Studiengang: Fachbachelor Biologie

Bachelorarbeit

Seasonal changes in energy reserves of the cold-water coral *Desmophyllum dianthus* in its natural habitat in Comau Fjord, Chile

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Sektion Bentho-Pelagische Prozesse

Rastede, 09.08.2022

Diese Bachelorarbeit wurde in der Sektion “Bentho-Pelagische Prozesse” am Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung in Bremerhaven durchgeführt.

Table of Contents

List of Figures

List of Tables

List of abbreviations

°C	degree centigrade
µl	microlitre
cm^2	square centimetre
CWCs	Cold-water corals
D. dianthus	*Desmophyllum dianthus*
DOM	Dissolved organic matter
e.g.	for example
et al.	et alii, Latin for “and other”
g	gram
J cm^{-2}	Joule per square centimetre
J	Joule
km	kilometer
L	Liter
L. pertusa	*Lophelia pertusa*
m	meter
M	Mol
m^{-2}	square metre
max.	maximum
mg cm^{-2}	milligram per square centimetre
mg	milligram
mL	millilitre
mm	millimetre
nm	nanometre
pCO_2	partial pressure of carbon dioxide
POM	Particulate organic matter
ROV	Remotely operated vehicle
sec.	seconds
TER	Total Energy Reserves
Ω_{arag}	Aragonite saturation

Zusammenfassung

Die Kaltwasserkorallenart *Desmophyllum dianthus* kommt im Comau Fjord (Patagonien, Chile) sowohl im Flachwasser (20 m) als auch in einer Tiefe von 300 m in großen Dichten vor. Der Fjord weist ausgeprägte horizontale und vertikale Umweltgradienten auf, wobei die Variabilität der Umweltbedingungen (z.B. Temperatur und Salinität) in flachen Gewässern größer ist als in der Tiefe. Darüber hinaus unterscheidet sich der pH-Wert zwischen dem Kopf und der Mündung des Fjords, mit einem höheren pH-Wert an der Mündung des Fjords. Entlang des vertikalen Gradienten ist der pH-Wert und die Sauerstoffkonzentration in flachen Gewässern höher und nimmt zur Tiefe hin ab. Entlang dieser Umweltgradienten wurden die Energiereserven (Lipide, Kohlenhydrate und Proteine) von *D. dianthus* in verschiedenen Jahreszeiten (Sommer, Herbst und Winter) gemessen. Dafür wurden Korallenproben an sechs Stationen in 20 m Wassertiefe und an einer Station in 300 m Wassertiefe entlang des Fjordes gesammelt. Zusätzlich wurde ein Kreuztransplantationsexperiment durchgeführt, bei dem Korallen entlang des horizontalen Gradienten zwischen Kopf und Mündung des Fjords sowie zwischen einer flachen Station in 20 m und einer tiefen Station in 300 m transplantiert wurden. Nach der Aufbereitung der Proben wurden Unterproben für die jeweiligen Analysen genommen. Dabei wurden die Lipide und Kohlenhydrate mittels Microplate Reader gemessen und die Proteine mittels Photometer. Die Energiereserven von *D. dianthus* unterscheiden sich klar zwischen den Wassertiefen, wobei Korallen aus der Tiefe insgesamt signifikant höhere Energiereserven aufweisen im Vergleich mit den Korallen im Flachwasser. Zudem unterscheiden sich die Energiereserven entlang des horizontalen Gradienten mit signifikanten Unterschieden der Energiereserven zwischen dem Kopf und der Mündung des Fjords. Entlang des horizontalen Gradienten zeigt sich zudem ein saisonales Muster mit signifikant höheren Energiereserven im Herbst und niedrigeren Energiereserven zum Winter hin. Das Kreuztransplantations-experiment hat gezeigt, dass transplantierte Korallen ihre Energiereserven schnell an die neuen Umweltbedingungen anpassen, was ihr hohes Anpassungspotential unterstreicht. Die Ergebnisse der Energiereserven stimmen mit vorangegangenen physiologischen Messungen (Wachstum und Respiration) überein, die unter anderem stark von der Variabilität der Umweltbedingungen bestimmt werden.

Zudem deuten die Werte darauf hin, dass auch Faktoren wie die Konkurrenz um Raum und Nahrung einen Einfluss auf die Energiereserven haben, was den Korallen möglicherweise stressbedingt eine verminderte Nahrungsaufnahme ermöglicht. Die höheren Energiereserven in der Tiefe legen zudem die Vermutung nahe, dass das Nahrungsangebot in der Tiefe größer ist und Zooplanktonarten wie Krill, die eine energiereiche Futterquelle für *D. dianthus* darstellen, möglicherweise in großer Abundanz in der Tiefe vorkommen.

Abstract

The scleractinian cold-water coral *Desmophyllum dianthus* thieves in Comau Fjord with high abundances in both shallow waters (20 m) and at depth (300 m). The fjord features pronounced horizontal and vertical environmental gradients with higher environmental variability (e.g., temperature and salinity fluctuations) in shallow waters and more stable conditions at depth. Environmental gradients also differ between the head and the mouth of the fjord, with a higher pH at the mouth of the fjord and between depths, with a higher pH and oxygen concentrations at shallow waters and a decreasing pH and oxygen concentrations at the deep. To characterize the corals along these different gradients, their total energy reserves (lipids, carbohydrates, proteins) were measured seasonally from austral summer, autumn, and winter. Corals were collected at six stations at 20 m water depth and at one station at 300 m water depth in the fjord. In addition, corals were transplanted along a horizontal gradient from head to mouth of the fjord and between 20 m and 300 m depth to test whether total energy reserves acclimate to a novel environment. After sample preparation, sub-samples were taken for the respective analyses. Lipids and carbohydrates were measured using a microplate reader and the proteins were measured using a photometer. The energy reserves of *D. dianthus* differed between water depths, with overall higher energy reserves in corals in deep waters. Along the horizontal gradient, energy reserves were heterogeneous, and a significant difference was found between the head and the mouth of the fjord. Moreover, a seasonal pattern emerged, with significant higher energy reserves in austral autumn and decreasing energy reserves towards winter. The reciprocal transplantation experiment showed acclimation of energy reserves of novel corals to their new environment, underlining its high acclimatization potential. The measured energy reserves are consistent with previous physiological measurements (growth and respiration), which are influenced by environmental variability, but also other factors like competition for space and food, which may negatively affect the feeding time of corals due to stress. The higher energy reserves at depth suggest a higher food availability in the deeper waters, probably especially larger zooplankter like krill.

1. Introduction

1.1 Cold-water corals (CWCs)

Cold-water corals are cnidarians encompassing stony corals, soft corals, black corals, and hydrocorals. They are found in deep waters worldwide, primarily associated with colder conditions at depths of up to 4000 m and temperatures between 4°C and 12°C (Freiwald et al. 2004, Roberts et al. 2009). However, some species can deal with higher temperatures of up to 17°C (Orejas et al. 2009, Naumann et al. 2013) and occasionally even 23°C in some regions (Roder et al. 2013). Furthermore, some species were also discovered in much shallower areas, a phenomenon called deep water emergence (Häussermann et al. 2021), for example in New Zealand at ~ 4 m water depth (Grange et al. 1981), in Norway at ~ 39 m water depth (Rapp and Sneli 1999) and in Chilean Patagonia at ~ 20 m water depth (Försterra and Häussermann 2003). The distribution of CWCs is controlled by biotic and abiotic factors such as seawater temperature, salinity, pH, carbonate chemistry, oxygen concentration, food availability and topography (Freiwald et al. 2004, Guinotte et al. 2006, Cairns 2007, Davies et al. 2009, Orejas et al. 2009, Roberts et al. 2009). Yet, each CWC species has its own optimal environmental conditions and needs a stable, solid substratum on which to build its skeleton (Roberts et al. 2009). CWCs support high biodiversity, as their calcium carbonate skeleton forms a structurally and ecologically complex habitat for many organisms like sponges, polychaetes, crustaceans, molluscs, echinoderms, bryozoans, and fish (Jonsson et al. 2004, Freiwald et al. 2004).

Compared to their tropical coral counterparts, *in situ* physiological assessments are still scarce in CWCs, which is mostly due to the difficult and hence expensive accessibility in their natural habitat. As environmental changes due to climate change (e.g., seawater warming and ocean acidification) are thought to threaten CWCs (Roberts et al. 2009, Roberts and Cairns 2014, Mora et al. 2013, Doney et al. 2009, Crowley 2000), deep emerged CWCs like *Desmophyllum dianthus* in Comau Fjord offer great possibilities to explore a wide range of physiological traits (e.g. growth, respiration, calcification, energy reserves) *in situ* and provide an idea how corals may deal with future environmental changes.

So far, recent studies already identified CWCs to be less sensitive to changes in aragonite saturation (Maier et al. 2013, Maier et al. 2012, Hennige et al. 2014, Beck et al. 2022) and some species can deal with temperature changes (Dodds et al. 2007, Naumann et al. 2014). Reciprocal transplantation experiments proved valuable in this context, as they allow testing the coral's ability to deal with contrasting environmental conditions as a proxy for their potential to deal with future changes. A recent study found a high acclimatization potential of the CWC *D. dianthus* in terms of growth and respiration rates after transplantation between stations at different water depths and along a horizontal gradient with different environmental conditions like water temperature and salinity (Beck et al. 2022).

1.2 Feeding and energy reserves of CWCs

Unlike their tropical coral counterparts, CWCs do not receive their energy from photosynthetic products due to the lack of photoautotrophic symbionts (Freiwald et al. 2004). Instead, they actively catch zooplankton, particulate organic matter (POM) or take up dissolved organic matter (DOM) with their tentacles (Freiwald et al. 2004, Houlbrèque and Ferrier-Pagès 2009). Zooplankton is their most important food source (Carlier et al. 2009, Tsounis et al. 2010, Dodds et al. 2009, Kiriakoulakis et al. 2005, Maier et al. 2021, Höfer et al. 2018, Naumann et al. 2011) that enables the coral to sustain their metabolism (Maier et al. 2021, Rakka et al. 2021) and factors like water flow contribute to the efficiency of feeding (Orejas et al. 2016). Although the availability of food is key, it was found that CWCs can endure some time on minimal resources and sustain their growth rates (Larsson et al. 2013).

The feeding ecology of CWCs and their performance are mostly explored under controlled conditions in aquaria, however, less is known about their trophic ecology in the field and how it affects their fitness. Tissue biomarker studies can provide insight into the coral's trophic status in their natural environment. Here, lipid biomarkers already showed general differences in food availability (Dodds et al. 2009, Gori et al. 2018) as well as food source (Dodds et al. 2009, Kiriakoulakis et al. 2005, Imbs et al. 2016). Additionally, energy reserves can give insights into the health status of corals (Schoepf et al. 2013, Rocker et al. 2017).

In general, energy reserves can be summarized by the amount of lipid, carbohydrate and protein storage and are used in times of starvation (Grottoli et al. 2004, Houlbrèque and Ferrier-Pagès 2009). Lipids are the major tissue component of corals, which make up to 10-40% of their dry biomass (Harland et al. 1993, Imbs 2013) and serve as long-term energy stores (Harland et al. 1993, Seemann et al. 2013). The composition of lipids varies with season, depth, and other environmental factors (Imbs 2012). Beyond that, their constituent classes and fatty acids play important roles in the overall coral fitness, including its ability to grow, reproduce, survive and its capacity to offset stress (Bergé and Barnathan 2005, Anthony and Connolly 2004).

1.3 *Desmophyllum dianthus* in Comau Fjord

Chilean Patagonia is known for its many fjords, one of them being the Comau Fjord. It is in the northern part of the country located and connected to the Gulf of Ancud. It runs in a north-south direction and is therefore protected from the main westerly winds (Bustamante 2009). The Comau Fjord measures a total length of 45 km and a width of 2 to 8.5 km. The depth decreases from almost 500 m at the mouth of the fjord to ~ 50 m at the head of the fjord (Försterra and Häussermann 2009) with a high tidal range of up to 7.5 m (Lagger et al. 2009). The fjord is influenced by subantarctic waters and continental waters from rivers, freshwater runoff from glaciers and high precipitation, resulting in a thin brackish water layer at the surface (Bustamante 2009, Soto 2009). Precipitation rates are influencing the water masses in the fjord with higher precipitation rates in winter leading to seasonal fluctuations of the surface layer with deeper surface layers in winter than in summer (Pantoja et al. 2011). Moreover, the surface layer is seasonally influenced by changing water temperatures due to the high variability of solar radiation (Torres et al. 2011).

The Comau Fjord represents an interesting environment for CWCs as it is one of the few places where CWCs emerge from the deep and conquer shallow habitats as outlined above. Shallow CWCs in Chilean fjords deal with variations in both biotic and abiotic conditions at different temporal scales from seasonal to more frequent (weekly to daily) fluctuations. In Comau Fjord, highest thermal variability is found in shallow waters in austral summer, while water temperatures at 300 m show almost no variability throughout the year.

Also average conditions differ between depth with a mean annual temperature of 12.5 ± 0.9 °C, a pH of 8.1 (resulting in aragonite oversaturation), high oxygen concentrations (approx. 212 µmol kg^{-1}) and a low salinity layer (approx. 32) in shallow waters compared to a mean annual water temperature of 11.4 ± 0.2 °C, a pH of 7.4, high salinity (approx. 99), low oxygen (approx. 450 µmol kg^{-1}) and aragonite undersaturation at 300 m water depth (Beck et al. 2022). Besides thermal variability in shallow waters, a horizontal pH gradient is found from head to mouth of the fjord with a lower pH at the head and a higher pH at the mouth as a possible result of higher freshwater run-off from rivers (Beck et al. 2022, Jantzen et al. 2013).

These abiotic conditions together with other drivers like light availability and freshwater inflow determine the occurrence as well as distribution of phytoplankton and zooplankton. It was shown that zooplankton occurrence varies seasonally, (Garcia-Herrera et al. 2022, González et al. 2010, Iriarte et al. 2007) driven by a higher primary production in spring and austral summer compared to winter (González et al. 2010). Similarly, a seasonal degradation of the pycnocline in winter negatively influences the phytoplankton and zooplankton populations (Sanchez et al. 2011). In the region, a higher zooplankton abundance and biomass is available in shallow waters with smaller copepods during daytime and larger during the night due to diel vertical migration. In deeper waters of 300 m, the food availability is lower and is composed of mainly large zooplankton prey like calanoid copepods and mysids (Garcia-Herrera et al. 2022). With seasonal fluctuations of zooplankton, the coral's energy reserves are very important to withstand and counteract periods of lower food availability as well as changes or limiting conditions in their environment (Maier et al. 2019, Dodds et al. 2009).

The cosmopolitan CWC *D. dianthus* (Esper 1794) is the organism of interest for this study and is found worldwide, from the sub-Antarctic to the North Sea (Miller et al. 2011). It generally occurs at water depths between 25-2500 m (Cairns et al. 2005), but single corals also occur as shallow as 8 m in the study region (Försterra and Häussermann 2003). It is a slow-growing species with a growth rate of 0.5-2 mm per year and a long-life span of up to 200 years (Risk et al. 2002). Individuals of *D. dianthus* are gonochoric as each individual has its separate sex with a seasonal reproductive cycle (spawning starting at the end of austral winter and gamete production in early spring (Feehan et al. 2019).

Within the Comau Fjord, it appears to be the most abundant coral species and co-occurs with two other scleractinian CWC species (*Tethocyathus endesa (*Cairns et al. 2005*)* and *Caryophyllia huinayensis* (Cairns et al. 2005)). The coral is a framework builder (Försterra and Häussermann 2003), as this solitary living species can form pseudo colonies and therefore provides a diverse habitat for other benthic organisms (Försterra et al. 2005, Freiwald et al. 2004). In shallow waters of Comau Fjord, high population density banks of more than 1500 ind./m² are found, mainly on hard substratum, e.g., rock walls and boulders and in a “head-down” position under overhangs (Försterra and Häussermann 2003).

The aim of this thesis is to investigate seasonal changes in the energy reserves of the CWC *D. dianthus* in Comau Fjord in Chilean Patagonia. For this, lipids, carbohydrates, and proteins were extracted from coral tissue samples and used to analyze the concentrations to get insight into the energy reserves of the coral from both horizontal and vertical gradients along the fjord. With the recent findings of the CWC *D. dianthus* in Comau Fjord at sites as shallow as 20 m (Försterra and Häussermann 2003), the fjord offers a great possibility to study how energy reserves of CWCs differ horizontally as well as vertically in the fjord under consideration of seasonality and environmental variability.

1.4 Research questions and hypotheses

With information from the above-mentioned studies, I therefore propose the following hypotheses for this study:

H0A: Total energy reserves show statistically significant differences between shallow stations along a horizontal gradient

H1A: Total energy reserves do not show statistically significant differences between shallow stations along a horizontal gradient

H0B: Total energy reserves significantly differ between coral samples from the shallow station Es and the deep station Ed

H1B: Total energy reserves do not differ significantly between coral samples from the shallow station Es and the deep station Ed

H0C: Transplanted coral samples (novel corals) adapt quickly to the new environment and show equal energy reserves as native corals

H1C: Transplanted coral samples (novel corals) do not adapt quickly to the new environment and show differences in energy reserves compared to native corals

2. Material and methods

2.1 Coral stations

Within the fjord, stations were established along a spatial gradient from the fjord head (station A) to its mouth (station F), with 6 shallow stations at ~ 20 m water depth located at the steep eastern walls of Comau Fjord and one deep station at ~ 300 m water depth (Figure 1A). For all shallow stations (A-F), a total of 30 Individuals of *D. dianthus* were collected and prepared and 24 individuals at the deep station (Ed). For the reciprocal transplantation, 30 individuals were collected at station A, F and Es and 8 corals at Ed. All in all, a total of 302 corals were collected representing 204 native corals and 98 novel corals.

2.2 Coral sampling and re-installation

All coral samples were collected in September 2016 using SCUBA diving and a ROV (Commander 2, Mariscope Ingeniería, Puerto Montt, Chile; modified with manipulator arms and high-resolution camera). At the shallow stations, corals were carefully chiseled from the fjord walls and put into closed 1 L plastic containers filled with seawater to avoid contact with the low salinity surface layer and light during transportation on the boat to the laboratory facilities at the research station. At the deep station, corals were collected using a remotely operated vehicle (ROV) with a wire frame and a bag attached to scrape the corals from the wall to collect them. The bag was then transferred to a cooler box filled with seawater for the transportation to the research station.

At the research station, all corals were maintained in 20-30 L flow-through aquaria filled with natural seawater pumped from 20 m water depth from the fjord in front of the research station and were not additionally fed. At the laboratory, the bare skeleton below the coral tissue was removed using a submerged grinding disc attached to a rotary tool (Dremel 4000, Dremel, Breda, The Netherlands) to reduce bioerosion affected parts of the skeleton. Coral samples were then glued on polyethylene screws using underwater easy glue (Preis Aquaristik, Germany). Handling was only done by touching the screws to avoid any disturbance by direct contact with the corals.

After 3 weeks, corals were returned into the fjord following an experimental design that included to reinstall corals at their collective site (native corals) as well as reciprocal transplantation between deep (Ed) and shallow (Es) and between head (A) and mouth (F) of the fjord (novel corals) (Figure 1C). For reinstallation of the corals at the shallow stations, divers fixed stainless-steel holders on the fjord wall in a way that allowed them to re-install the corals in their natural downward orientation. Corals on screws were fixed on special plastic plates that were mounted on these holders in the fjord wall (2-3 plates per station, max. 34 corals per plate). For re-installation, corals were transported in peli cases through the water column to avoid exposure to the low salinity surface layer of the fjord. For re-installation of corals at the deep station, two coral plates were installed on holders on a metal rack of a mooring at 20 m water depth by divers. The metal rack was attached to a pulley and lowered down to 300 m water depth (Figure 1B). For re-collection of corals, the metal rack with the fixed coral plates attached to it was pulled up to 20 m water depth where divers then removed the coral plates and transferred them in peli cases through the water column and on the boat to the research station.

Coral samples were recollected seasonally during the next year in austral summer (January 2017), autumn (May 2017) and winter (August 2017). During each season, 10 native corals were recollected at each shallow station and 10 novel corals at stations A, F, Ed and only in austral summer, 8 native and 8 novel corals were recollected at station Es and Ed. After recollection, corals were unscrewed from the holders and maintained in flow-through aquaria in the laboratory for max. 4 days. Afterwards, corals were removed from the screws, shock frozen in liquid nitrogen and transferred to the Alfred Wegener Institute (AWI) in Bremerhaven in liquid nitrogen containers (dry shippers) and stored at -80 °C until processing. Due to logistical problems, almost all coral samples collected in austral summer were thawed (except for corals from stations F and Ed) and therefore, unusable for tissue analysis.

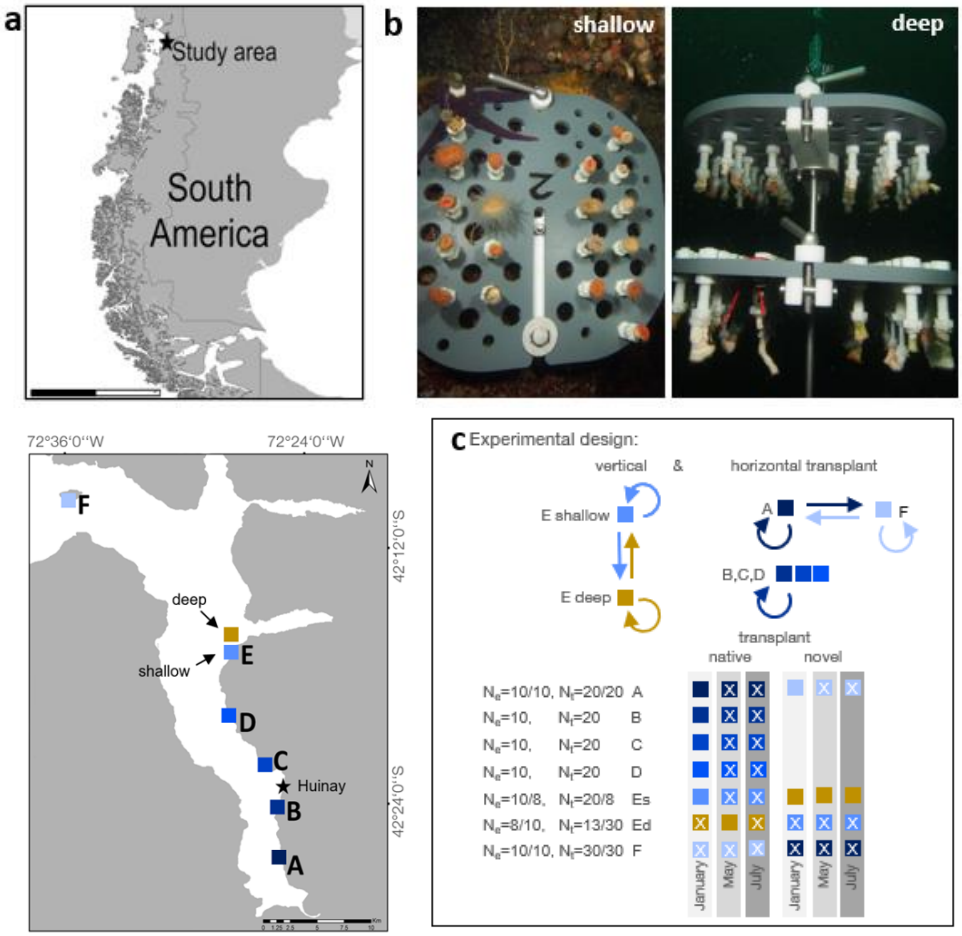

Figure 1: Study site and experimental design A) Map of geographic location of Comau Fjord in South America with six coral stations at 20 m water depth (A-F shallow, blue colors) and one deep station at 300 m water depth (yellow color). **B)** *Desmophyllum dianthus* glued on white polyamide screws and fixed on gray plastic plates in downward orientation at shallow stations (left) and on the metal rack of a pulley at the deep station (right). **C)** Experimental design and coral sampling scheme. The experimental design includes vertical and horizontal cross-transplantation of novel corals between shallow (Es) and deep (Ed) and between the shallow stations at the head (A) and the mouth of the fjord (F). Coral samples from stations B, C and D were returned to their respective stations. Individuals of *D. dianthus* were re-collected in austral summer (January), autumn (May) and winter (August).

2.3 Preparation of coral samples

Coral samples were taken separately from -80 °C and prepared for tissue analyses. Work was done on ice to prevent the samples from thawing. Whole coral samples from shallow stations were used for the tissue analyses, whereas coral samples from the deep station were cut in half lengthwise using a saw (FKS/E, Proxxon S.A., Wecker, Luxemburg). Using an airbrush at 5 bar (Starter Class set, Revell GmbH, Bünde, Germany) and filtered seawater, the coral tissue was separated from the skeleton until all tissue was removed. For this, the coral fragments were held without touching the tissue area. The tissue samples were then homogenized using an Ultra Turrax (T18 basic, IKA GmbH & Co. KG, Staufen, Germany) and tissue samples (12-20 mL) were divided into aliquots for protein, carbohydrate, and lipid analysis. The tissue samples were stored in cryovials at -80°C until further processing. For the analysis, samples were thawed at room temperature until they were completely liquified again.

2.4 Lipid analysis

The lipid analysis was conducted after Folch et al. (1957) and Cheng et al. (2011) and adapted for the *D. dianthus* samples using the “coral lipid assay for 96-well plates” protocol from Bove and Baumann (2021). After the coral samples were thawed, three times 600 µl of each sample were transferred to a 1.5 mL safe lock tube (triplicate samples). To each tube, 400 µl of chloroform and 200 µl of methanol was added. The mixture was shaken on a vortexer (Vortex Genie 2, Scientific Industries) for 20 minutes. This was followed by the addition of 160 µl of 0.05 M NaCl solution to achieve a final mixture of $CHCl_3$:CH_3OH:NaCl with a ratio of 2:1:0.8. After inverting the tubes twice, the cap of the tubes were carefully opened and closed again to allow gasses to escape. The samples were centrifuged at 3000 rpm at room temperature (20°C) for five minutes (Tischkühlzentrifuge 5417R, Eppendorf). The upper phase (CH_3OH) was carefully pipetted off and discarded and 100 µl from the lower phase were transferred into new safe lock tubes for the assay. 150 µl methanol was added and the solution was mixed using a vortexer for ~30 seconds. The tubes were then placed into a water bath at 90°C for 20 minutes. The lid had to be open so that the methanol could evaporate completely. After that, 300 µl 98% sulfuric acid was added and mixed again using a vortexer for ~ 30 seconds. The tubes were placed into the water bath for another 20 minutes and cooled on ice for 2 minutes afterwards.

After 75 µl of each standard and sample were transferred into the wells of a microplate, the absorbance was measured at 530 nm on a microplate reader (TriStar LB941 Multimode Reader, Berthold Technologies, Germany). In the original protocol from Bove and Baumann (2021), the absorbance was measured at 540 nm, however, this was not possible with the microplate reader used for this study. Therefore, a spectrum profile was measured first to see where the peak was highest, which was the case at 535 nm (Supplementary Figure 1). Therefore, the absorbance was measured at a wavelength of 530 nm.

After the background was measured at 530 nm, 34.6 µl of 0.2 mg/mL vanillin solution in phosphoric acid was added to each well using a multichannel pipette. After adding the vanillin reagent to each well, the color changed from yellow to pink. The plate was incubated for 10 minutes, and the measurement was repeated. For the calculation of the lipid concentration, the first measurement (background absorbance) was subtracted from the second measured absorbance. For normalization of the lipid concentration, the tissue covered surface area of the corals (see below) was used with the resulting unit of mg cm^{-2}. Since energy reserves are usually specified in the unit of energy, conversion factors (39.5 kJ/g) were used to convert the concentration into J cm^{-2} (Gnaiger and Bitterlich 1984).

2.5 Carbohydrate analysis

The carbohydrate concentration was measured using phenol and sulfuric acid for the colorimetric detection after Dobois et al. (1956), with a known standard dilution series of d-glucose. After the coral samples were thawed, they were vortexed and each sample was diluted 1:2 using 100 µl of the sample and 100 µl of Milli-Q water in a 2 mL tube. 200 µl from each standard were transferred into a 2 mL tube and 200 µl of 5 % phenol solution and 1 mL of 100 % sulfuric acid added to each standard and sample. After 10 minutes, the lid was closed and the tube carefully shaken, incubated at 30 °C in a water bath for 20 minutes and shaken again. For the measurements, three times 200 µl of each standard and sample (in triplicates) were pipetted into the wells of a 96 well microplate and the absorbance measured at 485 nm on the same microplate reader as for the lipid analysis. A standard curve was prepared by plotting the blank corrected average absorbance for each glucose standard against its concentration in µl/mL.

The standard curve was used to determine the carbohydrate concentration of each sample. For normalization of the carbohydrate concentration, the tissue covered surface area of the corals (mg cm^{-2}) and conversion factors (17.5 kJ/g) were used to convert the concentration into J cm^{-2} (Gnaiger and Bitterlich 1984).

2.6 Protein analysis

The total protein content was determined after Lowry et al. (1951) using a protein assay kit (Detergent compatible (DC) Protein Assay Kit, Bio-Rad Laboratories Inc., Hercules, USA) and bovine serum albumin (BSA) as standard. Samples were thawed and a standard dilution series was created using filtered seawater. 5 µl of reagent S and 250 µl of reagent A were mixed to make reagent A' (durable for a week). 25 µl of each standard and sample were transferred into a new safe lock tube, 125 µl of reagent I added, vortexed for one minute and incubated for another minute. Afterwards, 125 µl of reagent II were added, vortexed and centrifuged for 5 minutes at 15.000 g. The upper phase was carefully removed by placing the tube on a cellulose cloth. Then 127 µl of reagent A' was added, vortexed and incubated for 5 minutes, until the protein pellet was fully resolved. Before the next step, the solution was vortexed again and 1 mL of reagent B added. The tube was vortexed, incubated for 15 minutes and the absorbance measured at 750 nm on a photometer (UV-1800 spectrophotometer, Shimadzu Corporation, Kyoto, Japan). For normalization of the protein concentration, the tissue covered surface area of the corals was used (mg cm^{-2}) and converted into Joule using a conversion factor of 23.9 kJ/g (Gnaiger and Bitterlich 1984).

2.7 Tissue covered surface area

The tissue covered surface area of the corals was used for normalization of the energy reserve data. The outer surface of the corals was measured using a digital caliper (reading to 0.01 mm) before the tissue was sprayed off. Using this outer surface, the total surface area of the coral was calculated according to Beck et al. (2022) including the outer and inner surface area of the calyx that is covered with tissue, but not the surface area of the individual septa.

2.8 Statistical analysis

For statistical analysis, the software R (Version 1.4.1106) was used. To test for normality of the data, a Shapiro-Wilk test was used and for homogeneity of variances, a Levene test was performed. The data did not meet the normality standards; therefore, a generalized linear model (*glm*) was used to check for the relationship between the fixed factors depth, season, station, and transplantation with the response variables. We compared different models using the *performance* package with best results given for log-transformed data of the Gamma distribution (Supplementary Figure 2). To test for differences in the energy reserves along the horizontal gradient and for seasonal effects, only shallow native corals were used with season and site as fixed effects. To test for the effect of transplantation and depth, both native and novel corals from A, F, Es and Ed were used with site and transplant as fixed effects. For both models, post-hoc comparisons were tested using the *lsmeans* package.

3. Results

3.1 Lipids

The lipid concentration of *D. dianthus* differed significantly between the shallow station Es and the deep station Ed, with higher concentrations at the deep station. In shallow waters, concentrations were highest at station C and lowest at station D. Beyond that, a significant difference was also found between the head and the mouth of the fjord (GLM, A - F: p value = <0.0001; Figure 2, Supplementary Figure 3a, Supplementary Table 1). In addition, a seasonal pattern emerged, with significantly higher lipid concentrations in austral autumn than in winter (GLM, May - August: p value = <0.0001; Figure 2, Supplementary Figure 3a, Supplementary Table 1). Novel corals quickly adjusted their concentrations after transplantation to the same levels as native corals at the respective station (GLM, native - novel: p value = 1.0000; Figure 2, Supplementary Figure 3a, Supplementary Table 1).

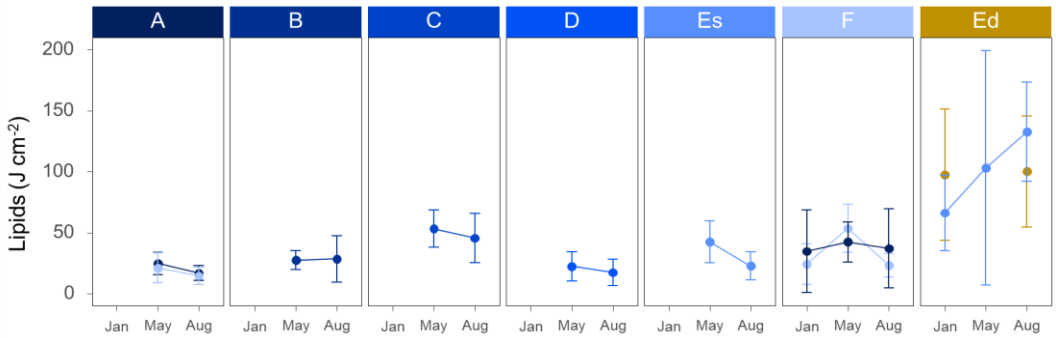

Figure 2: Seasonal lipid concentration of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. Lipid concentrations of corals at six shallow stations (A-F, blue) and one deep station (Ed, yellow) are shown in austral summer (January), autumn (May) and winter (August) (Supplementary Table 2). Data from January is missing for stations A, B, C, D and Es because the samples were thawed due to logistical difficulties.

3.2 Carbohydrates

Just like the lipids, the carbohydrate concentrations differed between depths, with significantly higher values at the deep station Ed compared to the shallow station Es (GLM, Es - Ed: p value = <0.0001; Figure 3, Supplementary Figure 3b, Supplementary Table 3). The carbohydrate concentrations at shallow stations differed significantly between seasons (GLM, May - August: p value = <0.0001; Figure 3, Supplementary Figure 3b, Supplementary Table 3), with higher concentrations in austral autumn and lower concentrations in winter. Along the horizontal gradient, a significant difference was also found between the head (station A) and the mouth of the fjord (F) (GLM, A - F: p value = 0.0001; Figure 3, Supplementary Figure 3b, Supplementary Table 3). The carbohydrate concentrations did not differ between native and novel corals from shallow and deep stations (GLM, native - novel: p value = 1.0000; Figure 3, Supplementary Figure 3b, Supplementary Table 3).

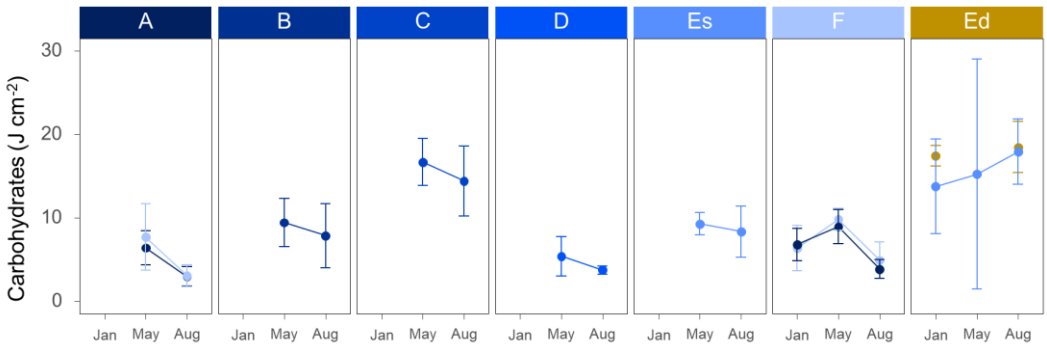

Figure 3: Seasonal carbohydrate concentration of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. Carbohydrate concentrations of corals at six shallow stations (A-F, blue) and one deep station (Ed, yellow) are shown in austral summer (January), autumn (May) and winter (August) (Supplementary Table 2). Data from January is missing for stations A, B, C, D and Es because the samples were thawed due to logistical difficulties.

3.3 Proteins

The protein concentrations were significantly higher at the deep station Ed compared to the shallow station Es (GLM, Es - Ed: p value = <0.0001; Figure 4, Supplementary Figure 3c, Supplementary Table 4). Just like the lipids and carbohydrates, a seasonal pattern was found, with higher protein concentrations in austral autumn than in winter (GLM, May - August: p value = <0.0001; Figure 4, Supplementary Figure 3c Supplementary Table 4). Additionally, the protein concentrations of native and novel corals did not differ significantly at shallow and deep stations (GLM, native - novel: p value = 1.0000; Figure 4, Supplementary Figure 3c, Supplementary Table 4).

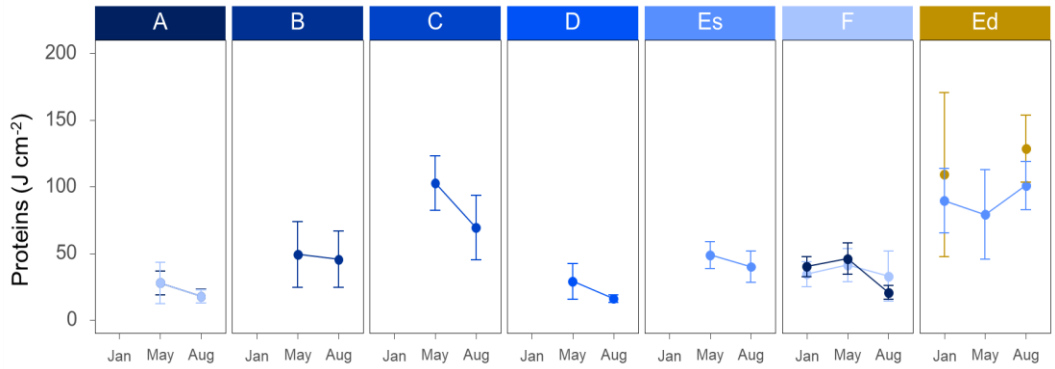

Figure 4: Seasonal protein concentration of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. Protein concentrations of corals at six shallow stations (A-F, blue) and one deep station (Ed, yellow) are shown in austral summer (January), autumn (May) and winter (August) (Supplementary Table 2). Data from January is missing for stations A, B, C, D and Es because the samples were thawed due to logistical difficulties.

3.4 Total energy reserves

Coral samples at the deep station Ed had significantly higher total energy reserves compared to the shallow station Es (GLM, Es - Ed: p value = <.0001; Figure 5, Supplementary Table 5). The energy reserves at all shallow stations were significantly higher in austral autumn compared to winter (GLM, May - August: p value = <0.0001, Figure 5, Supplementary Table 5) and highest energy reserves were found at station C and lowest at station A and D. At the deep station Ed, native corals had slightly higher energy reserves in austral summer compared to novel corals, but novel corals rapidly increased their energy reserves towards winter. Likewise, as lipids, carbohydrates and proteins, total energy reserves did not differ between native and novel corals at shallow and deep stations (GLM, native - novel: p value = 1.0000; Figure 5, Supplementary Table 5).

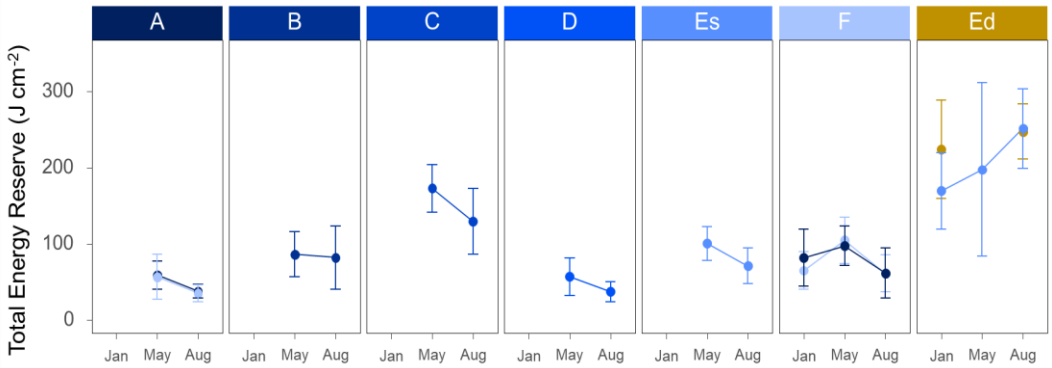

Figure 5: Seasonal total energy reserves of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. Total energy reserves of corals at six shallow stations (A-F, blue) and one deep station (Ed, yellow) are shown in austral summer (January), autumn (May) and winter (August) (Supplementary Table 2). Data from January is missing for stations A, B, C, D and Es because the samples were thawed due to logistical difficulties.

4. Discussion

This is the first *in situ* study which determined the total energy reserves of the CWC *D. dianthus* in Comau Fjord, Chilean Patagonia. By sampling corals seasonally along a horizontal and vertical gradient as well as after transplantation to a novel environment, it was possible to observe seasonal as well as depth related differences. Moreover, it was found that the corals were able to acclimatize to sites with contrasting environmental conditions. We found overall higher energy reserves at 300 m water depth and seasonal differences with higher energetics during austral autumn compared to winter along the horizontal gradient at 20 m water depth.

4.1 Energy reserves between water depths

Higher energy reserves were expected in corals in shallow waters of Comau Fjord due to the higher zooplankton density in shallow waters and lower zooplankton abundance and biomass at 300 m water depth (Garcia-Herrera et al. 2022), as it is suspected that energy reserves are directly linked to food availability (Maier et al. 2019). However, a recent performance assessment similarly observed contradictory results of fitter and healthier coral phenotypes at deeper depth (Beck et al. 2022). This is further underscored by Wall et al. (in review), who found higher lipid concentrations in corals at depth compared to shallow living corals. The measured energy reserves in this study align with the latter observations (higher growth rates and lipid concentrations at depth) and were also found to be elevated at the deep station. At the shallow station, energy reserves of corals were significantly lower and there are several explanations for these contradicting results.

One explanation is the high environmental variability at 20 m depth (Beck et al. 2022), which might contribute to lower energy reserves in corals in shallow waters. Previous studies tried to identify environmental drivers responsible for site specific changes in coral performance and found a correlation between environmental variability with growth rates of *D. dianthus* in Comau Fjord (Beck et al. 2022). Shallow waters in the fjord feature strong temperature fluctuations with daily swings of more than 3°C and overall higher temperatures in austral summer compared to winter which may affect the feeding time of the corals due to tentacle retraction and polyp inactivity at elevated temperatures (Chapron et al. 2021).

It is assumed that environmental variability in shallow waters is more stressful for corals as they need more energy to cope with it, whereas deeper water layers show less thermal variability (Beck et al. 2022) and corals may need less energy to compensate for stress, resulting in higher energy reserves at depth. Moreover, rapid salinity fluctuations at 20 m depth due to the high tidal range in the fjord region may influence the zooplankton community, both in abundance and composition, as they cause osmotic stress, leading to increased mortality in some zooplankton taxa and therefore, to changes in abundance and changes of food availability (Wells et al. 2022).

In addition, other factors may contribute to *D. dianthus* being exposed to more stress in shallow waters, such as competition for space. In shallow waters of Comau Fjord, high population densities of *D. dianthus* are found, which are often associated with a diverse benthic community (Fillinger and Richter 2013). Competition for space also includes competition for food (Buss 1979), therefore corals in shallow waters might be exposed to higher levels of stress, which can have a direct negative impact on their feeding time and thus, their ability to build up energy reserves.

Highest zooplankton biomass and abundance was sampled from 0-50 m by Garcia-Herrera et al. 2022, however, it is not known if the zooplankton was homogeneously spread over this depth range or accumulated in a certain depth. Especially larger zooplankton individuals able to form swarms can possibly be found in a certain depth and thus, do not represent the exact zooplankton community at 20 m depth, where the corals occur (Garcia-Herrera et al. 2022). Moreover, zooplankton includes a wide variety of taxa with different sizes and the mobility of some taxa like krill (*Euphausia vallentini,* Stebbing, 1900) must be considered, as mobile taxa are able to avoid the plankton nets (Brinton 1962). As zooplankton tows were conducted in the centre of the fjord, the catch may not reflect the zooplankton community at the fjord walls, where the stations were established, and the caught zooplankton community therefore might not reflect the exact zooplankton composition in the areas where corals occur (Garcia-Herrera et al. 2022). Especially krill as a larger sized zooplankton taxa has not been caught efficiently (Garcia-Herrera et al. 2022), even though it is common in Comau Fjord (Sanchez et al. 2011, Palma and Silva 2004) and provides a crucial energy supply for *D. dianthus* (Maier et al. 2021).

It is assumed that mobile taxa like krill are potentially denser in the deeper layers, which can be an additional explanation for the higher energy reserves of the corals at depth.

4.2 Energy reserves along horizontal gradient

Along the horizontal gradient, highest energy reserves were found at station C and lowest at station D. Furthermore, the energy reserves differed between the head and mouth of the fjord with overall higher reserves at the mouth. It is likely that differences along the fjord are attributed to higher levels of stress, e.g., competition for space, as sessile epibenthic organisms like corals require space to live, grow and reproduce (Hennessey and Sammarco 2014). As shallow waters in Comau fjord are known to be densely populated (Fillinger and Richter 2013), is it assumed that lower energy reserves were found at stations that were densely populated. However, our results contradict this explanation, as higher energy reserves were measured at very densely populated stations (e.g., station F) with a diverse community (M. Wall, personal communication). Thus, other drivers may be more critical along the horizontal gradient, e.g., temperature variability.

Highest temperature fluctuations were found at the head of the fjord (Beck et al. 2022), where energy reserves were almost twice as low compared to energy reserves at the mouth of the fjord. As elevated temperatures affect the feeding time of the corals, (Chapron et al. 2021), it is likely that differences of energy reserves between the head and the mouth of the fjord can be attributed to temperature fluctuations with higher fluctuations having a negative effect on the energetics of the corals, which is additionally underscored by the lowest performance of *D. dianthus* at the head of the fjord (Beck et al. 2022).

As highest and lowest energy reserves were measured at two central stations (station C and D), other factors besides thermal variability may be considered for differences of energy reserves. Shallow living corals in Comau Fjord, in particular coral samples at station C had one of the lowest tissue covered surface areas (Beck et al. 2022). Low tissue covered surface areas are often associated with higher infestation of endolithic photoautotrophic organisms (Försterra et al. 2005, Hassenrück et al. 2013, Försterra et al. 2008).

As a possible stressor for shallow corals, the coral's fitness may be impaired by these endolithic photoautotrophic organisms (Hassenrück et al. 2013), explaining the observed response heterogeneity along the horizontal gradient.

Another influence for differences of energy reserves along the fjord could be the aquaculture sector in Chile, which has been exponentially growing since the late 1980s. Up to now, Chile is thus the second largest global producer of farmed salmon (Quiñones et al. 2019, Avendaño-Herrera 2018). With the rising aquaculture sector, negative impacts on ecosystems were also rising. Especially lost fish nets were found to entangle in coral banks, leading to reduced water flow and reduced food availability (Häussermann et al. 2013). For CWCs, highest risks occur due to increased sedimentation and nutrient enrichment near the farms (Hargrave 2010), leading to reduced diversity and altered macrofauna (Häussermann et al. 2013). CWCs produce and release large amounts of organic matter as cleaning mucus into the surrounding water when they are affected by increased sedimentation. As an increased expanse of energy is required to produce cleaning mucus (Häussermann et al. 2013), lower energy reserves were expected in corals living close to these farms (e.g., coral specimens at station C). However, the latter explanation does not explain the highest measured energy reserves at station C, and it is assumed, that corals may build up energy reserves when living close to these farms as a local adaptation to cope with the stress. However, more research is required to explore the effect of aquaculture, in particular salmon farms on the performance of corals. We therefore mainly link environmental variability to differences of energy reserves along the fjord, but also consider locally differing factors like aquaculture stations and differences in the tissue coverage of the corals to the observed response heterogeneity.

Seasonal differences

Energy reserves of *D. dianthus* were highest in austral autumn and decreased towards winter. Seasonality is most likely linked to increased productivity in austral summer, primarily due to seasonal differences in temperature, solar radiation, wind, and precipitation rates (Pickard 1971). Seasonal fluctuations of freshwater from rain and glacial melt are the main factors affecting primary production in fjord systems as they cause strong tidal stratifications (Silva et al. 1997).

Several studies reported high chlorophyll a and primary production in spring, promoting an increase of biomass and subsequently abundance of zooplankton as secondary producers (González et al. 2010, Iriarte et al. 2007, Thomas et al. 2001). The overall higher energy reserves of the corals in austral autumn lead to the assumption of higher food availability during this time, additionally underscored by Maier et al. 2020 who also found seasonal variations of tissue reserves in CWCs. They attributed variations of tissue reserves primarily to seasonal dynamics in terms of temperature fluctuations, increased productivity and thus, higher food availability. Decreasing energy reserves towards winter are most likely a result of lower food availability during this time of the year. As energy reserves are also used in times of starvation when no food is available (Grottoli et al. 2004; Houlbrèque and Ferrier-Pagès 2009), it is assumed that *D. dianthus* uses its energy reserves towards winter or does not build up energy reserves.

However, it can also be considered that physiological processes such as reproduction also contribute to changes in energy reserves. Reproduction is one of the key life processes besides growth that requires energy (Feehan et al. 2019). As a broadcast spawner, *D. dianthus* releases unfertilized eggs and sperm into the surrounding environment (Harrison and Wallace 1990), which is a highly energy demanding process (Maier et al. 2020, Feehan et al. 2019). The reproduction of *D. dianthus* follows a seasonal cycle but was only studied in shallow waters of Comau Fjord so far (Feehan et al. 2019, Försterra and Häussermann 2003, Försterra et al. 2005). The reproductive cycle in shallow waters peaks with spawning at the end of August and the beginning of gamete production in early September (Feehan et al. 2019). It is assumed that corals use energy reserves when spawning (Maier et al. 2020), which would explain the lower energy reserves towards winter. However, it is most likely that the coral samples were collected before the spawning event and seasonal differences in the energy reserves are mainly attributed to seasonal differences in productivity in the fjord.

4.3 Energy reserves between native and novel corals

Our results suggest a high acclimatization potential of *D. dianthus*, as corals transplanted between the shallow stations A and F and between deep and shallow adjusted their energy reserves to their native counterparts. This finding is underscored by a fast acclimatization of growth and respiration rates of *D. dianthus* after the reciprocal transplantation experiment (Beck et a. 2022).

The energy reserves of novel corals at the deep station differed from native corals only in austral summer but increased rapidly and reached similar levels of energy reserves as native corals in winter. Further, the composition of energy reserves of novel corals changed after transplantation to a novel environment. The carbohydrate and protein concentrations were approximately 3-fold higher at the deep station compared to the shallow stations, whereas lipids showed an almost 4-fold higher concentration at the deep station compared to the shallow stations. Not only did novel corals adjust their energy reserves after transplantation to a novel environment, but also adjusted and changed their tissue composition. These results are in line with the study from Rocker et al. 2019, who conducted a reciprocal transplantation experiment with the tropical coral *Acropora tenuis* (Dana, 1846) along a water quality gradient on the Great Barrier Reef in Australia. They showed rapid lipid and fatty acid adjustment within four months after transplantation, underlining a high acclimatization potential of the biochemical composition of this coral species, which is in line with the results of the present study. The transplantation experiment from the present study therefore underscores that *D. dianthus* can accommodate a wide range of habitats with different environmental conditions.

5. Conclusions

Overall, differences of energy reserves in *D. dianthus* between water depths in Comau Fjord can be explained by differences in food availability between shallow and deep stations and by environmental variability in shallow waters, which affects the performance of corals. Seasonal differences are driven by higher temperatures in summer and resulting higher productivity and higher food availability during this time. We also identified the growing aquaculture sector as a possible influence for differences of energy reserves along the horizontal gradient, indicating local adaptation. The reciprocal transplantation experiment indicates a high acclimatization potential of *D. dianthus*, leading to the assumption that *D. dianthus* can cope with changing environmental conditions, especially important for future changes due to climate change.

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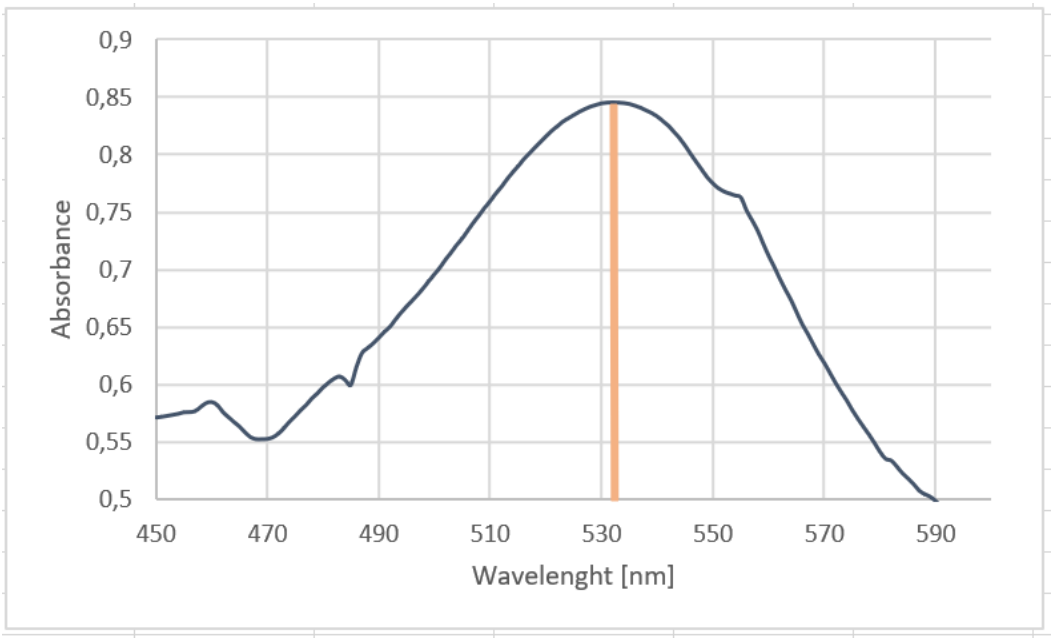
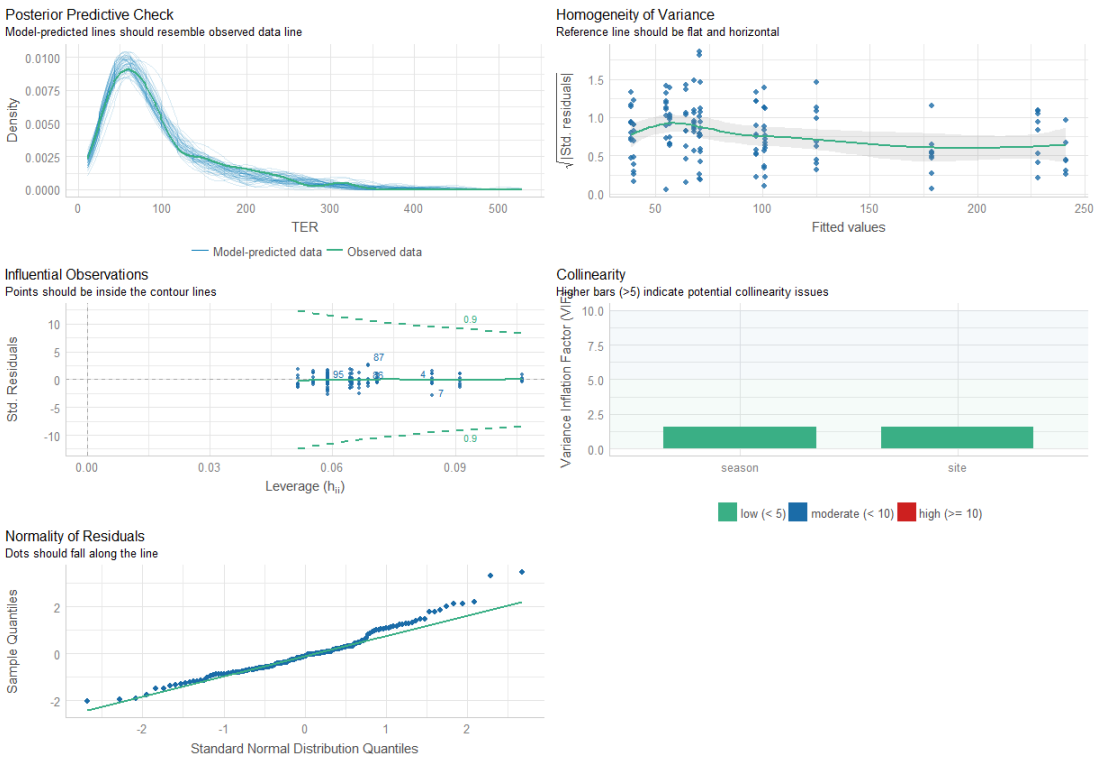
7. Supplements

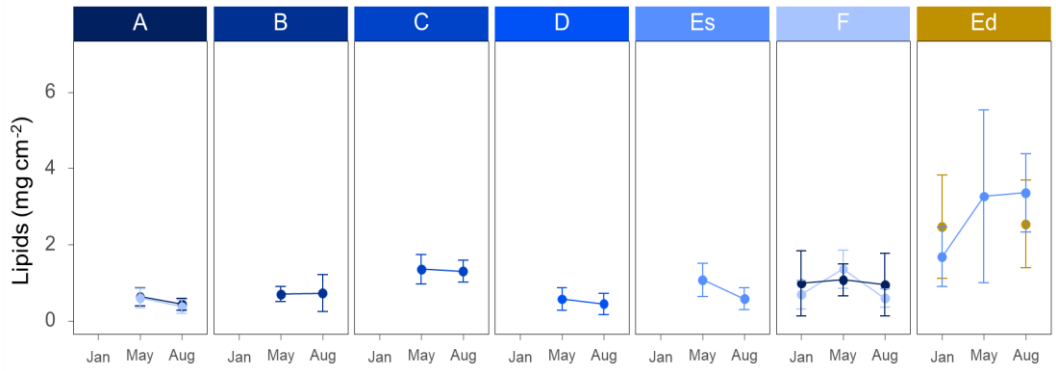


Supplementary Figure 1: Spektrum profile of absorbance of lipid sample with highest peak at 530 mm (marked in orange)



Supplementary Figure 2: Model comparison (GLM, gamma distribution) using the *performance* package in R Studio

a



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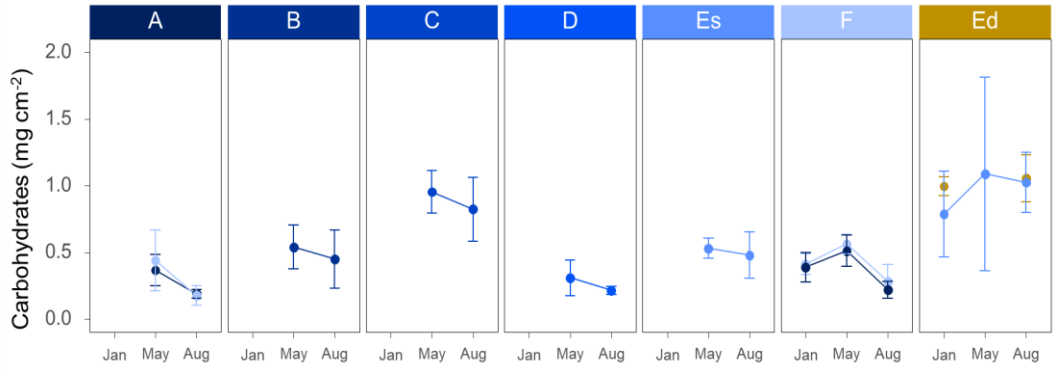

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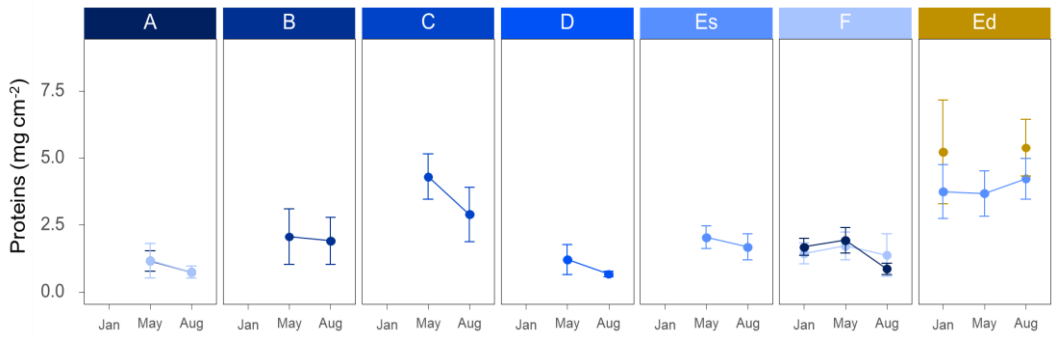

Supplementary Figure 3: Seasonal variation of tissue components of native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. a) Lipid, b) carbohydrate and c) protein concentration (mg cm^{-2}) at six shallow stations at 20 m water depth along a horizontal gradient from head to mouth of the fjord (A-F, blue stations) and along a vertical gradient, one deep station at 300 m water depth (Ed, yellow station). Native corals were re-installed in their respective station after collection in September 2016 and novel corals were cross transplanted between head (station A) and mouth (station F) of the fjord and between shallow (station Es) and deep (Ed). Coral samples were recollected in January 2017, May 2017, and August 2017.

Supplementary Table 1: Post hoc tests for generalized linear models for lipids of *Desmophyllum dianthus*. Statistical analysis was conducted using the software R (Version 1.4.1106). Significant p values are shown in bold.

Fixed effects	Contrast	Estimate	SE	df	t. ratio	p-value
Lipids (model1: shallow stations)						
season	Jan-Aug	0.0311	0.1438	113	0.216	0.9746
	May-Aug	-0.3585	0.0661	113	-5.427	**<.0001**
	Jan-May	-0.3895	0.1438	113	-2.709	0.0211
station	A - B	-0.57875	0.115	113	-5.032	<.0001
	A - C	-115238	0.113	113	-10.174	<.0001
	A - D	0.02533	0.110	113	0.230	0.9999
	A - Es	-0.58280	0.115	113	-5.061	<.0001
	A - F	-0.53126	0.110	113	-4.819	0.0001
	B - C	-0.57363	0.118	113	-4.865	0.0001
	B - D	0.60408	0.115	113	5.252	<.0001
	B - Es	-0.00405	0.120	113	-0.034	1.0000
	B - F	0.04749	0.115	113	0.413	0.9984
	C - D	1.17771	0.113	113	10.398	<.0001
	C - Es	0.56958	0.118	113	4.825	0.0001
	C - F	0.62112	0.113	113	5.484	<.0001
	D - Es	-0.60813	0.115	113	-5.281	<.0001
	D - F	-0.55659	0.110	113	-5.049	<.0001
	Es - F	0.05154	0.115	113	0.448	0.9977
Lipids (model 2: stations A, F, Es, Ed)						
station	A - F	-0.5139	0.0810	154	-6.345	**<.0001**
	Ed - Es	0.9887	0.1221	154	8.096	**<.0001**
station* transplant	A (native) - A (novel)	0.0244	0.0676	154	0.361	1.0000
	F (native) - F (novel)	0.0244	0.0676	154	0.361	1.0000
	Es (native)- Es (novel)	0.0244	0.0676	154	0.361	1.0000
	Ed (native) - Ed (novel)	0.0244	0.0676	154	0.361	1.0000

Supplementary Table 2: Seasonal energy reserves from native and novel *Desmophyllum dianthus* in Comau Fjord, Chile. Lipid, carbohydrate, protein and total energy content of *D. dianthus* (mean ± standard deviation) at six shallow stations at 20 m water depth along a horizontal gradient (A-F) and along a vertical gradient, one deep station (Ed) at 300 m water depth. Native corals were re-installed in their respective station after collection in September 2016 and novel corals were cross transplanted between head (station A) and mouth (station F) of the fjord and between shallow (station Es) and deep (Ed). Coral samples were recollected in January 2017, May 2017, and August 2017.

Season	Transplantation	Station	Lipids (J cm²)		Carbohydrates (J cm²)		Proteins (J cm²)		Total energy reserves (J cm²)	
			Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd
Summer (January)	native	F	24,30	16,71	6,39	2,70	1,44	0,40	65,14	24,48
		Ed	97,56	53,77	17,44	1,25	5,22	1,93	224,16	64,19
	novel	F	34,82	33,89	6,81	1,94	1,68	0,32	81,80	37,66
		Ed	66,33	30,87	13,78	5,66	3,74	1,01	169,55	50,16
Autumn (May)	native	A	24,80	9,28	6,42	2,05	1,17	0,38	59,07	18,69
		B	27,41	7,79	9,45	2,87	2,06	1,03	86,18	29,45
		C	53,38	15,30	16,69	2,82	4,30	0,85	172,90	31,06
		D	22,55	11,93	5,41	2,34	1,21	0,56	56,93	24,33
		Es	42,53	17,24	9,29	1,34	2,04	0,42	100,52	21,96
		F	53,63	19,77	9,84	1,30	1,72	0,52	104,66	30,68
	novel	A	23,49	10,09	7,71	3,98	1,17	0,65	56,74	29,66
		F	42,51	16,51	8,96	2,07	1,68	0,32	97,52	25,86
		Ed	128,96	89,75	19,05	12,68	3,68	0,84	219,43	95,83
Winter (August)	native	A	17,01	6,16	3,32	0,56	0,74	0,22	37,72	8,88
		B	28,52	19,01	7,88	3,82	1,91	0,88	81,98	41,85
		C	45,62	20,02	14,43	4,20	2,90	1,01	129,28	43,20
		D	17,47	10,90	3,75	0,52	0,67	0,11	37,25	13,25
		Es	22,68	11,45	8,39	3,07	1,67	0,49	71,10	23,45
		F	23,41	9,52	4,94	2,19	1,38	0,78	61,25	24,20
		Ed	100,35	45,56	18,48	3,07	5,38	1,05	247,44	36,02
	novel	A	14,54	7,18	3,09	1,31	0,74	0,21	35,39	11,14
		F	37,19	32,46	3,86	1,12	0,86	0,21	61,70	33,06
		Ed	132,72	40,62	17,93	3,92	4,23	0,76	251,63	52,22

Supplementary Table 3: Post hoc tests for generalized linear models for carbohydrates of *Desmophyllum dianthus*. Statistical analysis was conducted using the software R (Version 1.4.1106). Significant p values are shown in bold.

Fixed effects	Contrast	Estimate	SE	df	t. ratio	p-value
Carbohydrates (model1: shallow stations)						
season	Jan-Aug	0.0311	0.1438	113	0.216	0.9746
	May-Aug	-0.3585	0.0661	113	-5.427	**<.0001**
	Jan-May	-0.3895	0.1438	113	-2.709	0.0211
station	A - B	-0.57875	0.115	113	-5.032	<.0001
	A - C	-1.15238	0.113	113	-10.174	<.0001
	A - D	0.02533	0.110	113	0.230	0.9999
	A - Es	-0.58280	0.115	113	-5.061	<.0001
	A - F	-0.53126	0.110	113	-4.819	0.0001
	B - C	-0.57363	0.118	113	-4.865	0.0001
	B - D	0.60408	0.115	113	5.252	<.0001
	B - Es	-0.00405	0.120	113	-0.034	1.0000
	B - F	0.04749	0.115	113	0.413	0.9984
	C - D	1.17771	0.113	113	10.398	<.0001
	C - Es	0.56958	0.118	113	4.825	0.0001
	C - F	0.62112	0.113	113	5.484	<.0001
	D - Es	-0.60813	0.115	113	-5.281	<.0001
	D - F	-0.55659	0.110	113	-5.049	<.0001
	Es - F	0.05154	0.115	113	0.448	0.9977
Carbohydrates (model 2: stations A, F, Es, Ed)						
station	A - F	-0.5139	0.0810	154	-6.345	**<.0001**
	Ed - Es	0.9887	0.1221	154	8.096	**<.0001**
station* transplant	A (native) - A (novel)	0.0244	0.0676	154	0.361	1.0000
	F (native) - F (novel)	0.0244	0.0676	154	0.361	1.0000
	Es (native) - Es (novel)	0.0244	0.0676	154	0.361	1.0000
	Ed (native) - Ed (novel)	0.0244	0.0676	154	0.361	1.0000

Supplementary Table 4: Post hoc tests for generalized linear models for proteins of *Desmophyllum dianthus*. Statistical analysis was conducted using the software R (Version 1.4.1106). Significant p values are shown in bold.

Fixed effects	Contrast	Estimate	SE	df	t. ratio	p-value
Proteins (model1: shallow stations)						
season	Jan-Aug	0.0311	0.1438	113	0.216	0.9746
	May-Aug	-0.3585	0.0661	113	-5.427	**<.0001**
	Jan-May	-0.3895	0.1438	113	-2.709	0.0211
station	A - B	-0.57875	0.115	113	-5.032	<.0001
	A - C	-1.15238	0.113	113	-10.174	<.0001
	A - D	0.02533	0.110	113	0.230	0.9999
	A - Es	-0.58280	0.115	113	-5.061	<.0001
	A - F	-0.53126	0.110	113	-4.819	0.0001
	B - C	-0.57363	0.118	113	-4.865	0.0001
	B - D	0.60408	0.115	113	5.252	<.0001
	B - Es	-0.00405	0.120	113	-0.034	1.0000
	B - F	0.04749	0.115	113	0.413	0.9984
	C - D	1.17771	0.113	113	10.398	<.0001
	C - Es	0.56958	0.118	113	4.825	0.0001
	C - F	0.62112	0.113	113	5.484	<.0001
	D - Es	-0.60813	0.115	113	-5.281	<.0001
	D - F	-0.55659	0.110	113	-5.049	<.0001
	Es - F	0.05154	0.115	113	0.448	0.9977
Proteins (model 2: stations A, F, Es, Ed)						
station	A - F	-0.5139	0.0810	154	-6.345	**<.0001**
	Ed - Es	0.9887	0.1221	154	8.096	**<.0001**
station* transplant	A (native) - A (novel)	0.0244	0.0676	154	0.361	1.0000
	F (native) - F (novel)	0.0244	0.0676	154	0.361	1.0000
	Es (native) - Es (novel)	0.0244	0.0676	154	0.361	1.0000
	Ed (native)- Ed (novel)	0.0244	0.0676	154	0.361	1.0000

Supplementary Table 5: Post hoc tests for generalized linear models for total energy reserves of *Desmophyllum dianthus*. Statistical analysis was conducted using the software R (Version 1.4.1106). Significant p values are shown in bold.

Fixed effects	Contrast	Estimate	SE	df	t. ratio	p-value
Total Energy Reserves (model1: shallow stations)						
season	Jan-Aug	0.0562	0.1108	126	0.507	0.8681
	May-Aug	-0.3556	0.0634	126	-5.605	**<.0001**
	Jan-May	-0.4118	0.1171	126	-3.516	0.0018
station	A - B	-0.57855	0.112	126	-5.186	<.0001
	A - C	-1.15226	0.110	126	-10.489	<.0001
	A - D	0.02535	0.107	126	0.237	1.0000
	A - Ed	-1.80923	0.135	126	-13.426	<.0001
	A - Es	-0.58247	0.112	126	-5.215	<.0001
	A - F	-0.53869	0.104	126	-5.180	<.0001
	B - C	-0.57372	0.114	126	-5.016	<.0001
	B - D	0.60389	0.112	126	5.413	<.0001
	B - Ed	-1.23069	0.139	126	-8.871	<.0001
	B - Es	-0.00393	0.116	126	-0.034	1.0000
	B - F	0.03986	0.109	126	0.366	0.9998
	C - D	1.17761	0.110	126	10.720	<.0001
	C - Ed	-0.65697	0.137	126	-4.792	0.0001
	C - Es	0.56979	0.114	126	4.977	<.0001
	C - F	0.61358	0.107	126	5.734	<.0001
	D - Ed	-1.83458	0.135	126	-13.614	<.0001
	D - Es	-0.60782	0.112	126	-5.442	<.0001
	D - F	-0.56403	0.104	126	-5.424	<.0001
	Ed - Es	1.22676	0.138	126	8.906	<.0001
	Ed - F	1.27055	0.115	126	11.062	<.0001
	Es - F	0.04379	0.109	126	0.403	0.9997
Total Energy reserves (model 2: stations A, F, Es, Ed)						
station	A - F	-0.5139	0.0810	154	-6.345	**<.0001**
	Ed - Es	0.9887	0.1221	154	8.096	**<.0001**
	A (native) - A (novel)	0.0244	0.0676	154	0.361	1.0000

station* transplant	F (native) - F (novel)	0.0244	0.0676	154	0.361	1.0000
	Es (native)- Es (novel)	0.0244	0.0676	154	0.361	1.0000
	Ed (native) – Ed(novel)	0.0244	0.0676	154	0.361	1.0000

8. Acknowledges

Ich möchte mich bei allen bedanken, die mich während meiner Zeit des Schreibens der Bachelorarbeit unterstützt haben, insbesondere bei meiner Familie. Danke, dass ihr mich bei allem immer so unterstützt und an mich glaubt. Ein großes Danke für die Umarmungen, wenn ich mal nicht weitergekommen bin und ihr mich aufgemuntert habt, aber auch ein Danke, wenn ihr euch mit mir über Erfolge gefreut habt. Ein großes Dankeschön gilt dabei meiner Mama, die mich während des Schreibens fleißig mit Kaffee und Nervennahrung versorgt hat! Das hat besonders die etwas schwierigeren Phasen immer etwas einfacher gemacht.

Ich bin sehr dankbar, dass ich die Möglichkeit bekommen habe, meine Bachelorarbeit in Kooperation mit dem Alfred-Wegener-Institut zu schreiben. Dabei gilt ein besonderes Dankeschön meinen beiden Betreuerinnen, Marlene und Krissi. Danke, dass ihr immer ein offenes Ohr für mich hattet, mir viele Anregungen und Anmerkungen für die Bachelorarbeit gegeben habt und mich so großartig unterstützt habt in den vielen online Meetings. Ich hatte sehr viel Glück, euch beide als Betreuerinnen zu haben. Danke!

Danke auch an meine Labor-Betreuerin Steffi, die mich gerade zur Anfangszeit Tatkräftig im Labor unterstützt hat, viel recherchiert- und Zeit investiert hat, um mir zu helfen. Die Zeit im Labor mir dir hat sehr viel Spaß gemacht. Danke dafür!