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In situ Skeletal Growth Rates of the Solitary Cold-Water Coral *Tethocyathus endesa* From the Chilean Fjord Region

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Cold-water corals (CWC) can be found throughout a wide range of latitudes (79°N–78°S). Since they lack the photosymbiosis known for most of their tropical counterparts, they may thrive below the euphotic zone. Consequently, their growth predominantly depends on the prevalent environmental conditions, such as general food availability, seawater chemistry, currents, and temperature. Most CWC communities live in regions that will face $CaCO_3$ undersaturation by the end of the century and are thus predicted to be threatened by ocean acidification (OA). This scenario is especially true for species inhabiting the Chilean fjord system, where present-day carbonate water chemistry already reaches values predicted for the end of the century. To understand the effect of the prevailing environmental conditions on the biomineralization of the CWC *Tethocyathus endesa*, a solitary scleractinian widely distributed in the Chilean Comau Fjord, a 12-month *in situ* experiment was conducted. The *in situ* skeletal growth of the test corals was assessed at two sites using the buoyant weight method. Sites were chosen to cover the naturally present carbonate chemistry gradient, with pH levels ranging between 7.90 ± 0.01 (mean ± SD) and 7.70 ± 0.02, and an aragonite saturation (Ω_{arag}) between 1.47 ± 0.03 and 0.98 ± 0.05. The findings of this study provide one of the first *in situ* growth assessments of a solitary CWC species, with a skeletal mass increase of 46 ± 28 mg per year and individual, at a rate of 0.03 ± 0.02% day. They also indicate that, although the local seawater chemistry can be assumed to be unfavorable for calcification, growth rates of *T. endesa* are comparable to other cold-water scleractinians in less corrosive waters (e.g., *Lophelia pertusa* in the Mediterranean Sea).

Keywords: CWC, calcification, *in situ* growth, scleractinian, coral

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INTRODUCTION

More than 50% of the approximately 5,100 recent coral species are deep and cold-water corals (CWC) (Roberts et al., 2009). These corals are typically heterotrophic, lacking the photosymbionts known for most of their tropical counterparts (Freiwald et al., 2004; Roberts et al., 2009). Thus, most CWC species are found throughout a wide range of latitudes (79°N–78°S) and at depths below the euphotic zone, with vertical distributions ranging from below 8 m (Försterra and Häussermann, 2003) down to the abyssal plain at depths down to 4,000 m (Freiwald et al., 2004, 2021; Roberts et al., 2006; Cairns, 2007). In the absence of light-enhanced calcification processes (Falkowski et al., 1984), growth rates of scleractinian CWCs largely depend on other prevailing environmental factors, including food availability, currents, temperature, and in particular seawater carbonate chemistry (Mortensen et al., 1998; Flögel et al., 2014). As a result, their skeletal mass is reported to increase relatively slow (Orejas et al., 2011; Büscher et al., 2017, 2019) in comparison to that of their photosymbiotic tropical conspecifics, with only a few exceptions (see e.g., *Desmophyllum dianthus* in Jantzen et al., 2013a).

As biomineralization is a key physiological parameter for the fitness of calcifying organisms (Allemand et al., 2011), assessing skeletal growth over time allows addressing various research questions on the response of organisms to biotic and/or abiotic changes in the ecosystem, as well as their resilience to ongoing and persistent environmental changes (Lartaud et al., 2019). While the factors influencing growth and biomineralization rates of tropical, photosymbiotic corals have been intensively studied in recent decades (see e.g., Gattuso et al., 1998; Allemand et al., 2011; Chan and Connolly, 2013), growth rates of their cold-water and deep-sea congeners are less well known. This lack of information is mainly due to the difficulty of accessing their habitats, and consequently, there are few studies on the long-term growth of CWCs, especially *in situ*. A few studies have so far assessed long-term growth rates of the most common framework forming cold-water scleractinian *Lophelia pertusa* (Roberts et al., 2009) both, *in situ* (e.g., Larcom et al., 2014; Büscher et al., 2019) and under different laboratory conditions, e.g., different food supply (Büscher et al., 2017) or different pCO_2 levels (Hennige et al., 2014; Büscher et al., 2017). However, knowledge on skeletal growth rates of other CWC species, especially solitary and non-hermatypic corals, is very limited (Jantzen et al., 2013a), although some of these species may constitute a major component of the benthic community and provide three-dimensional structures and habitat for other species (e.g., in the Chilean fjord region; Försterra et al., 2016). Assessing their growth is, therefore, crucial to understand their general ecology, but also their vulnerability to regional and global impacts, and their likely resilience in future scenarios (Jaap, 2000; Rinkevich, 2014).

Ocean acidification (OA), caused by an increase in anthropogenic carbon dioxide (CO_2) emissions which result in lowered seawater pH and a decrease in oceans carbonate ion concentrations, consequently diminishes the calcium carbonate ($CaCO_3$) saturation state. For this reason, OA is predicted to impair the formation of biogenic $CaCO_3$ in marine calcifiers in general (Orr et al., 2005; Guinotte et al., 2006; Comeau et al., 2009) and in CWCs in specific (e.g., McCulloch et al., 2012a,b; Jantzen et al., 2013b; Hennige et al., 2014; Büscher et al., 2017). CO_2 levels in the oceans are predicted to likely reach 900–1,000 μatm by the end of the century, exceeding the levels experienced by most marine species over the past 30 million years (Lüthi et al., 2008). In addition, more than 70% of the global CWC communities live in regions that are predicted to be undersaturated with $CaCO_3$, particularly in the form of aragonite (Ω_{arag}) (Maier et al., 2013; Zheng and Cao, 2014). Especially the predicted decline in seawater pH and the associated problems of pH homeostasis in organisms are hypothesized to cause changes in calcification rates under predicted future OA conditions (Fabry et al., 2008; Cyronak et al., 2016).

In some regions of the world, for example the Patagonian fjord system, present-day carbonate water chemistry already resembles (and presumably even exceeds) these predictions for the world's oceans by the end of the century (Caldeira and Wickett, 2003; Orr et al., 2005). This environment makes the area an ideal "natural laboratory" for the *in situ* "future ocean scenario," and several studies have already investigated the response of the local biota to these extreme conditions (e.g., Fillinger and Richter, 2013; Jantzen et al., 2013a,b). In Patagonian fjords, pH levels can be as low as 7.60 (Jantzen et al., 2013b; Försterra et al., 2014), and waters can be undersaturated with aragonite (Ω_{arag} as low as 0.78; Jantzen et al., 2013b). With an area of 240,000 km^2 and a total length of 1,500 km, the region is also one of the largest connected fjord systems on Earth (Pantoja et al., 2011), highly structured by various channels, islands, fjords, and archipelagos (**Figure 1A**). Patagonian fjords receive freshwater discharges and organic material originating from rivers and continental run-offs that generate large vertical and horizontal density gradients (Bustamante, 2009). These factors presumably shape the species assemblages in the region, resulting in a structurally and functionally unique ecosystem (Palma and Silva, 2004; Castro et al., 2011). The prevailing environmental conditions are also assumed to be the reason why some of the local CWC species display a surprisingly large vertical distribution range, from shallow depths of about 8 m down to 1,900 m, and probably even beyond (Cairns et al., 2005; Häussermann and Försterra, 2009; Försterra et al., 2016). Comau Fjord (42°22′ S, 72°27′ W), known for its pronounced vertical and horizontal pH gradients (Försterra et al., 2008; Fillinger and Richter, 2013; Jantzen et al., 2013a,b; Rossin et al., 2017), is a typical U-shaped fjord characterized by steep rocky walls with various slopes and overhangs, inhabited by a highly diverse benthic community. One locally common species is the solitary stony coral *Tethocyathus endesa* (Försterra et al., 2005; **Figure 1B**). This scleractinian reaches up to 11 mm in diameter, 8 mm in height, and is composed of a corallite and a polyp part. It occurs in association with the scleractinians *Desmophyllum dianthus* and *Caryophyllia huinayensis* (Cairns et al., 2005; Häussermann and Försterra, 2009; Försterra et al., 2016). However, while *D. dianthus* and *C. huinayensis* are mostly found under overhangs and on the steep slopes of the rock faces of these fjords, *T. endesa* is often found on plateau areas, with their calyx facing toward the water surface and has been reported at

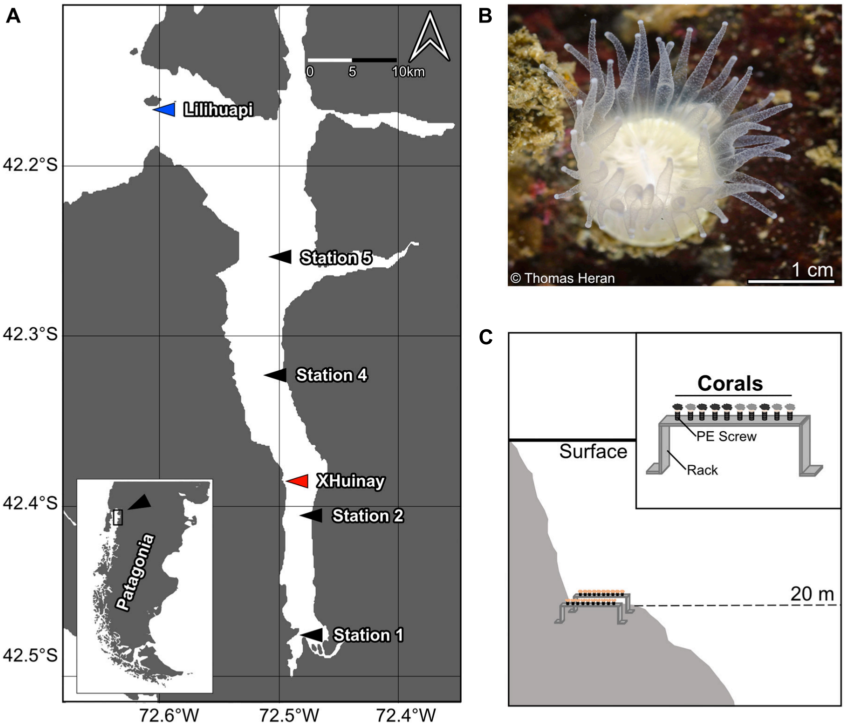

FIGURE 1 | (A) Overview of Patagonian fjord region with Comau Fjord (black rectangle) and 6 CTD stations within the fjord, including the experimental stations XHuinay in the central region of Comau Fjord (red arrow) and Lilihuapi at its mouth (blue arrow). **(B)** Close-up of a specimen of *Tethocyathus endesa* (top view). **(C)** Set-up of coral holder at a depth of 20 m, with coral specimens glued onto polyethylene (PE) screws, which are randomized attached to a mounted rack.

depths of up to 240 m, but also as shallow as 11 m (Häussermann and Försterra, 2009).

This study provides one of the first *in situ* assessments on skeletal growth rates of a solitary cold-water scleractinian species, *Tethocyathus endesa*. It also investigates the naturally present carbonate chemistry gradient in Comau Fjord (from the end to the mouth of the fjord; including low pH and occasional undersaturation of aragonite) in summer 2014 and summer 2015. The carbonate chemistry of the environment can be assumed to be unfavorable for biomineralization. A subset of experimental corals was also cross-transplanted between two sites (at the center and at the mouth of the fjord) to eliminate the possibility of incorrectly transferring the growth of two subpopulations, each genetically adapted to its own location, to the population occurring in the entire fjord.

MATERIALS AND METHODS

Characterization of Site

Comau Fjord is located in the northernmost part of the Chilean fjord region, east of Chiloé island (42°10′ to 42°50′ N and 72°40′ to 72°60′ W) (**Figure 1A**). It has a total length of 45 km and reaches a maximum width of 8.5 km (Häussermann et al., 2012). As a typical fjord in northern Patagonia (Silva, 2008), Comau Fjord is characterized by a strong vertical stratification, as it receives freshwater from precipitation (approx. 6,000 mm yr^{-1}) and rivers, mainly in winter and early spring (September–October), which creates a low salinity surface layer (0.5 m in summer—10 m in winter) with salinities as low as 2 (PSU) (Pantoja et al., 2011; Addamo et al., 2021). Below 18 m water depth, however, salinity is relatively constant at 32 (PSU) (Addamo et al., 2021), and the intermediate water layer, consisting of Modified Sub-Antarctic Water (MSAAW), compensates the freshwater outflow (Palma and Silva, 2004; Valle-Levinson et al., 2007). Due to the high tidal amplitudes in the region (Schwabe et al., 2006) organisms in the upper water layer (down to approx. 15–20 m) of the fjord are exposed to pronounced fluctuations in salinity and temperature (Häussermann and Försterra, 2009; Jantzen et al., 2013b). Below the pycnocline, monthly mean water temperatures fluctuate seasonally between 8 and 12°C (Häussermann et al., 2012; Jantzen et al., 2013b).

The experiment was conducted at two sites, (1) "XHuinay," a site at the western coast of the central fjord area (42°23′25″ S, 72°27′32″ W) and at (2) "'Lilihuapi" (42°09′43″ S, 72°35′27″ W), located at the mouth of the fjord (**Figure 1A**). Sampling sites were chosen based on the prevailing horizontal gradient in seawater carbonate chemistry (e.g., pH, total alkalinity (TA), and Ω_{arag}) between the end and the mouth of the fjord (Jantzen et al., 2013b). On the basis of previous assessments of the environmental conditions at the selected experimental sites (see Jantzen et al., 2013b), it was expected that the water at XHuinay would display a lower pH, TA, and Ω_{arag} than at Lilihuapi.

Assessment of Physical Parameters and Carbonate Chemistry

In February 2014, vertical profiles of pH and salinity were taken at six stations from the end of the fjord to its mouth (i.e., Station 1, Station 2, XHuinay, Station 4, Station 5, and Lilihuapi; **Figure 1A**), using a CTD multi-probe (SBE 19plus-SEACAT Profiler - Conductivity, Temperature, and Pressure with RS 232 Interface, Sea-Bird Electronics Inc.) equipped with a pH sensor (PHC301, Hach Lange GmbH, Germany). All casts were conducted by hand, and with maximum depths between 83 and 216 m; only the relevant averages for water depths between 17 and 23 m are reported here, as the experimental corals were located in a water depth of 20 m (for the full dataset see Laudien et al., 2014).

Additionally, seawater samples were taken between January and February 2015, at a water depth of 20 m at the two experimental sites (n = 4 per site), using a 2.5 L Niskin-type water sampler (Hydrobios GmbH, Altenholz, Germany). The pH was immediately determined manually with a portable pH probe (PHC301, Hach Lange Company, Düsseldorf, Germany). To further assess the carbonate chemistry at the experimental sites, seawater samples (n = 4 per site) were collected on the same day at a depth of 20 m, using SCUBA. For the sampling, a 500 mL borosilicate bottle (Schott Duran, Germany) was filled with seawater at a depth of 20 m, leaving no air space. Before these seawater samples were analyzed for total alkalinity (TA; i.e., the total concentration of bases and total dissolved solids), they were filtered through glass microfiber filters (Whatman GF/F 25 mm, GE Healthcare Europe GmbH, Freiburg, Germany) to remove particulate organic matter. For each sample, triplicate measurements of TA were performed using potentiometric titration (TitroLine alpha plus+TA05plus, SIAnalytics GmbH, Mainz, Germany and TitriSoft 2.72, Schott Instruments, Mainz, Germany) (Gran, 1952) using certified seawater as reference material (CRM) (Andrew Dickson, Scripps Institution of Oceanography). Further parameters of the carbonate system, i.e., dissolved inorganic carbon (DIC), total alkalinity (TA), partial pressure of carbon dioxide ($_p\mathrm{CO}_2$), aqueous carbon dioxide [CO_2(aq)], as well as aragonite and calcite saturation (Ω_{arag} and Ω_{calc}, respectively), were then calculated with the R package Seacarb (Lavigne and Gattuso, 2013) using first and second carbonate system dissociation constants of Lueker et al. (2000), as well as the dissociations of HF and $\mathrm{HSO_4}^-$(Dickson and Goyet, 1994), respectively.

In addition, ambient seawater temperature was recorded at the two experimental sites and at a depth of 20 m throughout the experimental period (1 year, from February 2014 till January 2015) using autonomous data loggers (TidbT V2 Temp Logger, Onset Computer Corporation, United States) with a 15-min recording interval.

Cross-Transplantation Experiment

In February 2014, 20 specimens of *T. endesa* (**Figure 1B**) with an average height of 4.1 ± 0.9 cm (mean ± SD) were collected by hand in a depth of 20 m at each of the two experimental sites (total = 40) by SCUBA divers. To minimize the risk of damage and stress during the sampling process, mainly corals growing on a biogenic substrate (primarily on shells of alive limpets *Crepidula* sp.) were collected together with their substrate. For the transport to the laboratory, specimens were placed in plastic containers, sealed water-tight at the collection site, ensuring no contact with either the brackish surface water layer or air. Experimental specimens were maintained for 48 h in a 30 liter flow-through aquarium, supplied with unfiltered seawater, continuously pumped up from 25 m water depth. Corals were then cut from their settling substrate, using a grinding disc attached to a rotary tool (Dremel 4,000, Dremel, The Netherlands), and any additional organic material adhered to the base of coral specimens was removed. Individual corals were then fixed (Super Flex Glue Gel, UHU GmbH und Co KG, Germany) to polyethylene (PE) screws and their initial skeletal mass was determined using the buoyant-weighing method (see below). Finally, corals were brought back to the field and attached (facing upwards) on a customized coral holder installed at a depth of 20 m at the respective sampling sites (**Figure 1C**).

Of the original 20 specimens collected per site (i.e., XHuinay and Lilihuapi), ten were returned to the site of origin, serving as a control referred to as "X" and "L" corals, respectively. The remaining corals were cross-transplanted to the respective other site (**Figure 1C**) and are now referred to as "X to L" (for corals transplanted from XHuinay to Lilihuapi) and "L to X" (for those transplanted from Lilihuapi to XHuinay). In this way, 20 *T. endesa* specimens were installed at each site, with ten control and ten cross-transplanted specimens randomly placed on the previously mounted holding racks. This cross-transplantation of corals between the two experimental sites was conducted to eliminate the possibility of incorrectly transferring the growth of two subpopulations, each genetically adapted to its own location, to the population occurring in the entire fjord.

Skeletal Growth Rate

The growth rate of *T. endesa* (as mass increase in mg per year and normalized for % increase per day) was determined using the buoyant-weighing technique (Jokiel, 1978; Davies, 1989), a method widely used for tropical, temperate, and CWCs (e.g., Marubini et al., 2001; Jantzen et al., 2013a; Comeau et al., 2014; Büscher et al., 2019). The buoyant mass of the corals in water ($\mathrm{m_{water}}$ in grams) was assessed using an analytical balance (CP 225D-OCE, Sartoris, Germany, precision 0.001 g) at the beginning of the experiment in February 2014 and then again at the end in February 2015. The mass of the specimens in air (m_{air}) was then calculated after Jokiel (1978):

$$m_{air} = \frac{m_{water}}{(1 - \frac{\rho_{water}}{\rho_{aragonite}})} \tag{1}$$

where ρ_{water} is the seawater density (g cm^{-3}), and $\rho_{\mathrm{aragonite}}$ is the skeleton density of aragonite (g cm^{-3}).

To calculate seawater density during the weighing process (Bialek, 1966), temperature and salinity were assessed using a temperature sensor (WTW ama-digit, Wissenschaftlich-Technische Werkstätten GmbH, Germany) and a refractometer (Sinokit Enterprise Limited, Hong Kong). Seawater temperature was kept at 12 ± 0.5°C. The difference between the coral mass in 2014 and 2015 was taken as the skeletal growth per year (mg yr^{-1}). In order to compare the growth rates of *T. endesa* with those of other CWC and tropical coral species, growth rates (G), were normalized to mass increase per day, as a percentage of the initial mass of the coral (G % d^{-1}) using Equation 2:

$$G = \frac{(m_2 - m_1)}{m_1 \times (t_2 - t_1)} \times 100 \quad (2)$$

where m_1 is the initial dry mass (in mg), m_2 is the dry mass at the end of the experiment, and $t_2 - t_1$ is the duration of the experiment between the final (t_2) and initial (t_1) time in days.

Statistical Analyses

To compare the skeletal mass increase of *T. endesa* between the four different groups (i.e., "X," "L," "X to L," and "L to X") and to test for significant differences ($p \leq 0.05$) between the *in situ* skeletal growth at the two experimental sites (i.e., XHuinay and Lilihuapi), pairwise Wilcoxon tests and Kruskal-Wallis tests were used. All statistical analyses were performed using R (Foundation for Statistical Computing, Austria, Version 3.5.3).

RESULTS

Physical Parameters and Carbonate Chemistry

In 2014, the seawater pH (averaged for a depth between 17 and 23 m; for the full dataset, see Laudien et al., 2014), assessed at the six sampling sites (i.e., Station 1, Station 2, XHuinay, Station 4, Station 5, and Lilihuapi; **Figures 1A**, **2A**) highlighted the pronounced horizontal gradient from the end of the fjord toward its mouth. The seawater pH ranged from 7.57 ± 0.01 (Station 1; mean ± SD) *via* 7.63 ± 0.02 at XHuinay, to an average of 7.90 ± 0.01 at Lilihuapi (**Figure 2A** and **Table 1**). The additional manual pH measurements from 2015, conducted only at the experimental sites (i.e., XHuinay and Lilihuapi), at a depth of 20 m further underline these particularly low seawater pH values in the region, with 7.70 ± 0.02 at XHuinay and 7.90 ± 0.01 at Lilihuapi (**Table 1**; for full dataset see Diercks et al., 2015a,b). Low TA also characterized the seawater at the two sites, with 2,234 ± 36 μmol l^{-1} at XHuinay, and 2,216 ± 19 μmol l^{-1} at Lilihuapi, resulting in an undersaturation (Ω_{arag} 0.98 ± 0.05) at XHuinay and a low aragonite saturation (Ω_{arag}1.47 ± 0.03) at Lilihuapi (**Table 1**).

Between February 2014 and January 2015, the mean water temperature at the central fjord at XHuinay was 11.5 ± 0.5°C, with monthly variations ranging from 10.55 ± 0.15°C in August 2014 (austral winter) to 12.64 ± 0.89°C in March 2014 (austral summer; **Figure 2B** and **Table 1**). The highest water temperature of 15.30°C was recorded in December 2014, and the lowest of 9.93°C was logged in August 2014. Maximum monthly temperature fluctuations of Δ0.89°C and Δ0.77°C were recorded in March 2014 and December 2014, respectively. At Lilihuapi, the average annual water temperature was 12.9 ± 0.9°C, with the water coldest in August 2014 (10.41 ± 0.17°C) and warmest in February 2014 (12.85 ± 0.93°C; **Figure 2B** and **Table 1**). The highest water temperature at this site (15.53°C) was recorded in February 2014, the lowest in August 2014 (9.46°C). The largest monthly temperature fluctuations of Δ0.93°C were recorded in February and December 2014 at Lilihuapi.

The salinity-driven pycnocline was very pronounced at XHuinay (**Figure 2C**; for full dataset see Laudien et al., 2014), extending between 5 and 12 m water depth, with an average salinity of 25.3 ± 0.07 in surface waters (<5 m) and 32.5 ± 0.2 in waters below 12 m. At Lilihuapi, the pycnocline was less pronounced but also present between 5 and approximately 12 m water depth, with a salinity of 30.1 ± 0.4 in shallower waters (<5 m) and 32.5 ± 0.1 below 12 m (**Figure 2C**). Consequently, the salinity at 20 m, the respective depth at which the *T. endesa* specimens were mounted on the coral holders, was similar at the two experimental sites, with 32.7 ± 0.1 at XHuinay and 32.6 ± 0.1 at Lilihuapi (**Table 1**).

Skeletal Growth

In January 2015, all experimental specimens were alive and none showed any obvious visible sign of degradation (e.g., tissue damage/loss or bioerosion). Overall, there was no significant difference between the skeletal growth rates of *T. endesa* specimens at the two experimental sites XHuinay and Lilihuapi (**Figure 3** and **Supplementary Table 1**). Neither between specimens of the control groups (i.e., "X" and "L"), which remained at their site of origin, nor between the cross-transplanted individuals (i.e., "X to L" and "L to X"). Therefore, growth rates of *T. endesa* from Comau Fjord were averaged for all specimens, indicating an increase of skeletal mass of 46 ± 28 milligrams per year and individaul, or 0.03 ± 0.02 % per day. Out of the 40 corals in the experimental setup, only two transplanted specimens showed a decrease or stagnation in mass over the experimental period, one from the group "X to L" with an average decrease of –0.02% per day, and one specimen of the group "L to X," where the mass remained almost identical (< –0.002% d^{-1}) between 2014 and 2015.

DISCUSSION

Physical Parameters and Carbonate Chemistry of Comau Fjord

Patagonian fjords are known for their low seawater pH, which is assumed to result from the high geological activity and seeps of volcanic origin in the region (Pantoja et al., 2011; Jantzen et al., 2013b; Muñoz et al., 2014). The emerging gradient from the mouth to the end of these fjords is also reflected in the carbonate chemistry of the seawater in Comau Fjord, characterized by an overall comparatively low pH and a horizontal pH gradient with the lowest values at the end of the fjord (Station 1 with 7.57 ± 0.01). In the center (Station XHuinay), a pH of 7.70 ± 0.02 was measured, and the highest pH of 7.90 ± 0.01 at its mouth (Station Lilihuapi). Here, the influence of the Pacific Ocean increases (Pickard, 1971), and the fjord water mixes with that of the Gulf of Ancud. Combined with the low total alkalinity (TA) of the fjord water, the carbon equilibrium shifts toward CO_2, leading to a reduction in the overall aragonite

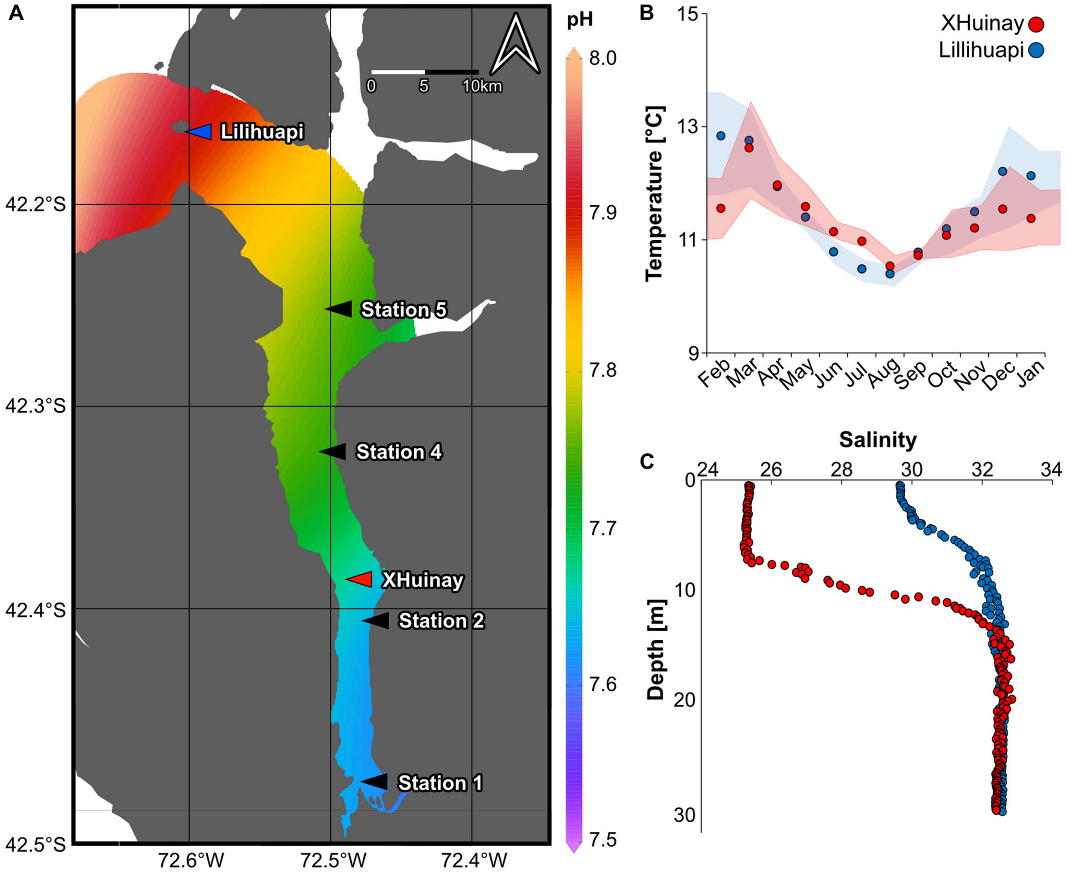

FIGURE 2 | Environmental parameters of Comau Fjord (2014–2015). **(A)** Average pH (17–23 m water depth; February 2014) throughout the fjord (end–mouth), resolved from six CTD casts at different stations within the fjord, including the two experimental stations XHuinay (red) and Lilihuapi (blue). **(B)** Monthly average water temperature (January 2014–February 2015) at a depth of 20 m at the two experimental sites. Dots refer to the monthly means, the shaded areas to the variation between minimum and maximum temperature during the respective month. **(C)** Salinity at the two experimental sites from the surface to 30 m depth (February 2014); XHuinay = red and Lilihuapi = blue.

TABLE 1 | Physical parameters and carbonate chemistry.

Station	Year	Depth [m]	Temp [°C]	Sal (PSU)	pH	TA [μmol l^{-1}]	DIC [μmol l^{-1}]	pCO$_2$ [μatm]	CO$_{2\ (aq)}$ [μmol l^{-1}]	Ω_{arag}	Ω_{calc}
XHuinay	2014	17–23	11.5 ± 0.5	32.5 ± 0.1	7.63 ± 0.02	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
	2015	20		32.7 ± 0.1	7.70 ± 0.02	2,234 ± 36	2,182 ± 34	955 ± 42	941 ± 42	0.98 ± 0.05	1.54 ± 0.08
Lilihuapi	2014	17–23	12.9 ± 0.9	32.6 ± 0.1	7.90 ± 0.01	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
	2015	20		32.6 ± 0.1	7.90 ± 0.01	2,216 ± 19	2,098 ± 21	577 ± 21	568 ± 21	1.47 ± 0.03	2.31 ± 0.06

Average annual water temperature (February 2014–January 2015; mean ± SD), CTD derived salinity and pH from 2014 for XHuinay (measurements at depth range: n = 26) and Lilihuapi (n = 34), as well as other carbonate chemistry parameters [i.e., pH, TA, DIC, pCO$_2$, CO$_2$ (aq), Ω_{arag} and Ω_{calc}; assessed with a handheld probe; n = 4] in 2015.

saturation state (Kleypas et al., 1999; Zeebe and Wolf-Gladrow, 2001), with occasional undersaturation of the waters, for example at XHuinay (Ω_{arag} 0.98 ± 0.05). Seawater that is undersaturated (<1) in aragonite is assumed to be corrosive and thus inhibits calcification as it may promote the dissolution of unprotected aragonite structures (Feely et al., 1988, 2008). However, it has also been suggested that the increased availability of bicarbonate, due to an enhanced pCO$_2$ may facilitate calcification, although it simultaneously decreases the Ω_{arag} (Marubini et al., 2008; Jury et al., 2010). Comparing the seawater chemistry at the two experimental sites in 2014 and 2015 with the previous reports from 2010 and 2011 (Jantzen et al., 2013b) also shows that it is subjected to temporal variations. While the seawater pH and salinity at the experimental sites remained stable over these five years, the TA in 2010/11 at both sites were slightly lower than the ones measured in the present study. Salinity mainly influences TA of the ocean and thus the corresponding Cl$^-$ and Na$^+$ concentrations, as well as biogeochemical processes such as the production of particulate organic matter by microalgae and the precipitation of calcium carbonate (Wolf-Gladrow et al.,

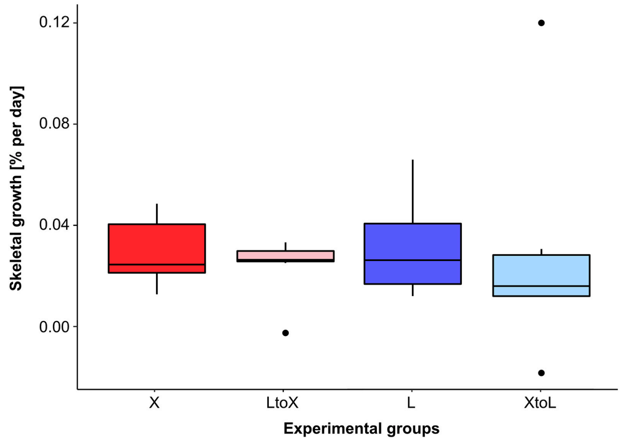

FIGURE 3 | Skeletal growth rates [% d^{-1}] of *T. endesa* specimens from four experimental groups. Growth rates of control corals from the central region of Comau Fjord at XHuinay (X; red) and of corals transplanted from Lilihuapi to XHuinay (L to X, light red), as well as the control corals at the mouth of the fjord at Lilihuapi (L, blue) and of corals transplanted from XHuinay to Lilihuapi (X to L; light blue).

2007). Since salinity did not change during the respective years, the amount of organic matter and the precipitation of calcium carbonate may be the cause of these TA differences. This observation may also be an indication of the dynamics of the abiotic environmental conditions in the region.

Given this, and the fact that the present study only includes the assessment at two time points (i.e., in February 2014 and February 2015), it remains unclear whether the differences in carbonate chemistry at the two experimental sites (i.e., XHuinay and Lilihuapi) persist throughout the year and/or if they are subject to fluctuations. Since the assessed skeletal growth rates of *T. endesa* at the two experimental sites (for both, cross-transplanted and control corals) were not significantly different, we report below on the general *in situ* skeletal growth rates of *T. endesa* in Comau Fjord.

In situ Skeletal Growth Rates of *T. endesa*

On average, the skeletal mass of *T. endesa* specimens increased by 46 ± 28 milligrams per year, corresponding to 0.03 ± 0.02% per day. These growth rates are comparable to those reported for other CWC species, such as *L. pertusa* from the North-Atlantic (0.01 ± 0.01% per day; Büscher et al., 2019), or *Dendrophyllia cornigera* (0.04 ± 0.02% per day; Orejas et al., 2011).

However, the growth of CWC species can be influenced by various environmental factors, such as temperature (Grigg, 1974; Matsumoto, 2007; Silverman et al., 2007), current speed (Purser et al., 2010), prey abundance (Silverman et al., 2007; Purser et al., 2010; Naumann et al., 2011), and the aragonite saturation status (Gattuso et al., 1998; Silverman et al., 2007; Jury et al., 2010; Form and Riebesell, 2012; Büscher et al., 2019). The relatively harsh environmental conditions of Comau Fjord (with particularly low pH and Ω_{arag}) may thus challenge the calcium precipitation in *T. endesa*, resulting in reduced growth rates than would be the case under more calcification-favorable conditions. The variety of growth responses of marine calcifiers to a low seawater pH may thus reflect the actual range and plasticity of acclimatization potentials of some species to maintain their skeletal growth rates, over a range of seawater Ω_{arag} (McCulloch et al., 2012a,b; Cohen et al., 2017). For instance, some solitary and temperate coral species, such as *Caryophyllia smithii* (McCulloch et al., 2012a) and *D. dianthus* (Wall et al., 2016), are suspected being capable of an active physiological adaption to the low pH of ambient seawater by regulating their internal pH through an increased Ca^{2+}-ATPase activity (McCulloch et al., 2012a,b). Consequently, these species are capable to regulate the pH in their tissues up to 0.78 units above the pH of the surrounding seawater (McCulloch et al., 2012a,b). As *T. endesa* shows skeletal growth rates comparable to those of other CWC species from less corrosive seas (e.g., Mediterranean Sea), this species may also be capable of such an up-regulation of the internal pH, when seawater Ω_{arag} is below 1 as it was the case in January 2015 in XHuinay (**Table 1**). However, the physiological responses of this species to its environment are still unknown and need future investigation. Such a pH elevation would also be accompanied by an increased energetic expenditure, leading to a reduction of energy for other physiologically important processes. A 0.1 unit decrease in seawater pH may result in a 10% increase in energy budget (McCulloch et al., 2012b). The finding that the majority of the corals in this experiment (95%) sustain net positive calcification rates under the prevalent, harsh environmental conditions thus suggests that such an potentially increased energy demand would be met by the relatively large zooplankton abundances and amounts of particulate and dissolved organic matter that the local fjord systems receive, either from marine or terrestrial primary production (Montero et al., 2011; Sánchez et al., 2011), or anthropogenic sources, such as detritus from terrestrial plants, urban, and aquaculture waste (Rojas and Silva, 2005). However, further research, including extension of the experiments reported here (e.g., over several years), but also on the physiological mechanisms involved, is needed to understand how *T. endesa* can sustain its growth rates and calcification over long term under the harsh local environmental conditions.

Comparison to Other Cold-Water Corals and Photosymbiotic Coral Species

Skeletal growth of tropical and photosymbiotic scleractinians has been extensively studied in the past, both *in situ* and under a variety of experimental conditions in the laboratory, for example under different light intensities (e.g., Rodolfo-Metalpa et al., 2008; Schutter et al., 2012), feeding regimes (e.g., Houlbrèque et al., 2003; HoulbreÌque et al., 2004), water temperatures (e.g., Carricart-Ganivet, 2004; Rodolfo-Metalpa et al., 2008), and nutrient availabilities (e.g., Ferrier-Pagès et al., 2000; Tanaka et al., 2007). However, data on growth rates of cold-water scleractinians are scarce, mainly because CWC ecosystems have only recently gained attention (Freiwald et al., 2004). This is particularly true for CWC that are part of benthic communities in remote areas, such as the solitary coral species *T. endesa* from the Chilean fjord region. Like other benthic species in this region (e.g., other CWC species such as *C. huinayensis*), *T. endesa* was only recently described (Cairns et al., 2005) and thus information on its ecology and physiology is still extremely scarce. The general lack of data for CWC is also due to the fact that there are only a few locations worldwide where these organisms are relatively easy to access, such as the Patagonian fjord system and some Norwegian fjords. As a consequence, only few studies have assessed long-term growth rates of CWCs (e.g., Brooke and Young, 2009; Orejas et al., 2011; Larcom et al., 2014; Büscher et al., 2019). However, these mainly focused on the most common framework forming cold-water scleractinian (Roberts et al., 2009) *L. pertusa*, and the solitary CWC species *D. dianthus* (Hassenrück et al., 2013; Jantzen et al., 2013a; Martínez-Dios et al., 2020), and their growth rates were assessed both, under different laboratory conditions, e.g., different food supply (Büscher et al., 2017) or different pCO_2 levels (Hennige et al., 2014; Büscher et al., 2017), and *in situ* (e.g., Brooke and Young, 2009; Larcom et al., 2014; Büscher et al., 2019). These studies also used a range of different techniques, such as geochemical analysis of skeletal isotopes (Mikkelsen et al., 1982; Mortensen et al., 1998), visual growth banding patterns (Brooke and Young, 2009), estimates from *in situ* video recordings (Larcom et al., 2014), or buoyant weighing (Orejas et al., 2011; Jantzen et al., 2013a; Büscher et al., 2019). The results of this study are therefore not only the first scientific report on skeletal growth rates of the CWC *T. endesa*, but also one of the first *in situ* assessments of a solitary CWC species in general.

The comparison of skeletal growth rates of *T. endesa* from this study to previous reports on other heterotrophic cold-water, or temperate coral species (**Table 2**) reveals that growth rates can vary considerably depending on species, location, and experimental approach (i.e., *in situ* or laboratory; long-term or short-term measurements). This highlights the importance of further studies on CWC species to gain a better understanding of their ecology, physiology, and response to a changing ocean. For instance, the 1-year *in situ* skeletal growth of *T. endesa* (0.03 ± 0.02% d^{-1}) was comparable to rates previously reported for *L. pertusa* from the North Atlantic (with a long-term *in situ* skeletal growth rate of 0.01 ± 0.01% per day; Büscher et al., 2019), and the Mediterranean (long-term rate of 0.02 ± 0.01% per day assessed in laboratory experiment; Orejas et al., 2011), as well as from *Dendrophyllia cornigera* (long-term growth rate of 0.04 ± 0.02% per day assessed in the laboratory; Orejas et al., 2011). However, the short-term (2 weeks) skeletal growth rates of *D. dianthus*, also from Comau Fjord, were between three times (when assessed *in situ*) and eight times (when assessed in a laboratory experiment) higher (Jantzen et al., 2013a) than those of *T. endesa*. However, it is noteworthy that the reported short-term growth rates of *D. dianthus* of 0.25 ± 0.18% per day (Jantzen et al., 2013a) is also one of the rare occasions when a heterotrophic CWC species exhibits growth rates comparable to photosymbiotic, tropical conspecifics, such as *Pocillopora damicornis* (0.2–0.3% d^{-1}; Piniak and Brown, 2008) or *Stylophora pistillata* (0.35 ± 0.07% d^{-1}; Ferrier-Pagès et al., 2000). These comparatively high growth rates, reported by Jantzen et al. (2013a) might also be biased by seasonal effects, as it has been shown that *D. dianthus* increases its feeding response linearly with prey abundance (Höfer et al., 2018). As the short-term growth rates of *D. dianthus* were assessed during austral summer, the potential oversupply of food during this season may have led to a temporary peak in skeletal growth, leading to an overestimation of the overall growth rates of this species.

When comparing the skeletal growth rates of different CWC species obtained in different studies, the limitations of the respective experimental approaches must also be taken into account. While *in situ* measurements are limited in determining all potential influencing factors responsible for coral metabolism and growth rates (e.g., food availability, as well as daily or seasonal variations of various water parameters), it has been shown that in laboratory experiments, the quality of the cultivation of the CWCs may have a significant impact (Jantzen et al., 2013a; Lartaud et al., 2014). Direct comparison of coral growth rates between different studies should thus be considered with some caution, as variations in the cultivation setups, divergent measurement methods, and time frames, as well as other factors (e.g., temperature, feeding regime, or ambient carbonate chemistry), may influence growth.

Other Considerations

Although we did not observe any obvious traces of bioeroding organisms (e.g., boring sponges, polychaetes or gastropods) on the experimental specimens, it cannot be excluded that the latter

TABLE 2 | Comparison of skeletal growth (% increase per day ± SD) between different cold-water, temperate, and tropical/photosymbiotic coral species.

Species	Location	% increase d^{-1}	Time	Exp. Setup	Temp (°C)	Method	References
Tethocyathus endesa	Comau Fjord, Chile	0.03 ± 0.02	1 year	*In situ*	12°C	Buoyant weight	This study
Desmophyllum dianthus	Comau Fjord, Chile	0.09 ± 0.08	2 weeks	Laboratory	12°C	Buoyant weight	Jantzen et al., 2013b
Desmophyllum dianthus	Comau Fjord, Chile	0.25 ± 0.18	2 weeks	*In situ*	12°C	Buoyant weight	Jantzen et al., 2013b
Lophelia pertusa	North Atlantic	0.01 ± 0.01	1 year	*In situ*	8°C	Buoyant weight	Büscher et al., 2019
Lophelia pertusa	Mediterranean Sea	0.02 ± 0.01	1 year	Laboratory	12°C	Buoyant weight	Orejas et al., 2011
Dendrophyllia cornigera	Mediterranean Sea	0.04 ± 0.02	8 months	Laboratory	12°C	Buoyant weight	Orejas et al., 2011
Desmophyllum dianthus	Mediterranean Sea	0.06 ± 0.03	8 months	Laboratory	12°C	Buoyant weight	Orejas et al., 2011
Madrepora oculata	Mediterranean Sea	0.11 ± 0.04	2 years	Laboratory	12°C	Buoyant weight	Orejas et al., 2011
Stylophora pistillata	Red Sea	0.35 ± 0.07	18 weeks	Laboratory	25°C	Buoyant weight	Ferrier-Pagès et al., 2000
Pocillopora damicornis	Hawaii, North Pacific	0.2–0.3	3 months	*In situ*	27°C	Buoyant weight	Piniak and Brown, 2008

may not have influenced the long-term *in situ* skeletal growth rates on a micro scale (Försterra et al., 2005), thus potentially leading to an underestimation of growth rates (Jantzen et al., 2013a). The possible colonization by bioeroding organisms also provides another potential explanation for the stagnation, or even decrease in skeletal mass in two of the experimental specimens. Though the *T. endesa* specimens in this study thrive under the comparatively harsh conditions of Comau Fjord, the exponentially growing economic interest in the fjord region increases anthropogenic pressure. The input of nutrients, sediment due to mariculture and road construction, and the input of pharmaceutical and anti-fouling substances (introduced by the salmon-farming industry) is already a severe threat to vulnerable benthic communities of the Patagonian fjord region (Bustamante, 2009; Försterra et al., 2014, 2016).

CONCLUSION

This study reports on the skeletal growth rates of the CWC *T. endesa*, inhabiting the Patagonian fjord region, providing one of the first assessments of *in situ* growth of a solitary CWC species. While *T. endesa* specimens in Comau Fjord are exposed to environmental conditions (in particular with respect to the carbonate chemistry of the surrounding seawater) that can be considered unfavorable for calcification, this species displays skeletal growth rates comparable to other scleractinian coral species from less corrosive cold-water and temperate environments, such as *L. pertusa* and *D. cornigera* from the North Atlantic and the Mediterranean.

However, it remains unclear whether *T. endesa* will also be able to sustain and adapt to future environmental conditions, as benthic communities of the Chilean fjord region may be further threatened by proceeding climate change, including ocean acidification. In addition there is an increase in direct anthropogenic pressure from expanding fisheries, land use and road building (Häussermann and Försterra, 2007; Buschmann et al., 2009; Försterra et al., 2016). Although Patagonia represents one of the most important fjord systems in the subpolar margin, only little is known about local benthic communities and the physiological and ecological responses of these systems to regional oceanographic conditions (Pantoja et al., 2011). It is therefore indispensable to continue investigations on ecological processes and dependencies of this unique biocenosis. This will promote the endeavors for legal protection of CWC habitats (Häussermann and Försterra, 2007), as the highly diverse communities of this region may otherwise be irretrievably lost before even been investigated (Häussermann and Försterra, 2009).

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: PANGEA: https://doi.org/10.1594/PANGAEA.846927, https://doi.org/10.1594/PANGAEA.846928, and https://doi.org/10.1594/PANGAEA.832187.

AUTHOR CONTRIBUTIONS

JL, VH, GF, and SR designed the experiment and contributed reagents, tools, and materials. SR, FR, and JL conducted the measurements. SR and FR analyzed the data, ran the formal analyses, and prepared the first draft. All authors contributed to improving the manuscript, read and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.757702/full#supplementary-material

Supplementary Table 1 | Buoyant weight data of the corals used in this study, and calculated growth (see also Fromula 2 in the main text).

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