es, Fs and coloured in dark blue, blue and light blue, respectively, and the deep site by Ed and coloured in dark yellow. Data are mean ± 95%-confidence intervals.



Supplementary Figure 3: Heatmaps of fatty acid and fatty alcohol composition of individual corals. Heatmaps depict the relative percentage of individual fatty acid (a) and alcohol (b) markers per sample. Trees are hierarchical clustering of samples based on a complete linkage method of the relative abundance across sample or marker. Coral samples were collected at shallow waters (20 m depth) of Comau Fjord at sites As, Es, Fs (dark blue, blue and light blue colours, respectively) and at one deep site (300 m depth) at site Ed (dark yellow).



Supplementary Figure 4: Fatty acid ratio as putative health indicators. Ratio of specific markers across sites that have been used as putative health indicators in tropical corals (Rocker et al., 2019; Kim et al., 2021). A) represents the ratio EPA / ARA (EPA: eicosapentaenoic acid 20:5(n-3) and ARA: arachidonic acid, 20:4(n-6)) and B) PUFA(n-3) / PUFA(n-6) (PUFA: polyunsaturated fatty acids and n-3 and n-6 represent the sum of all omega-3 and omega-6 PUFA, respectively). Shallow sites are indicated by As, Es, Fs and coloured in dark blue, blue and light blue, respectively, and the deep site by Ed and coloured in dark yellow. Data are mean ± 95%-confidence intervals.

Supplementary Discussion

Comparison of the biochemical composition with other **Desmophyllum** *and other cold-water coral species*

Deep coral lipid composition markedly differs from other CWCs analysed so far. CWCs show a pan-global distribution inhabiting oligotrophic waters like the Mediterranean Sea (Freiwald & Roberts, 2005; Lo Iacono et al., 2018) and high productivity areas as described for the North and South Atlantic (Dodds et al., 2009; Hebbeln et al., 2020). In the latter, they can even endure anoxic conditions as observed in subtropical oxygen minimum zones (Colman et al., 2005; Le Guilloux et al., 2009; Hebbeln et al., 2020). In terms of lipid composition derived from various CWC reefs, the contrasting content of PUFA sticks out particularly. PUFAs are the major FA group in *Dendrophyllia cornigera* in both Menorca and Cantabria (Gori et al., 2018: 67 %) as well as *D. dianthus* or *Madrepora oculata* in the Mediterranean and NE Atlantic (Naumann et al., 2015: approx. 50%, Kiriakoulakis et al., 2005: 42-45 %) and they share this characteristic with *D. dianthus* obtained in shallow stations in the Comau Fjord (40 %). *Lophelia pertusa* samples from the NE Atlantic represent an exception with similarly low or even lower values like the deep *D. dianthus* in Comau Fjord (Kiriakoulakis et al., 2005: 7-25 %). Previously, PUFA dominance was explained as an expected characteristic of marine lipids (Yamashiro et al., 1999), yet not supported in the deep CWCs in Comau Fjord with highest growth rates. This stark difference is accompanied by a 2.9-fold higher level of storage compounds compared to structural lipids. However, even the storage to structural ratio of shallow *D. dianthus* corals is significantly higher compared to *D. cornigera* (Gori et al., 2018), but similar to *D. dianthus* from the Mediterranean (Naumann et al., 2015). This might reflect species-specific differences, but may also reflect limited food supply. Often a higher proportion of PUFA coincides with low productivity areas as reflected in *D. cornigera* in the Menorca channel (Gori et al., 2018). Similarly, *L. pertusa* corals collected in the NE Atlantic are characterized by enrichment in storage lipids likewise as the deep coral phenotype in this study (or even up to 8-fold higher enrichment in storage compounds; Kiriakoulakis et al., 2005; Dodds et al., 2009) and therefore, indicate high productivity regions beneficial for CWC populations. It can be expected that these populations employ similarly elevated growth rates, respiration rates and coral biomass as observed for the deep coral population in Comau Fjord and may indicate flourishing 3-dimensional reef structures in these regions.

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Manuscript 4:

Seasonal energy reserves of the cold-water coral *Desmophyllum dianthus* from Comau Fjord, Chile

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Key words: lipids, carbohydrates, proteins, lipid classes, calcification, seasonality, reciprocal transplantation, acclimatization

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Abstract

The composition of energy reserves and lipid classes has been studied in few cold-water coral (CWC) species and information on their seasonal changes and environmental controls is still limited. This study explores the seasonal and spatial variation of total energy reserves (proteins, carbohydrates and lipids) and lipid classes of the CWC *Desmophyllum dianthus* along pronounced gradients in the physico-chemical and feeding conditions in Comau Fjord (Chile). We examined the adaptation of energy reserves and lipid classes in an *in situ* reciprocal transplantation experiment (20 m vs. 300 m and fjord head vs. mouth) and compared total energy reserves to coral calcification. Surprisingly, the deep corals had highest calcification rates, with higher total energy reserves and storage lipids (wax esters and triacylglycerols), while seasonal changes of energy reserves were more pronounced in shallow waters. The rapid increase in energy reserves of novel (i.e. cross-transplanted) deep corals underscores the fast acclimatisation potential of *D. dianthus*, whereas the adjustment of the lipid class composition took up to one year. Novel corals in shallow waters had the same amount of energy reserves as native corals at the respective station. Total energy reserves correlated positively with calcification rates.

Introduction

Cold-water corals (CWCs) are mostly found in deep waters worldwide, where they form important ecosystems for other benthic organisms and fish (Freiwald et al., 2004; Roberts et al., 2009). However, even in deep waters, they are affected by environmental changes (Guinotte et al., 2006; Roberts et al., 2006; Hoegh-Guldberg et al., 2007). In some regions, CWCs are also found in shallow waters of fjord environments. Deep-water emergence of species from greater depths (> 200 m) conquering the shallow euphotic zone (Häussermann et al., 2021) has been observed in Alaska (Waller et al., 2014), New Zealand (Parker et al., 1997), Norway (Brooke & Järnegren, 2013), Sweden (Wisshak et al., 2005) and Chile (Försterra & Häussermann, 2003). In the shallow habitats, CWCs experience more fluctuating environmental conditions than at depths (Wisshak et al., 2005; Montero et al., 2011; Guihen et al., 2012; Rossbach et al., 2021; Beck et al., 2022) and are likely more susceptible to future environmental changes.

Many CWCs occur in regions with high primary productivity with direct food supply from the surface ocean (Duineveld et al., 2004, 2007; Kiriakoulakis et al., 2004; Carlier et al., 2009; Davies et al., 2009), but they are also found under contrasting productivity regimes (Dodds et al., 2009; Gori et al., 2018). Generally, CWCs are opportunistic filter feeders, which feed on zooplankton (Carlier et al., 2009; Naumann et al., 2011, 2015; Höfer et al., 2018) and a wide range of other food sources, including dissolved organic matter, bacteria and phytoplankton (Sherwood et al., 2008; Mueller et al., 2014), but zooplankton is considered the most important food source (Naumann et al., 2011, 2015; Rakka et al., 2020, 2021; Maier et al.,

2021). However, information about *in situ* food availability in CWC habitats are still scarce due to their remoteness and difficult accessibility. The biochemical and stable isotope composition provide a loophole to the corals' nutrition and health status (e.g. Schoepf et al., 2013; Rocker et al., 2017, 2019a). One example is the metabolic fractionation leading to enrichment of stable isotopes along the food chain (e.g. Sherwood et al., 2008) and another is the energy surplus from feeding that is stored as lipids, although it is also partly excreted as mucus (Anthony & Fabricius, 2000).

The biochemical composition is critical for the coral to maintain its metabolism under limiting feeding conditions, but also to be able to withstand future environmental changes (Anthony et al., 2009). The total tissue energy reserves of corals consist of lipids, proteins and carbohydrates. Lipids can account for up to 40 % of the total organic dry mass (Harland et al., 1993; Imbs, 2013) and provide almost twice as much energy per unit mass as proteins and carbohydrates (Gnaiger & Bitterlich, 1984), which have the lowest energy density (Leuzinger et al., 2003; Schoepf et al., 2013). Polar lipids are essential for the formation of cell membranes (phospholipids and sterols; Oku et al., 2003; Imbs et al., 2010), but non-polar lipids are also used for short- and long-term energy storages (e.g. wax esters and triacylglycerols; Harland et al., 1993). In addition, they are involved in many biochemical and physiological processes and the stress resistance of corals (Rodrigues et al., 2008; Anthony et al., 2009).

Several previous studies investigated the total lipid or fatty acid content (Larsson et al., 2013; Movilla et al., 2014; Baussant et al., 2017), lipid classes (Hamoutene et al., 2008) as well as fatty acid composition (Dodds et al., 2009; Naumann et al., 2015; Gori et al., 2018; Maier et al., 2019, 2020) of CWCs, but little is known so far about the entire biochemical composition (lipids, proteins and carbohydrates) of CWCs (only laboratory study by Chapron et al., 2021). The lipid content of the CWC *Lophelia pertusa* (syn. *Desmophyllum pertusum*) was not significantly affected by food concentration in previous laboratory studies (Larsson et al., 2013; Baussant et al., 2017), which indicates that CWCs can resist food deprivation over several months (Larsson et al., 2013; Baussant et al., 2017). However, decreasing trends in both studies and a significant decrease of lipid concentrations in Chapron et al. (2021) showed that *L. pertusa* depletes its lipid stores after few months. In contrast, CWCs may downregulate their metabolism under food deprivation to prevent the depletion of energy reserves (Dodds et al., 2009) as reduced respiration (Baussant et al., 2017) and calcification rates (Naumann et al., 2011) indicate. Therefore, energy reserves can give information about the coral metabolism and the metabolization of energy reserves when limiting energy is available, but little is known so far about natural temporal and spatial variations in energy reserves of CWCs. Energy reserves of corals vary during the year because they have to divide their metabolic energy between the most important physiological processes, such as maintenance, growth, reproduction and competition (Leuzinger et al., 2003, 2012). Therefore, food limitations in winter coinciding with lower temperatures may lead to a reduction of their metabolism and thus contribute to energy conservation as CWCs likely build up lipid reserves during periods of high food availability and use these reserves under suboptimal feeding conditions (Dodds

et al., 2009; Maier et al., 2019). For tropical shallow-water corals, it has been shown that the energy reserves vary seasonally due to changes in abiotic conditions, such as temperature, light and nutrients (e.g. Ben-David-Zaslow & Benayahu, 1999; Oku et al., 2003; Hinrichs et al., 2013; Imbs & Dang, 2021). The energy reserves of the CWC *L. pertusa* were found to decrease during the spawning season in winter due to the high energetic cost for reproduction (Maier et al., 2020), whereas Dodds et al. (2009) found no significant seasonal variation in the lipid content and composition of *L. pertusa*, only a similar decreasing trend in winter.

As primary productivity is projected to decrease due to climate change (Steinacher et al., 2010; Mora et al., 2013; Sweetman et al., 2017; Seifert et al., 2020), this will have a cascading effect on zooplankton consumers which constitute the main food for CWCs. The corals may need more energy to cope with changing environmental conditions, but will face a limited energy supply. Lower energy reserves are expected to lower the resistance of corals to changing environmental conditions (Anthony et al., 2009). For instance, it was proposed that CWCs may be able to maintain their calcification rate under unfavourable environmental conditions, such as low pH, by mobilizing their lipid reserves (Maier et al., 2013; Hennige et al., 2014). However, this is only possible in the short term (i.e. weeks to months), until lipid reserves are depleted (Maier et al., 2013). In aquarium experiments, it has been shown that reduced pH had no effect on energy reserves of *Corallium rubrum* (Bramanti et al., 2013) and the CWCs *Desmophyllum dianthus* and *Dendrophyllia cornigera* (Movilla et al., 2014), compared to elevated temperatures that led to lower energy reserves in *L. pertusa* (Chapron et al., 2021).

The aim of the present study was to shed light into CWC energetics and investigate the spatial and temporal changes of *in situ* energy reserves (proteins, carbohydrates and lipids). We were particularly interested in the seasonal lipid class management and the spatial differences in the accumulation of storage lipids compared to structural lipids. We used the ubiquitous CWC *D. dianthus* as our study species, taking advantage of its wide-spread occurrence over steep environmental gradients in its natural habitat in Comau Fjord (Chile) and its tolerance to transplantation to novel environments. In a year-long *in situ* reciprocal transplantation experiment, we examined shifts in energy reserves of *D. dianthus* at its natural location and after transplantation to contrasting physico-chemical and feeding conditions. For the first time, we gathered a comprehensive data set of CWC seasonal energetics and compared the observed seasonal patterns in energy reserves to simultaneously assessed coral calcification in this region.

Material and methods

Study site and organisms

This study was conducted in Comau Fjord, which is located in the northern part of Chilean Patagonia (Figure 1). The fjord is characterized by a high tidal range of up to 7.5 m depth and a low salinity surface layer in the upper 7-15 m depth due to high precipitation and terrestrial freshwater input (Häussermann & Försterra, 2009; Fillinger & Richter, 2013; Iriarte et al., 2014). As a result, oxygen and pH are high near the surface and low in deep waters (Silva, 2008; Garcia-Herrera et al., 2022). Variability is also higher in shallow than in deep waters, with large near-surface fluctuations in temperature, salinity, oxygen and pH in summer and autumn, and smaller fluctuations in winter and spring (Beck et al., 2022). CWCs occur between 7 m and the maximum depth of 480 m of the fjord (Försterra et al., 2005; Häussermann & Försterra, 2009; Häussermann et al., 2021). The solitary, azooxanthellate CWC *D. dianthus* is the most abundant and important coral in the Chilean fjord region (Försterra & Häussermann, 2003; Försterra et al., 2005; Häussermann & Försterra, 2007). This species occurs between 15 m and the maximum depth of Comau Fjord (Försterra et al., 2005; Häussermann & Försterra, 2009; Fillinger & Richter, 2013) and its wide distribution in the fjord provides a rare opportunity to investigate its *in situ* energy reserves under contrasting environmental conditions. Previous investigations found higher calcification rates of *D. dianthus* in deep (300 m) waters of the fjord compared to corals in shallow (20 m) waters (Beck et al., 2022; Wall et al., in review).

Experimental design and coral collection

At each of the six sampling stations between the head (A) and mouth (F) of the fjord, 30 individuals of *D. dianthus* were collected by SCUA divers at approx. 20 m water depth in September 2016 (Figure 1). At station Ed, an additional 15 individuals were collected at 300 m depth, using a remotely operated vehicle (Commander 2, Mariscope Ingeniería, Puerto Montt, Chile; modified with manipulator arms and high-resolution camera). For reciprocal transplantation, another 30 corals were sampled at each of the shallow stations A, F and Es and another eight corals at Ed. In the laboratory, the corals were glued on individually labelled polyethylene screws using underwater easy glue (Preis Aquaristik, Germany) and re-installed by divers on holders at the fjord wall at the shallow stations. At the deep station, corals were attached to a mooring at 20 m water depth by divers and lowered down to 300 m depth on a pulley. Corals were re-installed at their station of origin (native corals) or reciprocally transplanted (novel corals) between the head (A) and mouth (F) of the fjord and one shallow (Es) and the deep station (Ed; Figure 1). Over one year, native and novel corals were collected every three to four months in austral summer (January 2017), autumn (May 2017) and winter (August 2017) for seasonal tissue analyses. Ten native corals were collected at each of the shallow stations and ten novel corals at stations A, F and Ed in every season. Only in summer, eight native and eight novel corals were collected at station Ed and station Es, respectively.

After collection, corals were transported to the Huinay research station and maintained in flow-through aquaria for max. four days before they were shock frozen in liquid nitrogen. The frozen coral samples were transported to the Alfred Wegener Institute (AWI, Germany) in liquid nitrogen containers (dry shippers) and stored at -80 °C until further processing. Unfortunately, freezer failure caused thawing of most summer tissue samples. These samples had to be discarded, leaving only native and novel corals from stations F and Ed for tissue analysis. A full description of the field experiment and coral sampling is given in Beck et al. (2022).

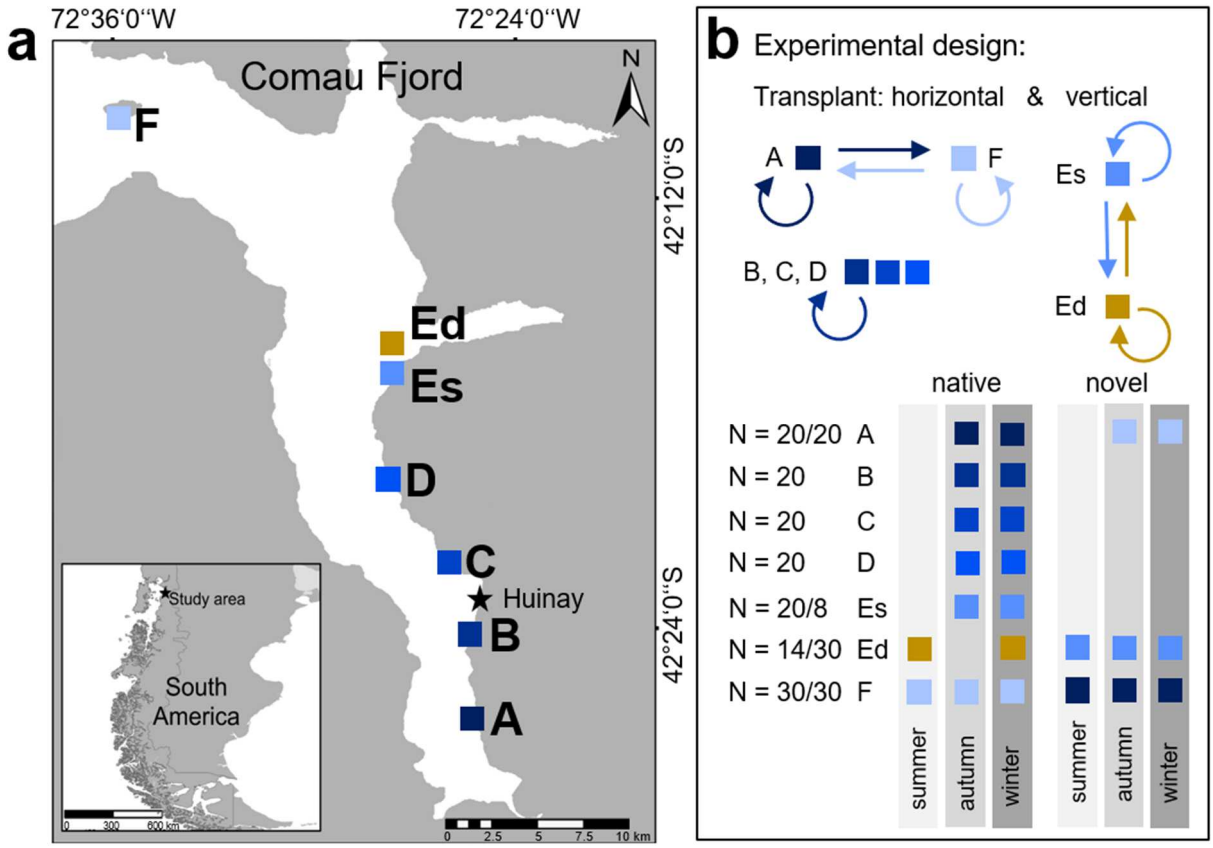

Figure 1: Experimental design and coral sampling scheme. A) Coral sampling stations in Comau Fjord, Chile: six stations at 20 m water depth (A, B, C, D, Es, F, blue colours) and one station at 300 m water depth (Ed, yellow). The research station in Huinay is located between stations B and C (star). B) The experimental design includes vertical and horizontal reciprocal transplantation of novel (i.e. cross-transplanted) corals between the shallow stations A and F as well as between shallow (E shallow: Es) and deep (E deep: Ed), where colours indicate the station of origin. Corals collected at stations B, C and D were only returned to their respective native station. At each of the stations, corals were collected after four, eight and eleven months in summer (January), autumn (May) and winter (August; N = 6-10 per station and sampling time point) for tissue analyses. Corals were initially also sampled at stations A-D and Es in summer but due to freezer failure, these samples thawed and could not be used for tissue analyses.

Energy reserves

For the shallow stations, whole coral samples were prepared for the tissue analyses whereas only one half of each deep coral specimen was used. Deep corals were cut in halves in a -30°C cold room using a saw equipped with a diamond blade (FKS/E, Proxxon S.A., Wecker, Luxemburg) to prevent the tissue from thawing during cutting. The coral tissue was separated from the skeleton using an airbrush (Starter Class set, Revell GmbH, Bünde, Germany) connected to pressurised air at 5 bar and filtered seawater while working on ice. The tissue slurry (10-22 mL) was homogenized using an Ultra Turrax (T18 basic, IKA GmbH & Co. KG, Staufen, Germany) and subsamples for C:N, protein, carbohydrate and total lipid content were stored at -80 °C.

For the determination of the C:N ratio, a 1 mL subsample of the tissue slurry was filtered on a pre-combusted (4 hours at 500°C) filter (Whatman GF/C, GF Healthcare Life Sciences, United Kingdom) and analysed using an elemental analyser Euro EA 3000 (EuroVector, HEKAtech GmbH, Wegberg, Germany).

One subsample (25 µL) was used for the protein measurements after Lowry et al. (1951) using a protein assay kit (DC Protein Assay Kit, Bio-Rad Laboratories Inc., Hercules, USA) and bovine serum albumin (BSA) as standard. The protein concentration was measured on a photometer (UV-1800 spectrophotometer, Shimadzu Corporation, Kyoto, Japan) at 750 nm.

One subsample (100 µL) was used for carbohydrate quantification using the phenol-sulfuric acid method after Dubois et al. (1956) with some slight modifications for measurements with a microplate reader and D-glucose as a standard. For the carbohydrate analysis, the thawed tissue slurry was 1:1 diluted with reverse osmotic water (conductivity: 18.0 MΩ cm^{-1}; Sartorius arium pro, Sartorius Corporate Administration GmbH, Germany). The samples were vortexed, phenol and sulfuric acid added to 200 µL of each sample and standard (dilution series: 0-400 µg/mL D-glucose) in safe lock tubes and incubated for 10 min. Afterwards, vials were incubated in a water bath at 30 °C for 20 min. and mixed. The absorbance of the samples and standards was measured in triplicates at 485 nm on a microplate reader (TriStar LB941 Multimode Reader, Berthold Technologies, Germany).

Another subsample (1800 µL) was used to determine the total lipid concentration in triplicates (600 µL each) using the colorimetric sulfo-phospho-vanillin (SPV) method for microplate measurements after Cheng et al. (2011) with some slight modifications and corn oil as standard. The thawed samples were homogenized with an Ultra Turrax for 2 min. before lipids were extracted with a 2:1 chloroform:methanol solution in safe lock tubes and vortexed for 20 min. Then 0.05 M NaCl was added and the tubes were inverted gently. The vials were centrifuged at 3,000 rpm for 5 min. with a 5417R centrifuge (Eppendorf AG, Hamburg, Germany). Afterwards, 1 mL of the upper phase (methanol) was removed and 300 µL of the lower phase (chloroform with soluble lipids) of each sample and standard (dilution series: 0-7 mg/mL corn oil) were used for the assay and pipetted into a new safe lock tube. 150 µL methanol was added and the vials were vortexed. The solvent was evaporated in a water bath

at 90 °C for approx. 20 min. 300 µL sulfuric acid was added and the vials vortexed again, incubated in a water bath at 90 °C for 20 min. and cooled on ice for 2 min. 75 µL of each sample were pipetted in triplicates into a well of a polystyrene microplate and the background absorbance measured at 530 nm on a microplate reader (TriStar LB941 Multimode Reader, Berthold Technologies, Germany). Afterwards, 34.5 µL 0.2 mg/mL vanillin was added to each well using a multichannel pipette, the microplate incubated for 10 min. and the absorbance measured. We subtracted the background from the absorbance of the samples and created a standard curve with the absorbance of the corn oil standard with a polynomial equation to calculate the total lipid concentration.

The protein, carbohydrate and total lipid concentrations were converted to kilojoules (kJ; protein: 23.9 kJ/g, carbohydrate: 17.5 kJ/g, lipids: 39.5 kJ/g; Gnaiger & Bitterlich, 1984) and standardized to the tissue covered surface area of the corals, which was measured before the tissue was removed from the skeleton using a digital calliper (for details on the determination of the surface area see Beck et al., 2022).

Lipid classes

Subsamples (1-10 mL) of native and novel corals from stations A, F, Es and Ed collected in austral summer and winter were used to determine the lipid class composition using the high-performance liquid chromatography (HPLC) method by Graeve & Janssen (2009). Subsamples were filtered on a pre-combusted (4 hours at 500°C) and pre-weighed filter (Whatman GFF, GF Healthcare Life Sciences, United Kingdom) and freeze dried for approx. 24 hours. The total lipid content was extracted three times with dichloromethane:methanol (DCM:MeOH, 2:1 per volume) after Folch et al. (1957). The raw extract was washed with 0.88 % KCl solution before centrifugation at low speed. Thereafter, the organic phase containing dissolved lipids was separated and evaporated under a stream of nitrogen. The lipid extract was re-dissolved in 3 mL dichloromethane to a known concentration. For lipid class analysis, 500 µL of the raw extract were evaporated and re-dissolved in cyclohexane (CH). Lipid classes were injected onto a LaChromElite HPLC system (VWR, Darmstadt, Germany) coupled to an evaporative light scattering detector (ELSD; Sedex 75, Sedere, France) and separated on a Chromolith®Performance-Si column (100 x 4,6mm; VWR, Darmstadt, Germany) after Graeve & Janssen (2009). Data acquisition was performed using the LaChrom Elite software (version 3.1.7; VWR, Darmstadt, Germany). The lipid classes of each individual coral sample were calculated as relative percentage in relation to the total lipid concentration.

Calcification

Calcification rates of *D. dianthus* were determined using the buoyant weighing technique (Jokiel, 1978) as part of Beck et al. (2022). A precision balance (Sartorius CPA 225D-OCE, Sartorius AG, Göttingen, Germany; precision: 0.01 mg) was mounted on a platform above a small aquarium filled with seawater from the fjord. Initial coral dry mass of eight to ten native and novel corals of each station was determined in September 2016. The same individuals

were weighed again after four, eight and eleven months in austral summer (January 2017), autumn (May 2017) and winter (August 2017), respectively. Here, we use the data to explore the relationship of coral performance in terms of calcification to energy reserves.

Statistical analysis

All statistical analyses were performed using the software R (version 4.1.0; R Core Team, 2021). We tested for normality using the Shapiro-Wilk test and for homogeneity of variances using the Levene test. As protein, carbohydrate, lipid, total energy reserve, C:N data and surface area were not normally distributed, we used a generalized linear model (g*lm*) to examine the relationship between the response variables with season, station and station*transplant as fixed factors. We compared different models with the package *performance*, which gave the best result for log-transformed data of the Gamma distribution. For each response variable, one model was run only with the native corals of the shallow stations to identify differences in energy reserves along the horizontal gradient and between seasons. For a second model, only data of native and novel corals from stations A, F, Es and Ed were used to identify differences between native and novel corals and between water depths. Post-hoc comparisons of significant effects were tested using the *lsmeans* function of the package *lsmeans*. Differences in the lipid class composition between stations were tested with a PERMANOVA using the function *adonis2* of the package *vegan*.

Results

Energy reserves

The biochemical composition of the corals showed consistent spatial and temporal patterns across the different tissue components. The concentration of proteins, carbohydrates and lipids was significantly higher at the deep station compared to shallow stations (GLM, Es – Ed: p-value < 0.001; Figure 2a-c, Supplementary Tables 1-3). In shallow waters, the protein and carbohydrate concentrations were highest at station C. Proteins, carbohydrates and lipids were significantly higher in austral autumn (May) than in winter (August; GLM, May-Aug: p-value < 0.001; Figure 2a-c, Supplementary Tables 1-3). All novel corals quickly adjusted their protein, carbohydrate and lipid concentrations after transplantation to the same level as native corals at the respective station (GLM, native – novel: p-value ≥ 0.196, Figure 2a-c, Supplementary Tables 1-3).

Total energy reserves, provided by all tissue components, were significantly higher (184 %) at 300 m compared to 20 m in both native and novel corals (GLM, Es – Ed: p-value < 0.001; Figure 2d, Supplementary Tables 1-3). In shallow waters, total energy reserves were highest at station C and differed between seasons with 30 % lower energy reserves in winter compared to autumn (GLM, May – Aug: p-value < 0.001, Figure 2d, Supplementary Tables 1-3).

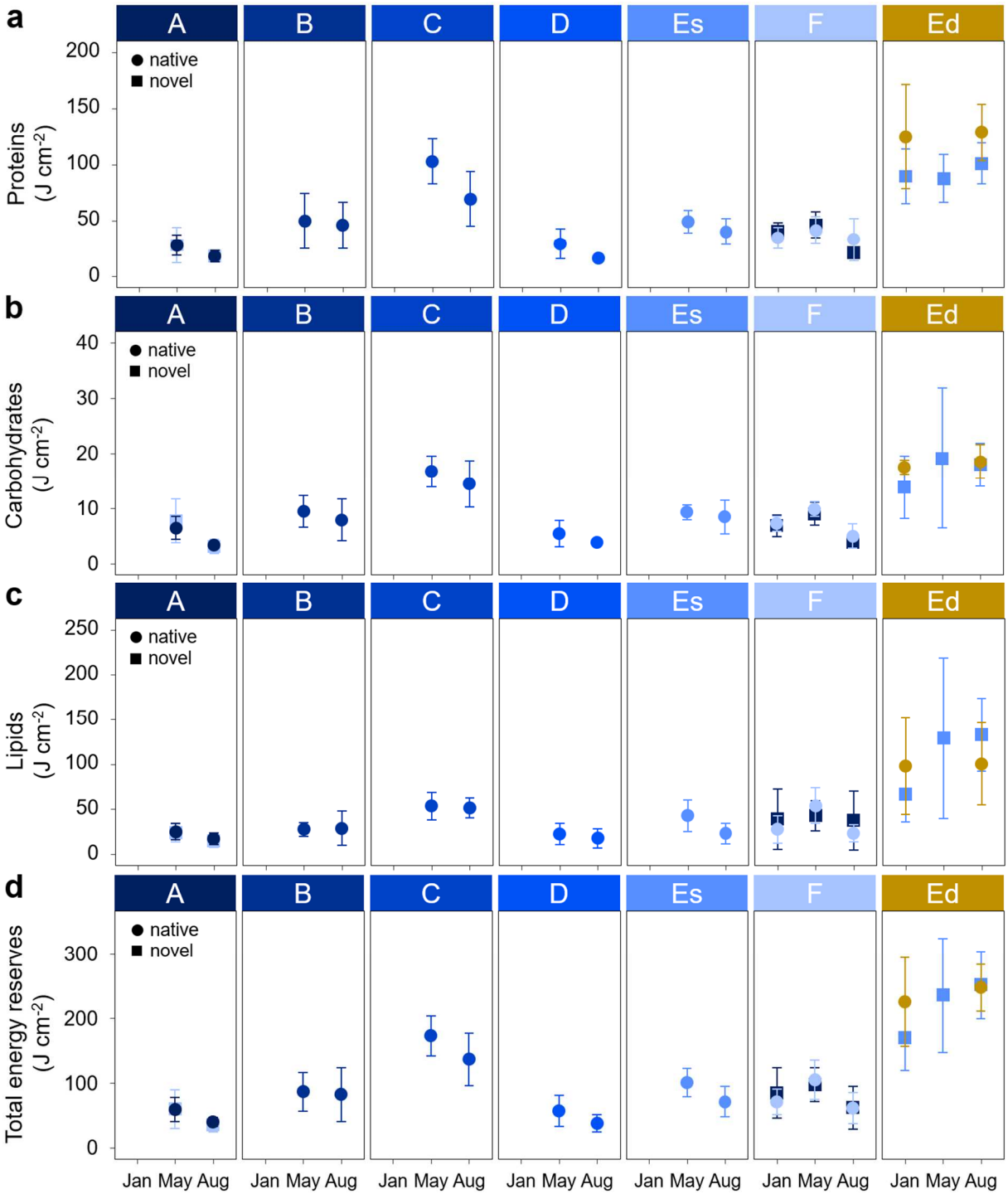

Figure 2: Seasonal energy reserves of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. a) Proteins, b) carbohydrates, c) lipids and d) total energy reserves of *D. dianthus* (mean ± standard deviation) at six stations at 20 m depth along the fjord from head to mouth (A-F) are shown in blue and at one station at 300 m depth (Ed) in yellow (N = 6-10). Native corals (circles) were re-installed at the same station after collection in September 2016 and novel corals (squares) were cross-transplanted between the shallow stations at the head (A) and the mouth (F) of the fjord and between shallow (Es) and deep (Ed). Samples for tissue analyses were collected after four, eight and eleven months in austral summer (January), autumn (May) and winter (August), respectively, and standardized to the tissue covered surface area of the corals.

The tissue covered surface area of corals at shallow stations was significantly lower at station C (GLM, C – A/B/D/Es: p-value < 0.001; Figure 3, Supplementary Tables 1-3), resulting in significantly higher area-specific energy reserves (Figure 2, Supplementary Tables 1). The surface area of native deep corals was 134 % higher than in shallow corals (GLM, Es – Ed: p-value < 0.001; Figure 3, Supplementary Tables 1-3). Novel deep corals transplanted from shallow waters increased their tissue covered surface area significantly over the whole time of the experiment and were only able to reach similar surface areas as native deep corals in August (GLM, p-value = 0.016; Figure 3, Supplementary Tables 1-3).

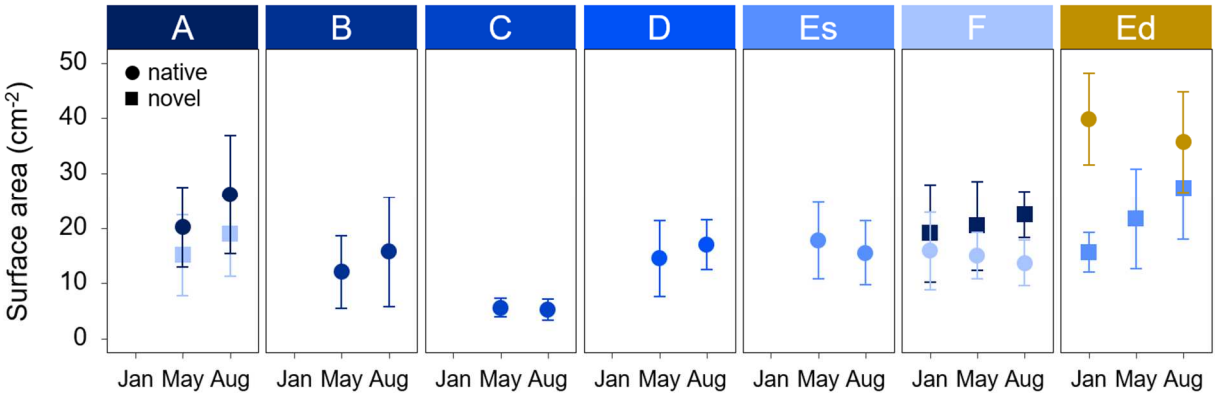

Figure 3: Surface area of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. The tissue covered surface area of *D. dianthus* (mean ± standard deviation) at six stations at 20 m depth along the fjord from head to mouth (A-F) is shown in blue and at one station at 300 m depth (Ed) in yellow (N = 6-10). Native corals (circles) were re-installed at the same station after collection in September 2016 and novel corals (squares) were cross-transplanted between the shallow stations at the head (A) and the mouth (F) of the fjord and between shallow (Es) and deep (Ed). Samples were collected after four, eight and eleven months in austral summer (January), autumn (May) and winter (August), respectively.

The C:N ratio of the deep corals was also significantly higher than in shallow corals (GLM, Es – Ed: p-value < 0.001; Figure 4, Supplementary Tables 1-3), but differed between native and novel deep corals (GLM, Ed native – novel: p-value < 0.001; Figure 4, Supplementary Tables 1-3). At the deep station, the C:N ratio increased from austral summer (January) to winter (August) in both native and novel corals, but was generally higher in native corals (Figure 4, Supplementary Table 1).

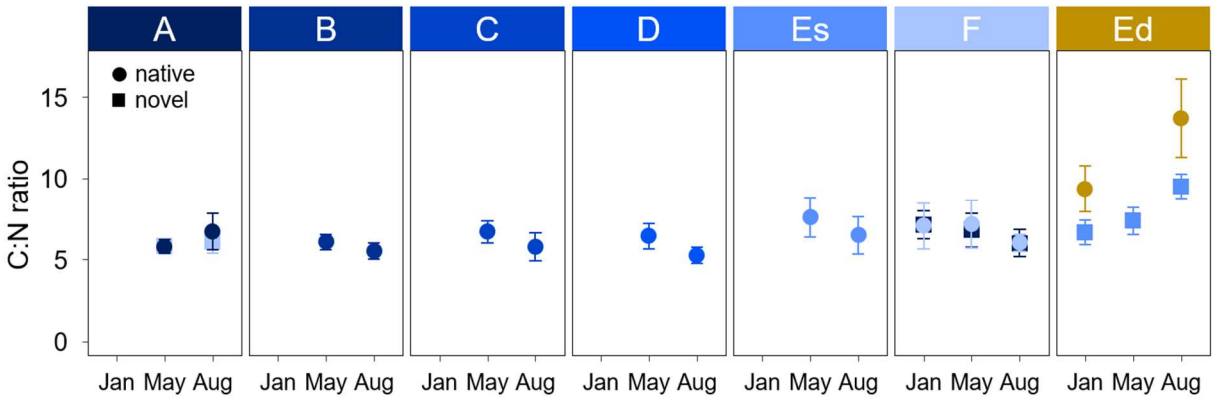

Figure 4: C:N ratio of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. C:N ratio of *D. dianthus* (mean ± standard deviation) at six stations at 20 m water depth along the fjord from head to mouth (A-F) are shown in blue and at one station at 300 m water depth (Ed) in yellow (N = 6-10). Native corals (circles) were re-installed at the same station after collection in September 2016 and novel corals (squares) were cross-transplanted between the shallow stations at the head (A) and the mouth (F) of the fjord and between shallow (Es) and deep (Ed). Samples for the analyses were collected after four, eight and eleven months in austral summer (January), autumn (May) and winter (August), respectively.

Lipid classes

While the total lipid concentration differed between stations and seasons, this also affected the relative composition of main lipid classes with significantly different composition between shallow and deep corals (PERMANOVA, Ed – A/Es/F: adjusted p-value = 0.01; Figure 5, Supplementary Tables 4 and 5). At the deep station, both native and novel corals were characterised by a dominance of the energy storage components (approx. 80 %), consisting of wax esters (WE) and triacylglycerols (TAG) in both seasons. In January, WE were 2.7-3 times more abundant than TAG (63.2 % and 23.7 %) in native corals and had proportions of 69.4 % and 20.1 % in August. In novel corals, WE and TAG reached proportions of 69.5 % and 21.7 % in August, respectively. Only novel deep corals in austral summer (January) had almost equal amounts of WE and TAG (43.4 % and 40.4 %, respectively; Figure 5, Supplementary Tables 4 and 5). In shallow corals, both storage lipid classes accounted for only 29-60 % with a higher proportion in austral summer (60 %) compared to winter (29-50 %) and visible station-specific differences in the relative abundance of the two lipid classes. In contrast, phospholipids dominated the lipid classes in shallow (19.8-47 %) compared to deep corals (5-11.5 %, Figure 5, Supplementary Tables 4 and 5).

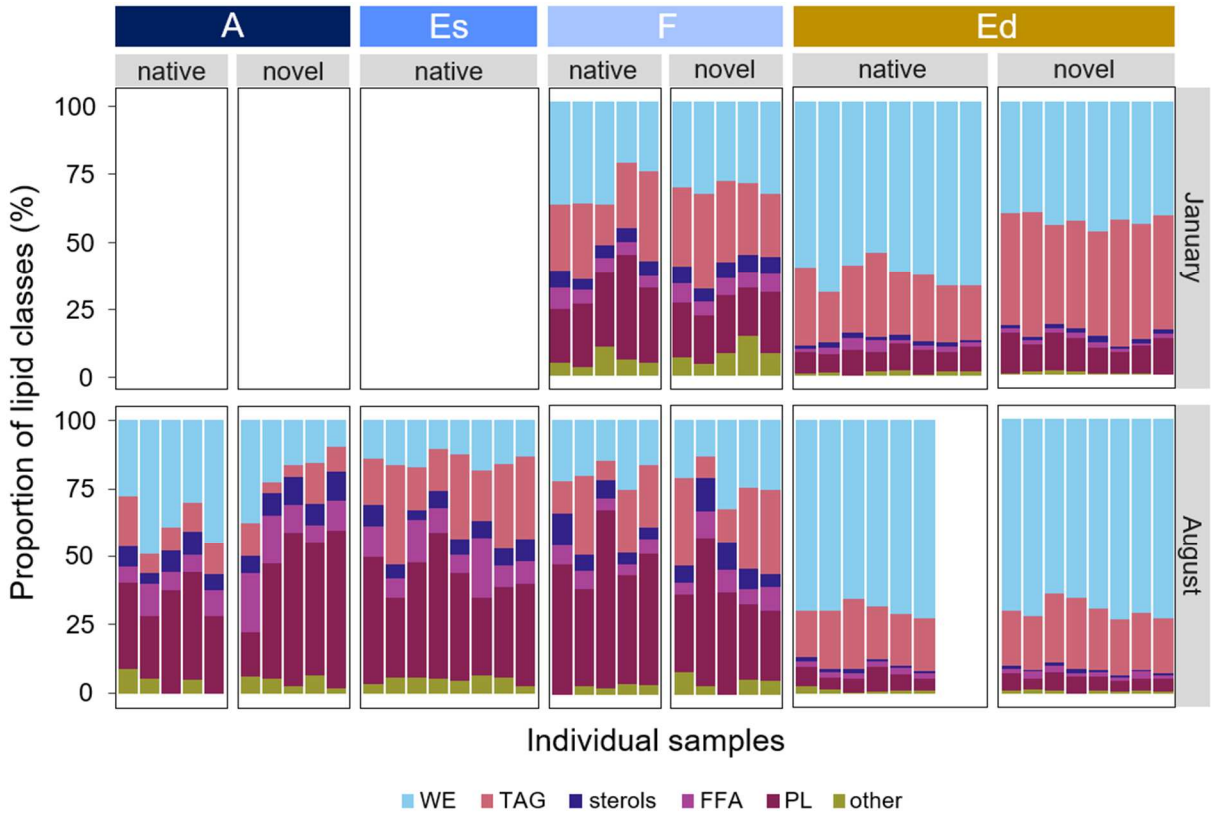

Figure 5: Lipid class composition of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. The proportion of the main lipid classes were determined for a subset of corals (N = 5-8) from the stations A, F, Es and Ed collected in austral summer (January) and winter (August). Empty panels are missing data due to freezer failure. WE = wax esters, TAG = triacylglycerols, sterols, DAG = diacylglycerols, FFA = free fatty acids, PL = phospholipids

Relation of energy reserves to calcification

Seasonal total energy reserves of *D. dianthus* were positively correlated with calcification rates (R^2 = 0.78, p-value < 0.001, Figure 6). Deep corals with highest calcification rates also had highest energy reserves in all three seasons, whereas energy reserves and calcification rates were lowest in corals at the head and the middle of the fjord (stations A, B and D) in austral winter.

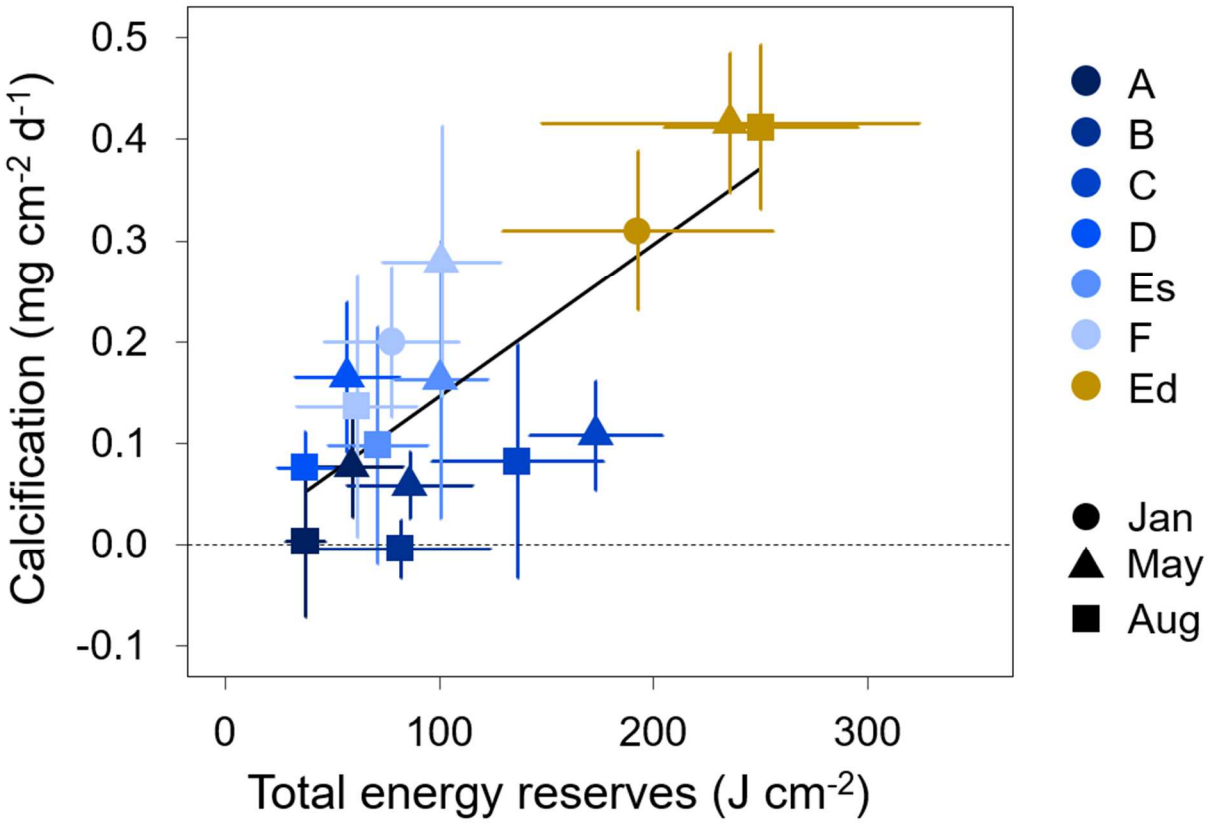

Figure 6: Relationship of energy reserves and calcification rates of *Desmophyllum dianthus* in Comau Fjord, Chile. Data at six shallow stations at 20 m depth along the fjord (A-F) are shown in blue and data at one deep station at 300 m depth (Ed) in yellow. Energy reserves and calcification rates of native and novel corals were measured after four, eight and eleven months in austral summer (January, circle), autumn (May, triangle) and winter (August, square), respectively. Note that native and novel corals at each station are combined in this graph (N = 4-19, $y = -0.004 + 0.0015x$, $R^2 = 0.78$, $p = 0.00035$).

Discussion

We found highest energy reserves and the greatest amount of storage lipids year-round in *D. dianthus* corals in deep waters of Comau Fjord. Deep corals also had the highest calcification and respiration rates (Beck et al., 2022). Here, we link the energetic status of the corals to their performance in terms of calcification rates and show that the conditions in deep waters are beneficial for the corals. This is consistent with findings showing higher energy storage in deep corals in austral winter (Wall et al., in review), and the hypothesis that stored energy reserves support increasing calcification rates of deep corals. Furthermore, all energy reserves of novel corals at the deep station increased rapidly within four months to levels similar to native corals, with the adjustment of storage lipid composition taking the longest. In shallow waters, corals had higher energy reserves in austral autumn compared to winter.

The clear correlation between the concentration of energy reserves and coral calcification (Figure 6) is in line with previous studies linking the biochemical composition of shallow-water tropical corals to their health status (Schoepf et al., 2013; Rocker et al., 2017, 2019a). The results of the present study show that also in CWCs, the investment into calcification increases linearly with the available energy. As our data show no indication of saturation, it would be interesting to determine in future studies if and when saturation is reached in this insatiable and voracious carnivore (Höfer et al., 2018). The rapid adjustment of the energy reserves of novel deep corals underscores the high acclimatisation potential of *D. dianthus* to novel environmental conditions after transplantation, which was also reflected in their metabolic response (Beck et al., 2022). This is in accordance with findings of the tropical coral *Acropora tenuis* that adjusted its lipid and fatty acid composition within four months after transplantation, compounding the notion that the corals' biochemical composition is strongly driven by the environment (Rocker et al., 2019b). However, while the relative amount of storage lipids in novel deep corals reached the same level as in native deep corals in a few months, the adjustment of the composition of storage lipids (WE vs. TAG) took up to one year (Figure 5). A delayed acclimatisation of novel deep corals also becomes apparent when the energy reserves are referred to the whole polyp (Supplementary Figure 2). Therefore, this indicates that although the relative proportion of energy reserves can be quickly adjusted, it takes longer for the absolute amount to reach the same level as in native deep coral, which is also related to the delayed increase in tissue covered surface area (Figure 3).

Unfortunately, we do not know if novel shallow corals transplanted from deep would have depleted their energy reserves to the same level as native shallow corals within the duration of this experiment. However, it is important to know if and how fast *D. dianthus* depletes its energy reserves under unfavourable environmental conditions as in shallow waters of Comau Fjord in order to be able to maintain other processes. Another possibility is a reduction of its metabolism instead without depletion of its energy reserves, which is indicated by reduced calcification and respiration rates of novel shallow corals transplanted from deep and the simultaneous maintenance of the tissue covered surface area (Beck et al., 2022). In contrast,

Chapron et al. (2021) showed that protein and lipid concentrations of *L. pertusa* and *Madrepora oculata* were reduced within two to six months at elevated temperature while calcification rates were maintained.

The year-round higher energy reserves of deep corals likely indicate an increased energy input as a result of either higher food availability or a higher quality zooplankton community in deep waters of the fjord. However, this contradicts the available zooplankton data from Comau Fjord showing much lower zooplankton abundance and biomass at 300 m depth than near the surface throughout the year (Garcia-Herrera et al., 2022). A higher zooplankton energy supply to corals would also be expected to lead to increased calcification rates and higher energy reserves in shallow waters, but the opposite is the case (Figure 6; Beck et al., 2022). In contrast to our findings, lipid content and storage lipid reserves of *L. pertusa* and *Dendrophyllia cronigera* were higher in high productivity regions than in areas with low productivity (Dodds et al., 2009; Duineveld et al., 2012; Gori et al., 2018). One explanation for the Comau Fjord paradox of energy-rich deep CWCs is that large zooplankton, mysids and krill, which were not quantitatively assessed in Garcia-Herrera et al. (2022) may be abundant in deep waters of the fjord. Euphausiids are known to be abundant in the Chilean fjord region (Palma & Silva, 2004) and represent an important food source, sustaining CWCs' scope for growth (Maier et al., 2021), while the smaller mesozooplankton appears to be most important for the maintenance of CWC metabolism (Naumann et al., 2011, 2015; Rakka et al., 2020, 2021; Maier et al., 2021). The higher energy reserves therefore indicate that deep corals have more food available than in shallow waters (but also see the Supplementary Discussion on contrasting results to the *in situ* studies and the relationship between storage fatty acids and food availability in laboratory studies).

In addition, the composition of the lipid classes provides further insights into the nutrition of the corals. The higher amount of storage lipid classes (wax ester and triacylglycerols) in deep corals in the present study is in accordance with the higher proportion of saturated (SFA) and monounsaturated fatty acids (MUFA) compared to polyunsaturated fatty acids (PUFA) of *D. dianthus* at 300 m compared to 20 m depth in Comau Fjord, which reflects the high storage capacity of deep corals (Wall et al., in review). In addition, the storage lipids of deep corals were dominated by wax esters (approx. 60-70 %), which was also found for *L. pertusa* (Dodds et al., 2009). The authors concluded that these corals mainly feed on calanoid copepods, which are rich in wax esters (Lee et al., 1971; Hagen & Auel, 2001). Copepods are the dominant group of the zooplankton community in Comau Fjord and it is assumed that *D. dianthus* in deep waters mainly feeds on mysids and large calanoid copepods (Garcia-Herrera et al., 2022; Wall et al., in review). This assumption is also supported by the dominance of fatty acid trophic markers (FATM) for zooplankton in deep corals, whereas shallow water CWCs have more algal FATM markers (Wall et al., in review) and fewer wax esters (Figure 5), which supports a more algal based diet of shallow corals or more likely predominant feeding on herbivorous zooplankton (Wall et al., in review). In addition, a study on *L. pertusa* shows that the C:N ratio is not only linked to the food composition but also the food concentration (van Oevelen et al.,

2016). Therefore, the higher C:N ratio in deep corals may also indicate that more food is available at the deep station (Figure 4). Consequently, the biochemical composition of *D. dianthus* in Comau Fjord shows that corals in deep waters of the fjord have likely more food available than corals in shallow waters.

The decreasing energy reserves of shallow corals in austral winter (Figure 2) may be a result of the lower zooplankton abundance and biomass in winter in Comau Fjord (Garcia-Herrera et al., 2022). By contrast, Maier et al. (2020) attributed decreasing tissue biomass of *L. pertusa* in winter primarily to spawning as the gametes of this broadcast spawning species are released in boreal winter (Brooke & Järnegren, 2013). In tropical corals, lipids are the main indicator of energy investment into reproduction with a large decrease in the lipid concentration after spawning, but only small changes in the protein and carbohydrate concentrations (Leuzinger et al., 2003). In Comau Fjord, *D. dianthus* in shallow waters spawns at the end of austral winter (August) and begins with the gamete production in early spring before the spring phyto- and zooplankton bloom and the productive summer season (September; Feehan et al., 2019). However, the observed decrease in lipid concentration in winter is small and also seasonal changes in protein and carbohydrate concentration were observed and can therefore rather be attributed to seasonal changes in food availability or environmental conditions than reproduction. In addition, corals were sampled at the beginning of August and therefore, likely before the release of the gametes. By contrast, energy reserves and the lipid class composition of native deep corals showed no seasonality, which is in accordance with previous studies on the lipid concentration and composition of *L. pertusa* collected at water depths of 130-1300 m (Dodds et al., 2009). The authors explain the missing seasonal pattern with a potential reduction of the metabolism of *L. pertusa* in response to lower food supply in winter, i.e. the metabolic response having a dampening effect on the energy reserves. A differential metabolic response was found in Comau Fjord, where respiration rates of *D. dianthus* were reduced in winter, but calcification rates were unaffected (Beck et al., 2022). This indicates that deep corals adjust to reduced food availability by sequentially reducing respiration and calcification, before tapping energy reserves. The C:N ratio of deep corals increased over the duration of this study (Figure 4), in line with the increase in C-rich lipids over N-rich proteins, which showed only minor changes (Figure 2). C and N isotope labelling showed that food abundance and composition may lead to differential C:N assimilation, altering tissue C:N (van Oevelen et al., 2016). Likewise, the high C:N ratio in winter may reflect both qualitative and quantitative changes in food availability (Garcia-Herrera et al., 2022).

In addition to differences in zooplankton composition between shallow and deep waters of the fjord, the higher energy reserves of deep corals may also be a result of the re-allocation of energy from other processes. Shallow corals in Comau Fjord are subject to greater environmental variability, which correlates with the performance of the corals, with lowest calcification rates at the fjord head where environmental fluctuations are largest (Beck et al., 2022). This underscores the importance of natural fluctuations in rendering coral

performance, but it is not yet entirely clear how this influences the corals. Environmental variability may either directly affect corals by limiting their physiological performance or indirectly by affecting their food source, but it is also possible that a combination of both is the case in Comau Fjord. Recurrent disturbances due to fluctuating environmental conditions, including short periods of elevated temperatures in austral summer and autumn may therefore lead to tentacle retraction and polyp inactivity (Chapron et al., 2021), which reduces the feeding time of the corals. In addition to the stronger environmental fluctuations, corals in shallow waters are exposed to other direct factors that may affect their physiological performance. For instance, competition for space is greater due to the diverse benthic community in shallow waters (Försterra et al., 2005, 2016) and shallow corals are therefore likely to be disturbed more frequently by other benthic organisms than deep corals. Apart from these direct effects, environmental variability may also indirectly affect the corals by also altering the abundance and composition of zooplankton in shallow waters of the fjord due to salinity fluctuations (Laprise & Dodson, 1994; Wells et al., 2021). The available zooplankton data integrate over the upper 50 m of the water column (Garcia-Herrera et al., 2022) and include the brackish surface layer where corals are not present. They may thus not fully represent the zooplankton community available to the corals at 20 m depth. Furthermore, the plankton tows were conducted in the centre axis of the fjord, so we cannot rule out possible differences with the zooplankton community at the fjord walls. However, considering the steep walls and the orders of magnitude larger patchiness in the vertical than in the horizontal domain (Haury et al., 1978), we are confident that the lateral differences are minor. A potentially important difference between shallow and deep corals is the infestation of skeletons with phototrophic endolithic algae (Försterra & Häussermann, 2008). While the association has been originally described as potentially mutualistic, microendoliths have been shown to exacerbate bioerosion under stressful conditions (Pernice et al., 2020). Infestation by endolithic organisms leads to tissue retraction and smaller tissue surface area in shallow corals in Comau Fjord (Hassenrück et al., 2013; Beck et al., 2022). As a result, shallow corals exposed to stronger infestation may only be able to partion less of the available energy to basic metabolic processes (e.g. maintenance, growth, reproduction) and the response to stressors (Leuzinger et al., 2012). In contrast, deep corals living without phototrophic endoliths and in more stable environmental conditions have to expend less energy to compensate for disturbances as is the case for shallow corals. The savings may be substantial and deep corals may have more energy available for somatic growth (Beck et al., 2022), calcification (Figure 6), reproduction (Feehan et al., 2019) and the build-up of energy reserves (Figure 2) and especially storage lipids (Figure 5).

The difference in energy reserves between shallow and deep corals in Comau Fjord may also give some insights into energetic trade-offs as the available energy has to be divided between various processes including reproduction (Leuzinger et al., 2003, 2012). Deep populations of the solitary CWC species *Fungiacyathus marenzelleri* have lower reproductive output due to reduced food availability (Waller et al., 2002; Flint et al., 2007; Waller & Feehan,

2013). However, this is probably not the case for *D. dianthus* in Comau Fjord, where Wall et al. (in review) and the present study found no indication of food limitation. As reproduction requires substantial energy (Maier et al., 2020), there is always a trade-off between available energy for reproduction on the one hand, and calcification, somatic growth and the build-up of energy reserves on the other. Shallow corals exposed to high environmental variability and potential infestation by endoliths responded with lower biomass (Beck et al., 2022), calcification rates and energy reserves (Figure 6). It is known that *D. dianthus* is actively reproducing in shallow waters of this fjord (Feehan et al., 2019) where dense aggregations can be found (Försterra & Häussermann, 2003; Försterra et al., 2005; Häussermann & Försterra, 2007). Elevated temperatures affect the reproduction of tropical corals (Randall et al., 2020; Liberman et al., 2021), but little is known so far about the impact of environmental variability on the reproduction of CWCs. Recent investigations showed that high temperature variability delays the spermatogenesis in shallow populations of the soft CWC species *Primnoa pacifica* (Johnstone et al., 2021). In addition, shallow populations of *P. pacifica* had smaller oocytes than deep corals, which may either be a result of a high phenotypic plasticity due to different environmental conditions or a premature arrest of gametogenesis as a result of stressful conditions in shallow waters (Waller et al., 2019). The same might be the case for shallow corals in Comau Fjord. The higher investment into energy storage in deep corals indicates that they have enough energy available for all metabolic processes, including calcification (Figure 6) and presumably also reproduction. Therefore, deep corals are likely more fecund than corals in shallow waters as has already been proposed by Feehan et al. (2019). It is possible that the reproductive output is lower in shallow waters and most settlers come from deep waters. Population genetic analyses of *D. dianthus* show gene flow within the whole fjord, where potentially deep corals may serve as a reproductive source for the whole population (Addamo et al., 2021), but a direct comparison of reproductive process of *D. dianthus* from shallow and deep waters of Comau Fjord is still missing.

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Author contributions

G.M.S.G., J.L. and C.R. designed the study. J.L. and G.M.S.G. led the collection of corals. A.S.K., J.W., A.K.L., M.Woll, K.K.B., M.Wall and S.M. prepared the coral samples and conducted the measurements. K.K.B. and G.M.S.G. contributed physiological background data. K.K.B., M.Wall, M.Woll and M.G. analysed the data. K.K.B. and M.Wall interpreted the data, conducted the statistical analysis and prepared the figures. K.K.B. and M.Wall wrote the first draft and all authors edited the manuscript.

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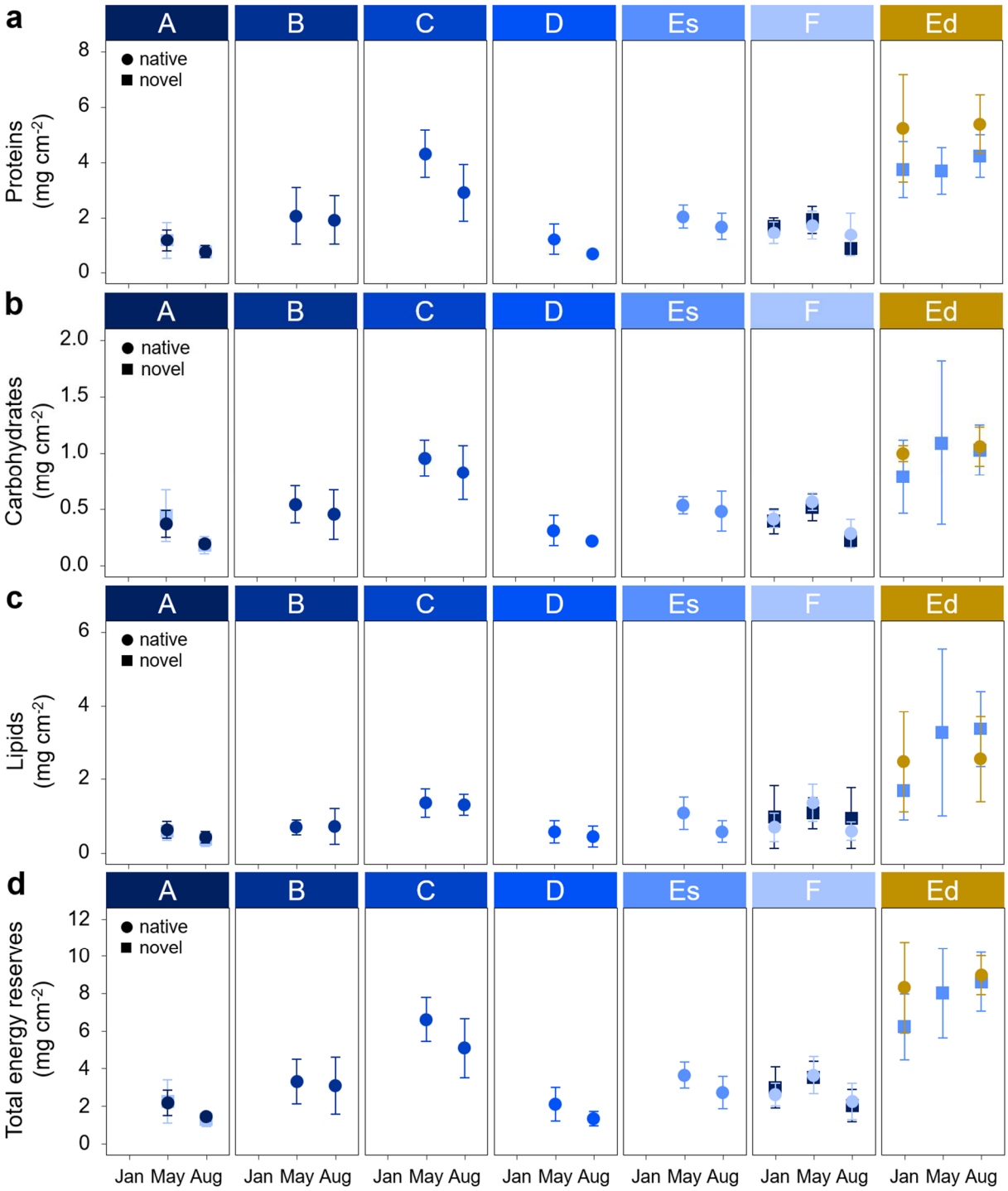
Supplementary Results

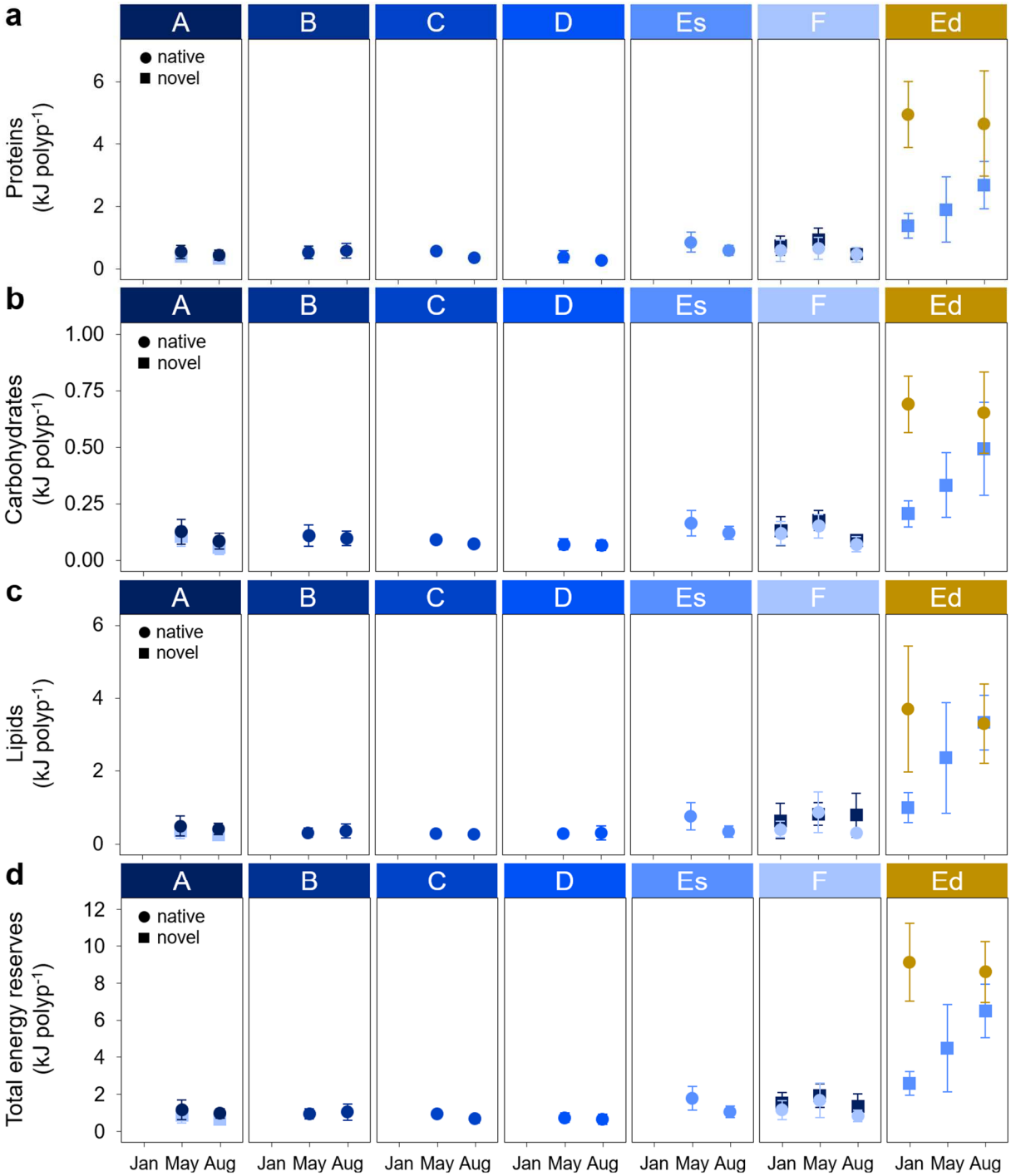
Supplementary Table 1: Seasonal energy reserves of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. Proteins, carbohydrates, lipids, total energy content, C:N ratio and tissue covered surface area of *D. dianthus* (mean ± standard deviation) at six stations at 20 m water depth along the fjord from head to mouth (A-F) and at one station at 300 m water depth (Ed). Native corals were re-installed at the same station after collection in September 2016 and novel corals were cross-transplanted between the shallow stations at the head (A) and the mouth (F) of the fjord, and between shallow (Es) and deep (Ed). Energy reserves were measured after four, eight and eleven months in austral summer (January), autumn (May) and winter (August), respectively. Note that energy reserves could not be assessed for all stations and seasons due to logistical problems. The tissue covered surface area was used as reference value (mg cm^{-2}), energy reserves converted into energy (J cm^{-2}) and also calculated per coral polyp (mg $polyp^{-1}$).

Station	N	Surface area (cm^2)	Proteins ($mg\ cm^{-2}$)	Carbohydrates ($mg\ cm^{-2}$)	Lipids ($mg\ cm^{-2}$)	Total energy reserves ($mg\ cm^{-2}$)	Proteins ($J\ cm^{-2}$)	Carbohydrates ($J\ cm^{-2}$)	Lipids ($J\ cm^{-2}$)	Total energy reserves ($J\ cm^{-2}$)
January 2017										
F (native)	8	15.88 ± 7.00	1.44 ± 0.40	0.41 ± 0.08	0.69 ± 0.38	2.61 ± 0.61	34.44 ± 9.50	7.19 ± 1.34	27.34 ± 14.97	70.54 ± 19.61
F (novel)	8-9	19.02 ± 8.78	1.68 ± 0.32	0.39 ± 0.11	0.98 ± 0.85	2.99 ± 1.10	40.18 ± 7.55	6.81 ± 1.94	38.68 ± 33.52	84.31 ± 39.05
Ed (native)	7-8	39.80 ± 8.25	5.22 ± 1.93	1.00 ± 0.07	2.47 ± 1.36	8.31 ± 2.43	124.75 ± 46.22	17.44 ± 1.25	97.56 ± 53.77	225.38 ± 69.23
Ed (novel)	10	15.62 ± 3.60	3.74 ± 1.01	0.79 ± 0.32	1.68 ± 0.78	6.21 ± 1.77	89.44 ± 24.10	13.78 ± 5.66	66.33 ± 30.87	169.55 ± 50.16
May 2017										
A (native)	10	20.14 ± 7.24	1.66 ± 0.38	0.37 ± 0.12	0.63 ± 0.23	2.16 ± 0.67	27.86 ± 9.09	6.42 ± 2.05	24.80 ± 9.28	59.07 ± 18.69
A (novel)	9-10	15.06 ± 7.34	1.17 ± 0.65	0.44 ± 0.23	0.59 ± 0.26	2.22 ± 1.15	27.89 ± 15.60	7.71 ± 3.98	23.49 ± 10.09	59.62 ± 29.94
B	9	12.01 ± 6.60	2.06 ± 1.03	0.54 ± 0.16	0.69 ± 0.20	3.30 ± 1.19	49.31 ± 24.73	9.45 ± 2.87	27.41 ± 7.79	86.18 ± 29.45
C	9	5.58 ± 1.70	4.30 ± 0.85	0.95 ± 0.16	1.35 ± 0.39	6.61 ± 1.17	102.82 ± 20.38	16.69 ± 2.82	53.38 ± 15.30	172.90 ± 31.06
D	10	14.45 ± 6.86	1.21 ± 0.56	0.31 ± 0.13	0.57 ± 0.30	2.09 ± 0.89	28.97 ± 13.42	5.41 ± 2.34	22.55 ± 11.93	56.93 ± 24.33
Es (native)	7	17.75 ± 6.95	2.04 ± 0.42	0.53 ± 0.08	1.08 ± 0.44	3.65 ± 0.70	48.70 ± 10.02	9.29 ± 1.34	42.53 ± 17.24	100.52 ± 21.96
Es (novel)	-	-	-	-	-	-	-	-	-	-
F (native)	9-10	14.97 ± 4.16	1.72 ± 0.52	0.56 ± 0.07	1.35 ± 0.50	3.64 ± 0.98	41.19 ± 12.37	9.84 ± 1.30	53.63 ± 19.77	104.66 ± 30.68
F (novel)	10	20.43 ± 8.07	1.93 ± 0.48	0.51 ± 0.12	1.08 ± 0.42	3.52 ± 0.87	46.05 ± 11.57	8.96 ± 2.07	42.51 ± 16.51	97.52 ± 25.86
Ed (native)	-	-	-	-	-	-	-	-	-	-
Ed (novel)	8-10	21.69 ± 9.10	3.68 ± 0.84	1.09 ± 0.72	3.26 ± 2.27	8.02 ± 2.41	87.86 ± 20.10	19.05 ± 12.68	128.96 ± 89.75	235.60 ± 88.35
August 2017										
A (native)	9-10	26.12 ± 10.70	0.74 ± 0.22	0.19 ± 0.03	0.43 ± 0.16	1.42 ± 0.22	17.72 ± 5.18	3.32 ± 0.56	17.01 ± 6.16	39.69 ± 6.71
A (novel)	10	18.98 ± 7.69	0.74 ± 0.21	0.18 ± 0.08	0.37 ± 0.18	1.29 ± 0.38	17.76 ± 5.06	3.09 ± 1.31	14.54 ± 7.18	35.39 ± 11.14
B	7-8	15.70 ± 9.88	1.91 ± 0.88	0.45 ± 0.22	0.72 ± 0.48	3.08 ± 1.51	45.58 ± 21.00	7.88 ± 3.82	28.52 ± 19.01	81.98 ± 41.85
C	8-9	5.23 ± 1.91	2.90 ± 1.01	0.86 ± 0.24	1.30 ± 0.28	5.08 ± 1.57	69.23 ± 24.23	14.99 ± 4.11	51.32 ± 11.13	136.33 ± 40.27
D	10	16.95 ± 4.45	0.67 ± 0.11	0.21 ± 0.03	0.44 ± 0.28	1.33 ± 0.38	16.02 ± 2.67	3.75 ± 0.52	17.47 ± 10.90	37.25 ± 13.25
Es (native)	10	15.46 ± 5.80	1.67 ± 0.49	0.48 ± 0.18	0.57 ± 0.29	2.73 ± 0.86	40.03 ± 11.63	8.39 ± 3.07	22.68 ± 11.45	71.10 ± 23.45
Es (novel)	-	-	-	-	-	-	-	-	-	-
F (native)	10	13.67 ± 4.10	1.38 ± 0.78	0.28 ± 0.13	0.59 ± 0.24	2.25 ± 0.97	32.90 ± 18.76	4.94 ± 2.19	23.41 ± 9.52	61.25 ± 24.20
F (novel)	10	22.43 ± 4.24	0.86 ± 0.21	0.22 ± 0.06	0.94 ± 0.82	2.03 ± 0.87	20.64 ± 5.03	3.86 ± 1.12	37.19 ± 32.46	61.70 ± 33.06
Ed (native)	6	35.68 ± 9.14	5.38 ± 1.05	1.06 ± 0.18	2.54 ± 1.15	8.98 ± 1.04	128.61 ± 25.07	18.48 ± 3.07	100.35 ± 45.56	247.63 ± 36.02
Ed (novel)	10	27.26 ± 9.24	4.23 ± 0.76	1.02 ± 0.22	3.36 ± 1.03	8.61 ± 1.58	100.98 ± 18.16	17.93 ± 3.92	132.72 ± 40.62	251.63 ± 52.22

Station	N	C:N ratio	Proteins (mg polyp^{-1})	Carbohydrates (mg polyp^{-1})	Lipids (mg polyp^{-1})	Total energy reserves (mg polyp^{-1})	Proteins (kJ polyp^{-1})	Carbohydrates (kJ polyp^{-1})	Lipids (kJ polyp^{-1})	Total energy reserves (kJ polyp^{-1})
January 2017										
F (native)	8	7.04 ± 1.40	24.00 ± 14.27	6.73 ± 2.99	10.02 ± 5.12	42.47 ± 20.01	0.57 ± 0.34	0.12 ± 0.05	0.40 ± 0.20	1.13 ± 0.52
F (novel)	8-9	7.13 ± 0.86	30.63 ± 13.00	7.31 ± 3.65	15.94 ± 11.61	55.49 ± 18.79	0.73 ± 0.31	0.13 ± 0.06	0.63 ± 0.46	1.53 ± 0.56
Ed (native)	7-8	9.33 ± 1.43	206.49 ± 44.08	39.36 ± 7.17	93.57 ± 41.01	334.88 ± 63.25	4.94 ± 1.05	0.69 ± 0.13	3.70 ± 1.62	9.11 ± 2.11
Ed (novel)	10	6.42 ± 1.88	57.15 ± 16.52	11.20 ± 3.04	24.99 ± 9.95	93.77 ± 23.14	1.37 ± 0.39	0.20 ± 0.05	0.99 ± 0.39	2.56 ± 0.64
May 2017										
A (native)	10	5.77 ± 0.41	22.35 ± 8.83	7.12 ± 3.19	12.37 ± 6.52	41.84 ± 18.15	0.53 ± 0.21	0.12 ± 0.06	0.49 ± 0.26	1.15 ± 0.52
A (novel)	9-10	5.81 ± 0.47	16.23 ± 7.66	5.94 ± 2.54	9.08 ± 5.06	31.84 ± 15.26	0.39 ± 0.18	0.10 ± 0.04	0.36 ± 0.20	0.86 ± 0.43
B	9	6.06 ± 0.48	21.44 ± 8.29	6.10 ± 2.65	7.68 ± 2.97	35.23 ± 10.11	0.51 ± 0.20	0.11 ± 0.05	0.30 ± 0.12	0.92 ± 0.26
C	9	6.68 ± 0.67	23.06 ± 4.18	5.12 ± 0.79	7.19 ± 1.72	35.37 ± 5.47	0.55 ± 0.10	0.09 ± 0.01	0.28 ± 0.07	0.92 ± 0.14
D	10	6.43 ± 0.77	15.76 ± 7.92	3.92 ± 1.44	6.95 ± 2.21	26.63 ± 10.37	0.38 ± 0.19	0.07 ± 0.03	0.27 ± 0.09	0.72 ± 0.26
Es (native)	7	7.28 ± 1.41	35.46 ± 13.08	9.27 ± 3.28	18.95 ± 8.80	63.67 ± 22.78	0.85 ± 0.31	0.16 ± 0.06	0.75 ± 0.35	1.76 ± 0.65
Es (novel)	-	-	-	-	-	-	-	-	-	-
F (native)	9-10	7.15 ± 1.46	27.29 ± 14.82	8.55 ± 2.95	21.77 ± 13.31	57.61 ± 30.72	0.65 ± 0.35	0.15 ± 0.05	0.86 ± 0.53	1.66 ± 0.93
F (novel)	10	6.80 ± 1.04	38.74 ± 15.07	9.95 ± 2.46	20.69 ± 7.58	69.39 ± 22.53	0.93 ± 0.36	0.17 ± 0.04	0.82 ± 0.30	1.92 ± 0.63
Ed (native)	-	-	-	-	-	-	-	-	-	-
Ed (novel)	8-10	7.56 ± 0.76	79.16 ± 43.47	18.86 ± 8.18	59.74 ± 35.97	152.85 ± 77.32	1.89 ± 1.04	0.33 ± 0.14	2.36 ± 1.42	4.46 ± 2.35
August 2017										
A (native)	9-10	6.70 ± 1.10	18.26 ± 6.71	4.71 ± 1.99	10.37 ± 3.86	33.96 ± 9.72	0.44 ± 0.16	0.08 ± 0.03	0.41 ± 0.15	0.94 ± 0.26
A (novel)	10	6.08 ± 0.68	13.52 ± 5.85	3.16 ± 1.76	6.01 ± 1.40	22.69 ± 7.57	0.32 ± 0.14	0.06 ± 0.03	0.24 ± 0.06	0.62 ± 0.18
B	7-8	5.50 ± 0.50	23.86 ± 9.48	5.50 ± 1.83	9.00 ± 4.67	38.36 ± 15.42	0.57 ± 0.23	0.10 ± 0.03	0.36 ± 0.18	1.02 ± 0.43
C	8-9	5.64 ± 0.75	14.20 ± 4.78	4.00 ± 0.86	6.44 ± 2.15	24.65 ± 8.04	0.34 ± 0.11	0.07 ± 0.02	0.25 ± 0.08	0.66 ± 0.22
D	10	5.24 ± 0.48	11.34 ± 3.56	3.70 ± 1.28	7.35 ± 4.63	22.39 ± 8.67	0.27 ± 0.08	0.06 ± 0.02	0.29 ± 0.18	0.63 ± 0.27
Es (native)	10	6.57 ± 1.17	24.30 ± 6.77	6.81 ± 1.69	8.36 ± 3.71	39.47 ± 11.21	0.58 ± 0.16	0.12 ± 0.03	0.33 ± 0.15	1.03 ± 0.31
Es (novel)	-	-	-	-	-	-	-	-	-	-
F (native)	10	6.01 ± 0.52	18.60 ± 10.05	3.91 ± 1.89	7.68 ± 2.41	30.18 ± 12.74	0.44 ± 0.24	0.07 ± 0.03	0.30 ± 0.10	0.82 ± 0.31
F (novel)	10	6.00 ± 0.81	19.41 ± 6.09	4.90 ± 1.45	19.95 ± 14.47	44.25 ± 17.97	0.46 ± 0.15	0.09 ± 0.03	0.79 ± 0.57	1.34 ± 0.65
Ed (native)	6	13.83 ± 1.87	194.31 ± 70.35	37.22 ± 10.23	83.38 ± 25.12	314.91 ± 71.61	4.64 ± 1.68	0.65 ± 0.18	3.29 ± 0.99	8.59 ± 1.66
Ed (novel)	10	9.94 ± 0.80	111.96 ± 31.69	28.07 ± 11.70	84.28 ± 17.95	224.31 ± 53.46	2.68 ± 0.76	0.49 ± 0.20	3.33 ± 0.71	6.50 ± 1.45



Supplementary Figure 1: Concentration of seasonal energy reserves of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. a) Protein, b) carbohydrate, c) lipid and d) total energy concentration of *D. dianthus* (mean ± standard deviation) at six stations at 20 m water depth along the fjord from head to mouth (A-F) are shown in blue and at one station at 300 m water depth (Ed) are shown in yellow (N = 6-10). Native corals (circles) were re-installed at the same station after collection in September 2016 and novel corals (squares) were cross-transplanted between the shallow stations at the head (A) and the mouth (F) of the fjord and between shallow (Es) and deep (Ed). Samples for the analyses were collected after four, eight and eleven months in austral summer (January), autumn (May) and winter (August), respectively, and standardized to the tissue covered surface area of the corals.



Supplementary Figure 2: Seasonal energy reserves of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. a) Protein, b) carbohydrate, c) lipid and d) total energy reserves per polyp of *D. dianthus* (mean ± standard deviation) at six stations at 20 m water depth along the fjord from head to mouth (A-F) are shown in blue and at one station at 300 m water depth (Ed) are shown in yellow (N = 6-10). Native corals (circles) were re-installed at the same station after collection in September 2016 and novel corals (squares) were cross-transplanted between the shallow stations at the head (A) and the mouth (F) of the fjord and between shallow (Es) and deep (Ed). Samples for the analyses were collected after four, eight and eleven months in austral summer (January), autumn (May) and winter (August), respectively, and calculated per coral polyp.

Supplementary Table 2: Generalized linear models for energy reserves (proteins, carbohydrates and lipids), C:N ratio and tissue covered surface area of *Desmophyllum dianthus*. Significant p-values are shown in bold.

Fixed effects	Df	Deviance Resid.	Df Resid.	Dev
Proteins (model 1: shallow stations)				
season	2	2.942	118	39.70
station	5	25.52	113	12.17
Proteins (model 2: stations A, F, Es, Ed)				
station	3	53.89	154	19.85
transplant	1	0.29	153	19.56
station*transplant	2	0.60	151	18.96
Carbohydrates (model 1: shallow stations)				
season	2	2.46	116	32.34
station	5	20.71	111	11.63
Carbohydrates (model 2: stations A, F, Es, Ed)				
station	3	35.13	152	26.73
transplant	1	0.06	151	26.67
station*transplant	2	0.24	149	26.44
Lipids (model 1: shallow stations)				
season	2	3.73	116	36.61
station	5	12.77	111	23.84
Lipids (model 2: stations A, F, Es, Ed)				
station	3	62.66	151	48.24
transplant	1	0.06	150	48.18
station*transplant	2	0.31	148	47.88
Total energy reserves (model 1: shallow stations)				
season	2	3.00	115	30.47
station	5	18.25	110	12.22
Total energy reserves (model 2: stations A, F, Es, Ed)				
station	3	52.6	149	20.61
transplant	1	0.03	148	20.58
station*transplant	2	0.07	146	20.51

Supplementary Table 2 (continued)

Fixed effects	Df	Deviance Resid.	Df Resid.	Dev
C:N ratio (model 1: shallow stations)				
season	2	0.34	115	2.73
station	5	0.46	110	2.27
C:N ratio (model 2: stations A, F, Es, Ed)				
station	3	3.55	150	5.53
transplant	1	0.55	149	4.99
station*transplant	2	0.76	147	4.23
Surface area (model 1: shallow stations)				
season	2	0.33	118	36.19
station	5	18.26	113	17.93
Surface area (model 2: stations A, F, Es, Ed)				
station	3	5.39	156	27.79
transplant	1	0.48	155	27.31
station*transplant	2	5.35	153	21.96

Supplementary Table 3: Post hoc tests of generalized linear models for energy reserves (proteins, carbohydrates and lipids), tissue covered surface area of *Desmophyllum dianthus*. Only relevant results are displayed here. Significant p-values are shown in bold.

Fixed effects	Contrast	Estimate	SE	t ratio	p-value
Proteins (model 1: shallow stations)					
season	Jan-Aug	-0.098	0.153	-0.642	0.797
	May-Aug	-0.333	0.070	-4.725	**<0.001**
	Jan-May	-0.234	0.153	-1.529	0.277
station	A-B	-0.757	0.123	-6.173	**<0.001**
	A-C	-1.333	0.121	-11.040	**<0.001**
	A-D	0.024	0.118	0.205	1.000
	A-Es	-0.699	0.123	-5.697	**<0.001**
	A-F	-0.505	0.118	-4.295	**<0.001**
	B-C	-0.576	0.126	-4.584	**<0.001**
	B-D	0.781	0.123	6.369	**<0.001**
	B-Es	0.058	0.128	0.450	0.998
	B-F	0.252	0.123	2.056	0.311
	C-D	1.357	0.121	11.240	**<0.001**
	C-Es	0.634	0.126	5.036	**<0.001**
	C-F	0.828	0.121	6.860	**<0.001**
	D-Es	-0.724	0.123	-5.894	**<0.001**
	D-F	-0.529	0.118	-4.500	**<0.001**
	Es-F	0.195	0.123	1.585	0.608
Proteins (model 2: stations A, F, Es, Ed)					
station*transplant	A (native) - A (novel)	-0.002	0.117	-0.015	1.000
	F (native) - F (novel)	0.017	0.096	0.177	1.000
	Es (native) - Ed (native)	1.065	0.136	7.809	**<0.001**
	Ed (native) - Ed (novel)	0.309	0.124	2.497	0.196

Supplementary Table 3 (continued)

Fixed effects	Contrast	Estimate	SE	t ratio	p-value
Carbohydrates (model 1: shallow stations)					
season	Jan-Aug	-0.203	0.139	-1.463	0.309
	May-Aug	-0.371	0.0616	-6.020	**<0.001**
	Jan-May	-0.168	0.1389	-1.209	0.448
station	A-B	-0.606	0.108	-5.610	**<0.001**
	A-C	-1.200	0.106	-11.275	**<0.001**
	A-D	0.043	0.104	0.411	0.999
	A-Es	-0.662	0.108	-6.115	**<0.001**
	A-F	-0.407	0.104	-3.923	**0.001**
	B-C	-0.594	0.109	-5.428	**<0.001**
	B-D	0.649	0.107	6.075	**<0.001**
	B-Es	-0.056	0.111	-0.503	0.996
	B-F	0.199	0.107	1.866	0.423
	C-D	1.243	0.105	11.821	**<0.001**
	C-Es	0.538	0.110	4.912	**<0.001**
	C-F	0.794	0.105	7.547	**<0.001**
	D-Es	-0.705	0.107	-6.592	**<0.001**
	D-F	-0.450	0.102	-4.391	**<0.001**
	Es-F	0.255	0.107	2.388	0.160
Carbohydrates (model 2: stations: A, F, Es, Ed)					
station*transplant	A (native) - A (novel)	-0.086	0.140	-0.614	0.999
	F (native) - F (novel)	0.114	0.115	0.986	0.977
	Es (native) - Ed (native)	0.714	0.158	4.511	**<0.001**
	Ed (native) - Ed (novel)	0.064	0.144	0.449	1.000

Supplementary Table 3 (continued)

Fixed effects	Contrast	Estimate	SE	t ratio	p-value
Lipids (model 1: shallow stations)					
season	Jan-Aug	0.108	0.204	0.530	0.857
	May-Aug	-0.358	0.090	-3.961	**<0.001**
	Jan-May	-0.466	0.204	-2.287	0.058
station	A-B	-0.316	0.157	-2.021	0.330
	A-C	-0.939	0.157	-5.996	**<0.001**
	A-D	0.033	0.150	0.220	1.000
	A-Es	-0.399	0.157	-2.543	0.112
	A-F	-0.573	0.150	-3.817	**0.002**
	B-C	-0.622	0.163	-3.824	**0.002**
	B-D	0.349	0.157	2.232	0.223
	B-Es	-0.082	0.163	-0.504	0.996
	B-F	-0.256	0.157	-1.637	0.574
	C-D	0.972	0.157	6.207	**<0.001**
	C-Es	0.540	0.163	3.312	**0.012**
	C-F	0.366	0.157	2.338	0.179
	D-Es	-0.432	0.157	-2.754	0.065
	D-F	-0.606	0.150	-4.037	**0.001**
	Es-F	-0.174	0.157	-1.111	0.877
Lipids (model 2: stations: A, F, Es, Ed)					
station*transplant	A (native) - A (novel)	0.107	0.182	0.590	0.999
	F (native) - F (novel)	-0.111	0.150	-0.742	0.996
	Es (native) - Ed (native)	1.163	0.205	5.687	**<0.001**
	Ed (native) - Ed (novel)	-0.089	0.186	-0.479	1.000

Supplementary Table 3 (continued)

Fixed effects	Contrast	Estimate	SE	t ratio	p-value
Total energy reserves (model 1: shallow stations)					
season	Jan-Aug	-0.039	0.145	-0.270	0.961
	May-Aug	-0.341	0.065	-5.277	**<0.001**
	Jan-May	-0.302	0.145	-2.083	0.093
station	A-B	-0.552	0.113	-4.891	**<0.001**
	A-C	-1.150	0.113	-10.198	**<0.001**
	A-D	0.051	0.108	0.474	0.997
	A-Es	-0.555	0.113	-4.909	**<0.001**
	A-F	-0.506	0.108	-4.672	**<0.001**
	B-C	-0.599	0.116	-5.166	**<0.001**
	B-D	0.603	0.111	5.409	**<0.001**
	B-Es	-0.003	0.116	-0.028	1.000
	B-F	0.046	0.111	0.412	0.999
	C-D	1.202	0.111	10.780	**<0.001**
	C-Es	0.595	0.116	5.127	**<0.001**
	C-F	0.645	0.111	5.782	**<0.001**
	D-Es	-0.606	0.112	-5.432	**<0.001**
	D-F	-0.557	0.107	-5.214	**<0.001**
	Es-F	0.049	0.112	0.441	0.998
Total energy reserves (model 2: stations: A, F, Es, Ed)					
station*transplant	A (native) - A (novel)	0.063	0.126	0.497	1.000
	F (native) - F (novel)	-0.021	0.103	-0.202	1.000
	Es (native) - Ed (native)	1.041	0.143	7.290	**<0.001**
	Ed (native) - Ed (novel)	0.079	0.130	0.605	0.999

Supplementary Table 3 (continued)

Fixed effects	Contrast	Estimate	SE	t ratio	p-value
C:N ratio (model 1: shallow stations)					
season	Jan-Aug	-0.123	0.067	-1.840	0.157
	May-Aug	-0.102	0.028	-3.620	**0.001**
	Jan-May	0.021	0.067	0.311	0.948
station	A-B	0.082	0.049	1.672	0.550
	A-C	0.007	0.048	0.154	1.000
	A-D	0.076	0.047	1.614	0.589
	A-Es	-0.107	0.049	-2.179	0.248
	A-F	-0.044	0.048	-0.926	0.940
	B-C	-0.075	0.050	-1.484	0.675
	B-D	-0.006	0.049	-0.125	1.000
	B-Es	-0.189	0.051	-3.699	**0.003**
	B-F	-0.126	0.050	-2.540	0.113
	C-D	0.068	0.048	1.417	0.716
	C-Es	-0.114	0.050	-2.273	0.205
	C-F	-0.051	0.049	-1.053	0.900
	D-Es	-0.183	0.049	-3.724	**0.003**
	D-F	-0.120	0.048	-2.519	0.119
	Es-F	0.063	0.050	1.266	0.803
C:N ratio (model 2: stations: A, F, Es, Ed)					
station*transplant	A (native) - A (novel)	0.048	0.055	0.864	0.989
	F (native) - F (novel)	0.014	0.048	0.296	1.000
	Es (native) - Ed (native)	0.481	0.063	7.641	**<0.001**
	Ed (native) - Ed (novel)	0.360	0.056	6.371	**<0.001**

Supplementary Table 3 (continued)

Fixed effects	Contrast	Estimate	SE	t ratio	p-value
Surface area (model 1: shallow stations)					
season	Jan-Aug	-0.067	0.167	-0.401	0.915
	May-Aug	0.069	0.077	0.895	0.644
	Jan-May	0.135	0.167	0.812	0.696
station	A-B	0.519	0.133	3.886	**0.001**
	A-C	1.448	0.131	11.023	**<0.001**
	A-D	0.386	0.128	3.017	**0.031**
	A-Es	0.343	0.134	2.568	0.105
	A-F	0.474	0.128	3.703	**0.003**
	B-C	0.930	0.137	6.797	**<0.001**
	B-D	-0.133	0.133	-0.995	0.920
	B-Es	-0.176	0.139	-1.263	0.805
	B-F	-0.045	0.133	-0.337	0.999
	C-D	-1.063	0.131	-8.086	**<0.001**
	C-Es	-1.105	0.137	-8.072	**<0.001**
	C-F	-0.975	0.131	-7.418	**<0.001**
	D-Es	-0.043	0.134	-0.321	1.000
	D-F	0.088	0.128	0.686	0.984
	Es-F	0.131	0.134	0.978	0.925
Surface area (model 2: stations: A, F, Es, Ed)					
station*transplant	A (native) - A (novel)	0.307	0.119	2.577	0.164
	F (native) - F (novel)	0.569	0.122	4.674	**<0.001**
	Es (native) - Ed (native)	0.841	0.136	6.193	**<0.001**
	Ed (native) - Ed (novel)	-0.332	0.098	-3.387	**0.016**

Supplementary Table 4: Lipid class composition of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. Main lipid classes in % and total amount per coral polyp (mean ± standard deviation) at stations A, F, Es and Ed in austral summer (January) and winter (August).

Station	N	Wax ester (%)	Triacyl-glycerols (%)	Sterols (%)	Free Fatty Acids (%)	Phospho-lipids (%)	Other lipid classes (%)
January 2017							
F (native)	5	31.8 ± 7.5	24.8 ± 6.5	5.0 ± 0.9	5.4 ± 1.3	27.1 ± 7.0	5.9 ± 2.9
F (novel)	5	31.3 ± 2.1	28.6 ± 4.2	5.8 ± 0.5	6.1 ± 0.9	19.8 ± 2.0	8.4 ± 3.7
Ed (native)	8	63.2 ± 4.8	23.7 ± 4.3	1.5 ± 0.3	2.3 ± 1.3	8.3 ± 1.1	1.0 ± 0.6
Ed (novel)	8	43.4 ± 2.3	41.4 ± 3.4	1.4 ± 0.3	1.5 ± 0.3	11.5 ± 2.5	0.8 ± 0.5
August 2017							
A (native)	5	38.3 ± 9.1	11.2 ± 4.4	6.7 ± 1.9	8.0 ± 2.5	31.8 ± 6.7	3.9 ± 3.9
A (novel)	5	20.7 ± 10.6	8.7 ± 4.8	8.7 ± 1.7	13.2 ± 6.1	44.0 ± 16.7	4.7 ± 2.0
Es (native)	8	15.0 ± 2.6	24.2 ± 8.6	6.3 ± 1.4	10.9 ± 5.2	38.5 ± 8.5	5.2 ± 1.3
F (native)	5	19.8 ± 4.3	18.7 ± 8.8	6.6 ± 3.0	5.3 ± 1.5	47.0 ± 11.4	2.5 ± 1.5
F (novel)	5	23.4 ± 7.0	22.5 ± 11.6	8.1 ± 3.0	7.3 ± 2.3	34.4 ± 11.7	4.3 ± 3.0
Ed (native)	6	69.4 ± 2.4	20.1 ± 2.9	1.2 ± 0.2	2.0 ± 0.2	6.0 ± 1.7	1.4 ± 0.8
Ed (novel)	8	69.5 ± 3.4	21.7 ± 2.4	1.0 ± 0.3	1.8 ± 0.6	5.1 ± 1.2	0.9 ± 0.5

Supplementary Table 4 (continued)

Station	N	Wax ester (mg polyp^{-1})	Triacyl-glycerols (mg polyp^{-1})	Free Fatty Alcohols (mg polyp^{-1})	Sterols (mg polyp^{-1})	Free Fatty Acids (mg polyp^{-1})	Cerebrosids (mg polyp^{-1})	Phospho-lipids (mg polyp^{-1})	All lipid classes (mg polyp^{-1})
January 2017									
F (native)	5	11.17 ± 3.54	9.07 ± 3.79	1.21 ± 0.16	1.75 ± 0.25	1.86 ± 0.27	1.61 ± 1.49	9.89 ± 3.95	35.77 ± 8.84
F (novel)	5	11.13 ± 3.58	10.24 ± 3.69	1.32 ± 0.48	2.06 ± 0.73	2.22 ± 0.95	1.28 ± 0.58	7.13 ± 2.61	35.57 ± 11.53
Ed (native)	8	46.46 ± 20.75	18.59 ± 11.83	0.95 ± 0.34	1.10 ± 0.46	1.65 ± 1.22	0.31 ± 0.14	6.13 ± 2.92	74.78 ± 36.28
Ed (novel)	8	10.00 ± 5.54	9.49 ± 5.49	0.25 ± 0.20	0.33 ± 0.18	0.35 ± 0.22	0.27	2.67 ± 1.62	23.09 ± 13.07
August 2017									
A (native)	5	3.17 ± 1.08	1.09 ± 0.76	0.45 ± 0.20	0.66 ± 0.47	0.66 ± 0.24	0.25 ± 0.11	3.05 ± 2.05	9.04 ± 4.74
A (novel)	5	1.03 ± 0.39	0.47 ± 0.27	0.22 ± 0.06	0.48 ± 0.20	0.68 ± 0.27	0.14 ± 0.02	2.45 ± 1.33	5.34 ± 1.33
Es (native)	8	4.30 ± 2.00	7.59 ± 5.56	0.82 ± 0.42	1.77 ± 0.64	2.80 ± 0.85	0.66 ± 0.36	10.61 ± 3.16	28.56 ± 11.30
F (native)	5	3.89 ± 2.65	4.30 ± 3.42	0.52 ± 0.21	1.02 ± 0.42	1.00 ± 0.65	0.38 ± 0.14	8.62 ± 5.34	19.44 ± 12.35
F (novel)	5	3.64 ± 2.10	4.29 ± 3.64	0.64 ± 0.22	1.12 ± 0.41	1.06 ± 0.53	0.62 ± 0.51	4.95 ± 2.14	15.93 ± 9.06
Ed (native)	6	88.32 ± 14.85	25.99 ± 8.25	1.24 ± 0.36	1.52 ± 0.46	2.51 ± 0.59	0.44 ± 0.20	7.57 ± 1.88	127.64 ± 23.57
Ed (novel)	8	41.19 ± 12.10	12.84 ± 3.73	0.61 ± 0.26	0.57 ± 0.25	1.05 ± 0.44	0.13	3.07 ± 1.38	59.29 ± 17.19

Supplementary Table 5: Results of PERMANOVA for comparison of lipid class composition of *Desmophyllum dianthus* between coral stations in Comau Fjord, Chile. Significant p-values are shown in bold.

Station 1	Station 2	p-value	adjusted p-value
C	A	0.020	0.20
Es	A	0.005	**0.05**
Es	C	0.370	1.00
Es	Ed	0.001	**0.01**
F	A	0.014	0.14
F	C	0.321	1.00
F	Es	0.025	0.25
F	Ed	0.001	**0.01**
Ed	A	0.001	**0.01**
Ed	C	0.001	**0.01**

Supplementary Discussion

In contrast to *in situ* studies, previous laboratory studies found no significant relationship between zooplankton food concentration and storage fatty acid content of *L. pertusa* over three months (Larsson et al., 2013; Baussant et al., 2017), but only a non-significant increasing trend (Larsson et al., 2013). Although *L. pertusa* can sustain long starvation periods (Baussant et al., 2017; Maier et al., 2019) without reduction of its metabolism during short-term food deprivation of four weeks (Maier et al., 2019), its metabolism is depressed after six months (Baussant et al., 2017). *Desmophyllum dianthus* even decreased its metabolism during a starvation period of just three weeks (Naumann et al., 2011). However, this may not only be related to differences between species, but may also depend on different feeding conditions and energy reserves of the corals in these experiments. As CWCs can have high amounts of storage lipids (Dodds et al., 2009; Larsson et al., 2013), these lipid reserves may enable them to sustain starvation periods of a certain period of time before its physiological performance is affected. For instance, the calcification rate of *Caryophyllia huinayensis* decreased only after three months of exposure to elevated temperature and reduced feeding, presumably due to sufficient energy reserves at the beginning of the experiment that enabled the corals to withstand these conditions for several months (Beck et al., in prep). In addition, decreasing protein and lipid concentrations were found in *L. pertusa* and *M. oculata* after two to six months at elevated temperature (Chapron et al., 2021). It is therefore important to take the nutritional status of corals in laboratory experiments into account, as increased feeding can mask and delay the effect.

6

Synthesis

This thesis advances our understanding how cold-water corals (CWCs) respond to environmental changes, in particular the impact on early life stages, the interactive effects of multiple environmental drivers, including food availability, and the effect of natural environmental variability. I uniquely combined direct observations in the field with aquarium experiments, which refine our understanding of corals' physiological performance, phenotypic plasticity and their underlying environmental drivers. In addition, the investigation of CWCs' biochemical composition provides more detailed insights into their natural diet and ability to build-up and maintain energy reserves under different environmental and feeding conditions.

In this thesis, I took advantage of the unique CWC culturing system and the established multi-generation population of *Caryophyllia huinayensis* at the Alfred Wegener Institute. I conducted a multi-driver experiment with different life stages and observed different physiological responses of juvenile and adult corals (**manuscript 1**). Contrary to expectations, adult corals were not the most resilient life stage to changes in temperature and food availability due to their high mortality rates. However, the experiment also showed that warming may delay CWC maturation under future environmental conditions. This indicates that early life stages can represent an important bottleneck for the resistance of CWC populations, which has consequences for the maintenance of the whole population. Thus, I showed for the first time that considering different life stages is essential for a better prediction of the response of CWCs to future environmental changes. This experiment also underlines the importance to study the response of CWCs to multiple environmental factors as they will be affected by a simultaneous change of several parameters in the future. In addition, by relating the environmental conditions in CWCs' natural habitat to their physiological performance, I showed that fluctuating environmental factors can have detrimental effects (**manuscript 2**). Therefore, multi driver experiments and the inclusion of

natural environmental variability give more realistic insights into the behaviour of CWCs under climate change than examining the influence of individual factors under stable conditions. For the first time, I included food availability as one factor in a CWC experiment with multiple physico-chemical drivers, which showed that adequate nutrition is indispensable (**manuscript 1**). Furthermore, the delayed response of the corals also demonstrated the need for long-term experiments over several months. The detailed investigation of the biochemical composition of CWCs from Comau Fjord, including their seasonal energy reserves, fatty acid composition and lipid classes, allowed to get a better insight into their trophic ecology and unravel previously conflicting data on coral physiology and zooplankton abundance in the fjord (**manuscripts 3 and 4**). Linking this information to coral physiology, environmental conditions and zooplankton availability enabled a better understanding of CWCs' resilience to future environmental changes in regions with different food availabilities. Finally, the *in situ* reciprocal transplantation experiment provided the opportunity to discover the rapid acclimatisation potential of several traits of *Desmophyllum dianthus* to a new environment (**manuscripts 2 and 4**).

Answers to research questions

1) **How do different life stages of cold-water corals react to extreme environmental conditions?**

The effect of environmental changes on early and late juveniles as well as adult corals of *C. huinayensis* was studied in a controlled aquarium experiment, which revealed energetic trade-offs between juvenile and adult corals, but also between the two juvenile stages (**manuscript 1**). The energy input balanced or exceeded the energy demand of juvenile corals under ambient and Ω conditions, while the energy demand of adult corals was barely met. Elevated temperature alone and in combination with aragonite undersaturation increased the corals' energy demand. These treatments had the largest effect on somatic growth as well as calcification and respiration rates of early juvenile corals, whereas reduced food availability had a slightly smaller effect (Figure 1). In contrast, these two parameters had the smallest effect on all of these traits in adult corals, yet clearly reduced their chances of survival.

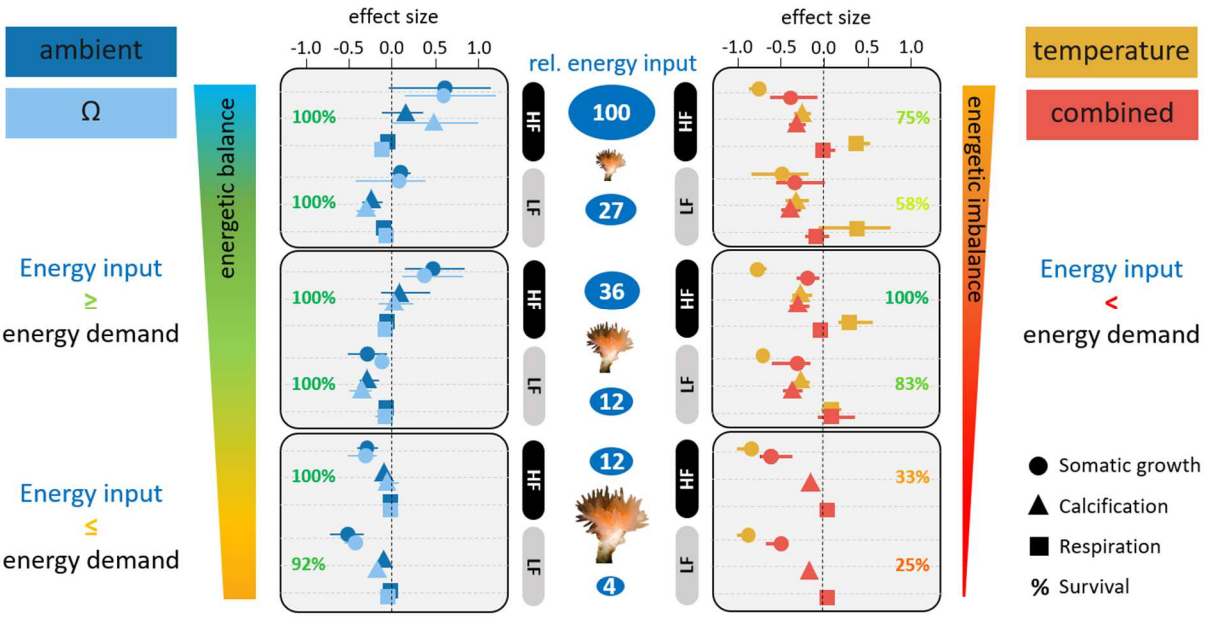


Figure 1: Summarised results of the aquarium experiment with *Caryophyllia huinayensis* under different Ω, temperature and feeding conditions. The effect sizes (mean difference) of somatic growth (circle), calcification (triangle) and respiration rates (square) after six months under treatment conditions are displayed in the colours of the four physico-chemical treatments (ambient = dark blue, Ω = light blue, temperature = yellow, combined = red). The effect sizes were calculated after six months under these treatment conditions in relation to initial ambient conditions. Percentages indicate the survival rate for each life stage. The relative energy input for each life stage and feeding regime was calculated from measurements of the prey capture rates of the corals that were normalised to their tissue covered surface area and expressed relative to the highest energy input of early juvenile corals in the high feeding (HF) regime. All traits show that the energy input exceeded the energy demand of early and late juvenile corals at ambient temperature (ambient and Ω treatments), but not in adult corals. In addition, all life stages were barely able to maintain their growth rates in the low feeding (LF) regime under ambient temperature (temperature and combined treatments). However, elevated temperature of 15 °C, both as single driver and in combination with aragonite undersaturation, clearly exceeded the tolerance limit of *C. huinayensis*, leading to reduced growth and survival rates as well as elevated respiration rates, that may be an indication of metabolic stress.

This clearly indicates that adults were not the most resilient life stage, which is in contrast to expectations and previous studies (Maier et al., 2009; Movilla et al., 2014; Martínez-Dios et al., 2020). Additionally, the response and sensitivity were dependent on the investigated trait. Calcification rates, which are predominantly used to assess performance (e.g. Form & Riebesell, 2012; Büscher et al., 2017; Martínez-Dios et al., 2020), are likely not the best parameter to determine the resilience of adult corals due to their generally low calcification rate. Calcification of adult corals was less affected in this study, although they responded severely in terms of somatic growth and survival to both elevated temperature and reduced food supply. While reduced calcification of juvenile corals likely prolongs the duration of the juvenile, non-reproductive stage, a combination with high mortality rates in adult corals in

turn will affect the population structure. This leads to shifts in the size structure domination by smaller corals, delays maturity and results in an overall reduced reproductive output and population size (Done, 1999).

None of the life stages of *C. huinayensis* were affected by aragonite undersaturation alone. This is in contrast to previous investigations that found a large decrease in calcification rates of small, young CWC polyps (Maier et al., 2009; Movilla et al., 2014; Martínez-Dios et al., 2020) and tropical coral recruits (e.g. Albright et al., 2008, 2010; Albright & Langdon, 2011; Foster et al., 2015, Jiang et al., 2018), but is in line with many CWC studies that found no effect on adult corals (e.g. Hennige et al., 2014, 2015; Rodolfo-Metalpa et al., 2015; Gori et al., 2016). This may be due to species-specific differences, as *C. huinayensis* seems to be more robust than other CWC species to adverse environmental conditions (e.g. methane and sulfide enriched water; Försterra et al., 2014). This work demonstrates that especially ocean warming and projected reductions in food availability may have critical impacts on multiple life stages of CWCs, thus affecting the resilience of entire CWC populations.

2) How do cold-water corals react to simultaneous changes of multiple environmental factors?

Multi driver responses are usually classified as additive, synergistic or antagonistic (e.g. Crain et al., 2008). So far, multi driver experiments with CWCs found an additive response of coral calcification to simultaneous changes of temperature and pH within the same feeding regime (Hennige et al., 2015; Büscher et al., 2017; this study) and only Gori et al. (2016) observed an antagonistic effect. Single drivers often showed a neutral response (Hennige et al., 2015; Gori et al., 2016; this study) and no cumulative effect was found (Hennige et al., 2015; Gori et al., 2016; Büscher et al., 2017). In the present experiment, the response to multiple drivers was strongly dependent on individual factors (elevated temperature and food supply), which pushed the corals towards their tolerance limit and also dominated in combination (**manuscript 1**). As the corals already reached their limit in response to these single factors, we only observed a slightly stronger response to the combination of drivers. Thus, unless individual factors are also tested, such a combined response makes it more complicated to clearly identify the main drivers of changes in physiological performance *in situ*, where they act in concert.

For the aquarium experiment, we used natural environmental conditions and the extremes measured so far. From a physiological perspective, the applied elevated temperature of 15 °C certainly exceeded the corals' optimal window and was potentially close to their upper critical tolerance limit as their thermal performance likely follows a classical performance curve (discussion of **manuscript 1**). By contrast, the aragonite saturation levels seemed to be in a rather optimal range in terms of calcification, despite aragonite undersaturation, and their critical limit is much lower. So far, performance assays are very limited in CWCs (Dorey et al., 2020; Martínez-Dios et al., 2020; Chapron et al., 2021 Reynaud

et al., 2021), but are important to place *in situ* environmental conditions and the extremes defined here in a physiological context.

In contrast to aquarium experiments, where most water parameters are kept constant and only the target conditions are modified, corals *in situ* are always subject to multiple environmental parameters. Therefore, a different approach is needed to determine the most important factors that drive the response of the corals in the field. Here, I used a multifactorial analysis of various environmental conditions in comparison to coral calcification (**manuscript 2**). This revealed that besides specific environmental drivers like temperature, also their variability matters and needs to be assessed and considered. The shallow waters in Comau Fjord are characterised by strong environmental variability and have been identified as an important driver in this region that influence the physiological performance of CWCs. This aligns with observation in other ecosystems (e.g. Helmuth, 1998; Helmuth & Hofmann, 2001; Bernhardt et al., 2020; Kroeker et al., 2020; Marshall et al., 2021) and the role of natural variability in determining organisms' performance (Wahl et al., 2016; Bates et al., 2018; Morash et al., 2018; Ziegler et al., 2021; Gómez et al., 2022).

3) How do cold-water corals cope with short- and long-term exposure to extreme current and future environmental conditions? Do they have the potential to acclimatise to environmental changes?

In the short-term, *C. huinayensis* was able to cope with environmental changes (elevated temperature and reduced food supply). This corroborates other short-term studies that found no effect of reduced pH (e.g. Maier et al., 2012, 2013; Hennige et al., 2014; Rodolfo-Metalpa et al., 2015), but contrasts others findings of clear responses also over short periods (Maier et al., 2009, 2016; Lunden et al., 2014; Gómez et al., 2018). This discrepancy does not seem to be species- or location-specific (see Table 1 of **manuscript 2**), but rather an effect of differences in energy availability, and thus, energy reserves of the corals. While the corals maintained the same physiological performance for at least one month under extreme environmental conditions, this response clearly changed after three to six months (**manuscript 1**). Sufficient energy reserves may allow them to maintain their physiological performance for a certain period of time, which begins to decline once the reserves are depleted. This conclusion can be drawn from the correlation between total energy reserves and calcification rates in *D. dianthus* (**manuscript 3**), which is in line with feeding studies on *D. dianthus* (Naumann et al., 2011; Martínez-Dios et al., 2020). However, interestingly, this is not always the case. Other laboratory studies found no effect of reduced food supply and complete food deprivation on calcification rates of *Lophelia pertusa* and *Madrepora oculata* even after several months in some cases (Larsson et al., 2013a; Maier et al., 2016; Baussant et al., 2017; Büscher et al., 2017). The energetics and metabolic responses may thus be species-specific, but also related to treatment levels, as discussed in **manuscript 1**. This warrants more detailed investigations of CWCs' energetic status. Such a delayed response should always be

considered in aquarium experiments and can be addressed by more detailed analyses of the energetic composition of the corals and more long-term observations.

The *in situ* experiment in Comau Fjord showed that several traits (calcification, respiration, total energy reserves) of *D. dianthus* acclimatise fast to environmental changes within four months (**manuscripts 2 and 4**). This underscores its strong phenotypic plasticity, but also contrasting environmental conditions in its natural environment. However, by measuring several traits, I also showed that the strength of the response and CWCs' ability to adjust to a new environment depend on the investigated trait. A similar trait-dependent response is known from reciprocal transplantation experiments with tropical corals (Bay & Palumbi, 2017; Rocker et al., 2019a) and allows a more refined insight into the physiological performance of corals. For instance, the tissue covered surface area of novel shallow corals was not reduced to the same level as of native shallow corals within the one year of the study (**manuscript 2**). In addition, the lipid class composition of novel deep corals was still distinct after four months (**manuscript 4**), but a reassessment after eleven months revealed the same relative composition as the native deep corals. This highlights the necessity to study several traits of an organism to gain a more holistic view of its adaptation potential to future environmental conditions. In addition, we must also consider the time frame in which corals can withstand and overcome unfavourable conditions.

However, acclimatisation is not always positive, as the environment can also negatively influence traits (e.g. Bay & Palumbi, 2017). This maladaptation was also observed in **manuscript 2** as novel shallow corals transplanted from deep reduced their physiological performance within four months. While novel deep corals quickly acclimatised to generally more favourable conditions in deep waters, novel shallow corals quickly reduced their calcification and respiration rates as they were affected by the more negative environmental conditions in shallow waters within a short time. Interestingly, some traits showed a clear acclimatisation, while others were maintained in novel shallow corals, which likely also reflects a delayed response. However, we do not know if novel shallow corals were able to maintain their energy reserves or if they started to deplete these reserves in order to maintain their tissue covered surface area. The observed response indicates energetic trade-offs and the corals may sacrifice calcification (potentially adjusted to the energy supply) in favor of somatic maintenance (potentially more closely linked to the ability to accumulate energy reserves). Yet, this is in contrast to the maintenance of calcification rates of *C. huinayensis* in the aquarium experiment and underscores our lacking knowledge about CWCs' energy reserves and energetic trade-off.

4) How much do environmental conditions fluctuate in the natural habitat of cold-water corals, especially at shallow sites where they have emerged from the deep? How does natural environmental variability affect the physiological performance of cold-water corals?

The water temperature in shallow waters (20 m depth) in Comau Fjord fluctuates in a similar range as determined previously for other CWC habitats at much greater depth (50-900 m depth range; Mienis et al., 2007, 2014; Guihen et al., 2012; Brooke et al., 2013; Gugliotti et al., 2019) and correlates strongly with salinity fluctuations and presumably also other physico-chemical parameters (**manuscript 2**). Therefore, deep-water emergent CWCs are by far not the only CWCs that regularly experience environmental variability, which highlights the importance of this parameter for CWCs in general. Consequently, the Comau Fjord represents a natural laboratory for investigations of CWCs to contrasting environments due to its small-scale heterogeneity of environmental conditions and large difference between spatially close shallow and deep water habitats.

For the first time, I was able to show that natural environmental variability reduces the physiological performance (**manuscript 2**) and affects the biochemical composition (**manuscript 4**) of CWCs. I found reduced calcification and respiration rates as well as energy reserves and storage lipids of *D. dianthus* in shallow waters. This is consistent with the hypothesis that enhanced environmental variability reduces CWCs' physiological performance and is in line with previous findings of decreasing growth rates of other organisms under variable compared to constant temperatures (Bernhardt et al., 2018; Marshall et al., 2021). However, native shallow corals were not more resilient to environmental variations than novel shallow corals, since the latter adjusted their calcification to the same level as the former, but not to a lower level. A further reduction of calcification rates by novel shallow corals would have indicated an adaptive advantage of native shallow coral, as was partly the case for the gorgonian coral *Antillogorgia bipinnata* (Calixto-Botía & Sánchez, 2017). This indicates that CWCs regularly experiencing fluctuations are not better adapted to future environmental changes. This finding contrasts studies on tropical corals that found a better adaptability of corals to increasing temperatures when they were regularly exposed to natural temperature fluctuations (Oliver & Palumbi, 2011; Kenkel et al., 2013; Schoepf et al., 2015; Safaie et al., 2018) and positive effects of increased pH variability on calcification (Dufault et al., 2012; Comeau et al., 2014). Unlike many tropical corals, CWCs do not seem to be accustomed to the continuous fluctuations, nor do recurring recovery periods in between seem to sufficiently compensate for the more energy-demanding conditions.

However, organisms are never exposed to single environmental factors *in situ*, but to a whole range of factors which can have positive, neutral or negative effects on their physiology. Environmental variability is a proxy for several co-varying factors, leading to differences in CWC calcification and energy reserves between shallow and deep waters of Comau Fjord. However, it is important to know whether environmental variability affects the corals directly

or indirectly via their food source, as the environmental fluctuations may also alter the zooplankton abundance and composition in shallow waters of the fjord. Here, further analyses of the biochemical composition of *D. dianthus* can provide a more detailed understanding and link to potential differences in food availability.

5) How variable is the *in situ* biochemical composition of CWCs and which factors influence it most? How much do the energy reserves influence the physiological performance of the corals?

The biochemical composition of CWCs in Comau Fjord is certainly driven by the availability and composition of zooplankton, but also modulated by other co-varying factors (in particular those affecting coral calcification). Both the zooplankton community and the abiotic environmental conditions are more favourable for CWCs in deep waters of the fjord as indicated by the overall higher calcification rates and energy reserves of *D. dianthus* and the high amount of storage lipids. Observations of the natural zooplankton community showed low plankton concentrations in deep waters of Comau Fjord (Garcia-Herrera et al., 2022). Yet, the composition of fatty acids and lipids of the corals differed significantly across water depths, which reveals differences in corals' feeding strategies (**manuscripts 3 and 4**). This direct investigation of the energy reserves and biochemical composition indicate the opposite of the natural zooplankton data and support a flourishing zooplankton community in deep waters of the fjord. The discrepancy between the biochemical composition of *D. dianthus* and direct investigations of the zooplankton community in Comau Fjord emphasise the importance to investigate the corals' biochemical composition. This gives us better insights into their nutritional status and warrants further zooplankton studies that captures more mobile and abundant species like krill.

This thesis shows a clear link between total energy reserves and coral calcification (**manuscript 4**), indicating that *D. dianthus* uniformly invests into calcification and the build-up energy reserves when enough energy is available. This is in line with previous findings of tropical corals, where energy reserves provide important information about their health status (e.g. Schoepf et al., 2013; Rocker et al., 2017, 2019b). Therefore, CWCs' biochemical composition clearly indicates their resilience and ability to deal with environmental changes, similar to tropical corals (Anthony et al., 2009). However, this raises the question whether saturation is reached at some point and energy excess is not invested into calcification anymore. The clear accumulation of energy reserves in deep corals may indicate such saturation and energetic trade-offs, yet this needs to be investigated in more detail in future studies.

6) How does reduced food availability affect the ability of cold-water corals to cope with environmental changes?

The aquarium experiment clearly showed that food availability is one of the most important determinants of the response of *C. huinayensis*, especially in the long term with clear negative effects on its metabolism due to reduced food supply. This is consistent with previous findings that food supply is an important factor for CWCs' occurrence (Hebbeln et al., 2019; da Costa Portilho-Ramos et al., 2022) and their ability to resist stressful environmental conditions (e.g. Baco et al., 2017; Hanz et al., 2019; Hebbeln et al., 2020). In addition, the biochemical composition and reduced calcification rates of corals in shallow waters of Comau Fjord indicate that they have access to less food than corals in deep waters. As the zooplankton community in shallow waters may be affected by the high environmental variability, shallow corals cannot compensate for the unfavourable environmental conditions due to the presumably reduced food supply. However, it is unclear whether more food would allow the corals to better withstand these conditions. The corals' biochemical composition and the clear correlation with coral calcification revealed that a high amount and quality of food is beneficial for deep corals and enables them to thrive at aragonite undersaturated conditions. This is consistent with the occurrence of CWC habitats in unfavourable conditions of aragonite saturation (Thresher et al., 2011; Baco et al., 2017), temperature (Mienis et al., 2014) or oxygen concentration (Hanz et al., 2019; Hebbeln et al., 2020; Orejas et al., 2021), most likely due to high food supply in these regions. Therefore, adequate food availability and sufficient energy reserves are crucial for CWCs to resist unfavourable current and future environmental conditions.

The findings of this thesis clearly show that additional food supply can only compensate for unfavourable environmental conditions to some extent. Some environmental conditions, e.g. long-term exposure to high extreme temperatures, simply exceed the tolerance limit of the corals. However, the interplay of reduced food availability, increasing warming and acidification will affect CWCs in the future, accompanied by increasing variability and short-term fluctuations of these factors. The present work indicates that CWCs will be particularly affected by reduced food availability, extreme temperatures and increasing environmental variability.

Cold-water corals in the natural laboratory of Comau Fjord (Figure 2)

This thesis indicates that the conditions in deep waters of Comau Fjord are more beneficial for *D. dianthus* due to more stable environmental conditions and expectedly higher food availability, coupled with better zooplankton composition (presumably dominated by energy-rich calanoid copepods and krill). This enables deep corals to calcify more and build up more energy reserves and storage lipids. On the one hand, deep corals have enough food available. On the other hand, the abiotic conditions also allow them to invest a high amount of energy into calcification and the build-up of energy reserves, as little energy is expended on coping with fluctuating and likely stressful environmental conditions. This also allows the corals to thrive at aragonite undersaturation in deep waters of the fjord as other abiotic and biotic parameters are favourable. The highest calcification rates of novel deep corals shows that *D. dianthus* can cope with sudden environmental changes as long as these are beneficial. By contrast, corals in shallow waters suffer from an unfavourable environmental setting with high environmental fluctuations, likely more disturbances from other benthic organisms, a presumably higher infestation rate with endolithic algae and a lower food supply (with a zooplankton community presumably dominated by non-calanoid copepods). The higher environmental variability in shallow waters reduces the corals' physiological performance either directly or via their food source. Therefore, shallow corals are exposed to environmental conditions that increase their energy demand to resist these disturbances. At the same time, less energy is available to shallow corals than to deep corals. Although CWCs were able to conquer shallow environments in Comau Fjord, the results of this thesis show that this is likely only possible in plankton-rich environments, as shallow corals in Comau Fjord are already at their limit. To complete our understanding of CWCs' energy allocation in Comau Fjord, it is also critical to investigate the corals' reproductive investments. A previous study postulated that mainly deep water populations maintain populations in shallow waters (Addamo et al., 2021). Our findings of higher calcification rates and energy reserves in deep waters may support this hypothesis, but it is also possible that the reduced energy reserves in shallow corals derive from a similar investment into reproduction.

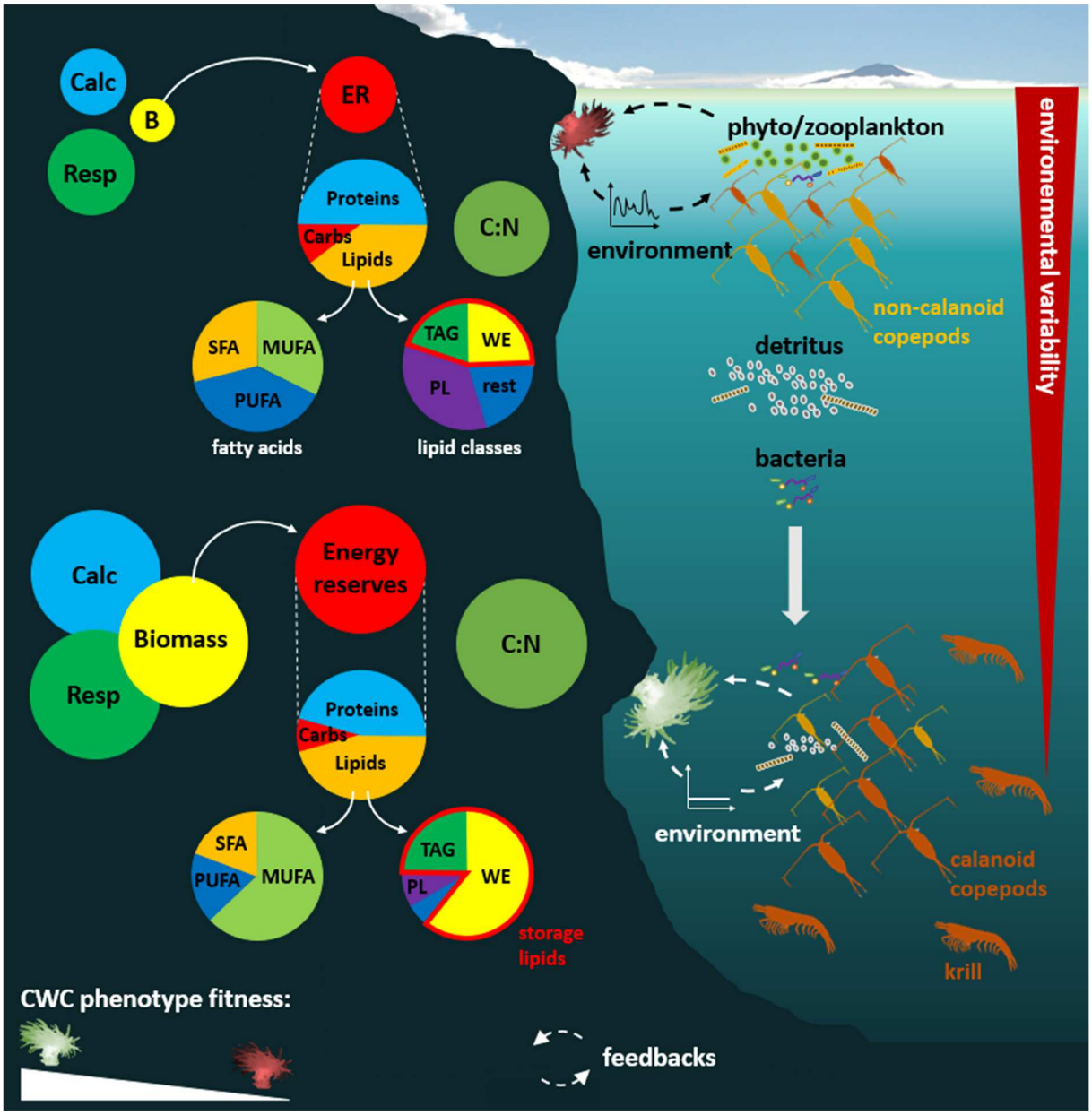


Figure 2: Summarised results of the *in situ* experiment with *Desmophyllum dianthus* in Comau Fjord, Chile. Results of the physiological parameters and biochemical composition are displayed for native and novel corals together in this figure. Calcification (Calc), respiration (Resp), biomass (B), total energy reserves (ER) and the C:N ratio of deep corals are displayed as 100 % for deep corals and the total amounts for shallow corals are shown in relation to deep corals. Only relative proportions are shown for energy reserves, fatty acids and lipid classes (total energy reserves display absolute differences). Shallow corals are negatively affected by high environmental fluctuations (e.g. temperature, salinity, pH, oxygen concentration etc.), which may also affect the zooplankton community as their most important food source, leading to reduced coral calcification, which in turn is also reflected in the lower proportion of energy reserves. Corals in shallow waters feed presumably more on non-calanoid copepods, which is displayed in their low amount of wax esters. In contrast, corals in deep waters of the fjord benefit from more stable environmental conditions (despite aragonite undersaturation) and a different zooplankton community as food source, which is most likely dominated by calanoid copepods and krill. The higher C:N ratio in deep corals gives indication that more food is available in deep waters of Comau Fjord (van Oevelen et al.,

2016). Therefore, deep corals have higher calcification rates, higher tissue coverage and biomass as well as more energy reserves. Even though both shallow and deep corals gain the same amount of energy from proteins, lipids and carbohydrates (Carbs), the relative and absolute amounts of storage lipids (WE = wax esters and TAG = triacylglycerols) and the fatty acid class ratio (SFA+MUFA)/PUFA, displaying their storage capacity, are higher in deep than in shallow corals. MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids, SFA = saturated fatty acids, PL = phospholipids, rest of lipid classes = sterols, free fatty acids, free fatty alcohols, diacylglycerols, monoacylglycerols and cerebrosides.

Outlook

Environmental changes affect CWCs differently across life stages. Therefore, future aquarium experiments and *in situ* studies should not solely focus on studying adult CWCs. Additionally, very little is known so far about the effect of environmental changes on the reproductive investments and success of CWCs, including fertilisation, ranging from larval development and survival, settlement success as well as metamorphosis into coral recruits, which are also critical phases in the corals' life cycle and for the maintenance of coral populations. Among tropical corals, increasing temperatures reduce the fertilisation success and lead to embryo and larval mortality (Randall & Szmant, 2009a, 2009b; as summarised in Randall et al., 2020) and decreasing seawater pH can reduce the fertilisation, settlement success and metamorphosis of coral larvae (as reviewed by Kurihara, 2008; Albright et al., 2010; Albright, 2011; Albright & Langdon, 2011; Albright & Mason, 2013; Nakamura et al., 2011). In addition, simultaneous changes of temperature and pH can change the timing of the brooding event, reduce larval survival and metamorphosis (Liberman et al., 2021), but did not negatively impact early life stages of tropical corals in all cases (Negri et al., 2007; as reviewed by Ross et al., 2011; Chua et al., 2013; Foster et al., 2015). Therefore, future studies should also investigate the effects of climate change on the early reproductive and developmental stages of CWCs to clarify whether future environmental changes may negatively affect these early life stages. This would substantiate findings that elevated temperature affects embryo and larval development of a deep-sea octocoral species (Rakka et al., 2021). In addition, we need more multi-trait assessments and should also identify the most important and critical traits for each life stage. For instance, adult corals do not invest as much energy into growth as juvenile corals and although growth is important, investments into reproductive output may be even more critical for the whole population. By contrast, growth is a good indicator for juvenile performance, since they need to reach a certain size before they become reproductively active.

Fluctuating conditions can modulate an organisms' response (Bernhardt et al., 2018, 2020; Kroeker et al., 2020; Marshall et al., 2021), and I showed that they also negatively affect *D. dianthus* in Comau Fjord. Therefore, future aquarium experiments should also consider short-term/diurnal and long-term/seasonal environmental variability (of single and multiple

factors) in CWCs' natural habitat, instead of conducting them under controlled stable environmental conditions. This would give us more realistic results when the conditions in aquarium experiments better mimic the natural environment of CWCs (Wahl et al., 2016; Bates et al., 2018; Morash et al., 2018; Ziegler et al., 2021). A recent short-term laboratory study investigated the effect of temperature variability on *L. pertusa*, however keeping the temperature stable for one week (Gómez et al., 2022). Also considering short-term and diurnal fluctuations of environmental parameters will greatly improve our understanding of corals' response to ongoing and future environmental changes, as investigations with average environmental parameters may over- or underestimate organism responses (Bates et al., 2018) and therefore distort the predictions. An alternative would be more costly and logistically challenging *in situ* experiments under natural environmental conditions, including natural fluctuations. In any case, future studies rely on *in situ* measurements of biotic and abiotic conditions at the scale and extent they can be found in CWC natural habitats, which can also provide background data for the parameters in aquarium experiments.

In addition to accounting for environmental variability, including multiple environmental factors will greatly enhance our understanding of CWC resilience to future climate change. Only this broader setup provides more realistic results as CWCs will be exposed to a combination of changes in various factors due to climate change. Therefore, future studies should focus on multi instead of single driver investigations. Apart from the combined effects of reduced pH and elevated temperature (Hennige et al., 2015; Gori et al., 2016; Büscher et al., 2017), future research should also include other environmental factors that are predicted to change in the future due to climate change and anthropogenic activities, such as oxygen concentration (Sweetman et al., 2017; first investigation as single driver by Lunden et al., 2014) and sedimentation (first investigations as single and multiple driver by Larsson et al., 2013b; Weinnig et al., 2020; Baussant et al., 2022). As my dissertation shows, aquarium experiments must also account for predicted reductions of food availability, which is a key factor influencing the physiological performance of CWCs and an important aspect for the resilience of CWCs to future changes (da Costa Portilho-Ramos et al., 2022). Here, mesocosm approaches are a way forward that would allow to study multi-species responses and to get a better understanding of the impact on CWC ecosystems (Wahl et al., 2016).

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Contribution to multi-author article/manuscript

Declaration on the contribution of the candidate to a multi-author article/ manuscript which is included as a chapter in the submitted doctoral thesis

<u>Manuscript 1:</u> Ontogenetic differences in the response of the cold-water coral *Caryophyllia huinayensis* to ocean acidification, warming and food availability

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design:	ca. 80 %
Experimental work and/or acquisition of (experimental) data:	ca. 90 %
Data analysis and interpretation:	ca. 90 %
Preparation of figures and tables:	ca. 90 %
Drafting of the manuscript:	ca. 90 %

<u>Manuscript 2:</u> Environmental stability and phenotypic plasticity benefit the cold-water coral *Desmophyllum dianthus* in an acidified fjord

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design:	ca. 20 %
Experimental work and/or acquisition of (experimental) data:	ca. 80 %
Data analysis and interpretation:	ca. 80 %
Preparation of figures and tables:	ca. 60 %
Drafting of the manuscript:	ca. 80 %

<u>Manuscript 3:</u> Lipid biomarkers reveal trophic relationships and energetic trade-offs in contrasting phenotypes of the cold-water coral *Desmophyllum dianthus* in Comau Fjord, Chile

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design:	ca. 20 %
Experimental work and/or acquisition of (experimental) data:	ca. 20 %
Data analysis and interpretation:	ca. 10 %
Preparation of figures and tables:	ca. 20 %
Drafting of the manuscript:	ca. 10 %

<u>Manuscript 4:</u> Seasonal energy reserves of the cold-water coral *Desmophyllum dianthus* from Comau fjord, Chile

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design:	ca. 20 %
Experimental work and/or acquisition of (experimental) data:	ca. 30 %
Data analysis and interpretation:	ca. 70 %
Preparation of figures and tables:	ca. 70 %
Drafting of the manuscript:	ca. 90 %

Date:

Signature:

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