Growth and Respiration of the Cold-Water Corals *Tethocyathus endesa* and *Caryophyllia huinayensis* in the Fjord Comau, Chile

Wachstum und Respiration der Kaltwasserkorallen *Tethocyathus endesa* und *Caryophyllia huinayensis* im chilenischen Comau-Fjord

BACHELOR THESIS

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List of Abbreviations

Ω_{ar}	Aragonite saturation state
in situ	"At site" (latin)
O_2BR	Background respiration due to microorganisms, oxygen value measured in the 'empty' glass bottles after incubation.
w_{water}	Buoyant weight of coral in seawater [g]
$CaCO_3$	Calcium carbonate
Ca^{2+}	Calcium ions
P	Calculated probability
A_{calyx}	Calyx surface area [cm^2]
CO_3^{2-}	Carbonate ions
CO_2	Carbon dioxide
H_2CO_3	Carbonic acid
C. huinayensis	*Caryophyllia huinayensis* (C)
cm	Centimeter
R^2	Coefficient of determination
CWC	Cold-water corals
w_{air}	Coral weight in air [g]
cm^3	Cubic centimeter
d	Day
ρ_{water}	Density of sewater [g cm^{3-}]
Δ	Delta
°C	Degree Celcius
°S	Degree South
°W	Degree West
D. dianthus	*Desmophyllum dianthus*
e.g.	*exempli gratia*, latin for "for example"
Fig.	Figure
g	Gram
h	Hour
HCO_3^-	Hydrogen carbon
H^+	Hydrogen ion
O_2i	Initial seawater oxygen concentration of the control bottles containing no corals, measured right after collection
km	Kilometer
LG	Liliguapi island
l	Liter
MWRS	Mann-Whitney Rank Sum test
m	Meter
μmol	Mikromol
mg	Milligram
ml	Milliliter
mm	Millimeter
pH	Negative common logarithm of the hydrogen ion concentration of a solution, a measure for acidity
OA	Ocean acidification

O_2	Oxygen
O_2C	Oxygen concentration in the glass bottles containing corals after incubation
ΔO_2	Oxygen consumption over 12h
pers. com.	Personal comment
PVC	Polyvinylchlorid
R	Respiration rates [μmol O_2 cm^{-2} d^{-1}]
SCUBA	Self-contained underwater breathing apparatus
ρ_{sd}	Skeletal density of the coral [g cm^{3-}]
m^2	Square meter
St.Dev	Standard Deviation
Tab.	Table
T. endesa	*Tethocyathus endesa* (T)
t_i	Incubation time [h]
V_i	Incubation volume [l]
H_2O	Water
XH	Cross-Huinay
XHN	Cross-Huinay North
yr	Year

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Abstract

The ongoing anthropogenic carbon dioxide (CO_2) release into the atmosphere is leading to a concurrent increase of CO_2 in the oceans, resulting in a reduction of pH through ocean acidification. Though cold-water corals are thought to be highly vulnerable, previous studies have shown that some of them may be resilient to lower pH values. Chile's Comau fjord shows a pronounced horizontal pH gradient, partly reaching such low pH values as they are predicted for most oceans by the end of the century, offering the opportunity to conduct *in situ* experiments investigating the effects of reduced pH regimes. Two coral species that are abundant and ecologically important in the fjord Comau, *Tethocyathus endesa* and *Caryophyllia huinayensis*, were used in a reciprocal cross-transplantation experiment in 2014 - 2016 between sites of high and low pH to investigate the influence of different pH regimes on the corals. An interspecific comparison of the respiration rates, mass and calyx surface area increase in 2015 - 2016 and the mortality of the two species was carried out. Results for the respiration rates of *T. endesa* and *C. huinayensis* were similar between the species, but were strongly elevated compared to studies from previous years. The transplant from low to high pH showed a higher carbonate accretion rate for *T. endesa*, suggesting that higher pH regimes may be favoured by this species. Results for the calyx surface area increase corresponded to the results in mass increase for both species, though *C. huinayensis* even showed negative results. The physical environment at the investigated sites was compared through pH, oxygen and temperature data. Sites of low pH showed similar pH and oxygen values that were lower than those at the site of high pH at rising tide. Furthermore, the mass increase was intraspecifically compared between the two years. *T. endesa* showed a reduced mass increase in the second year at the site of low pH, whereas *C. huinayensis* showed similar results for all treatments in both years. As ocean acidification will require long-term adaptions, this suggests that *C. huinayensis* may be able to adapt to different pH regimes better than *T. endesa* and over a longer period of time.

Zusammenfassung

Der anthropogene Ausstoß von Kohlenstoffdioxid (CO_2) in die Atmosphäre führt zu einem simultanen Anstieg des CO_2-Gehalts der Ozeane und zu einer dadurch verursachten Reduktion des pH-Wertes durch Ozeanversauerung. Besonders Kaltwasserkorallen gelten dadurch als gefährdet, jedoch haben Studien gezeigt, dass einige dieser Korallen resistent gegen solche Veränderungen sein könnten. Der Comau-Fjord im südlichen Chile bietet optimale Bedingungen, um *in situ* Experimente durchzuführen, die den Einfluss von reduzierten pH-Werten untersuchen. Grund hierfür ist ein horizontaler pH-Gradient, durch den in einigen Bereichen des Fjordes so niedrige Werte erreicht werden, wie sie für die meisten Ozeane im Zuge der Ozeanversauerung vorausgesagt werden. Zwei Korallenarten, die im Comau-Fjord individuenreich und ökologisch wichtig sind, *Tethocyathus endesa* und *Caryophyllia huinayensis*, wurden in einem zweijährigen Kreuz-Transplantations-Experiment zwischen Standorten mit hohem und niedrigem pH verwendet. Respirationsraten, Massen- und Calyxoberflächenzuwachs in 2015 - 2016 sowie die Mortalität wurden interspezifisch verglichen. Die gemessenen Respirationsraten von *T. endesa* und *C. huinayensis* waren ähnlich, jedoch stark erhöht im Vegleich zu früheren Jahren. Bei der Transplantation von einem niedrigen zu einem hohen pH-Wert zeigte *T. endesa* einen erhöhten Massenzuwachs. Dies lässt vermuten, dass *T. endesa* einen Standort mit höherem pH-Wert bevorzugt. Der Calyxoberflächenzuwachs zeigte ähnliche Ergebnisse, wobei *C. huinayensis* teilweise negative Werte aufwies. Um die physikalische Umwelt zu beschreiben, wurden pH-, Sauerstoff- und Temperaturmessungen durchgeführt und zwischen den Standorten verglichen. Standorte mit niedrigerem pH-Milieu zeigten ähnliche pH- und Sauerstoffwerte, die bei steigender Tide niedriger waren als Messungen am hohen pH-Standort. Zusätzlich wurde das Wachstum der beiden Korallenarten in 2015 - 2016 mit dem Vorjahr verglichen. Am Standort mit niedrigen pH-Werten zeigte *T. endesa* ein verringertes Wachstum im zweiten Jahr, wohingegen *C. huinayensis* unveränderte Wachstumsraten in beiden Jahren zeigte. Da Ozeanversauerung langfristige Anpassung erfordern wird, lassen die Ergebnisse vermuten, dass sich *C. huinayensis* besser und längerfristig an zukünftige pH-Werte anpassen kann als *T. endesa*.

1 Introduction

About 60% of all coral species known today are cold-water corals (CWC) found globally throughout a wide range of latitudes and with a vertical distribution ranging from less than 50 m down to the abyssal plane (4000 - 7000 m) (Freiwald et al. 2004; Cairns 2007; Roberts et al. 2009). Like their tropical counterparts, CWC can either build extensive reef structures or provide structural habitats solely through their abundance (Roberts et al. 2006 and 2009).

Tethocyathus endesa and *Caryophyllia huinayensis* (Cairns, Häussermann and Försterra 2005) both belong to the familiy Caryophylliidae in the order Scleractinia (Cairns et al. 2005; Roberts et al. 2009). Their coral polyp consists of a cylindric body made up of two cell layers, the ecto- and endoderm, that encase the mesoglea, a supporting lamella (Wehner and Gehring 2007). From the mouth, which is located at the center of the oral disc and surrounded by tentacles, the pharynx leads down to the gastrovascular cavity and at the aboral end, the polyp is attached to the substrate with its basal plate (Wehner and Gehring 2007; Fig. 1A). The polyp is divided longitudinal by lamellar sheets called mesenteries (Roberts et al. 2009).

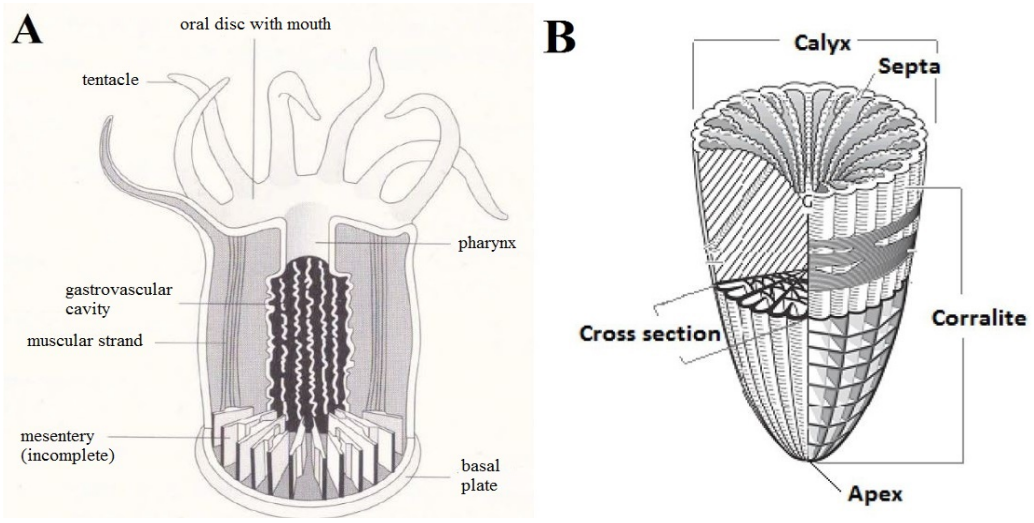

Figure 1: Morphology of a scleractinian coral polyp (A) and its encasing skeleton (B). After Wehner and Gehring (2007) (A) and Stolzenberg-Ramirez (2010), edited by Diercks (2015)(B).

As all scleractinian CWC, both coral species produce calcified skeletons of aragonite and the polyps are solitary, encased by individual skeletons (corallites) (Freiwald et al. 2004;

Häussermann and Försterra 2009; Roberts et al. 2009; Fig. 1B). The inside of the corallite, the calyx, is divided by vertical plates (septa) which grow from the theca (corallite wall) inward and of which both species usually have a total of 48 (Cairns et al. 2005; Häussermann and Försterra 2009). *T. endesa* shows a height of up to 8 mm and a maximum calyx diameter of 11 mm (Häussermann and Försterra 2009). With a calyx diameter of up to 10 mm and a maximum height of 20 mm, *C. huinayensis* is taller, but slender than *T. endesa* (Häussermann and Försterra 2009).

T. endesa and *C. huinayensis* are found globally in the south-east Pacific Ocean and have so far been encountered along various sites in the fjord region of southern Chile (Cairns et al. 2005; Häussermann and Försterra 2009). Here, specimens of *T. endesa* and *C. huinayensis* have been found growing as shallow as 11 m and down to 240 and 800 m depth, respectively (Cairns et al. 2005; Häussermann and Försterra 2009). Their shallow occurrence makes them two of the three scleractinian corals, the third one being *Desmophyllum dianthus*, of the *Caryophyliidae* family known from Chilean Patagonia to grow in shallow waters accessible to SCUBA divers (Cairns et al. 2005; Häussermann and Försterra 2009). In the fjord region of Chile, all three species are often found growing in close proximity of each other and especially in the fjord Comau situated in the northern part of the fjord region, *T. endesa* and *C. huinayensis* contribute to dense banks of *D. dianthus* (Cairns et al. 2005; Häussermann and Försterra 2009). However, both *T. endesa* and *C. huinayensis* show high abundances in the fjord Comau themselves, varying between 87 and up to 1000 specimens per m^2 (Wurz 2014; Diercks 2015). Their abundance and production of carbonate structures makes them ecologically important for the diverse benthic community found in the fjord (Försterra and Häussermann 2003; Freiwald et al. 2004).

The fjord Comau has been the subject of several studies in recent years, as it shows pronounced vertical and horizontal pH gradients (Fillinger and Richter 2013; Jantzen et al. 2013; Wurz 2014; Diercks 2015). From the upper 20 m down to 200 - 300 m, the pH drops from 8.42 to 7.26 (Fillinger and Richter 2013). At the mouth of the fjord, pH values reach 7.94 and lower values of 7.6 have been measured around the center of the fjord (Wurz 2014; Diercks

2015). Thus, the central part of the fjord as well as the deeper water layers, show pH values lower than currently found in the Pacific Ocean (between 7.8 - 7.9; Millero 2016). They also resemble and may even exceed values predicted for most oceans by the end of the century (Haugan and Drange 1996; Caldeira and Wickett 2003; Orr et al. 2005; IPCC 2014). Oceanic pH values are predicted to drop due to ocean acidification (OA), which mainly results from the uptake of atmospheric carbon dioxide (CO_2) by the oceans (Gattuso and Hansson 2011). The anthropogenic influence on the global climate has continuously increased in the past years and rising CO_2 emissions have lead to an increase of global temperatures and atmospheric CO_2 concentrations (IPCC 2014). About a quarter of atmospheric carbon is taken up by the oceans annually, which has a severe impact on the ocean carbon system (Caldeira and Wickett 2003; Gattuso and Hansson 2011). CO_2 and water (H_2O) react to carbonic acid (H_2CO_3), which is unstable and dissociates to hydrogen carbonate (HCO_3^-) and carbonate (CO_3^{2-}) in two consecutive reactions (Gattuso and Hansson 2011). If more CO_2 is added to the system, the hydrogen ion (H^+) concentration is raised, the pH drops concurrently and consequently the CO_3^{2-} concentration is reduced, making the water more acid and the precipitation of calcium carbonate more difficult for calcifying organisms (Orr et al. 2005; Hoegh-Guldberg et al. 2007 (and references therein)).

Scleractinian corals produce their aragonite skeleton through the process of calcification, which takes place externally between the calicoblastic epithelium (the aboral ectoderm) and the existing skeleton (Allemand et al. 2004; Braun and Erez 2004). Since corals use calcium and carbonate ions (Ca^{2+} and CO_3^{2-}, respectively) from the ambient seawater, $CaCO_3$ formation is dependent on the water's aragonite saturation state Ω_{ar} (Cohen and Holcomb 2009a). The Ω_{ar} describes the relation between the actual Ca^{2+} and CO_3^{2-} concentrations found in the seawater and their concentrations at equilibrium (Cohen and Holcomb 2009a). If $\Omega_{ar} > 1$, calcification is favoured, if $\Omega_{ar} < 1$, the ambient seawater becomes corrosive (Roberts et al. 2009). Since seawater Ca^{2+} concentrations are high and relatively stable, the Ω_{ar} is mainly determined by the concentration of CO_3^{2-} and thus influenced by OA (Orr et al. 2005; Cohen and Holcomb 2009a).

Although it has been predicted that OA will impact many coral species and other calcifying organisms (see for example Orr et al. 2005; Hoegh-Guldberg et al. 2007; Carpenter et al. 2008), there are also studies suggesting that some corals may be resilient to future changes in seawater carbonate chemistry (see for example Carpenter et al. 2008; McCulloch et al. 2012; Maier et al. 2013a and 2013b). In the fjord Comau, *T. endesa* and *C. huinayensis* seem to be unaffected by the low pH values due to their distribution and abundance described above. In addition, two studies conducted in the same fjord investigated the influence of different pH regimes on the mass increase of the corals and results suggested that both corals may be able to adapt to higher levels of ocean acidity (Wurz 2014; Diercks 2015).

Another parameter to measure a coral's reaction to changes in environmental factors are respiration rates, as higher rates indicate higher metabolic activity, which can be induced by different factors such as food availability, stress response or the temperature and oxygen content of the ambient seawater (Telesnicki and Goldberg 1995; Dodds et al. 2007; Naumann et al. 2011; Larsson et al. 2013). Since calcification is an energetically costly process (Allemand et al. 2004; Cohen and Holcomb 2009a), it was hypothesised by Maier et al. (2013a) that a higher need for maintaining calcification rates under unfavourable conditions (reduced pH, OA) may be reflected by higher respiration rates. However, the study by Maier et al. 2013a found no correlation between elevated CO_2 concentrations in the ambient seawater and elevated respiration rates for the CWC *Madrepora oculata* and *Lophelia pertusa*, suggesting that the maintenance of calcification rates does not require higher metabolic rates. Corresponding to this, a study by Diercks (2015) revealed no effect of the pH gradient found in the fjord Comau on respiration rates of *T. endesa*. On the contrary, *in vitro* experiments by Wurz (2014) have shown that respiration rates of *C. huinayensis* increase with decreasing pH values, with the maximum respiration rate measured at the lowest tested pH value (7.4). With these varying results, the question remains to what extend the different pH regimes found in the fjord Comau influence the metabolism of *T. endesa* and *C. huinayensis*.

Aims of the Study

Only speculations can be made about the full impact that OA will have on marine and especially benthic organisms like cold-water corals in the future. However, regions such as the fjord Comau that show naturally low pH values can be used to assess these impacts through corresponding experiments (Andersson et al. 2011 and references therein).

This Bachelor thesis thus aims to investigate the influence of the oceanic carbonate chemistry on the growth and health of *T. endesa* and *C. huinayensis*. For this, a two-year reciprocal cross-transplantation experiment was carried out, in which corals were transplanted between sites of higher and lower pH. To characterise the physical environment found at the sampling sites, temperature, pH and oxygen were measured and compared between them. Since the fjord Comau experiences a high tidal amplitude, it was hypothesised that this will have an effect on the physical parameters. The physical environment at the three sampling sites was thus compared per tide.

Mass increase [% yr^{-1}], respiration rates [μmol O_2 cm^{-2} d^{-1}] and the health and mortality of the corals were investigated as parameters for coral growth and wellbeing. Since previous studies have shown that corals are not necessarily influenced by the carbonate chemistry of the ambient seawater (see for example Fillinger and Richter 2013; Maier et al. 2013a and b, Wurz 2014; Diercks 2015), it was hypothesised that the reduced pH will have no effect on growth and respiration rates and overall coral health. As both species often grow in close proximity of each other and are both ecologically important for the benthic community in the fjord (Försterra and Häussermann 2003; Freiwald et al. 2004; Cairns et al. 2005; Häussermann and Försterra 2009), an interspecific comparison was carried out. Furthermore, an interannual comparison of the mass increase between 2014 to 2015 and 2015 to 2016 was examined for each species. As OA will require long-term adaptions, this may help to identify whether these corals are able to adapt to different pH regimes over a longer period of time.

2 Material and Methods

2.1 The Fjord Comau

The fjord Comau is situated approximately between 42.1°S and 42.3°S in the north of Chile's fjord region (Fig. 2). It is about 45 km long, 2 - 8.5 km wide and its depth reaches a maximum of about 500 m (Häussermann et al. 2012). At its northern end, it opens into the Golfo de Ancud, which connects the fjord with the Pacific Ocean. The fjord receives high amounts of freshwater input from rivers and precipitation, which creates a brackish surface layer low in salinity with a seasonally varying depth of 0.5 - 10 m (Bustamante 2009; Sánchez et al. 2011; Häussermann et al. 2012; Jantzen et al. 2013). It is also shifted vertically by the high tidal amplitude of over seven meters, resulting in high fluctuations of hydrological parameters such as salinity, temperature, pH and oxygen in the first few meters of the water column (Silva 2008; Bustamante 2009; Häussermann et al. 2012).

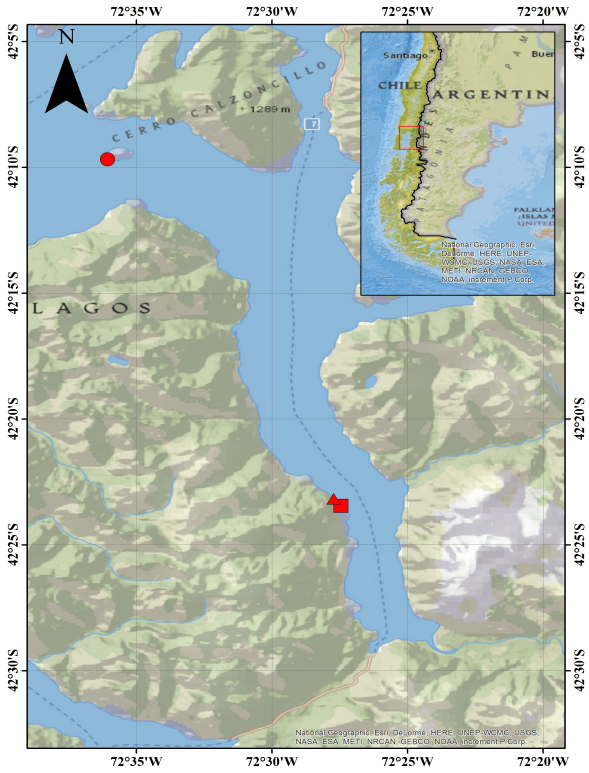

Figure 2: Study area. Overview of the fjord Comau (large map) situated in the north of Chilean Patagonia in South America (small map). Red symbols show the three study sites: circle = Liliguapi island (LG), triangle = Cross-Huinay North (XHN), square = Cross-Huinay (XH).

Below this surface layer, salinity and temperature ranges are relatively stable, between 31.2 - 33.0 and 8 - 12.0 °C, respectively (Häussermann et al. 2012; Fillinger and Richter 2013). The oxygen saturation decreases by 45% in the fist 180 m below the brackish surface layer and lowest O_2 values of 91 μmol l^{-1} are found below 300 m (Fillinger and Richter 2013; Jantzen et al. 2013).

2.1.1 The Sampling Sites

For the cross-transplantation experiment, three sampling sites, where both coral species grow, along the horizontal pH gradient of the fjord Comau were chosen (Fig. 2). Two sites, one for each species, were located inside the fjord across from the Huinay Scientific Field Station. *Tethocyathus endesa* was collected at Cross-Huinay North (XHN) (S42°23'10.56" W72° 27' 43.08"), *Caryophyllia huinayensis* at Cross-Huinay (XH) (S42°23'27.6" W72°27'26.7"). Both sites show a lower pH than the third sampling site (Wurz 2014; Diercks 2015) located outside the fjord, at Liliguapi island (LG) (S42°09'41", W72°36'04"). Here, only one sampling site was used for both species. At all three sampling sites, the coral holders used for the cross-transplantation experiment described below were installed at a depth of about 20 m.

2.1.2 Physical Environment

To characterise the physical environment, water samples were frequently taken at the three sampling sites (XHN, XH and LG) at various dates and tides throughout the expedition. Water samples were collected at XHN and XH on 15, at LG on eight days between March 22 and April 23 2016. For each location and sampling day, three water samples from 20 m depth were taken using a 2.5 l Niskin-Type plastic water sampler (Hydrobios Apparatebau GmbH, Altenholz, Germany) and each water sample was measured three times. These triplicate measurements served as measurement controls and were combined to one value. Oxygen [mg l^{-1}] was measured with a Standard Luminescent-Probe for dissolved oxygen and pH with a Standard-Electrode filled with liquid electrolyte (LDO101 and PHC301, Hach Lange

GmbH, Düsseldorf, Germany). At each sampling site, a temperature logger (TidbiT V2 Water Temperature Data logger, ONSET Computer Corporation, Bourne, USA) was installed next to the coral holders and data collected between January 2015 and April 2016 (LG: Jan 28 2015 - Apr 13, 2016; XHN: Jan 2015 - Apr 15, 2016; XH: Jan 29 2015 - Apr 12, 2016). At LG, temperature [°C] was recorded every 15 minutes, while in XHN and XH, temperature could only be measured once every hour due to a malfunction in the installed loggers that was not noticed until they were recollected.

2.2 Cross-Transplantation Experiment

A cross-transplantation experiment was started with *Caryophyllia huinayensis* in March 2013 and with *Tethocyathus endesa* in February 2014 during two expeditions, for which the first specimens were collected and installed by scientific SCUBA divers. To minimize the risk of damage and stress, the corals were collected together with their substrate, mostly the limpet *Crepidula sp.*, and placed in plastic containers, filled with ambient seawater from the sampling site, for transport. The containers were sealed air-tight at the site of collection, ensuring no contact with either the brackish surface layer found in the fjord or the air. In the laboratory of the Huinay Scientific Field Station, debris was removed and the corals were cut from the sea shells using a sanding disc attached to a rotary tool (Dremel 4000, Dremel, Dreda, The Netherlands). The corals were glued onto polyvinylchloride (PVC) screws, weighted and photographed. For the duration of the laboratory work, the corals were maintained in a 30 l aquarium which was supplied with unfiltered water continuously pumped up from the fjord from 25 m depth. After the laboratory work was finished, the corals were installed on polyethylene coral holders set up at the three sampling sites (Fig. 3). *T. endesa* was installed facing upwards and *C.huinayensis* downwards. For both coral species, ten corals collected at XHN and XH, respectively, were reinstalled at their site of collection to serve as control groups, while the other ten specimens were cross-transplanted to LG and vice versa, giving a total of 20 specimens per coral species and site. Thus, a total of 80 corals were used in the cross-transplantation experiment, 40 per species. Corals that were reinstalled at their

collection site will hereafter be referred to as "control groups".

After the initial setup in 2013 and 2014, respectively, the corals were recollected from the coral holders annually (2014 - 2016) during expeditions by scientific SCUBA divers and brought to the laboratory for the described experiments, lastly during the expedition in April 2016. To collect the corals, 100 ml glass bottles (Schott AG, Mainz, Germany) were filled air-free with aquarium water from the lab. On site, the water was exchanged with ambient sea water and the corals were attached to the lid of the glass bottle, which had an implemented mount, through their screws. In the laboratory, the corals were held in an aquarium as described before and were reinstalled at the according coral holders after experiments were completed.

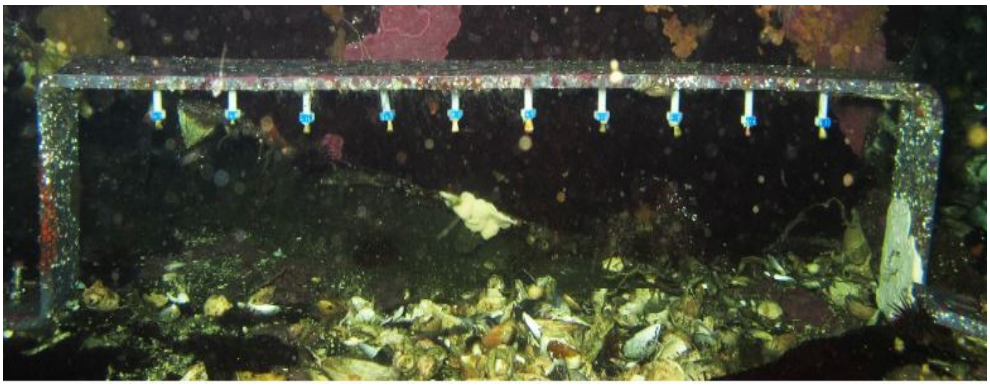

Figure 3: Coral holder used for the cross-transplantation experiment with *Tethocyathus endesa* and *Caryophyllia huinayensis* in the fjord Comau, Chile (after Wurz 2014). Corals were collected at sampling sites of high and low pH, glued onto polyvinylchlorid screws and reinstalled at the according holder and site. The photo shows *C. huinayensis* at the sampling site "Cross-Huinay".

2.3 Respiration Rates

During the preparation of the glass bottles used to collect the corals (see description above), a small magnetic stir bar was added to each of the bottles. The experimental setup for the respiration rates comprised a water bath which was placed on a magnetic stirring table (IKA RO15, IKA-Werke GmbH & Co. KG, Staufen, Germany). Using the water supply system of the field station, ambient seawater, the same as was used in the holding tanks, was constantly pumped through the water bath to ensure the same water temperatures as in the aquarium. The water temperature varied around 13.17 ± 1.15°C due to the natural fluctuations occuring in the fjord at 25 m depth. Immediately after the corals were brought to the lab, they were

placed in the water bath, inside the glass bottles, and incubated for 12 h. Together with the magnetic stir bar inside each bottle, the stirring table ensured a constant water movement throughout the incubation period (see Fig. 4).

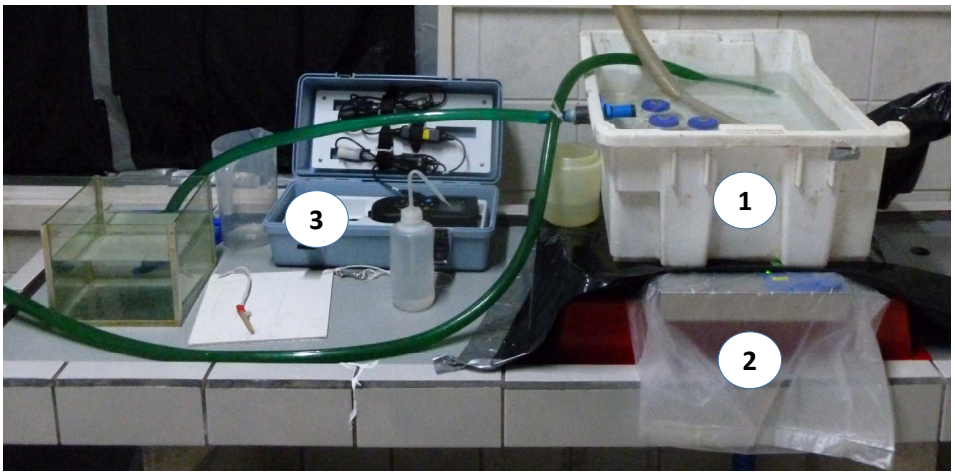

Figure 4: Setup for the respiration measurements. Corals were collected in 100 ml Schott glass bottles containing a magnetic stir bar and placed in a water bath (1) on a stirring table (2). The water supply system of the Huinay Scientific Field Station was used to pump seawater from the fjord (25 m depth) through the water bath. The oxygen content of two glass bottles serving as controls and containing only seawater was measured before the incubation (12h), while all remaining glass bottles (including another two control bottles with no corals) were measured afterwards. Measurements were done using a Standard Luminescent-Probe for dissolved oxygen (LDO101, Hach Lange GmbH, Düsseldorf, Germany) (3).

Four glass bottles were used as control samples and contained no corals, but were still filled with ambient seawater at the coral sampling site. The oxygen content for two of the control bottles was measured directly after sampling on board the dive boat, while the other two were incubated together with the corals. After 12 h, the corals were removed from the glass bottles and the water oxygen content was measured for all samples, including the two control samples, using a Standard Luminescent-Probe for dissolved oxygen (LDO101, Hach Lange GmbH, Düsseldorf, Germany). The start and end oxygen values were used to calculate the oxygen consumption by the corals, which was also corrected for background respiration from microorganisms using formula 1 (after Hatcher 1989):

$$\Delta O_2 = \Delta[(O_2 i)(O_2 C)] - \Delta[(O_2 i)(O_2 BR)] \quad (1)$$

with:

ΔO_2 = oxygen consumption over 12 h

$O_2 i$ = initial seawater oxygen concentration of the control bottles containing no corals, measured right after collection

$O_2 C$ = oxygen concentration in the glass bottles containing corals after incubation

$O_2 BR$ = background respiration from microorganisms, oxygen value measured in the empty glass bottles after incubation.

The oxygen consumption was then corrected for the volume of the glass bottles and the incubation time and the respiration rate calculated using formula 2 (after Hatcher 1989 and Wurz 2014):

$$R = \frac{(\frac{\Delta O_2 \times V_i}{t_i})}{A_{calyx}} \times 24 \times \frac{1000}{32} \quad (2)$$

with:

R = respiration rate [μO$_2$ cm^{-2} d^{-1}]

ΔO_2 = oxygen consumption over 12h

V_i = incubation volume [l]

t_i = incubation time [h]

A_{calyx} = calyx surface area [cm^2]

24 = correction for daily respiration rate

$\frac{1000}{32}$ = conversion factor from g to μmol O$_2$

The amount of respiring polyp tissue is estimated from the calyx surface area (Diercks 2015), which is why it can be used as a representation of the living surface area of the coral. To normalize the respiration rates to the living surface area of each coral, the calyx was photographed and the surface area calculated, as described below.

2.4 Calyx Surface Area

To measure the calyx surface area, a camera (OLYMPUS digital camera OM-D E-M5, Olympus Corporation, Tokyo, Japan) with a waterproof housing (NA-EM5 Underwater Camera Housing, Nauticam International Ltd., Hong Kong) was submerged in a black plastic tub. The tub was filled with filtered seawater from the holding aquarium. The corals were photographed next to a sliding calliper functioning as scale (Fig. 5). The calyx surface area was then measured and calculated from the photos using Photoshop CS6 (Adobe Systems Incorporated, San Jose, USA).

Photos taken of the corals in 2015 and 2016 were used to calculate the increase in calyx surface area [% yr^{-1}] over the past year. In order to assure the application of the same method to all samples, photos of the corals taken during the expedition in 2015 were remeasured using Photoshop CS6. In total, 35 corals of *T. endesa* were used to investigate the calyx surface area increase in 2015 - 2016. Concerning *C. huinayensis*, this could only be done for ten specimens, as photos from 2015 were either missing or unusable.

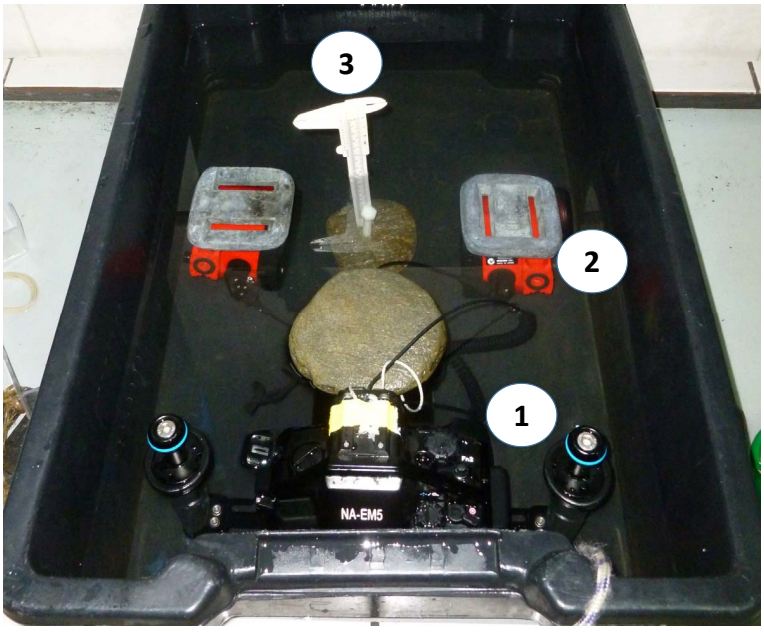

Figure 5: Camera setup for the photography of the calyx surface area. A camera (1) (OLYMPUS digital camera OM-D E-M5, Olympus Corporation, Tokyo, Japan) with a waterproof housing and external flash lights (2) (NA-EM5 Underwater Camera Housing, Nauticam International Ltd., Hong Kong) was placed in a black tub filled with filtered seawater. Both the camera and flash lights were held in position using weights and rocks. To take topview photos of the calyx, corals were held next to the sliding calliper (3).

2.5 Mass Increase

The buoyant weight technique as described by Davies (1989) was used to determine the mass increase of the corals used in the cross-transplant experiment over the past year (2015 - 2016). This method has not only been proven to be accurate and practicable, it also makes it possible to handle the corals without damaging them or taking them out of the water (Jokiel et al. 1978; Davies 1989). It is based on Archimedes' Principle, after which an object's weight in air equals the weight of the object in a liquid and the weight of the displaced liquid combined (Jokiel et al. 1978). First, the corals were weighed using a high-precision scale (CPA225D-OCE, Sartorius, Göttingen, Germany), which was set up on a weighing platform on concrete floor to ensure the most stable surroundings possible. A weighing basket was attached to the underside of the scale through tungsten filament. Below the scale, a 7 l aquarium was set up, which was filled high enough with seawater from the holding aquaria so that the weighing basket was fully submerged. It was also made sure that any air bubbles adhering to the coral or the weighing basket were removed. The temperature of the water inside the weighing aquarium was kept at $\pm$ 0.5 °C from the holding tanks and was regulated using cooling packs placed around the aquarium and a frequent exchange of water (Fig. 6).

Temperature and salinity of the water inside the weighing tank were measured for each coral to determine the density of the seawater inside the aquarium. The corals themselves were weighed three times each from which a mean value was calculated. Afterwards, the coral mass in air was calculated using formula 3 (Davies 1989):

$$w_{air} = \frac{w_{water}}{(1 - \frac{\rho_{water}}{\rho_{sd}})} \tag{3}$$

with:

w_{air} = coral weight in air [g]

w_{water} = buoyant weight of coral in water [g]

ρ_{water} = density of sea water [g cm^{-3}]

ρ_{sd} = skeletal density of the coral [g cm^{-3}]

The skeletal density of the corals could not be determined as done by Davies (1989) as no spare samples were available. For this reason, a skeletal density of 2.835 g cm^{-3} as calculated by Naumann et al. (2011) for *Desmophyllum dianthus* was used. As no records on the skeletal density were found for neither *T. endesa* nor *C. huinayensis*, the measurements for *D. dianthus* served as a good approximation for the density of both corals studied.

Figure 6: Setup of the high-precision scale (CPA225D-OCE, Sartorius, Göttingen, Germany) used to determine the buoyant weight of the corals. The scale (1) was set up above a 7 l aquarium (2) filled with with seawater from the holding tanks of the corals. A weighing basket was attached to the underside of the scale with tungsten filament. Corals were weighted three times from which a mean value was calculated. Temperature of the seawater was kept at ± 0.5°C of the holding tanks and was recorded along with salinity to calculate the density of the seawater.

Data acquired during the 2016 expedition was used in combination with the data from the previous two expeditions to calculate the mass increase between 2014 and 2016. Findings have already been presented in previous studies (Wurz 2014; Diercks 2015), but some calculations had to be redone in order to present all results uniformly. For the past year (Feb 2015 - Apr 2016), this was done successfully with 35 specimens of *T. endesa* and 13 specimens of *C. huinayensis*. Mass increase for *T. endesa* in 2014 - 2015 is presented as previously done by Dierks (2015), though calculations had to be remade. This was successfully done with 38 specimens of *T. endesa*. For *C. huinayensis*, calculations of the mass increase are only available for 2013 - 2014 (Wurz 2014) and thus calculations were made anew for 2014 - 2015 with the data collected during the 2015 expedition to be used in this study. Only for 14 corals was the available data sufficient to calculate the mass increase in 2014 - 2015. Reasons for the small amount of *C. huinayensis* specimens that could be used are severe shortages in the data available from the past years. Many specimens were missing in 2015 and previous records of the corals (photos or coral numbering) were not always sufficient to identify the corals properly.

2.6 Data Analyses

Data handling and organization was done using Microsoft Excel 2010. The seawater density needed for the buoyant weight method was determined using the function "swRho" of the R-package "oce" (Kelley and Richards 2016; R Core Team 2016). For the analysis of the oxygen and pH values at all three sampling sites, the collected data was sorted by location as well as tide (falling or rising). Secondly, statistical differences between different tides and locations were tested. Statistical analyses were carried out using SigmaPlot (Version 12.5, Systat Software GmbH, Erkrath, Germany). All data was tested for normality using the Shapiro-Wilk test as well as equal variance. A t-test was carried out to test for significant differences in mass increase and respiration rates of the corals between sampling sites, coral species and years, as well as for differences between the physical environment (oxygen and pH values between sites). The minimum number of samples needed per treatment in order to

perform statistical tests was $n = 2$. Data for which the normality or equal variance test failed were analysed with the non-parametric Mann-Whitney Rank Sum test (hereafter: MWRS). Results are presented as mean with standard deviation. For the respiration rates and the interspecific mass increase in 2015 - 2016, the sample number n gives the number per coral specimen per treatment. For the intraspecific, interannual comparison, n gives the number of samples for which the mass increase in 2014 - 2015 was calculated.

3 Results

3.1 Environmental Parameters

3.1.1 pH and Oxygen

As it was hypothesized that the high tidal amplitude found in the fjord Comau will influence the physical environment, the pH and oxygen measurements from each location were compared per tide (Tab. 1, Fig. 7). However, pronounced differences between falling and rising tide were only found for oxygen concentrations (Appendix Tab. A.1). On four days, an oxygen saturation above 90% was recorded at XHN and XH that was higher compared to the rest of the sampling days, which not only resulted in elevated pH and oxygen measurements, but these results also influenced the measured differences between tides (Appendix Tabs. A.3 - A.5).

Table 1: pH and oxygen values [mg l^{-1}] measured at the three sampling sites Cross-Huinay North (XHN), Cross-Huinay (XH) and Liliguapi island (LG). Data was collected at XHN and XH on 15, at LG on eight days between Mar 22 and Apr 23, 2016. For each measurement, three water samples were taken, each sample measured three times and these triplicate measurements combined to one value. The total mean value and standard deviation (St.Dev.) was then calculated from the data from all sampling days. The number gives the total amount of samples for each location and tide. Samples were taken at different days and at falling and rising tide. It was hypothesised that the high tidal amplitude will have an influence on the measurements, but pronounced differences were only found between tides for the oxygen values at LG (Appendix Tab A.1). The numbers in brackets give the total sample number per tide.

pH						
Location	LG (6, 18)		XHN (21, 21)		XH (33, 10)	
Tide	Falling	Rising	Falling	Rising	Falling	Rising
Mean Value	8.01	7.95	7.84	7.83	7.84	7.81
St. Dev.	0.04	0.17	0.21	0.15	0.20	0.08
Oxygen [mg l^{-1}]						
Location	LG (6, 18)		XHN (21, 21)		XH (33, 10)	
Tide	Falling	Rising	Falling	Rising	Falling	Rising
Mean Value	7.07	8.85	7.54	6.65	7.71	5.85
St. Dev.	0.10	0.94	3.06	2.57	2.64	1.12

At falling tide, the pH measured at LG was similar to the pH measurements at XHN and XH (MWRS P = 0.307 for LG vs. XHN and P = 0.083 for LG vs. XH; Tab. 1; Fig. 7A; Appendix Tab. A.2). At rising tide, the pH was lower at XHN and XH compared to LG (MWRS P = 0.021 for LG vs. XHN and P = 0.039 for LG vs. XH; Tab. 1; Fig. 7A; Appendix Tab. A.2).

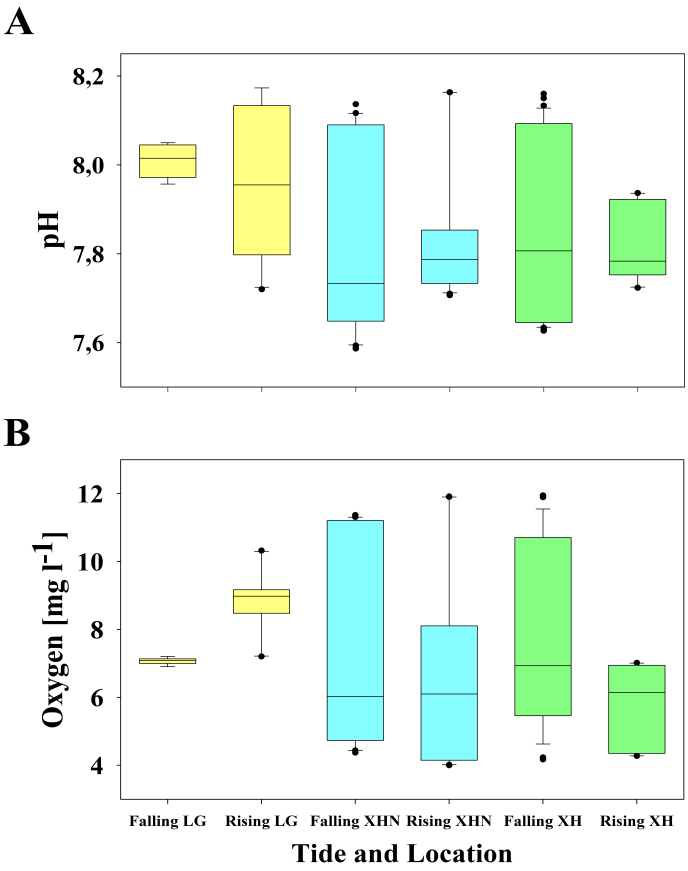

Figure 7: pH (A) and oxygen (B) values [mg l^{-1}] measured at the three sampling sites Liliguapi island (LG, yellow), Cross-Huinay North (XHN, blue) and Cross-Huinay (XH, green). Data was collected at XHN and XH on 15, at LG on eight days between Mar 22 and Apr 23, 2016. For each measurement, triplicate measurements that were combined to one value were taken for three water samples. Samples were taken at different days and at falling and rising tide. It was hypothesised that the high tidal amplitude found in the fjord Comau would influence the pH and oxygen concentrations and thus locations were compared per tide, though pronounced differences were only found in LG (Appendix Tab A.1).

PH values were similar at XHN and XH at both falling and rising tide (MWRS P = 0.922 falling tide and P = 0.933 for rising tide; Tab. 1; Fig. 7A; Appendix Tab. A.2).

Oxygen values measured at LG were similar to XHN and XH during falling tide (MWRS P = 0.620 for LG vs. XHN and P = 0.496 for LG vs. XH; Tab. 1; Fig. 7B; Appendix Tab. A.2). During rising tide, oxygen concentrations at XHN and XH were lower than at LG (MWRS P $<$ 0.001; Tab. 1, Fig. 7B; Appendix Tab. A.2). Oxygen values at XHN and XH were similar, independent of the tide (MWRS P = 0.582 for falling, P = 0.916 for rising tide; Tab. 1; Fig. 7B; Appendix Tab. A.2).

3.1.2 Temperature

The temperature development at all three sites was similar during the logging period from January 2015 to April 2016 (Fig. 8A - C). The hourly data logging resulted in varying diurnal temperature ranges, which became smaller during the austral winter from May/June to October.

At LG, temperatures ranged between 10.74 ± 0.16 °C and 13.02 ± 0.77 °C in August 2015 and March 2015, respectively (Fig. 8A). The maximum temperature was 15.51 °C and the minimum 9.83 °C, reached in January 2016 and July 2015, respectively (Fig. 8A). At XHN, monthly temperatures ranged between an average of 10.89 ± 0.31 °C in August 2015 and 12.63 ± 0.76 °C in February 2016, with the lowest and highest temperatures of 9.90 and 15.51 °C, respectively, reached in these months as well (Fig. 8B). Temperatures ranged between 10.86 ± 0.29 °C in August 2015 and 12.89 ± 0.86 °C in February 2016 at XH, with the lowest temperature of 9.73 °C reached in July 2015 and the highest temperature of 15.39 °C in February 2016 (Fig. 8C).

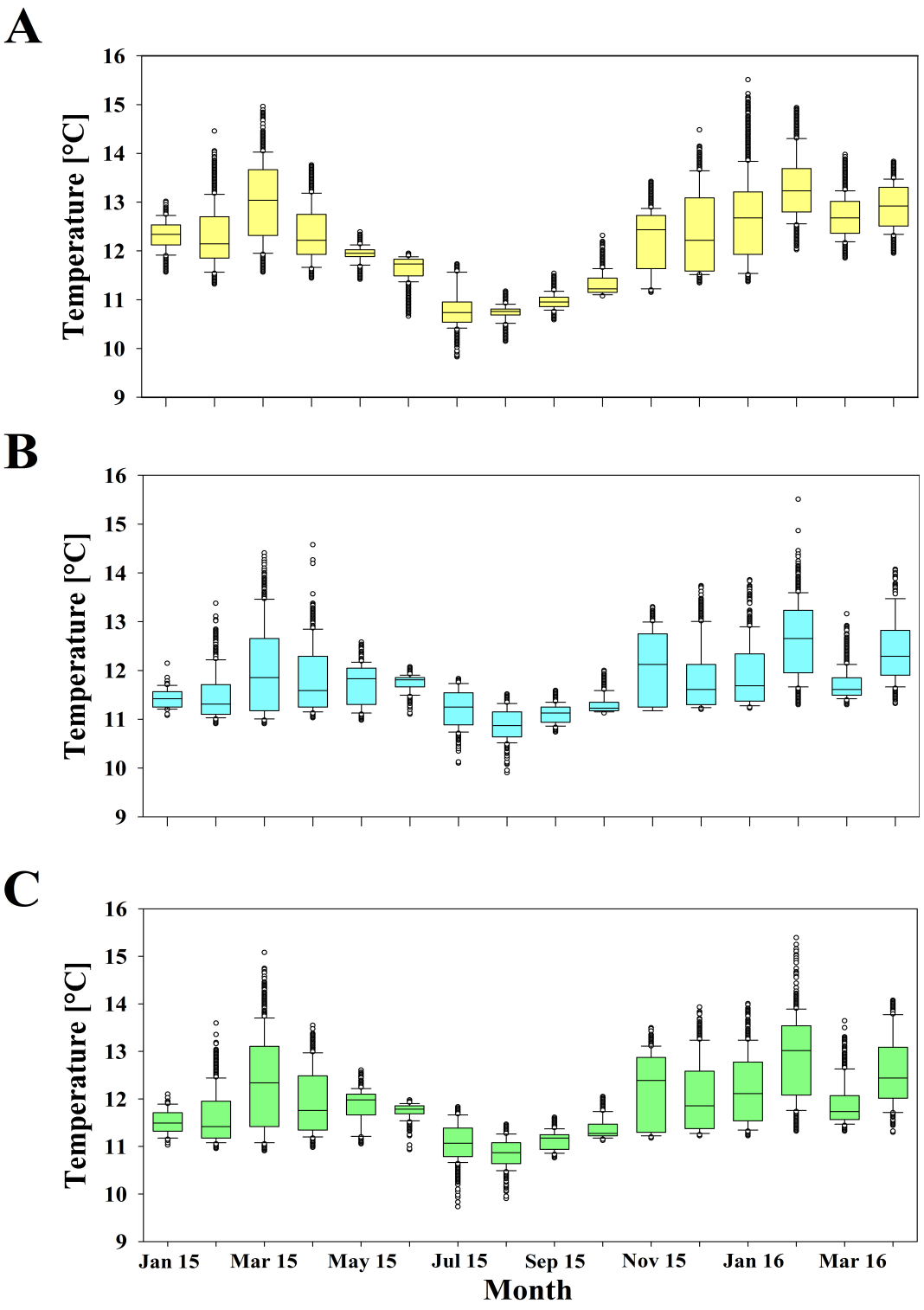

Figure 8: Monthly diurnal temperature ranges recorded at Liliguapi island (A, yellow), Cross-Huinay North (B, blue) and Cross-Huinay (C, green) between January 2015 and April 2016 (LG: Jan 28, 2015 - Apr 13, 2016; XHN: Jan 29, 2015 - Apr 15, 2016; XH: Jan 29, 2015 - Apr 12, 2016). In LG, temperature [°C] was recorded every 15 minutes, while in XHN and XH, temperature could only be measured once every hour.

3.2 Coral Quantity and Health

In 2016, a total of 37 specimens of *T. endesa* were recollected, with three corals missing. 27 corals were healthy, eight were alive but showed a mass loss over the past year and two corals were dead. For *C. huinayensis*, 20 specimens were recollected, of which one showed a mass loss from 2015 - 2016. Another five screws were found empty, with the attached corals missing. After the respiration rates were calculated for all corals recollected and the mass increase from 2014 - 2016 calculated for all available coral data, the data set was collocated according to treatment, leading to a reduction of the data to only a few samples per treatment.

3.3 Respiration Rates

Both species, *T. endesa* ($n = 9$) and *C. huinayensis* ($n = 3$), showed similar respiration rates of 28.94 ± 19.15 and 33.88 ± 20.84 μmol O_2 cm^{-1} d^{-1}, respectively, at LG, the site of high pH (t-test P = 0.712). Statistics failed to confirm the visually lower respiration rate of 14.83 ± 5.61 μmol O_2 cm^{-1} d^{-1} (Fig. 9A) that was measured for *T. endesa* transplanted from LG to XHN ($n = 6$) compared to their control group (MWRS P = 0.112). Similarily, *C. huinayensis* transplanted from LG to XH ($n = 7$) seemed to show lower respiration rates (19.84 ± 5.08 μmol O_2 cm^{-1} d^{-1}) than the control group at LG (Fig. 9A), but no statistical difference (t-test P = 0.110) was tested. Comparing the transplants from high to low pH of both species, *T. endesa* and *C. huinayensis* showed very similar values (t-test P = 0.120) and a clearly reduced variability in their respiration rates at XHN and XH, respectively, compared to their control groups.

At the low pH sites (XHN and XH), the control group of *T. endesa* ($n = 11$) showed lower respiration rates of 15.60 ± 3.85 μmol O_2 cm^{-1} d^{-1} at XHN than the control group of *C. huinayensis* at XH ($n = 5$) with an average of 23.46 ± 7.10 μmol O_2 cm^{-1} d^{-1} (Fig. 9B; t-test P = 0.011). Specimens of *T. endesa* that were transplanted from XHN to LG ($n = 9$) showed similar respiration rates of 23.81 ± 12.03 μmol O_2 cm^{-1} d^{-1} compared to their control group in XHN (MWRS P = 0.171; Fig. 9B). Results of transplanted specimens

of *C. huinayensis* (XH to LG; $n = 5$) were higher (t-test P = 0.035; 78.92 ± 48.36 μmol O_2 cm^{-1} d^{-1}) than the results of their control group in XH. Comparing the transplants of both species, *C. huinayensis* showed clearly higher respiration rates than *T. endesa* (t-test P = 0.006). Again respiration rates were generally less variable at the sites of low pH at XHN and XH than at LG.

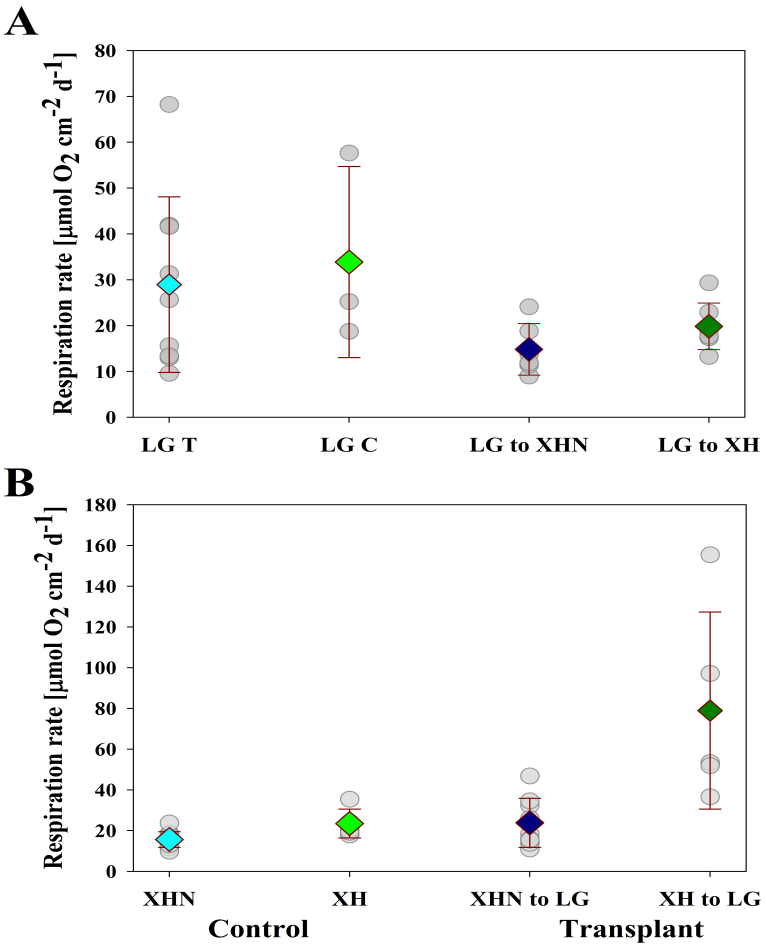

Figure 9: Respiration rates [μmol O_2 cm^{-1} d^{-1}] of *Tethocyathus endesa* (T) and *Caryophyllia huinayensis* (C) transplanted from sites of high to low pH (A) and from low to high pH (B). Single measurements for each treatments are given in grey and mean values in corresponding colors. Blue shows *T. endesa* and green *C. huinayensis*. Light colors show the control groups, dark colors the transplanted groups. LG = Liliguapi island (high pH); XHN = Cross-Huinay North (low pH); XH = Cross-Huinay (low pH).

3.4 Mass Increase

3.4.1 Interspecific Comparison

At LG, *T. endesa* ($n = 9$) showed a similar carbonate accretion as *C. huinayensis* ($n = 2$) with 12.11 ± 6.55 % yr^{-1} and 6.82 ± 6.1 % yr^{-1}, respectively (t-test P = 0.325; Fig. 10A). The transplanted corals of both species originating from the site of high pH showed no differences as well (t-test P = 0.062; Fig. 10A). With an average mass increase of -1.94 ± 8.44 % yr^{-1}, specimens of *T. endesa* transplanted from LG to XHN ($n = 6$) showed lower results than their control group in LG (MWRS P = 0.008; Fig. 10A). For specimens of *C. huinayensis* transplanted from LG to XH ($n = 6$), an almost identical mass increase of 6.90 ± 5.90 % yr^{-1} compared to the control group was observed (t-test P = 0.988; Fig. 10A).

Corals of both species at the low pH sites showed similar carbonate accretion rates (t-test P = 0.5), with *T. endesa* at XHN ($n = 11$) showing 2.16 ± 7.01 % yr^{-1} and *C. huinayensis* at XH ($n = 3$) 5.22 ± 5.18 % yr^{-1} (Fig. 10B). The carbonate accretion rate for *T. endesa* transplanted from XHN to LG ($n = 9$) was 11.15 ± 3.06 % yr^{-1}, which was higher than that of the control group at XHN (MWRS P = 0.004; Fig. 10B). Concerning *C. huinayensis*, carbonate accretion rates were similar between the transplanted specimens, showing an average of -1.12 ± 2.65 % yr^{-1} and the control group (t-test P = 0.221; Fig. 10B). Transplanted specimens of *T. endesa* showed a higher carbonate accretion rate than transplanted specimens of *C. huinayensis* (t-test P < 0.001; Fig. 10B).

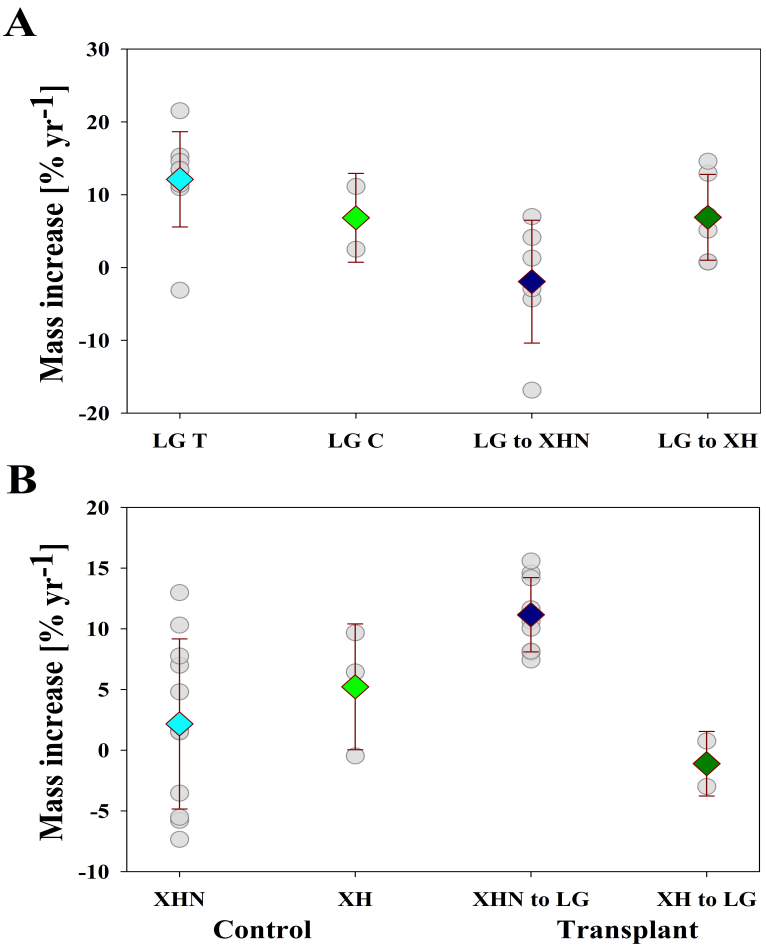

Figure 10: Mass increase [% yr^{-1}] of *Tethocyathus endesa* (T) and *Caryophyllia huinayensis* (C) in 2015 - 2016. Specimens were collected at a site of high pH and transplanted to a site of low pH (A) and vice versa (B). Light colors show the control groups installed at the site of collection, dark colors show the corals that were cross-transplanted to the other site, single measurements for each treatment are given in grey. Blue = mass increase of *T. endesa*; green = mass increase of *C. huinayensis*. LG = Liliguapi island, site of high pH; XHN = Cross-Huinay North and XH = Cross-Huinay, both sites of low pH.

3.4.2 Intraspecific Interannual Comparison

T. endesa at LG (n = 11) showed no difference in carbonate accretion between 2015 - 2016 and 2014 - 2015 (9.83 ± 4.37 % yr^{-1}; t-test P = 0.363; Fig. 11A). *T. endesa* transplants from LG to XHN (n = 8) had a reduced mass increase in 2015 - 2016 compared to 2014 - 2015 (7.58 ± 5.51 % yr^{-1}; t-test P = 0.025; Fig. 11A). In comparison to the mass increase at XHN in 2015 - 2016, *T. endesa* showed a higher growth during the previous year (n = 11) with 10.85 ± 4.46 % yr^{-1} in 2014 - 2015 (t-test P = 0.002; Fig. 11B).

Specimens transplanted from XHN to LG ($n = 9$) showed a similar mass increase in both years, as an average of 9.40 ± 13.92 % yr^{-1} was measured in 2014 - 2015, though results showed a higher variance in 2014 - 2015 (MWRS P = 0.052, Fig. 11B).

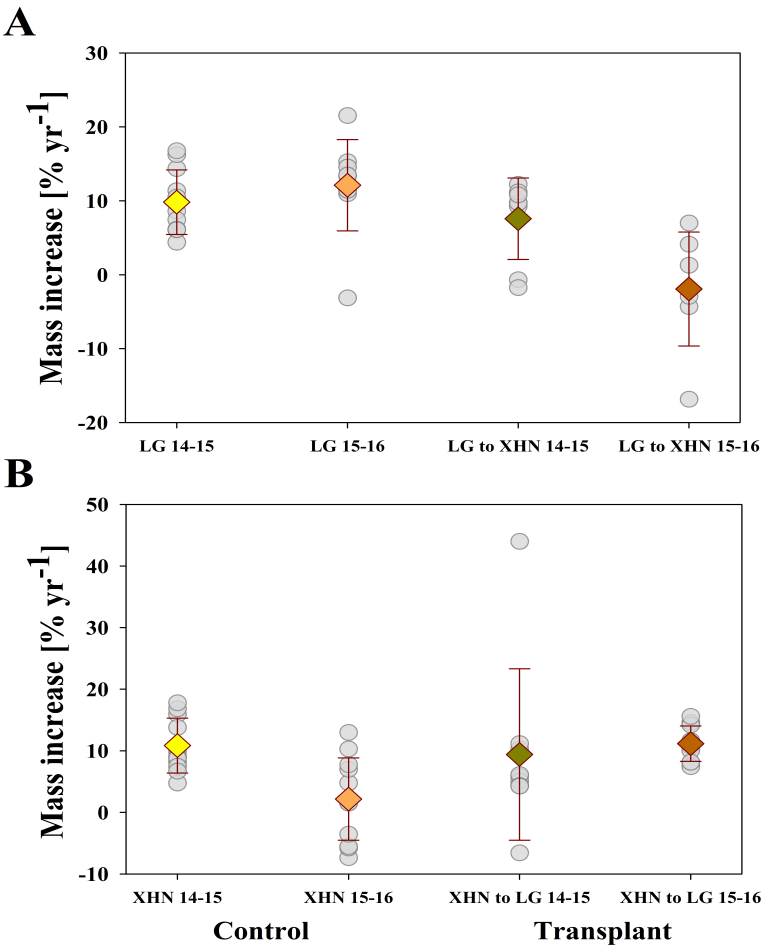

Figure 11: Mass increase [% yr^{-1}] of *Tethocyathus endesa* in 2014 - 2015 and 2015 - 2016. Specimens were collected at a site of high pH and transplanted to a site of low pH (A) and vice versa (B). Light colors show the control groups installed at the site of collection, dark colors show the corals that were cross-transplanted to the other site, while the single measurements for each treatment are given in grey. Yellow = mass increase in 2014 - 2015; orange = mass increase in 2015 - 2016. LG = Liliguapi island, site of high pH; XHN = Cross-Huinay North, site of low pH.

For *C. huinayensis*, the control group at LG and the transplanted group in XH showed similar results in both years. For corals in LG ($n = 4$), an average of 6.91 ± 4.99 % yr^{-1} was measured in 2014 - 2015, which was similar to the following year (t-test P = 0.986; Fig. 12A).

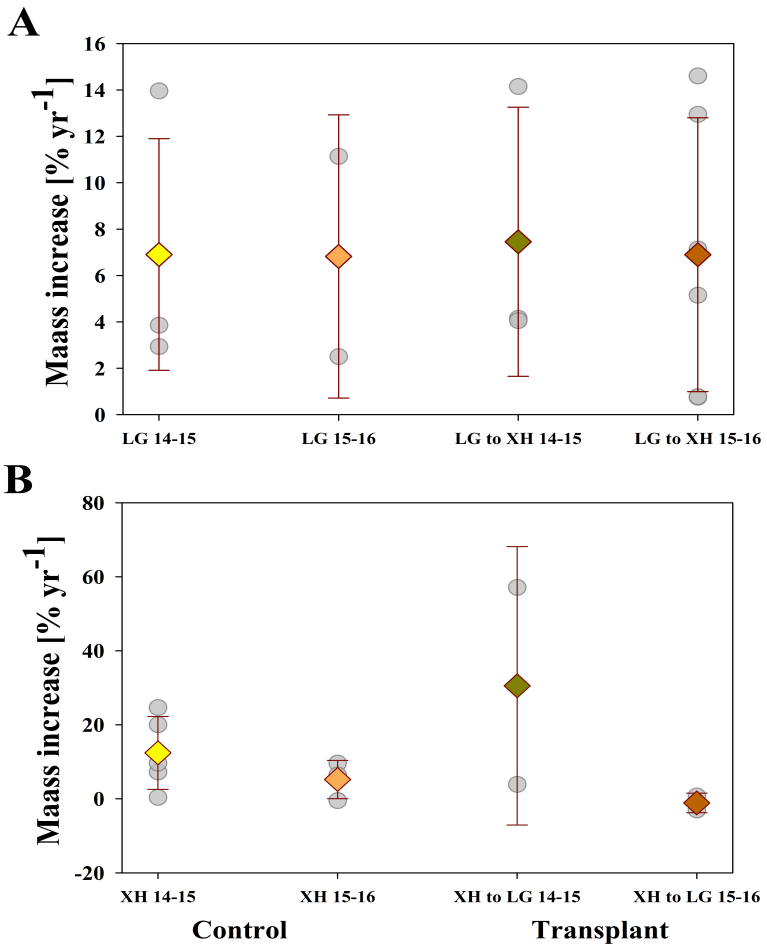

Figure 12: Mass increase [% yr^{-1}] of *Caryophyllia huinayensis* in 2014 - 2015 and 2015 - 2016. Specimens were collected at a site of high pH and transplanted to a site of low pH (A) and vice versa (B). Light colors show the control groups installed at the site of collection, dark colors show the corals that were cross-transplanted to the other site, while single measurements for each treatment are given in grey. Yellow = mass increase in 2014 - 2015; orange = mass increase in 2015 - 2016. LG = Liliguapi island, site of high pH; XHN = Cross-Huinay North, site of low pH.

With an average of 7.45 ± 5.80 % yr^{-1}, the mass increase of the transplanted group (LG to XH, $n = 3$) in 2014 - 2015 was also similar compared to the results from 2015 - 2016 (t-test P = 0.897; Fig. 12A). *C. huinayensis* transplanted from low pH at XH to high pH at LG showed similar results for both years as well. The average mass increase of 12.41 ± 9.84 % yr^{-1} measured for the control group in XH in 2014 - 2015 ($n = 5$) was seemingly higher than that from 2015 - 2016, but results proved to be similar (t-test P = 0.294, Fig. 12B). In 2014 - 2015, the mass increase for cross-transplanted specimens of *C. huinayensis* from XH to LG ($n = 2$) was calculated to be 30.53 ± 37.63 % yr^{-1}, with a much higher variance than in 2015 - 2016. The results for this transplant from the following year appeared to be lower, but were similar nonetheless (MWRS P = 0.333; Fig. 12B).

3.5 Calyx Surface Area Increase

At LG, the site of high pH, *T. endesa* (n = 9) showed a higher calyx surface area increase of 20.17 ± 18.69 % yr^{-1} than *C. huinayensis* (n = 2) with an average of -12.83 ± 11.1 % yr^{-1} (t-test P = 0.044; Fig. 13A). With an average of -12.62 ± 17.70 % yr^{-1}, transplanted specimens of *T. endesa* at XHN (n = 6) showed a lower calyx surface area increase compared to their control group in LG (t-test P = 0.005; Fig. 13A).

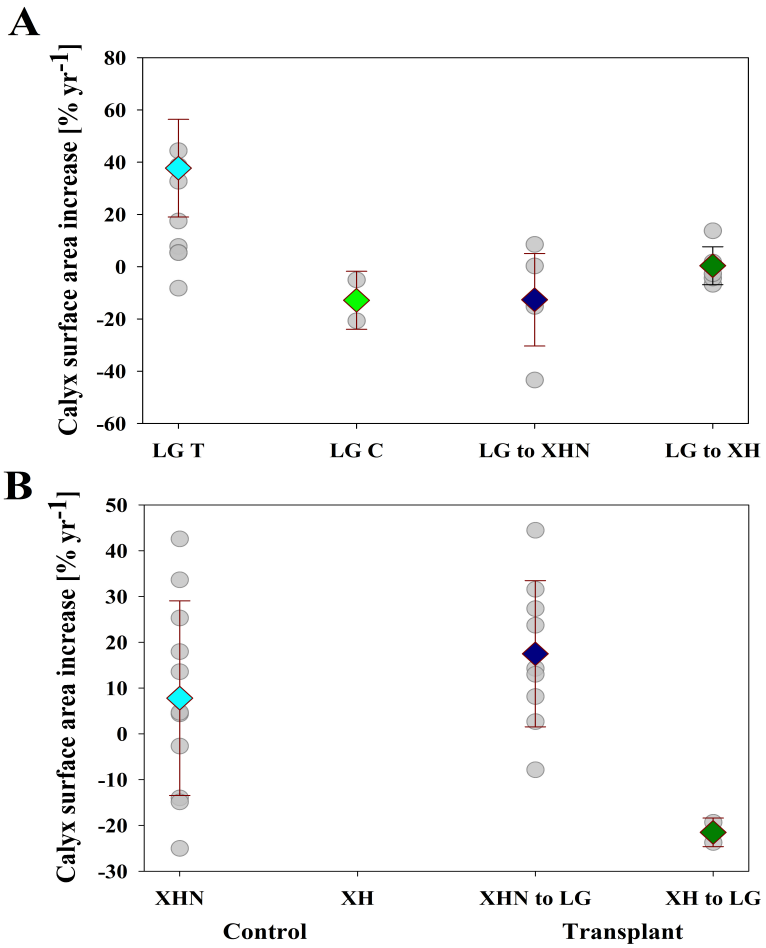

Figure 13: Calyx surface area increase [% yr^{-1}] of *Tethocyathus endesa* and *Caryophyllia huinayensis* in 2015 - 2016. Specimens were collected at a site of high pH and transplanted to a site of low pH (A) and vice versa (B). Light colors show the control groups installed at the site of collection, dark colors show the corals that were cross-transplanted to the other site, single measurements for each treatment are given in grey. Blue = calyx surface area increase of *T. endesa*; green = calyx surface area increase of *C. huinayensis*. LG = Liliguapi island, site of high pH; XHN = Cross-Huinay North and XH = Cross-Huinay, both sites of low pH.

Concerning *C. huinayensis*, the transplanted group at XH ($n = 6$) showed a similar calyx surface area increase of 0.40 ± 7.25 % yr^{-1} compared to their control group at LG (t-test P = 0.090; Fig. 13A). The transplantations showed similar results between the two species (t-test P = 0.126; Fig. 13A). Unfortunately, of the few specimens of *C. huinayensis* which could be used to calculate the calyx surface area increase in 2015 - 2016, non belonged to the control group at XH. At XHN, an average of 7.79 ± 21.25 % yr^{-1} in calyx surface area increase was measured for *T. endesa* ($n = 11$), which was similar to the transplanted group at LG ($n = 9$) with an average of 17.5 ± 15.97 % yr^{-1} (t-test P = 0.273; Fig. 13B). Specimens of *C. huinayensis* transplanted from XH to LG ($n = 2$) showed an average of -21.5 ± 3.13 % yr^{-1}, which was lower compared to the transplanted specimens of *T. endesa* (t-test P = 0.009; Fig. 13B).

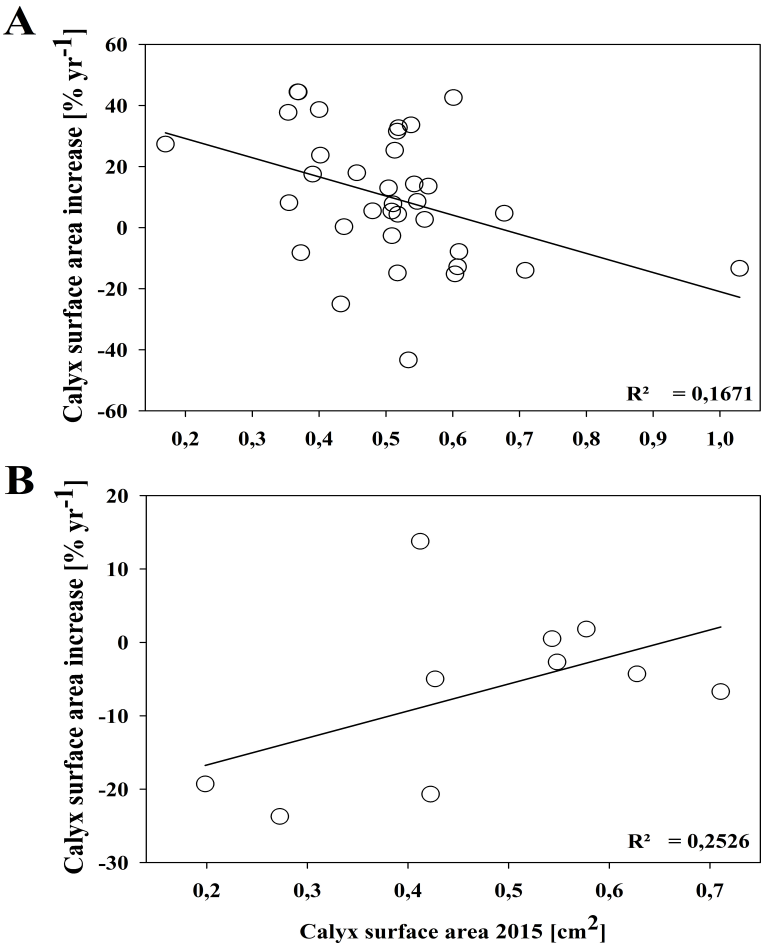

Figure 14: Calyx surface area increase [% yr^{-1}] in 2015 - 2016 as a function of the initial calyx surface area [cm^2] in 2015 for *Tethocyathus endesa* (A) and *Caryophyllia huinayensis* (B). Top-view photos of the corals were taken in 2015 and 2016, the calyx surface area for each year measured from these photos and the increase in calyx area calculated.

It was then tested if the calyx surface area and mass increase was correlated to the initial calyx surface area. For both species, no strong correlation between the initial calyx size in 2015 and calyx surface area increase in 2015 - 2016 could be found ($R^2 = 0.1671$ for Fig. 14A and $R^2 = 0.2526$ for Fig. 14B).

The mass increase in 2015 - 2016 proved to not be strongly correlated with the initial calyx surface area as well ($R^2 = 0.0963$ for Fig. 15A and $R^2 = 0.0324$ for Fig. 15B). Additionally, it was tested, if a correlation between the initial coral mass [g] and the mass increase in 2015 - 2016 could be observed. This test showed no correlation as well ($R^2 = 0.0258$ for Fig. 16A and $R^2 = 0.0634$ for Fig. 16B).

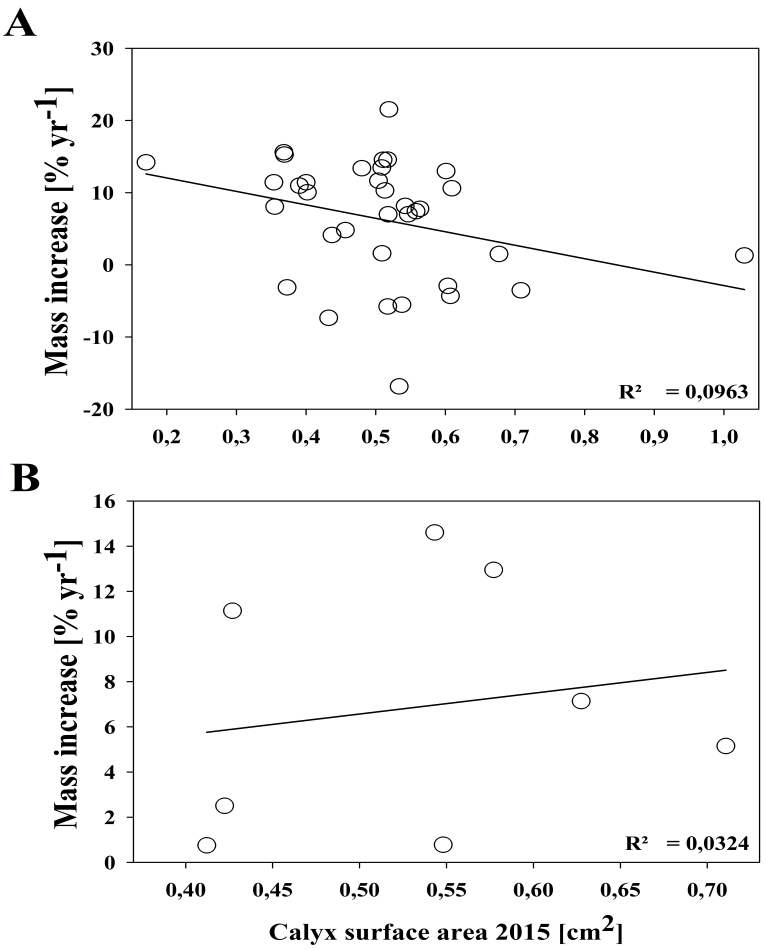

Figure 15: Mass increase [% yr^{-1}] in 2015 - 2016 as a function of the initial calyx surface area [cm^2] in 2015 for *Tethocyathus endesa* (A) and *Caryophyllia huinayensis* (B). Topview photos of the corals were taken in 2015 and the calyx surface area measured from these photos. The buoyant weight technique after Davies (1989) was used to calculate the coral mass in 2015 and 2016, from which the percental mass increase was calculated.

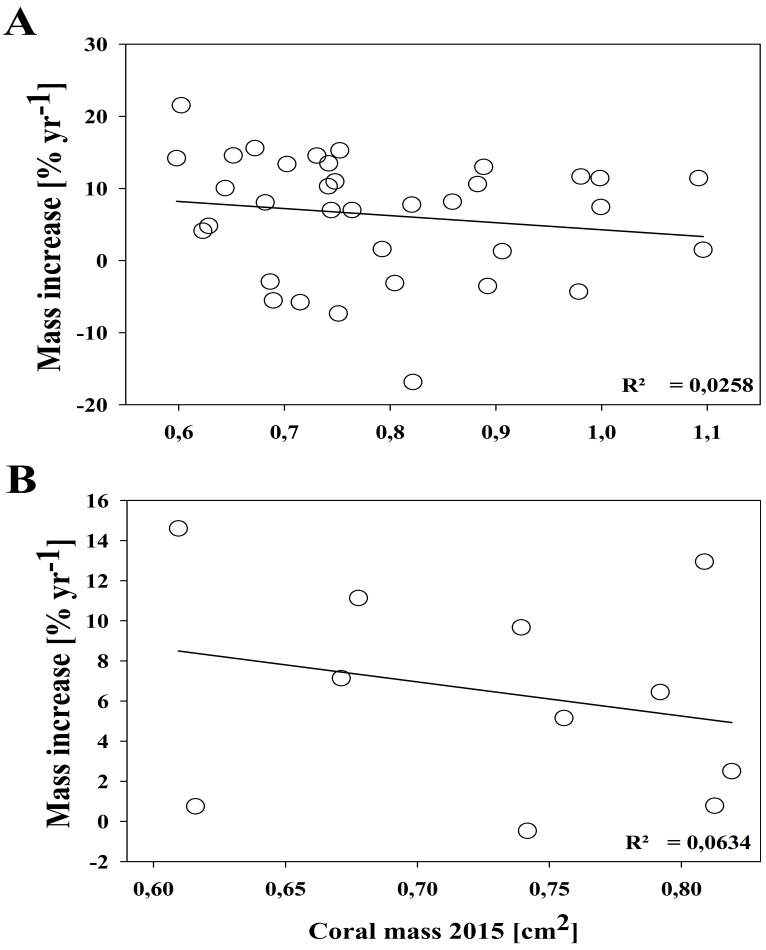

Figure 16: Mass increase [% yr^{-1}] in 2015 - 2016 as a function of the initial coral mass [g] in 2015 for *Tethocyathus endesa* (A) and *Caryophyllia huinayensis* (B). The buoyant weight technique after Davies (1989) was used to calculate the coral mass in 2015 and 2016, from which the percental mass increase was calculated.

3.6 Coral Mortality

Eventhough the cross-transplantation experiment was initially started with ten corals per species and treatment, this number varied over the years (Tab. 2). Of the two control groups at LG and XHN of *T. endesa*, no corals showed mass loss, were dead or missing in 2015, while in 2016, four corals at XHN and one at LG showed a mass loss and one coral at LG was dead (Tab. 2A). The transplant from LG to XHN showed corals with mass loss in both years, one more in 2016 than in 2015, and two missing corals in 2016 (Tab. 2A). The transplant from XHN to LG only showed one coral with mass loss in 2015 (Tab. 2A).

Results for *C. huinayensis* showed less corals with mass loss compared to *T. endesa*, but far more corals were missing in both years (Tab. 2B). In addition, a higher amount of data was not available for *C. huinayensis*. In 2015, no treatment showed corals with mass loss and only one coral of the control group at XH showed mass loss in 2016 (Tab. 2B).

Table 2: Overview of *Tethocyathus endesa* (A) and *Caryophyllia huinayensis* (B) used in the cross-transplantation experiment from 2014 - 2016. The experiment was setup in March 2013 for *C. huinayensis* and February 2014 for *T. huinaynesis*. For the presented study, data from 2014 - 2016 was assessed. Corals were cross-transplanted from sites of high to sites of low pH and vice versa. For each cross-transplant, a control group of corals was kept at the native collection site. The table gives the total numbers of corals, for which data was collected for each treatment, the number of healthy, dead and missing corals and those which showed a mass loss over the year or for which no data from either year is available. LG = Liliguapi island (site of high pH); XHN = Cross-Huinay North and XH = Cross-Huinay (sites of low pH).

A		**Total**	**Healthy**	**Mass loss**	**Dead**	**Missing**	**Data n.a.**
2015	**LG**	11	11	0	0	0	0
	XHN	11	11	0	0	0	0
	LG to XHN	9	6	2	1	0	0
	XHN to LG	9	8	1	0	0	0
2016	**LG**	11	8	1	1	1	0
	XHN	11	7	4	0	0	0
	LG to XHN	9	3	3	1	2	0
	XHN to LG	9	9	0	0	0	0
B		**Total**	**Healthy**	**Mass loss**	**Dead**	**Missing**	**Data n.a.**
2015	**LG**	8	4	0	0	3	1
	XH	10	5	0	0	3	2
	LG to XH	7	3	0	0	1	3
	XH to LG	7	2	0	0	3	2
2016	**LG**	7	2	0	0	4	1
	XH	10	2	1	0	5	2
	LG to XH	9	6	0	0	2	1
	XH to LG	7	2	0	0	4	1

4 Discussion

The aim of the presented study was to investigate the impact of the seawater acidity on the growth and respiration of the cold-water corals *Tethocythus endesa* and *Caryophyllia huinayensis*. A two-year *in situ* cross-transplantation experiment between sites of high and low pH with both species resulted in a higher respiration rate for *C. huinayensis* at the site of low pH and when transplanted to the site of high pH compared to *T. endesa*. For *T. endesa*, the inter- and intraspecific comparison of carbonate accretion rates showed higher rates at the site of high pH compared to *C. huinayensis* and reduced rates at the site of low pH in the second year. *C. huinayensis* showed similar results for all treatments and in both years. The calyx surface area increase of *T. endesa* was higher at the site of high pH and no correlation between the calyx surface area and the increase of the calyx and the coral mass for both species was found. The monitoring of the physical environment revealed that clear differences in pH and oxygen between the sites of low pH in the center of the fjord and high pH at the mouth of the fjord were only present during rising tide, whereas during falling tide the results were similar. Temperatures showed similar diurnal ranges in the course of one year (2015 - 2016).

Following the presentation of the results in the previous chapter, these will now be discussed and in particular compared to other studies. After that, the methodology will briefly be reviewed.

4.1 Hydrology of the Fjord Comau

Since the fjord Comau experiences high tidal amplitudes (Försterra 2009; Häussermann et al. 2012), it was hypothesised that this would influence the pH and oxygen values measured at the three sampling sites. This influence was only observed for the oxygen concentrations measured at Liliguapi island (LG) (Appendix Tab. A.1), but the tide did have an influence on the comparison of pH and oxygen between the three sites. At rising tide, Cross-Huinay North (XHN) and Cross-Huinay (XH) showed a mean pH of 7.83 compared to 7.95 at LG, while results were similar at falling tide and thus the pH showed a mean value of 7.9

throughout the fjord. Oxygen values at XHN and XH were 6.94 mg l^{-1} compared to 8.85 mg l^{-1} at LG during rising tide and the mean oxygen concentration in the fjord during falling tide was 7.44 mg l^{-1}. Previous studies have reported distinct horizontal gradients of pH and oxygen values throughout the fjord, though the effect of the tidal amplitude was not tested (Fillinger and Richter 2013; Jantzen et al. 2013; Wurz 2014; Diercks 2015). In contrast to this, the results presented in this study only show horizontal gradients between LG and XHN and XH at rising tide. From these findings it can be concluded that the water column down to at least 20 m permanently experiences dynamic changes in physical parameters such as pH and oxygen as well as temperature. As Fig. 8A - C show, temperatures can vary up to 4 °C between day and night at all three locations. Organisms growing in this zone thus have to be naturally adapted to changes in these parameters.

On four days, a significantly higher oxygen content was measured at XHN and XH for the water samples taken from 20m depth in the fjord. These measurements were tested against the data from the rest of the expedition and proved to be significantly higher (Appendix Tab. A.3). In the presented study, pH values ranged between 8.01 (falling tide at LG) and 7.81 (rising tide at XHN) and thus were slightly higher than previous results ranging between 7.94 at the mouth and 7.6 at the center of the fjord (Wurz 2014; Diercks 2015). The oxygen values measured in this study, ranging between 8.85 and 5.85 mg l^{-1}, resemble values Silva (2008) states for the well oxygenated surface layer, but values measured during the four discussed days were even higher, reaching an oxygen concentration of up to 11.90 mg l^{-1} (Appendix Tab. A.3). Excluding the days of elevated oxygen concentrations from the tidal comparison, differences between tides were also found between the pH measurement at XHN and XH and when comparing these two sites with LG (Appendix Tab. A.4 and Tab. A.5). It can thus be concluded, that measurements taken on the four days with unusually high oxygen values may not necessarily represent the usual pH and oxygen regimes found in the fjord Comau and may have altered the presented results. Instead, the high oxygen values could possibly be the result of short-term events such as an influx of water masses with a high oxygen saturation (Dr. J. Laudien pers. com.). It is also possible that the low-salinity surface layer was shifted

downwards through the high tidal amplitude on these days and thus processes influencing the oxygen and pH content (e.g., O_2 and CO_2 production and consumption, see Silva 2008) had an impact on deeper water layers. Nonetheless, the results do show that conditions in the upper meters of the water column can change considerably in a short period of time.

4.2 Respiration Rates

The interspecific comparison of the respiration rates of *T. endesa* and *C. huinayensis* showed similar results for both species at the site of high pH (LG) and for the transplant from high to low pH (LG to XHN and XH, respectively). At XHN and XH, respectively, and when transplanted from low to high pH, *C. huinayensis* showed higher respiration rates than *T. endesa*. Even though these results may suggest that a reduction of the pH has no effect on the respiration and with that on the metabolic activity of the corals, the respiration rates presented in this study were found to be much higher for both coral species and for all treatments compared to previous studies (Wurz 2014; Diercks 2015). Mean respiration rates for *T. endesa* and *C. huinayensis* presented in this study were 40 - 229 % and five to 25 times, respectively, higher compared to Diercks (2015) and Wurz (2014). Elevated respiration rates may be directly linked to an increased demand of carbon dioxide (CO_2) for calcification, as it has been suggested that a portion of the CO_2 used in calcification derives from respiration (Goreau 1977; Allemand et al. 2004). The generally higher energetic costs of maintaining carbonate accretion rates under unfavourable conditions may require a higher metabolic activity, as discussed below. Holding up their growth rates under reduced pH conditions may be highly costly for both coral species, requiring higher metabolic activity to compensate for the reduced carbonate ions concentrations in the ambient seawater. The high increase compared to the previous year, in combination with the partially reduced rates of carbonate accretion in 2015-2016 (see discussion below), may suggest that, at least for *T. endesa* and *C. huinayensis* used in this experiment, calcification requires higher metabolic rates in the longterm.

Various studies have shown that different parameters can have an influence on the respiration rates and that could have influenced the presented results. The elevated oxygen concentrations measured on four days mentioned above may likely have had an effect on the respiration rates, as three of those events occured on days when the corals were collected at XHN and XH and brought to the lab. Starving experiments with *Desmophyllum dianthus* and *Lophelia pertusa* have shown a reduction in respiration rates and thus metabolism with ongoing starvation (Naumann et al. 2011; Larsson et al. 2013). For *Dichocoenia stokesii* and *Meandrina meandrites*, two other scleractinian corals from Florida, it was shown that conditions requiring higher metabolic activity, in this case turbidity resulting in a higher production of mucus, led to an increase in respiration rates (Telesnicki and Goldberg 1995). As respiration was only once measured for this study it must be seen as a momentary record. This means, it is possible that the respiration was also influenced by environmental conditions such as changes in food availability, temperature or turbidity, occurring around the time of the collection of the corals.

4.3 Mass Increase

The control groups at LG and XHN and XH, respectively, of *T. endesa* and *C. huinayensis* showed similar growth rates. While the corals transplanted from high to low pH showed similar results for both species as well, *T. endesa* transplanted from low to high pH showed higher carbonate accretion rates than *C. huinayensis*. The two transplanted groups of *C. huinayensis* showed similar results compared to their corresponding control groups. Results for *T. endesa* revealed that carbonate accretion rates, compared to the control groups, were higher when transplanted to LG and lower when transplanted to XHN. From these results, it can be concluded that both corals seem to grow at the same rate under conditions they are adapted to. Moreover, carbonate accretion rates of *C. huinayensis* seem to be independent from the carbonate chemistry of the ambient seawater, while the conditions at LG may be more favourable for *T. endesa* than for *C. huinayensis*.

Comparing the growth rates for *T. endesa* and *C. huinayensis* measured in this study with results presented by Jantzen et al. (2014) shows that both corals grew slower in 2015 - 2016 than *Desmophyllum dianthus* that was used in the same experimental setup in the fjord Comau. While a growth rate of 0.05 ± 0.02 % day^{-1} for *D. dianthus* was measured in that study, the growth rates presented in this study ranged between 0.003 ± 0.006 % day^{-1} (for *C. huinayensis* transplanted from XH to LG) and 0.03 ± 0.015 % day^{-1} (for *T. endesa* at LG). However, it has to be noted that *D. dianthus* is much larger than both coral species (Häussermann and Försterra 2009). In comparison to this, the CWC *Madrepora oculata* grows even faster, with 0.2 ± 0.09 % d^{-1}, which is comparable to three tropical scleractinian corals (*Stylophora pistillata*, *Turbinaria reniformis* and *Galaxea fascicularis*) that were investigated in the same study (Orejas et al. 2011).

Between 2014 - 2015 and 2015 - 2016, both the control group at XHN and the transplanted specimens (LG to XHN) of *T. endesa* showed a reduced carbonate accretion in the second year. The transplant from XHN to LG showed similar results for both years. The presented results thus suggest that the carbonate accretion of *T. endesa* is influenced by the carbonate chemistry of the ambient seawater in the long-term. Since Diercks (2015) found no difference in the mass increase between high and low pH sites, but differences were measured with this study in the second year, *T. endesa* may not be able to uphold its carbonate accretion under reduced pH values for a longer period of time.

C. huinayensis did not show different rates of carbonate accretion in 2014-2015 and 2015 - 2016 for any of the four treatments. This suggests that this coral species may be able to uphold its carbonate accretion rate under reduced pH better than *T. endesa* and in the longterm. A study by McCulloch et al. (2012 and references therein) showed that various corals are able to up-regulate the pH at the site of calcification, which could be an explanation why *C. huinayensis* was unaffected by the reduced pH even in the second year. However, only five or less corals per treatment could be used for the calculation of the mass increase, which is a poor representation of the population. This was partly due to the fact that the data from 2015 and 2014 was incomplete, but there was also a generally high loss in corals

over the years. Results and tested differences should thus be interpreted with caution.

Since *T. endesa* already shows reduced carbonate accretion rates after two years, the question remains whether both coral species will be able to uphold their carbonate accretion rates in the years to come and at what costs. The process of calcification as such is already energetically costly under favourable conditions, as different kinetic barriers have to be overcome in order to make aragonite precipitation possible and enzyme activity is enhanced (Al-Horani et al. 2003; Allemand et al. 2004; Cohen and Holcomb 2009a). The amount of energy that corals can use on this process with rising carbon dioxide levels is not unlimited (Cohen and Holcomb 2009a; Andersson et al. 2011).

Current studies on the effects of OA on calcifying organisms are either based on laboratory work or experiments with a duration of only up to a year (see for example Orejas et al. 2011; Maier et al. 2013a and b; Wurz 2014; Diercks 2015). Longer-term studies such as the present one on the effect of OA may help to better understand the possible responses and acclimation potentials of cold-water corals as the real adaptation of the organisms will take place over a time period of unknown length in the future.

Another aspect that has to be considered are results presented in a study by Cohen et al. (2009b), which showed that corals may be able to build up their skeleton when held in conditions with an undersaturation of aragonite, but the skeletons were unhealthy and build up differently compared to unaffected corals. Experiments conducted with *D. dianthus* showed a significant up-regulation of genes that code for enzymes important in the stress response under elevated CO_2 conditions (Carreiro-Silva et al. 2014). Further studies investigating the state of the coral skeleton and the genes of *T. endesa* and *C. huinayensis* may help to identify whether the growth, especially the seemingly unaffected growth of *C. huinayensis* in the second year, under reduced pH conditions is a temporary acclimation, showing similar effects on the corals and thus may possibly be unhealthy for the coral in the longterm.

4.4 Calyx Surface Area Increase

The corals used in the cross-transplantation experiment showed initial differences in height and width. Percental results thus may be misleading, since larger corals will show a smaller percental growth than smaller corals even if both grow the same amount. However, since no correlation between the initial calyx surface area and the corresponding increase in either calyx surface area or mass was found, this bias can be ruled out. The presented results thus suggest that the rate of carbonate accretion is influenced by other factors discussed above than coral size. Comparing the results for mass and calyx surface area increase shows that *T. endesa* transplanted from high to low pH (LG to XHN) had a negative carbonate accretion in 2015 - 2016 and a corresponding reduced calyx surface area increase compared to their control group. Growth rates presented for the transplanted group of *T. endesa* may thus either be severely influenced by the carbonate chemistry of the ambient seawater or biased by either bioeroders or mechanical injuries to the skeleton. The increase in calyx surface area for *C. huinayensis* was similar between the control and transplanted group at LG and XH, respectively, corresponding to the similar carbonate accretion rates measured in 2015 - 2016 and supporting the statement made above that the growth of *C. huinaynesis* is not influenced by the pH regime of the ambient seawater. However, *C. huinayensis* showed a very low rate of calyx surface area increase for the transplanted group at XH and even negative rates for both (control and transplanted) groups at LG. Possible explanations include bioerosion through other organisms or faulties in the used method to measure the calyx surface area (see discussion below). There were also again very few specimens that could be used to calculate the calyx surface area increase and thus results and tested differences must be interpreted with caution.

4.5 Coral Quantity, Health and Mortality

Eight specimens of *T. endesa* collected in 2016 and three collected in 2015 showed a loss in coral mass over the past year. Of these corals, the majority was collected at XHN and only one at LG in both years. Of *C. huinayensis*, only one coral in 2016 showed a mass loss in 2015 - 2016. This could suggest, that the lower pH found at XHN/XH may be responsible for the deformation of the aragonite skeleton (Cohen et al. 2009b) and that this effect has a greater impact on *T. endesa*. However, since both corals of the control and transplant group were affected, the damage could also result from a mechanical force (e.g., falling rocks) or a predator was grazing on the holder or the corals themselves. Sea urchins are known to feed on algae turf and the coral holder was covered with red algae, making it a possible target for grazers (Häussermann and Försterra 2009; Appendix Fig). The sea urchin *Arbacia dufresnii* (Blainville, 1825) is assumed to occasionally feed on cold-water corals such as *Desmophyllum dianthus* and was encountered around the coral holders (Häussermann and Försterra 2009; Dr. J. Laudien pers. com. and unpublished data). Fish, for example *Prolatilus jugularis* (Valenciennes, 1833), and other bioeroders such as boring sponges or endolithic algae are also assumed to feed on or bore into the skeleton of different coral species (Dr. J. Laudien pers. com.).

4.6 Review of Used Materials and Methods

During all three expeditions in 2014 - 2016, the complete set of all 80 specimens was not successfully recollected. In general, there were always far less specimens of *C. huinayensis* recollected than *T. endesa* and especially in 2015, only 18 samples of *C. huinayensis* were recollected. A possible explanation could be the way in which the corals are glued onto the screws for the coral holders. With its growth form resembling an inverted cone, *C. huinayensis* has an especially small base with which the coral can be glued to the screw. When cutting the corals from the limpet *Crepidula sp.* using a rotary tool, a section large enough to provide a good base with which the coral can be glued onto the screw should be

cut. Additionally, *C. huinayensis* is attached to the coral holder upside down, while *T. endesa* grows upwards. If rocks fall onto the coral holder, the screws hanging downward may easily be pushed out of the holder, resulting in a loss of the entire screw. Securing the screws with a nut or other implements may help reduce the loss of specimens.

4.6.1 Respiration Rates

The respiraiton rates were measured using a Standard Luminescent-Probe for dissolved oxygen (LDO101, Hach Lange GmbH, Düsseldorf, Germany). To calculate the oxygen consumption over the incubation time, the start and end oxygen values were used. Diercks (2015) used both a manual and an automatic method to measure the oxygen consumption of *T. endesa*. The automatic method revealed that the oxygen consumption of the corals is linear and constant and no statistical differences were found between the results of both methods. Thus, the manual method used in this study is reliable and a valid method especially for expeditions, where complex setups may be difficult to realise (Diercks 2015).

4.6.2 Calyx Surface Area

To calculate the calyx surface area, topview photos were taken of the corals and then measured using Photoshop CS6. Measuring the diameter using a sliding calliper as it was done in previous expeditions was not redone during the expedition in 2016. Using a computer program to measure the calyx was more accurate, as the shape of the calyx can be considered. If a sliding calliper is used, it is assumed that the growth of the calyx follows the shape of a circle or ellipse and possible slightly irregular growth forms are not taken into account. Additionally, damage of the calyx can be considered. However, in order for this method to work, the photos must be of high quality with adequate lighting and magnification. This was not always the case, especially concerning the photos taken in 2015. In addition, some corals had their tentacles slightly extended while the photos were taken, meaning the calyx measurement could not be done accurately. An improvement of this method could be to make the photos

processible by a computer program, such as Photoshop or Matlab. This would mean that the calyx surface area would be detected automatically by the program and would not have to be measured by hand, which is another factor possibly responsible for biased results. For this, the calyx must be distinguishable from the surroundings, such as the holding hand and the screw. As both Photoshop and Matlab use color to distinguish between different areas, corresponding adjustments could be made by, e.g. wearing coloured gloves or framing the coral with a screen while taking the photos.

5 Conclusion and Outlook

In this thesis, the effects of the carbonate chemistry of the ambient seawater on the growth and respiration of the two cold-water corals *Tethocyathus endesa* and *Caryophyllia huinayensis* was studied for which a cross-transplantation experiment was conducted at sites of high and low pH. An interspecific and an intraspecific, interannual comparison of the corals as well as a comparison of physical parameters between the sites was carried out.
The environmental data proved to be highly variable with falling and rising tide. This emphasizes the influence of high tidal amplitudes on the environmental conditions in the water column and the generally high variablility to which marine organisms living in the upper zone of the water column have to be adapted.

Respiration rates measured for *Tethocyathus endesa* and *Caryophyllia huinayensis* in the context of this study did not show a clear effect of the carbonate chemistry, but were found to be greatly elevated in comparison with previous studies. Both the inter- and intraspecific comparison of the mass and calyx surface area increase indicate that *T. endesa* thrives better at high pH and that *C. huinayensis* seems to be better adapted to living in lower pH regimes than *T. endesa*. Both coral species seem to accrete carbonate at about the same rate when growing under conditions they are adapted to, but the results also suggest that *C. huinayensis* may be less effected by ocean acidification and the predicted reduction in pH. However, the question remains whether the elevated respiration rates indicate a high metabolic "cost" for the corals to maintain carbonate accretion rates.
Even though the respiration by *T. endesa* and *C. huinayensis* was likely influenced by other factors, further studies investigating the correlation of carbonate accretion and respiration of both corals are suggested. Identifying the mechanisms underlying the coral's adaption to reduced pH conditions, the state of the skeleton and active genes would help to assess the coral's health and metabolic activity and give a more detailed prediction of the future perspective of both coral species. All in all, the cross-transplantation experiment in the fjord Comau is a valuable approach to investigate the effects of reduced pH values, in particular by offering the opportunity of conducting longterm *in situ* experiments.

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A Appendix

Table A.1: Results for pH and oxygen values measured at different tides at the three sampling sites Liliguapi island, Cross-Huinay North and Cross-Huinay in the fjord Comau, Chile, during the expedition (Mar 17 - Apr 27 2016). Water samples were taken on 15 days in XHN and XH and on eight days in LG. For all days, triplicate measurements for each of the three water samples were taken and combined to one value for each water sample. Mean value and median per tide and location was then calculated from the samples. For each location, differences in the measurements taken at different tides were tested. For all tests a Mann-Whitney Rank Sum test was used.

Location	Parameter	Tide	Median	P-value
Liliguapi	pH	Falling	8.02	P = 0.057
		Rising	7.96	
	Oxygen	Falling	7.09	P <0.001
		Rising	8.98	
XHuinayN	pH	Falling	7.73	P = 0.291
		Rising	7.79	
	Oxygen	Falling	6.03	P = 0.606
		Rising	6.10	
XHuinay	pH	Falling	7.81	P = 0.807
		Rising	7.78	
	Oxygen	Falling	6.93	P = 0.114
		Rising	6.14	

Table A.2: Differences in pH and oxygen values between the three sampling sites at the three locations Liliguapi island (LG), Cross-Huinay North (XHN) and Cross-Huinay (XH) in the fjord Comau, Chile. During the expedition (Mar 17 - Apr 27 2016), water samples were taken on 15 days in XHN and XH and on eight days in LG. On each day, three water samples were taken, each sample measured three times and the triplicate measurements combined to one value. These values were then used for the analyses. As it was hypothesised that the high tidal amplitude will influence the measurements, locations were compared per tide. MWRS = Mann-Whitney Rank Sum test.

Parameter	Tested locations	Tide	P-value	Test
pH	LG vs. XHN	Falling	P = 0.307	MWRS
		Rising	P = 0.021	MWRS
	LG vs. XH	Falling	P = 0.083	MWRS
		Rising	P = 0.039	MWRS
	XHN vs. XH	Falling	P = 0.922	MWRS
		Rising	P = 0.933	MWRS
Oxygen	LG vs. XHN	Falling	P = 0.620	MWRS
		Rising	P <0.001	MWRS
	LG vs. XH	Falling	P = 0.496	MWRS
		Rising	P <0,001	MWRS
	XHN vs. XH	Falling	P = 0.582	MWRS
		Rising	P = 0.916	MWRS

Table A.3: Measurements and test results for sampling days with elevated oxygen values. On four of 15 sampling days during the expedition from Mar 17 - Apr 27 2016, elevated oxygen concentrations were measured at the two locations Cross-Huinay North (XHN) and Cross-Huinay (XH) in the fjord Comau, Chile. For all days, three water samples were taken, each sample measured three times and a mean value of the replicates calculated for each water sample. The results were then sorted for days of "low" and "high" oxygen values (saturation >90%) and a total mean value and standard deviation (St.Dev.) calculated. Statistical differences were tested between normal and elevated oxygen levels per tide at each location. For XHN, rising tide and XH, falling tide a t-test was used, for all others a Mann-Whitney Rank Sum test.

Location	Parameter	Tide	Oxygen	Mean	St. Dev.	Median	P-value
XHN	pH	falling	low	7.67	0.06	7.67	P <0.001
			high	8.07	0.06	8.09	
		rising	low	7.78	0.05	7.78	P <0.001
			high	8.16	0.00	8.16	
XHN	Oxygen	falling	low	5.00	0.65	4.78	P <0.001
			high	10.94	0.51	11.22	
		rising	low	5.77	1.44	6.05	P = 0.008
			high	11.90	0.01	11.90	
XH	pH	falling	low	7.70	0.08	7.66	P <0.001
			high	8.07	0.09	8.10	
XH	Oxygen	falling	low	5.86	1.00	5.54	P <0.001
			high	10.95	0.67	10.88	

Table A.4: Results for pH and oxygen values measured at different tides at the sampling sites Cross-Huinay North (XHN) and Cross-Huinay (XH) during the expedition from Mar 17 - Apr 27 2016 in the fjord Comau, Chile, excluding days with elevated oxygen concentrations. Water samples were taken on 15 days in XHN and XH and on eight days in LG. For all days, three water samples were taken, each sample measured three times and the triplicate measurements combined to one value for each water sample. A total mean value and median per tide was then calculated for each location. On four days, elevated oxygen concentrations (saturation >90%) were measured at XHN and XH, which resulted in higher pH and oxygen concentrations (Appendix Tab A.3) and were thus excluded below. For each location, differences in the measurements taken at different tides (falling and rising), excluding the measurements from days with elevated oxygen concentrations, were tested. For all tests a Mann-Whitney Rank Sum test was used.

Location	Parameter	Tide	Mean	St.Dev.	Median	P-value
XHN	pH	Falling	7.67	0.06	7.67	P <0.001
		Rising	7.78	0.05	7.78	
	Oxygen	Falling	5.00	0.65	4.78	P = 0.236
		Rising	5.77	1.44	6.05	
XH	pH	Falling	7.70	0.08	7.66	P = 0.008
		Rising	7.81	5.85	7.78	
	Oxygen	Falling	5.86	1.00	5.54	P = 0.866
		Rising	5.85	1.12	6.14	

Table A.5: Differences in ph and oxygen values between the three sampling sites at the three locations Liliguapi island (LG), Cross-Huinay North (XHN) and Cross-Huinay (XH) (fjord Comau, Chile) excluding measurements taken on days with elevated oxygen values. During the expedition (Mar 17 - Apr 27 2016), water samples were taken on 15 days in XHN and XH and on eight days in LG. On each day, three water samples were taken, each sample measured three times and the triplicate measurements combined to one value. On four days, elevated oxygen concentrations (saturation >90%) were measured in XHN and XH and these values were excluded from the analysis below. As it was hypothesised that the high tidal amplitude will influence the measurements, locations were compared per tide. For all comparisons a Mann-Whitney Rank Sum test (MWRS) was used.

Parameter	Tested locations	Tide	P-value	Test
pH	LG vs. XHN	Falling	$P < 0.001$	MWRS
		Rising	$P < 0.001$	MWRS
	LG vs. XH	Falling	$P < 0.001$	MWRS
		Rising	$P = 0.039$	MWRS
	XHN vs. XH	Falling	$P = 0.410$	MWRS
		Rising	$P = 0.415$	MWRS
Oxygen	LG vs. XHN	Falling	$P < 0.001$	MWRS
		Rising	$P < 0.001$	MWRS
	LG vs. XH	Falling	$P = 0.002$	MWRS
		Rising	$P < 0{,}001$	MWRS
	XHN vs. XH	Falling	$P = 0.019$	MWRS
		Rising	$P = 0.401$	MWRS

Table A.6: Monthly temperatures measured at the three sampling sites Liliguapi (LG), Cross-Huinay North (XHN) and Cross-Huinay (XH) in the fjord Comau, Chile. Data was collected using a data logger (TidbiT V2 Water Temperature Data logger, ONSET Computer Corporation, Bourne, USA) between January 2015 and April 2016 (LG: Jan 28 2015 - Apr 13 2016; XHN: Jan 2015 - Apr 15 2016; XH: Jan 29 2015 - Apr 12 2016). At LG, temperature was recorded every 15 minutes, while in XHN and XH, temperature could only be measured once every hour due to a malfunction in the installed loggers that was not noticed until they were recollected. Results are given in [°C] as mean value and standard deviation (St. Dev.) per month.

	Liliguapi		**Cross-Huinay North**		**Cross-Huinay**	
Month	**Mean**	**St. Dev.**	**Mean**	**St. Dev.**	**Mean**	**St. Dev.**
Jan 15	12,32	0,30	11,43	0,21	11,52	0,25
Feb 15	12,29	0,58	11,47	0,47	11,61	0,53
Mar 15	13,02	0,77	12,03	0,92	12,35	0,99
Apr 15	12,36	0,56	11,82	0,67	11,96	0,68
May 15	11,93	0,16	11,73	0,41	11,86	0,38
Jun 15	11,66	0,23	11,75	0,17	11,75	0,15
Jul 15	10,82	0,39	11,23	0,37	11,09	0,40
Aug 15	10,74	0,16	10,89	0,31	10,86	0,29
Sep 15	10,96	0,16	11,11	0,19	11,12	0,20
Oct 15	11,31	0,21	11,30	0,17	11,37	0,22
Nov 15	12,23	0,62	12,06	0,72	12,21	0,73
Dec 15	12,38	0,82	11,83	0,65	12,06	0,74
Jan 15	12,68	0,85	11,91	0,64	12,20	0,72
Feb 15	13,30	0,66	12,63	0,76	12,89	0,86
Mar 15	12,70	0,41	11,71	0,31	11,88	0,44
Apr 15	12,90	0,45	12,42	0,67	12,58	0,73

Table A.7: Measured respiration rates [μO_2 cm^{-2} d^{-1}] for *Tethocyathus endesa* (A) and *Caryophyllia huinayensis* (B), ordered by treatment. Corals were used in a reciprocal cross-transplantation experiment between sites of high and low pH in the fjord Comau, Chile. Respiration rates were measured with a Standard Luminescent-Probe for dissolved oxygen (LDO101, Hach Lange GmbH, Düsseldorf, Germany) after an incubation time of 12 hours. Results were then corrected for the incubation volume, background respiration by microorganisms and the calyx surface area. LG = Liliguapi island; XHN = Cross-Huinay North; XH = Cross-Huinay.

A	**LG**	**LG to XHN**	**XHN**	**XHN to LG**
	41,92	13,78	14,49	32,48
	68,24	9,01	16,31	25,96
	15,63	11,40	18,64	11,01
	41,62	11,87	12,84	13,78
	31,34	18,83	16,27	34,62
	9,60	24,11	17,94	46,86
	13,05		11,55	18,34
	13,40		9,91	15,82
	25,68		23,78	15,41
			16,81	
			13,07	
B	**LG**	**LG to XH**	**XH**	**XH to LG**
	18,75	17,35	17,90	155,44
	25,24	19,22	20,49	36,61
	57,65	13,28	19,24	97,15
		19,02	35,43	53,44
		22,93	24,22	51,97
		29,35		
		17,70		

Table A.8: Coral mass measured in 2014 - 2016 and the corresponding mass increase for *Tethocyathus endesa*. A two-year cross-transplantation experiment between sites of high and low pH was carried out in the fjord Comau, Chile. The mass of the specimens was calculated using the buoyant weight technique (Davies 1989) once a year during expeditions and the mass increase was calculated from these results. Specimens collected at the site of low (X) and high (L) pH were either reinstalled at the same, or transplanted (blue coloring) to the other site.

	Coral mass [g]			Mass increase [% yr^{-1}]	
No.	2014	2015	2016	2014-2015	2015-2016
X1	0,74	0,68	8,06	10,29	8,06
X2	0,98	0,88	10,61	44,00	10,61
X3	0,75	0,65	14,58	5,86	14,58
X4	0,70	0,75	-7,34	4,77	-7,34
X5	0,81	0,79	1,59	8,21	1,59
X6	0,66	0,63	4,81	15,92	4,81
X7	1,00	0,89	12,99	16,83	12,99
X8	0,68	0,60	14,20	-6,56	14,20
X9	1,07	1,00	7,43	5,07	7,43
X10	0,67	0,71	-5,77	9,91	-5,77
X11	0,71	0,64	10,05	6,14	10,05
X12	0,80	0,74	7,00	17,80	7,00
X13	0,65	0,69	-5,53	9,07	-5,53
X14	0,82	0,74	10,31	8,83	10,31
X15	0,78	0,67	15,59	4,36	15,59
X16	0,88	0,82	7,76	13,80	7,76
X17	0,93	0,86	8,16	4,27	8,16
X19	0,86	0,89	-3,53	7,49	-3,53
X20	1,09	0,98	11,65	11,17	11,65
X33	1,11	1,10	1,50	6,71	1,50
L1	0,89	0,98	0,94	9,77	-4,31
L2	0,72	0,72		-0,67	
L3	0,88	0,86		-1,73	
L4	0,83	0,91	0,92	9,26	1,29
L5	0,92	1,00	1,11	8,61	11,43
L6	0,75	0,82	0,68	9,74	-16,84
L7	0,48	0,54		12,23	
L8	0,53	0,60	0,73	14,37	21,54
L10		0,69	0,67		-2,92
L11	0,56	0,62	0,65	11,21	4,13
L12	0,68	0,73		7,46	
L13	0,71	0,75	0,87	6,07	15,28
L14	0,58	0,65		11,37	
L15	0,66	0,73	0,84	10,51	14,56
L16	0,69	0,76	0,82	10,82	7,00
L17	0,67	0,70	0,80	4,40	13,38
L18	0,64	0,74	0,84	16,26	13,49
L19	0,70	0,75	0,83	6,16	10,97
L88	1,03	1,09	1,22	6,10	11,43
L99	0,69	0,80	0,78	16,78	-3,13

Table A.9: Coral mass measured in 2014 - 2016 and the corresponding mass increase for *Caryophyllia huinayensis*. A two-year cross-transplantation experiment between sites of high and low pH was carried out in the fjord Comau, Chile. The mass of the specimens was calculated using the buoyant weight technique (Davies 1989) once a year during expeditions and the mass increase was calculated from these results. Specimens collected at the site of low (X) and high (L) pH were either reinstalled at the same, or transplanted (blue coloring) to the other site.

Sample No.	Coral mass [g]			Mass increase [% yr^{-1}]	
	2014	2015	2016	2014-2015	2015-2016
L0	0,78	0,81	0,91	4,15	12,95
L1	0,52	0,61	0,70	16,30	14,60
L9	0,66	0,76	0,79	14,15	5,15
L13	0,50	0,62	0,62	23,16	0,75
L18	0,64	0,67	0,72	4,06	7,14
NL2	0,79	0,82	0,84	3,86	2,51
NL3	0,79	0,81	0,82	2,94	0,78
NL6	0,59	0,68	0,75	13,96	11,14
NL8	0,65	0,69		6,87	
X1	0,53	0,84		57,13	
X2	0,70	0,73		3,93	
X10	0,63	0,68		7,27	
X12	0,62	0,74	0,81	20,06	9,67
X14	0,72	0,79	0,84	9,64	6,45
X15	0,55	0,69		24,67	
X21	0,74	0,74	0,74	0,40	-0,47
NX3		0,75	0,96		28,57
NX4		0,56	0,75		35,79

Table A.10: Calyx surface area measured in 2014 - 2016 and the corresponding increase for *Caryophyllia huinayensis*. A cross-transplantation experiment between sites of high and low pH was carried out in the fjord Comau, Chile. The calyx surface area was measured from top-view photos using Photoshop CS6 in 2015 and 2016 and the corresponding increase was calculated from these results. Specimens collected at the site of low (X) and high (L) pH were either reinstalled at the same, or transplanted (blue coloring) to the other site.

Sample No.	Calyx surface area [cm^2]		Calyx surface area increase [% yr^{-1}]
	2015	2016	2015-2016
L0	0,58	0,59	1,81
L1	0,54	0,55	0,50
L9	0,71	0,66	-6,71
L13	0,41	0,47	13,77
L18	0,63	0,60	-4,29
NL2	0,42	0,34	-20,68
NL3	0,55	0,53	-2,68
NL6	0,43	0,41	-4,99
NX3	0,27	0,21	-23,72
NX4	0,20	0,16	-19,29

Table A.11: Calyx surface area measured in 2014 - 2016 and the corresponding increase for *Tethocyathus endesa*. A cross-transplantation experiment between sites of high and low pH was carried out in the fjord Comau, Chile. The calyx surface area was measured from topview photos using Photoshop CS6 in 2015 and 2016 and the corresponding increase was calculated from these results. Specimens collected at the site of low (X) and high (L) pH were either reinstalled at the same, or transplanted (blue coloring) to the other site.

Sample No.	Calyx surface area [cm^2]		Calyx surface area increase [% yr^{-1}]
	2015	2016	2015-2016
X1	0,35	0,38	8,17
X2	0,61	0,56	-7,83
X3	0,52	0,68	31,58
X4	0,43	0,32	-24,99
X5	0,51	0,50	-2,65
X6	0,46	0,54	17,98
X7	0,60	0,86	42,59
X8	0,17	0,22	27,36
X9	0,56	0,57	2,69
X10	0,52	0,44	-14,84
X11	0,40	0,50	23,73
X12	0,52	0,54	4,37
X13	0,54	0,72	33,65
X14	0,51	0,64	25,32
X15	0,37	0,53	44,47
X16	0,56	0,64	13,59
X17	0,54	0,62	14,29
X19	0,71	0,61	-13,97
X20	0,50	0,57	13,02
X33	0,68	0,71	4,70
L1	0,61	0,53	-12,83
L4	1,03	0,89	-13,32
L5	0,35	0,49	37,73
L6	0,53	0,30	-43,32
L8	0,52	0,69	32,73
L10	0,60	0,51	-15,15
L11	0,44	0,44	0,32
L13	0,37	0,53	44,43
L15	0,51	0,55	7,79
L16	0,55	0,59	8,58
L17	0,48	0,51	5,50
L18	0,51	0,54	5,41
L19	0,39	0,46	17,53
L88	0,40	0,55	38,66
L99	0,37	0,34	-8,19

Plagiarism Declaration

I hereby declare that, to the best of my knowledge and belief, this Bachelor thesis entitled "Growth and Respiration of the Cold-Water Corals *Tethocyathus endesa* and *Caryophyllia huinayensis* in the Fjord Comau, Chile" is my own work. I confirm that each significant contribution to, and quotation in this thesis from the work, or works, of other people is indicated through the proper use of citations and references.

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Date Signature