What Happens After – Succession of an Epibenthic Hard-Bottom Community after Coral Mass Mortality in Chilean Patagonia

A Thesis Submitted in Partial Fulfillment of
an M. Sc. Degree in Marine Biology

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> “ Tief unten glaubt der Mensch ein Vogel zu sein.“
>
> \- Hans Hass

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Abstract

Climate-related extremes and anthropogenic impacts cause disturbances in benthic marine ecosystems. The fjords of Chilean Patagonia host a highly diverse benthic community, including three species of cold-water corals. The dominant scleractinian *Desmophyllum dianthus* Esper, 1794 shapes its habitat by forming calcareous skeletons and is assumed to be an important ecosystem engineer. After a significant disturbance in 2012 in Comau Fjord (42°20´S, 72°30´W), >99.9 % of the highly abundant scleractinian *D. dianthus* died along 8.4 km of coastline. This study analyzes the effect of the mortality event and subsequent recovery of the benthic community. To further investigate the role of *D. dianthus* in the community, a coral removal experiment was conducted. Underwater pictures of the community affected by the coral die-off (starting 2014) and the experimentally disturbed community (starting 2015) were taken annually to document the species succession, and abiotic parameters were measured. Image analysis was conducted to identify the occurring benthic species and measure abundance and percentage cover. Species richness *S*, Shannon-Wiener diversity *H'* and Pielou's evenness *J'* were calculated and statistical community analysis was applied.

After the mortality event, total abundance and percentage cover increased continuously from 2014 to 2016. The scleractinian *Caryophyllia huinayensis* Cairns, Häussermann and Försterra, 2005 became significantly more abundant. Octocorals and hydrozoans significantly increased in percentage cover, colonizing dead coral skeletons. No taxon exhibited continuous decline in abundance or cover. Individuals of *D. dianthus* resettled in the benthic community, exhibiting normal growth rates and a steady rise in abundance, and is expected to return to a dominant role in the community. Biodiversity indices were stable over the monitored time span and agreed with results of previous studies conducted in Comau Fjord. At coral removal sites, percentage cover increased due to expansion of encrusting bryozoans and immigration of actinians. Cover reached values comparable to control sites within one year. The changes in the benthic community in both monitoring stations could be attributed to the availability of free substrate and the relief of biotic pressure. The community showed high resilience and stability after the disappearance of the dominant species *D. dianthus* and no changes in biodiversity were shown. Due to the slow growth of cold-water communities, full recovery of the pre-mortality community structure is estimated to be a long process. This highlights the need for protection of this diverse ecosystem.

Zusammenfassung

Klimabedingte Extremereignisse und anthropogene Einflüsse verursachen Störungen der marinen benthischen Ökosysteme. Die patagonischen Fjorde Chiles beherbergen benthische Gemeinschaften mit sehr hoher Biodiversität, darunter auch drei Kaltwasserkorallenarten (Scleractinia). Die dominante Steinkoralle *Desmophyllum dianthus* Esper, 1794 prägt ihr Habitat durch das Bilden von Kalkskeletten und gilt als wichtiger Ökosystemingenieur. Im Jahr 2012 starben im Comau Fjord (42°20´S, 72°30´W) nach einer Umweltstörung >99.9 % der Individuen dieser Kaltwasserkorallenart entlang eines 8,4 km langen Küstenstreifens. In dieser Arbeit wurden die Auswirkungen der Korallenmortalität auf die benthische Gemeinschaft und dessen nachfolgende Erholung untersucht. Um die Rolle von *D. dianthus* innerhalb der Gemeinschaft genauer zu analysieren, wurden in einem experimentellen Ansatz die Korallen von einer designierten Fläche entfernt und die folgenden Veränderungen in der benthischen Gemeinschaft beschrieben. Unterwasseraufnahmen wurden jährlich von der Gemeinschaft, die durch die Korallenmortalität betroffen wurde (ab 2014), und von der Gemeinschaft der experimentell beschädigten Flächen (ab 2015) gemacht, um die Artensukzession zu dokumentieren. Zusätzlich wurden an diesen Stellen verschiedene abiotische Parameter gemessen. Anhand von Bildanalyse wurden sowohl die vorkommenden benthischen Arten identifiziert, als auch deren Abundanz und Flächenbedeckungsgrad gemessen. Artenreichtum *S*, Shannon-Wiener Diversität *H*‘ und Pielou’s Evenness *J*‘ wurden berechnet und multivariate Gemeinschaftsstatistik wurde angewandt.

Nach dem Korallensterben stiegen die Gesamtabundanz und der Gesamtflächenbedeckungsgrad zwischen 2014 und 2016 kontinuierlich. Die Steinkoralle *Caryophyllia huinayensis* Cairns, Häussermann und Försterra, 2005 wurde signifikant abundanter. Die abgestorbenen Korallenskelette wurden von Weichkorallen und Hydrozoen besiedelt, deren Flächenbedeckung signifikant zunahm. Kein Taxon wies stetige Abnahme in Abundanz oder Bedeckungsgrad auf. *D. dianthus* siedelte sich wieder in der benthischen Gemeinschaft an und wies normale Wachstumsraten und eine stete Abundanzzunahme auf. Es wird angenommen, dass diese Art wieder eine dominante Rolle in der Gemeinschaft erreichen wird. Die Biodiversitätsindizes blieben über den Untersuchungszeitraum stabil und stimmten mit den Werten aus vorherigen Studien im Comau Fjord überein. An Stellen wo Korallen experimentell entfernt wurden stieg der Flächenbedeckungsgrad der Gemeinschaft aufgrund der Ausbreitung von krustenbildenden Bryozoen und der Einwanderung von Seeanemonen (Actiniaria). Nach einem Jahr erreichte der Bedeckungsgrad vergleichbare Werte mit unbeschädigten Stellen. Die Veränderungen in der benthischen Gemeinschaft sind in beiden Untersuchungen auf das Angebot von freiem Substrat

und dem Nachlassen von biotischem Druck zurückzuführen. Die Gemeinschaft zeigte nach dem Verschwinden von *D. dianthus* eine hohe Widerstandsfähigkeit (resilience) und Stabilität. Die Biodiversität zeigte keine Veränderung. Aufgrund des langsamen Wachstums in Kaltwassergemeinschaften wird angenommen, dass die Wiederherstellung der vor der Störung herrschenden Gemeinschaftsstruktur ein langandauernder Prozess sein wird. Dies unterstreicht die Notwendigkeit von Schutzmaßnahmen für dieses vielfältige Ökosystem.

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List of Abbreviations

°C	degree Celsius
µmol	micromol
ANOVA	statistical analysis: Analysis of Variances
cf	"*confer*" Latin: compare, used to indicate possible species
cm	centimeter
CTD	Conductivity Temperature Depth
CWC	cold-water coral
DOM	dissolved organic matter
e.g.	*"exempli gratia",* Latin: for example
Feb	February
H'	Shannon-Wiener diversity
ind	individuals
J'	Pielou's Evenness
Jan	January
Jul	July
Jun	June

kg	kilogram
km	Kilometer
L	Liter
LG	Liliguapi
ln	natural logarithm
m	meter
m^2	square meter
Mar	March
max	maximum
min	minute
mm	millimeter
n	number
nMDS	statistical analysis: non-metric Multidimensional Scaling
O_2	oxygen
Oct	October
PERMANOVA	statistical analysis: Permutational Analysis of Variances
pH	negative decadic logarithm of the concentration of hydrogen ions in a solution, describing acidity
p_i	relative abundance of i^{th} taxon
S	species richness
SCUBA	self-contained underwater breathing apparatus
SD	standard deviation
SIMPER	statistical analysis: Similarity Percentages
SIMPROF	statistical analysis: Similarity Profile
SO	Soledad
sp.	species
spp.	species (plural)
TA	total alkalinity
XH	X-Huinay S
XHN	X-Huinay N
Σ	sum

1 Introduction

Ecosystem disturbances and succession

In recent decades, climate-related extremes and natural disasters attributed to climate change have increased in frequency and force, impacting terrestrial as well as marine ecosystems (IPCC, Summary for policy makers, 2014). In the Antarctic, climate-induced iceberg scouring has been shown to increase (Barnes and Souster, 2011), destroying benthic assemblages and possibly impacting biodiversity. Additionally*,* direct anthropogenic disturbances such as pollution, mining, fishing and eutrophication, as an effect of agri- and aquaculture, and resulting hypoxic conditions, cause damage to ecosystems, leading to mortalities and change in community structure, especially in the benthos (Gray *et al.*, 1990; Jones, 1992; Lim *et al.*, 2006; Buschmann *et al.*, 2009; Howarth *et al.*, 2011; Miljutin *et al.*, 2011; White *et al.*, 2012). These disturbances can cause the formation of free habitat, either by destruction of the old community or through the disappearance of dominant groups, such as hard corals (Norström *et al.*, 2009). Free habitat is recolonized by newly appearing or already present species. The process and sequence of taxa colonizing the substrate is called succession (Connell and Slatyer, 1977). Distinctions have to be made between primary succession, following the formation of new habitat, seasonal succession and long-term changes caused by climate fluctuation on a geological timescale, as well as secondary succession, following a temporary disturbance of the system (Platt and Connell, 2003). Different models are used to describe the dynamics of succession, which are assumed to be dictated by life history traits and competition (Connell and Slatyer, 1977). The FACILITATION and INHIBITION models are based on early arriving species shaping the environment and either facilitating or inhibiting the arrival and settlement of later species. The TOLERANCE model suggests that growth rates and life history dictate the sequence of species, where fast growing organisms are dominant early in the colonization, but other species are already able to settle. Due to slower growth, these taxa do not dominate until later in the succession. The community grows and is subject to interspecific competition for space or resources, until the species most tolerant to the conditions are dominant (Connell and Slatyer, 1977).

In the marine environment succession has been studied since the middle of the last century and across many habitats (Antoniadou *et al.*, 2010). Despite being well described in the rocky intertidal, knowledge on the succession of benthic communities on natural rocky substrate in the subtidal is scarce (Pacheco *et al.*, 2011). Studies on succession have been conducted on artificial new substrate, such as tiles and plates (Lotze *et al.*, 2002; Valdivia *et al.*, 2005; Pacheco *et al.*, 2010, 2011), as bio-fouling studies on anthropogenic structures (Rico *et al.*, 2012), mainly in temperate and tropical regions. The secondary succession of a community after disturbance events has been widely studied in polluted soft-bottom benthos (Borja *et al.*, 2006) and bleached or degraded coral reefs (Grigg, 1983; Brown and Suharsono, 1990; Sheppard and Loughland, 2010). In some cases, ecosystems do not return to their previous community structure but undergo a so-called phase shift to a new state. In coral reef studies, there are many cases of shifts from hard coral to macroalgal dominated communities (McManus and Polsenberg, 2004; Cheal *et al.*, 2010). Other taxa which have been reported to dominate communities after coral reef disturbances are soft corals, sponges, jewel and sea anemones as well as ascidians (Norström *et al.*, 2009).

Succession in cold-water ecosystems

In the polar and subpolar regions, where communities are subject to disturbances such as iceberg scouring, fluctuating salinity or effects of El Niño, studies of benthic succession revealed insights into ecosystem functioning (Arntz *et al.*, 2006; Beuchel and Gulliksen, 2008; Barnes and Souster, 2011). In Arctic Kongsfjorden, Svalbard, Beuchel and Gulliksen (2008) conducted a long-term study in the rocky subtidal on the development of the natural community versus areas where the rock had been cleared off. It took a recovery time of 20 years until the cleared area had reached a similar percentage cover as the natural community. This can be explained by the slow reproduction and growth rates of polar benthos. Studies by Pacheco *et al.* (2011) on artificial substrate in benthic systems off the coast of northern Chile lead to the assumption that convergence with the natural community would be achieved within three to four years. Disturbance was shown to affect the abundance and evenness of the subtidal community in north-central Chile and decrease the influence of the dominant species, leading to the re-emergence of less competitive species (Valdivia *et al.*, 2005; Cifuentes *et al.*, 2007).

Cold-water coral mortality event in Comau Fjord, Chile

In May 2012, Comau Fjord in Chilean Patagonia was affected by a significant disturbance which lead to the mass mortality of the scleractinian cold-water coral (CWC) *Desmophyllum dianthus* Esper, 1794. Försterra et al. (2014) observed a mortality event (over 99.9 %) of exclusively *D. dianthus* along more than 8.4 km of western coast line (42°22.429´S, 72°28.591´W to 42°26.439´S, 72°27.335´W) to a depth of at least 70 m. The coral skeletons remained attached to the wall and potentially provide new substrate (Figure 1). The rest of the benthic community was apparently unaffected. This also holds true for two other species of scleractinians: *Tethocyathus endesa* Cairns, Häussermann and Försterra, 2005 and *Caryophyllia huinayensis* Cairns, Häussermann and Försterra, 2005. Chilean Patagonia is a region with strong geothermal activity (Pantoja *et al.*, 2011). Seeps of strong reducing hydrothermal fluid occur in the fjords. In 2012, elevated concentrations of methane and sulfide were measured in Comau Fjord. Försterra *et al.* (2014) proposed these harmful conditions as one explanation for the coral death. In the last decades, aquaculture in the form of salmon farming has intensified in the fjords, with an over 300 % increase in yield in the Hualaihué province from 1995 to 2012. Resulting hypoxic events or a synergistic effect with methane/sulfide release might pose another explanation for the mortality event affecting *D. dianthus* (Försterra *et al.*, 2014).

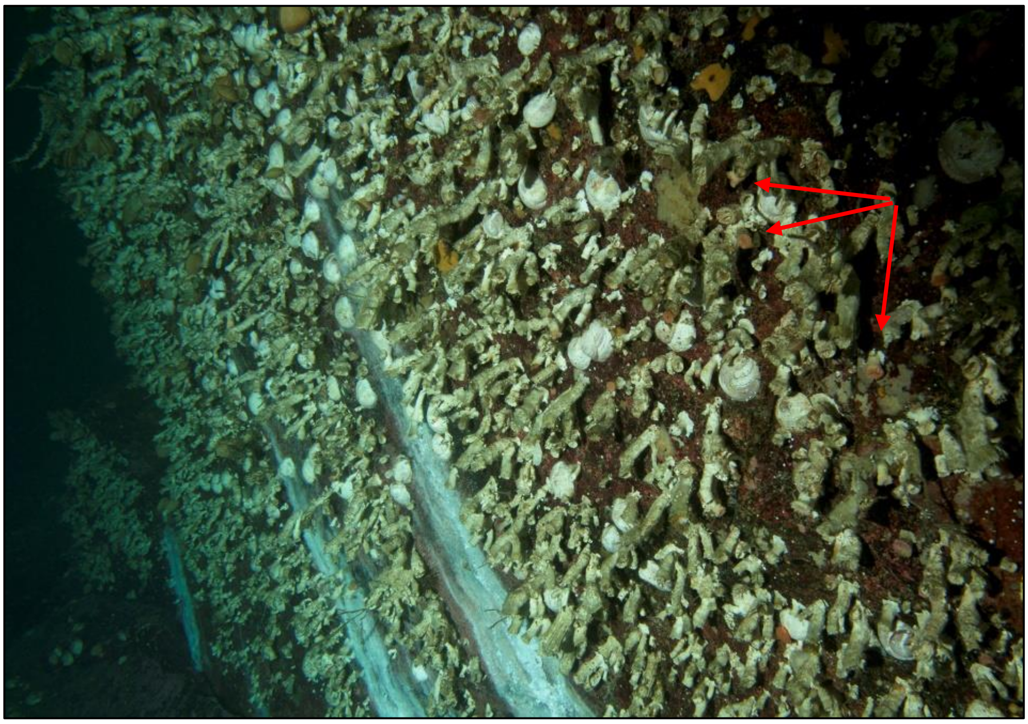

Figure 1: Dense bank of *D. dianthus* at X-Huinay N (XHN) in July 2013 after a mass mortality event occurred. White mats of filamentous bacteria can be seen. Only a few coral polyps survived the event (indicated by arrows, <0.01 % of the former coral abundance). ©V. Häussermann and G. Försterra, 2013.

Cold-water corals and ecosystem engineering

The scleractinian species, *D. dianthus*, is a cosmopolitan deep CWC species (occurring down to 2460 m), which is found in Comau Fjord in dense banks in unusually shallow depth (20 m, Försterra *et al.*, 2005). This allows the unique opportunity to perform *in situ* studies. CWC are cnidarians with the ability to live and grow in dark and cold environments without photosynthetic symbionts. These heterotrophic azooxanthellate taxa encompass stony corals (scleractinian), soft corals, black corals and hydrocorals (Freiwald, 2002; Roberts *et al.*, 2006). *D. dianthus* forms pseudo-colonies in high densities (over 1500 individuals m^{-2}; Försterra and Häussermann, 2009), where it can dominate the benthic hard-bottom community (Figure 2). Cairns *et al.* (2005) hypothesize *D. dianthus* to act as ecosystem engineer in the benthic ecosystem. In deep waters off New Zealand and Chile it is classified as a framework-building CWC (Fillinger and Richter, 2013).

Species that modify resources and their availability to other species within the ecosystem and thereby change, maintain or create habitats are called ecosystem engineers (Jones *et al.*, 1994). They can act as autogenic engineers, by modifying the environment through their own form or as allogenic engineers, by transforming resources into a different physical state, such as corals turning into coral sand (Wild *et al.*, 2013). Scleractinian zooxanthellate corals can form extensive reefs in the tropics, creating and maintaining a highly diverse and complex ecosystem. Likewise, azooxanthellate stony corals, such as *Lopehila pertusa* Linnaeus, 1758, which is the dominant framework species in deep waters of the Northeast Atlantic and related to *D. dianthus* (Addamo *et al.*, 2016), build complex matrices, supporting high biodiversity (Freiwald *et al.*, 2004). Studies revealed that along the Northeast Atlantic margin CWC reefs supported over 1300 species (Roberts *et al.*, 2009). Other framework building taxa might be gorgonians and octocorals, sponges, bivalves, ascidians and barnacles (Yakovis *et al.*, 2008; Cerrano *et al.*, 2010; Cathalot *et al.*, 2015). In Comau Fjord, multiple other benthic species construct complex habitats, such as the brachiopod *Magellania venosa* Dixon, 1789, the bivalve *Aulacomya atra* Molina, 1782 and the barnacle *Austromegabalanus psittacus* Molina, 1788 (Försterra *et al.*, 2016).

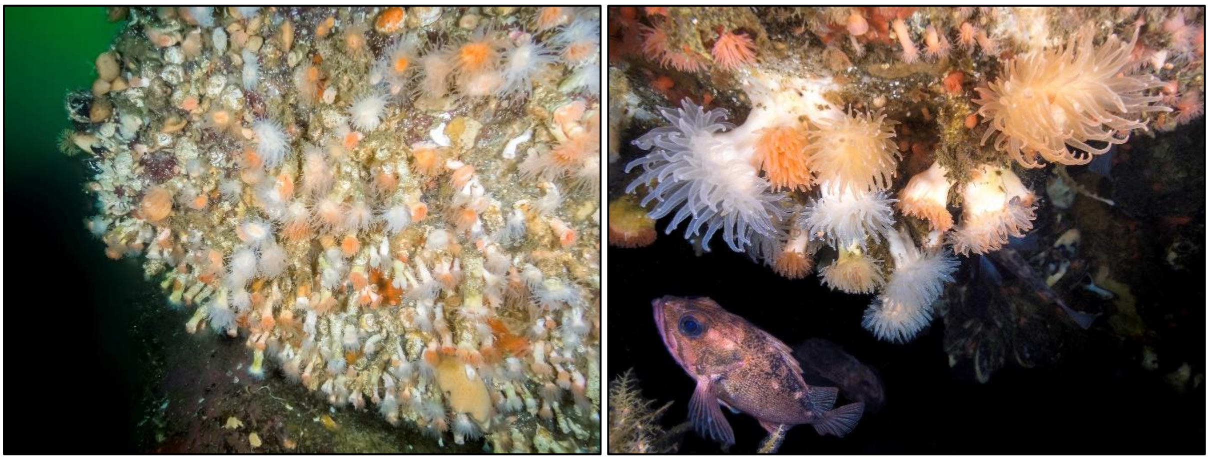

Figure 2: Scleractinian CWC *D. dianthus* forming dense banks in Comau Fjord (Chile), providing a habitat for multiple species (right: Patagonian redfish *Sebastes oculatus*, Valenciennes, 1833) in Comau Fjord, Chile. ©Thomas Heran Arce, 2017.

Ecology of Comau Fjord

Comau Fjord is a long-term study site in the Patagonian fjord system. It supports a high biodiversity in comparison with the fauna and flora in northern parts of Chile (Fernandez *et al.*, 2000; Försterra and Häussermann, 2009) and hosts a unique benthic fauna due to the phenomenon of deepwater emergence (Försterra and Häussermann, 2009). Due to its remoteness, parts of Chilean Patagonia are among the least studied marine systems in the world (Arntz, 1999; Schwabe *et al.*, 2006).

Considered a very fragile ecosystem (Iriarte *et al.*, 2010) and to support research, parts of Comau Fjord have been declared a Marine and Coastal Protected Area in 2001 (Försterra *et al.*, 2016). The fjord is characterized by a natural pH gradient from mouth to head as well as from surface to deep waters with values ranging from 8.1 at the surface to 7.4 at depth. This phenomenon has been studied in association with growth and respiration of the locally occurring calcifying scleractinians (Jantzen *et al.*, 2013b; Wurz, 2014; Diercks, 2015; Vossen, 2016). Long-term studies on primary succession of the benthic community have been conducted in Comau Fjord since 2009. Examples are the monitoring of community development on artificial substratum installed at different places in the fjord combined with different inclination angles and studies on sedimentation processes (Gottschlich, 2014). Reichel (2012) compared the succession of the benthic community at a site located at the central coast of the fjord (X-Huinay S, XH) with a site at the mouth of the fjord (Liliguapy, LG). Results indicated that the primary succession could be described by the TOLERANCE model where *D. dianthus* occupied the role of most tolerant and therefore dominant taxon. Serpulid polychaetes and encrusting bryozonas were identified as important early settlers. After three years, the community on the artificial substrate still significantly differed from the structure of the natural community, where scleractinians and octocorals were dominant, leading to the assumption that succession in Comau fjord is a slow process.

Objectives

The aim of the study is to make inferences about the role of *D. dianthus* in the succession of the benthic hard-bottom community in Comau Fjord in Chilean Patagonia. Photographic monitoring at seasonal intervals will be used to describe changes in abundance and percentage cover of benthic taxa following the death of *D. dianthus* at two stations affected by the coral mortality. The results may support the corals proposed role as ecosystem engineer and establish its importance for the ecosystem. The study will contribute to understanding how mortality events of single benthic components will affect the community in subantarctic systems and provide further insight into the dynamics of the benthos in Comau Fjord. It is based on the following working hypotheses:

1.1 In accordance with the TOLERANCE model, the species inventory will not change over the monitored time span. However, due to slow succession in cold-water ecosystems, the community will not return to its pre-mortality structure within the analyzed time.

1.2 The benthic community does not differ between the two stations. This hypothesis is based on the close vicinity of the stations and both being affected by the coral mortality event.

1.3 The benthic community undergoes a succession which will become visible as an increase in abundance and percentage cover over the years. Especially colonial species such as hydrozoans, octocorals and bryozoans will contribute to the difference.

1.4 *D. dianthus* will reappear in the community. Intact coral communities located north of the casualty area could act as seeding community and facilitate the resettlement of *D. dianthus*.

To further investigate how *D. dianthus* and the structure provided by its skeletons affects the benthic community, a *D. dianthus* removal experiment was conducted at a site unaffected by the observed coral mortality event. The succession of the treated areas in the following years was compared to unharmed communities at the same site. The dynamics will be described using abundance and percentage cover data obtained from images taken in 2015 and 2016. The preliminary results will be used in attempting to test the following hypothesis:

2.1 Cover and abundance of sessile benthic taxa increases during the monitored time span in areas where *D. dianthus* was removed and remain stable in untreated areas.

2 Materials and methods

2.1 Study area

The study was conducted in Comau Fjord (Figure 3) in the northern fjord system of Chilean Patagonia. The fjord extends over 45 km from its head in the south east, marked by the River Vodudahue, to its mouth in the north west, where the fjord connects to the Golf of Ancud. Comau Fjord is U-shaped with a maximum depth of 487 m and maximum width of 8.5 km, creating steep walls towards the coastline (Jantzen *et al.*, 2013b). The tidal amplitude can reach a maximum of 7 m. High precipitation (>5000 mm year^{-1}) and freshwater input from rivers create a layer of brackish surface water (Fillinger and Richter, 2013) followed by a strong thermo-pycnocline in up to 10 m water depth (Jantzen *et al.*, 2013b).

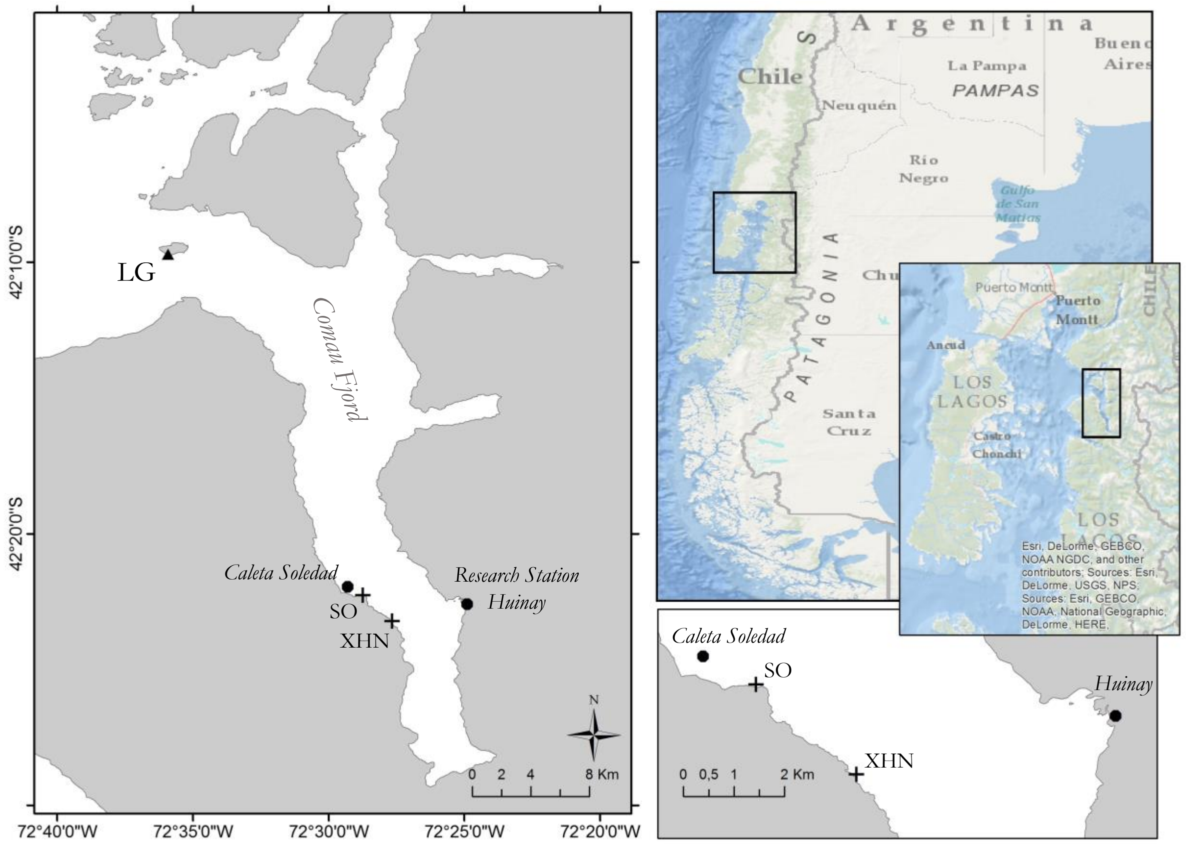

Figure 3: Map of Comau Fjord in Chilean Patagonia. Indicated are stations inside the fjord affected by the coral mortality (cross, SO and XHN) and a station at the mouth of Comau Fjord (triangle, LG), where an experiment studying the effects of coral removal was conducted. Black dots show the location of the salmon farm Caleta Soledad and the Research Station Fundación San Ignacio de Huinay.

Two stations inside Comau Fjord (Figure 3, Table 1) were selected to study the succession of the shallow benthic hard-bottom community after the coral mass mortality event in 2012. X-Huinay N (XHN) and Soledad (SO, ~ 1.5 km north of XHN) are located on the western side of the fjord across the research station Fundación Huinay. The stations are characterized by nearly vertical basaltic walls with overhangs, formerly colonized by banks of *D. dianthus*. Median water temperatures at 20 m depth range from 11 °C in the winter to 12.5 °C in the summer, with possible temperature extremes of 10 and 15 °C (Laudien *et al.*, 2017a, 2017b, 2017c). Soledad marks the northern endpoint of the coastal zone which was affected by the coral mortality. It is located at the tip of a land point formed by protruding rocks and in close vicinity to the salmon farm Caleta Soledad.

The study site Liliguapi (LG) is located at the southern tip of Isla Liliguapi at the entrance of Comau Fjord (Figure 3). An experiment was setup in 2015 to study the effect of the removal of *D. dianthus* on the secondary succession of the benthic hard-bottom community. The temperature curve is comparable to SO and XHN, with temperatures of 11 °C in winter and 12.5 °C in summer and temperature extremes of 10 to 16 °C.

Table 1 Coordinates and installation dates of the individual study sites.

Station	Position	Installation	
X-Huinay N (XHN)	S 42° 23.236’ W 72° 27.662’	02.2014	Study of benthic community affected by mass mortality of *D. dianthus* in 2012
Soledad (SO)	S 42° 22.274’ W 72° 28.737’	02.2014	
Liliguapi (LG)	S 42° 9.722‘ W 72° 35.915‘	02.2015	Study of benthic community after active removal of *D. dianthus*

2.2 Sampling design

2.2.1 Photo documentation

At the affected stations XHN and SO monitoring of the community by photography was set up in February 2014. Areas of 50×50 cm at 20 m water depth containing skeletons of *D. dianthus* were identified (XHN n = 11, SO n = 10). To mark the selected spots, holes were drilled into two corners of the 50×50 cm area by scientific divers on SCUBA using a pneumatic drill (Type DKR 36 with Dübellochbohrer 10mm, Atlas Copco, Nacka, Sweden). Stud bolts (V4A stainless steel M10) were fixed into the wall with glue (fischer© Injektionsmörtel FIS EM 390 S Fischerwerke GmbH & Co. KG, Waldachtal, Germany) and each area was marked with a yellow number plate. The bolts were used to attach a 50×50 cm custom photo frame, to ensure that the photographed area was consistent over the years and to match images to numbered spots. The frame is a custom-built aluminum construction with protruding wing nuts in the corners, which are adjustable to connect to the bolts in the wall. A camera can be attached in the middle of the frame to a raised crossbar, allowing for a central shot of the area in the frame (Figure 4).

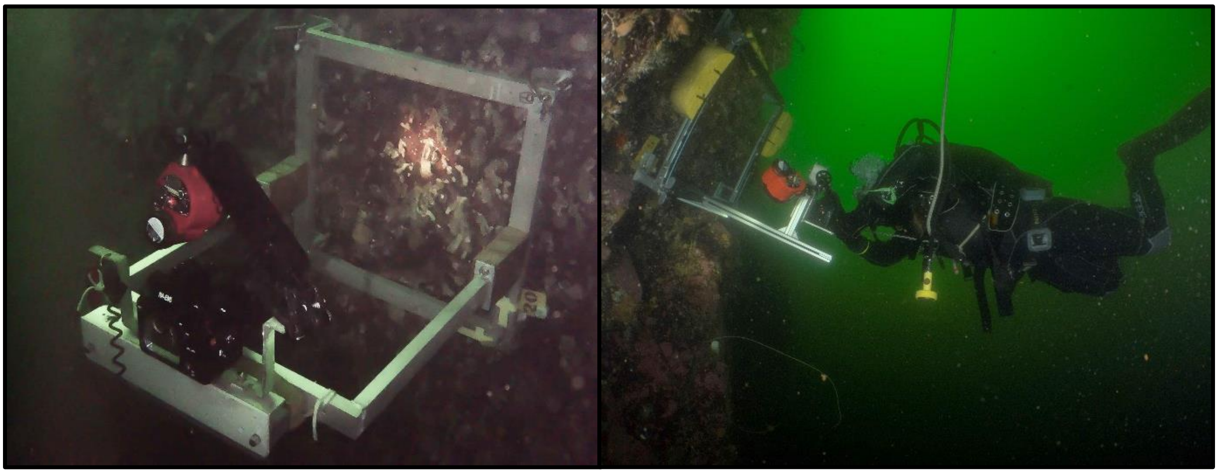

Figure 4: Photography setup consisting of aluminum frame and attached camera (left); diver on SCUBA conducting monitoring by photography (right, ©Felix Butschek, 2017). The frame marks the monitored area (here XHN), identifiable by the yellow number plate (right corner).

Photographs of the marked areas were taken quarter annually by scientific divers on SCUBA using an Olympus OM-D EM-5 digital camera (16.1x megapixel, rectilinear wide-angle zoom lens, Olympus, Tokyo, Japan) in an underwater housing (Nauticam, Hong Kong, Hong Kong) with two external strobes (D2000, INON, Kamakura, Japan). For the analysis, only annual pictures of the summer months were considered. Due to the poor quality of some images, single pictures taken in different seasons had to be used in the analysis (Table 2). At the station LG areas containing dense *D. dianthus* banks at 18 m depth were located in February 2015 (n = 10). The photography setup was installed identically to SO and XHN, to match the custom 50×50 photo frame with attached camera. Five spots were then selected as treatment areas and a wire brush was used to remove the corals and benthic fauna; five areas were left untreated as control. The areas were photographed annually.

Table 2 Dates of the annual photo monitoring at the different stations. Due to poor quality, single pictures taken during other seasons had to be used for the analysis (XHN Oct '14, Jun '15).

Station	**2014**	**2015**	**2016**
X-Huinay N (XHN)	Jun & Oct '14	Jan & Jun '15	Mar '16
Soledad (SO)	Feb '14	Jan '15	Mar '16
Liliguapi (LG)	/	Jul '15	Mar '16

2.2.2 Abiotic environmental parameters

Each station was equipped with a continuous temperature logger (HOBO TidbiT v2 Water Temperature Data Logger - UTBI-001, Onset Computer Corporation, Massachusetts, USA). The logger was fixed to a bolt at one of the marked areas and collected temperature data at 60 min intervals continuously for one year with precision of ±0.2 °C. The loggers were retrieved by divers annually, matching the dates of the summer pictures. To ensure a continuous data series, new loggers were installed prior to the retrieval of the old devices, to record parallel measurements. The temperature data was collected using the corresponding software (HOBOware, Onset Computer Corporation, Massachusetts, USA) and plotted with graphing software (Origin Pro 8 SRO 8.0724, Excel 2016). Raw data was uploaded in the world database PANGAEA (Laudien *et al.*, 2017d, 2017e, 2017a, 2017c, 2017b). Oceanographical data collection and water sampling was conducted at each station in February 2017 using a handheld CTD sensor (SBE19plus V2Seacat profiler, SBE43 Dissolved Oxygen Sensor, Sea-Bird Electronics, Washington, USA) coupled with a Niskin water sampler (Model 1010 Niskin Water Sampler, 5 L, General Oceanics, Miami, USA). Water samples were taken in triplicates at the depth of the fixed frames. Total alkalinity (TA) and pH of all water samples was measured in duplicates using the titrator TW alpha plus with TA05 plus (SI Analytics) with a pH electrode (SI Analytics Blue Line pH18). The water samples were filtered with a syringe using 25mm GF/F filters (Whatman) into 50 ml polypropylene test tubes. The titration was conducted in common practice using 0.05M HCl, which was prepared by diluting 0.1 N HCl Titrisol® (Merck, New Jersey, USA). As reference, certified reference material Batch No. 120 Dickson Standard (Scripps Institute of Oceanography, Massachusetts, USA) was measured in parallel.

2.3 Image analysis

2.3.1 Pre-Treatment

Prior to analysis, the pictures were sorted and selected for good quality, to ensure the same precision level in the later analysis for all images. Blurry or out of focus images were discarded. All pictures were corrected for chromatic aberration, angle and distortion using photo processing software (Adobe Photoshop Lightroom CC, Version 2015.12). Dark images were brightened up to make all structures visible. To ensure that measurements taken on the screen using imaging software represent the actual size of objects in reality, the image has to be straight and angles have to be corrected. The photo frame is constructed of two pairs of parallel lines. Using the "Guided Upright Tool", parallel lines were superimposed on the picture and fitted to the sides of the frame. This automatically rights the picture, correcting the angle the images were taken at (Figure 5.1

and 5.2). Distortion is an optical phenomenon caused by most lenses; the effect is also caused by taking photographs underwater. Using the right-angle sides of the frame as a representation of straight lines in reality, an overlaid grid was used to show straight lines on the screen (Figure 5.3). The distortion correction was then manipulated until the frame and the lines of the grid matched. For the combination of the wide-angle lens and the underwater housing, a setting of -10 was used to correct the distortion.

Figure 5: Processing of the raw images prior to analysis: 1) raw image, 2) correction of angle using parallel lines of frame 3) correction of distortion using grid overlay, 4) corrected picture ready for analysis.

After the images were adjusted to fit the real proportions of the objects, a custom scale was set using imaging software (Adobe Photoshop CC 2017, Version 2017.1.1). The yellow number plates attached to an expansion bolt in the corner of every picture have a uniform size (six centimeters width), which was used to set a custom scale, creating a scaling factor of pixel to centimeters. This factor is the basis for measuring distances and areas in images, scaling it and converting it to the appropriate unit. To avoid effects of the frame on the image analysis, such as shadows and blurring, a gap of five centimeters was kept between the frame and the analyzed area, creating a 40×40 cm square in the middle of the picture. This area was defined based on the latest images taken in April 2016.

2.3.2 Counting and measuring

The pictures were analyzed using imaging software (Adobe Photoshop CC 2017, Version 2017.1.1, Figure 6). All benthic immobile taxa bigger than 5 mm were identified and counted using a taxonomic key and identification guide for Chilean Patagonia (Försterra and Häussermann, 2009). This precision level was set based on the quality and resolution of the poorest images. Mobile species, excepting Actinians, were excluded from the analysis. Taxa were identified to lowest taxonomic level. Groups which were not clearly identifiable solely based on picture identification were classed in higher taxonomic groups (e.g. Porifera, Hydrozoa, Octocorallia). Bryozoans were classed into morphotypes (Försterra and Häussermann, 2009): erect-branched (e.g. *Cellaria* sp.), encrusting (e.g. *Smittina* sp.) and sheet-like (e.g. *Beania* sp.). Colonial organisms were counted as one, unless clear borders were discernible. Broken up colonies, which were identified in the previous year as single individual, were also counted as one organism in the following year. Octocorals with connected calyces and stolons were counted as single organism, unless clear gaps were visible. Unidentifiable taxa were grouped as "unidentified".

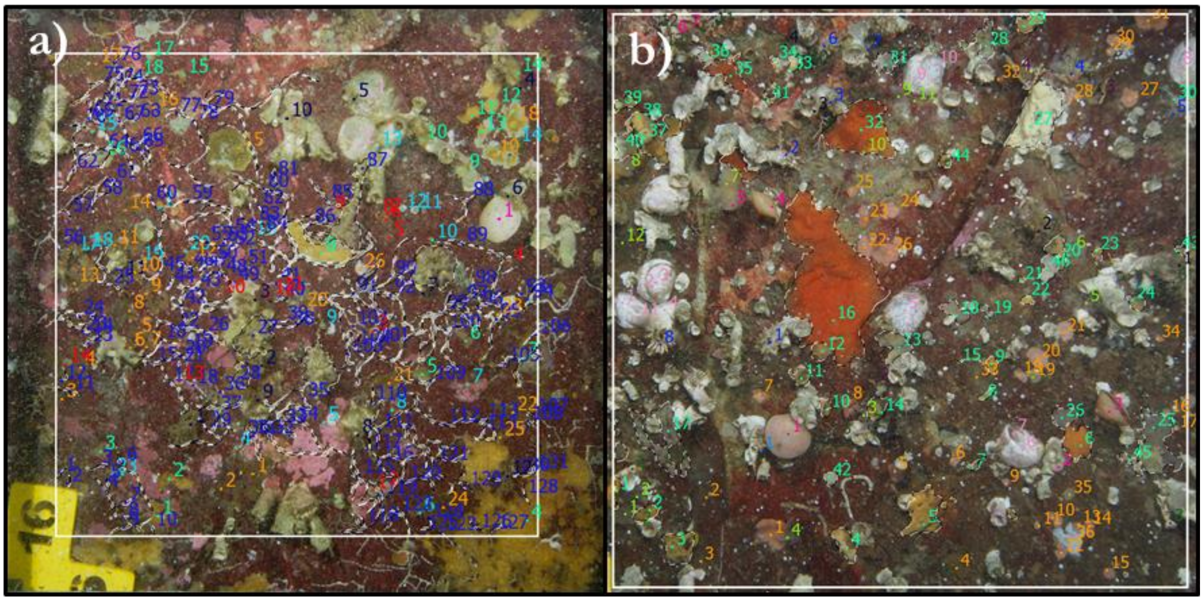

Figure 6: Image analysis: counting of different taxa, indicated by colors (blue: octocorals, orange: encrusting bryozoans, dark blue: hydrozoans, red: brachiopod *Novocrania lecointei*, light blue: scleractinian *Caryophyllia huinayensis*, light green: poriferans, pink: brachiopod *Magellania venosa*, lilac: gastropod *Crepidula dilatata*); area measurement (indicated by dashed line) of a) octocorals and b) poriferans in XHN, 2014. The white square marks the 40×40 cm analyzed area.

Area cover [cm^2] of the identified taxa was measured, using the “Lasso Tool” by tracing the organisms (Figure 6). Hereby only the top visible layer was considered, as described by Teixidó et al. (2002), (2004). It was converted into percentage cover based on the total area. Crustose Red Algae, not considered in abundance, were included in the cover analysis, as they can make up a large percentage of the area. The total area was defined as the set 40×40 cm sample area, subtracting non-analyzable space created by the topography of the wall, such as crevices. Taxa contributing with less than 1 % were not taken into consideration (Beuchel and Gulliksen, 2008). Counting data of individuals per taxon were converted into abundance [ind m^{-2}] using total area. Manual image analysis contains a human error. A high certainty for the identification and counting of the organisms can be assumed, as a total of 76 images were counted; the analysis was done in repeat to account for a learning curve. However, the manual measurement of cover using imaging software yields an error, which depends on the complexity of the organism. To keep this inaccuracy uniform, the analysis was conducted by a single person.

2.4 Data analysis

2.4.1 Community descriptors

To compare the biodiversity at the stations inside the fjord over the years, different community descriptors were calculated based on abundance data. Species richness *S* was defined as the number of different taxa in one sample, here different taxonomic levels were considered (Clarke and Gorley, 2006). The Shannon-Wiener diversity *H’* and Pielou’s evenness *J’* were calculated as described by Shannon and Weaver (1963) and Pielou (1966).

$$H' = -\sum_{i=1}^{s} p_i \times \ln p_i \tag{1}$$

$$J' = \frac{H'(s)}{H'(max)} \tag{2}$$

with s: number of taxa in sample, pi: relative abundance of the ith taxon in sample.

Species richness, Shannon-Wiener diversity and Pielou’s evenness were tested for significant differences over years and between stations using ANOVA (ANalysis Of Variances). Normal distribution (Shapiro-Wilks-Test) and equality of variances were tested before applying the ANOVA.

2.4.2 Ordination of samples

Abundance and cover data of the observed taxa by station and year were visualized using different graphing software (Excel 2016, OriginPro 8 SRO 8.0724). Statistical analysis was performed using the software PRIMER + PERMANOVA 6 (Anderson et al., 2008). Two data sets were built where the different taxa are considered variables and one defined area (identified by their yellow number plate) in one year (XHN_01_2014, XHN_01_2015) was treated as a sample. The metadata: station, year and treatment, were used as factors in the statistical analysis. To level the differing orders of magnitude of the data set, 4th root transformation was applied. This decreases the effect of stochastic occurrences of single taxa. (Clarke and Gorley, 2006). The Bray-Curtis coefficient was calculated and used to build a dissimilarity matrix. Based on this, cluster analysis and SIMPROF (SIMilarity PROFile,(Anderson et al., 2008) analysis were performed. The SIMPROF is an analysis based on null hypothesis testing to examine whether the observed similarities in the data match the similarities expected by chance. This reveals groups within the data that are not based on hierarchical clustering. It allows for a statistical validation of the cluster ordination. The results were plotted in a dendrogram and nMDS (non-metric multidimensional scaling) plot, showing the percentage similarity between the different samples and SIMPROF groups.

2.4.3 Multivariate statistics

A RELATE test, using Spearman rank correlation, was conducted to analyze possible correlation between the entire data set of abundance and cover in SO and XHN. The resulting rho-factor describes how well one data set can be explained by a second data set based on ranking. If the rho-factor is high, results of the statistical analysis and possible interpretations of e.g. “cover” can be transferred onto “abundance”. To test for significant differences in abundance and cover between years and stations, PERMANOVA (PERmutational ANalysis Of VAriance) testing was applied to all data sets, resulting in a pseudo F-statistic and a p-value. If the p-value is smaller than 0.05, the null hypothesis can be rejected. One-way pairwise and two-way designs with Monte-Carlo simulation were used to reveal the correlation between years and stations. Abundance and cover data from the station LG were additionally tested for differences between treatments. Based on the similarity matrices, a SIMPER (SIMilarity PERcentages) analysis was conducted for XHN and SO, to reveal the taxa which contributed most to the similarity within one and the dissimilarity between different groups.

3 Results

3.1 Abiotic environmental parameters

At the stations XHN and SO, abiotic parameters were measured at 20 m water depth using a CTD sensor. Salinity was 32.4 and oxygen saturation between 71 - 72 % (O_2 concentration ~190 µmol kg^{-1}). Water temperature was 12.1 °C and total alkalinity (TA) measured with 2233 µmol L^{-1} with pH values ranging from 7.77 to 7.80.

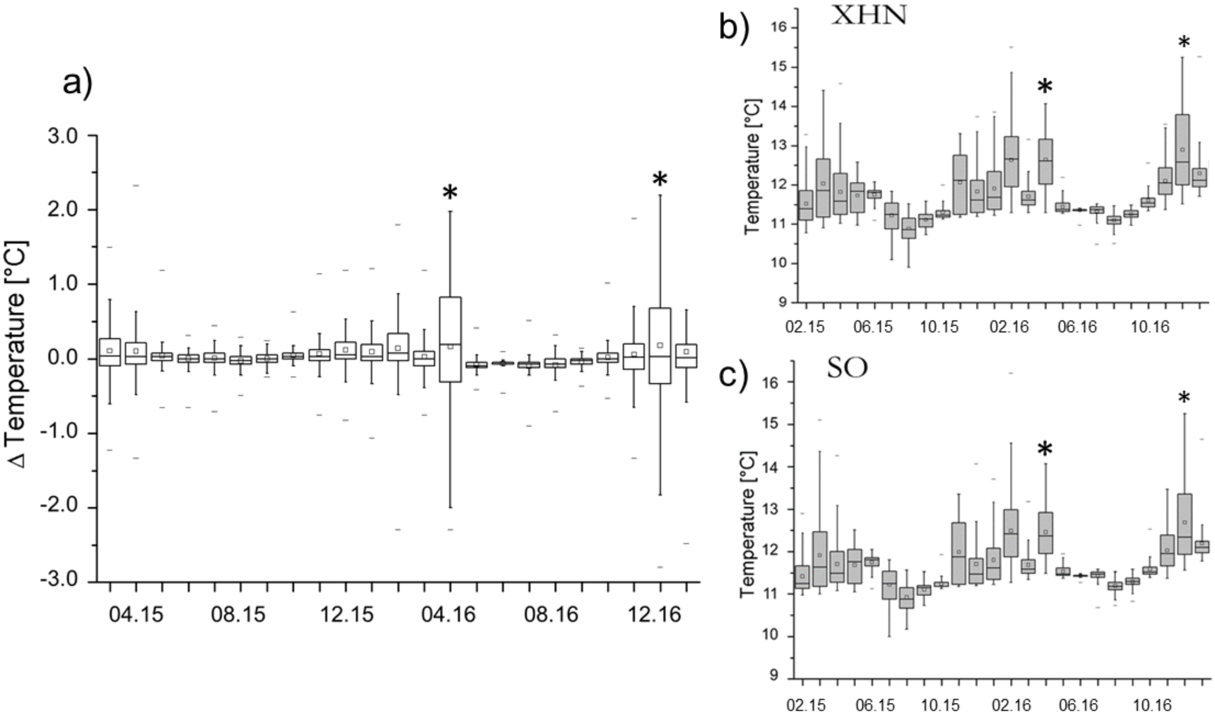

Figure 7: Left: a) Difference in water temperature [°C] between XHN and SO from February 2015 to January 2017 in 20 m depth measured with continuous temperature logger. Strongly deviating differences are marked with *. Right: Water temperature [°C] per months in b) XHN and c) SO from January 2015 to February 2017. The median is indicated by a square, the box represents the 25 and 75 percentiles, error bars show the 1.5× outliers, hyphen shows the maximum and minimum value.

No prevailing difference in water temperature [°C] was found over the course of two years (February 2015 - January 2017) between the two stations in 20 m depth (Figure 7a). The monthly average difference (ΔT) was 0 °C, with higher deviations from the average in the summer months. This reflects the water temperature fluctuations at XHN and SO, which follow a seasonality (Figure 7b and c). A high variation could be found in summer months (November – April), ranging from 11 - 15 °C, with extreme values of 16 °C. Temperatures in winter were more stable, ranging from 10 - 12 °C. A strong deviation from this pattern occurred in April 2016. In December 2016, the temperature in SO followed the course of XHN but with a slight lag, causing the high difference. A detailed temperature plot for these months (marked with *) can be found in Appendix 1. The measured abiotic conditions were different at the monitored areas in 18 m water depth at LG. Salinity was 32.4, water temperature 13.4 °C and oxygen saturation was 104 % (O_2 concentration ~ 272 µmol kg^{-1}). TA was 2241 µmol L^{-1} with a pH of 7.90. Water temperature [°C] shows clear seasonality with high variance in summer and lower stable values in winter (Figure 8).

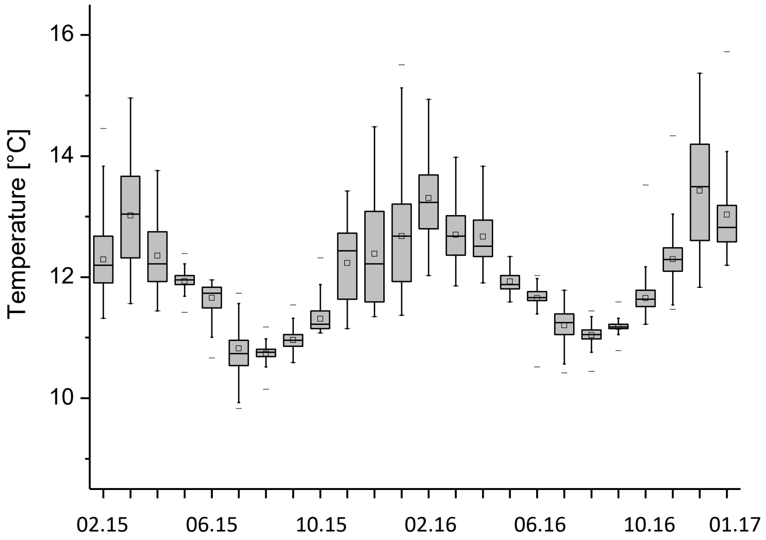

Figure 8: Water temperature [°C] per month at the station LG in 18 m depth from February 2015 to January 2017. The median is indicated by a square, the box represents the 25 and 75 percentiles, error bars show the 1.5× outliers, hyphen shows the maximum and minimum value.

3.2 Succession after coral mortality

3.2.1 Species inventory

A total of 17 taxa were identified, which are members of the benthic hard-bottom community at the stations XHN and SO from 2014 to 2016. Due to technical problems during photography, one area in SO had to be excluded from the analysis. In two cases, due to bad image quality, pictures of areas in XHN from a different season had to be analyzed, creating an irregular time interval between these analyzed images. In total, the analysis included nine areas in SO and eleven in XHN. Due to the quality of the images and the lack of taxonomic sampling, several taxa could not be identified to lower levels. This includes Porifera, Octocorallia and Hydrozoa. In some groups, such as Actiniaria, Polychaeta and Bryozoa, the association to a genus or species was possible for some individuals but not with enough certainty for all cases. Therefore, the identification was kept at a higher taxonomic level. Bryozoans were classed into three different morphotypes (erect-branching, encrusting, sheet-like), which are independent of taxonomic order or family. The species inventory at XHN and SO did not change from 2014 to 2016. This was supported by the species richness *S*

(S_{mean} ~ 11) which did not change significantly over the years at the stations inside the fjord. The Shannon-Wiener diversity *H*' did not differ between the stations. An increasing trend was visible over the monitored time span, but it was only significant (PERMANOVA p = 0.043) between 2014 (*H*' = 1.9) and 2016 (*H*' = 2.0). Evenness *J*' was stable (J' ~ 0.8) at both stations. All taxa which were present in 2014 could be found in the following years, no new taxon appeared over the course of the study. The only exception were sheet-like bryozoans, which increased in abundance and cover from 2014 to 2015 and disappeared in most areas in 2016.

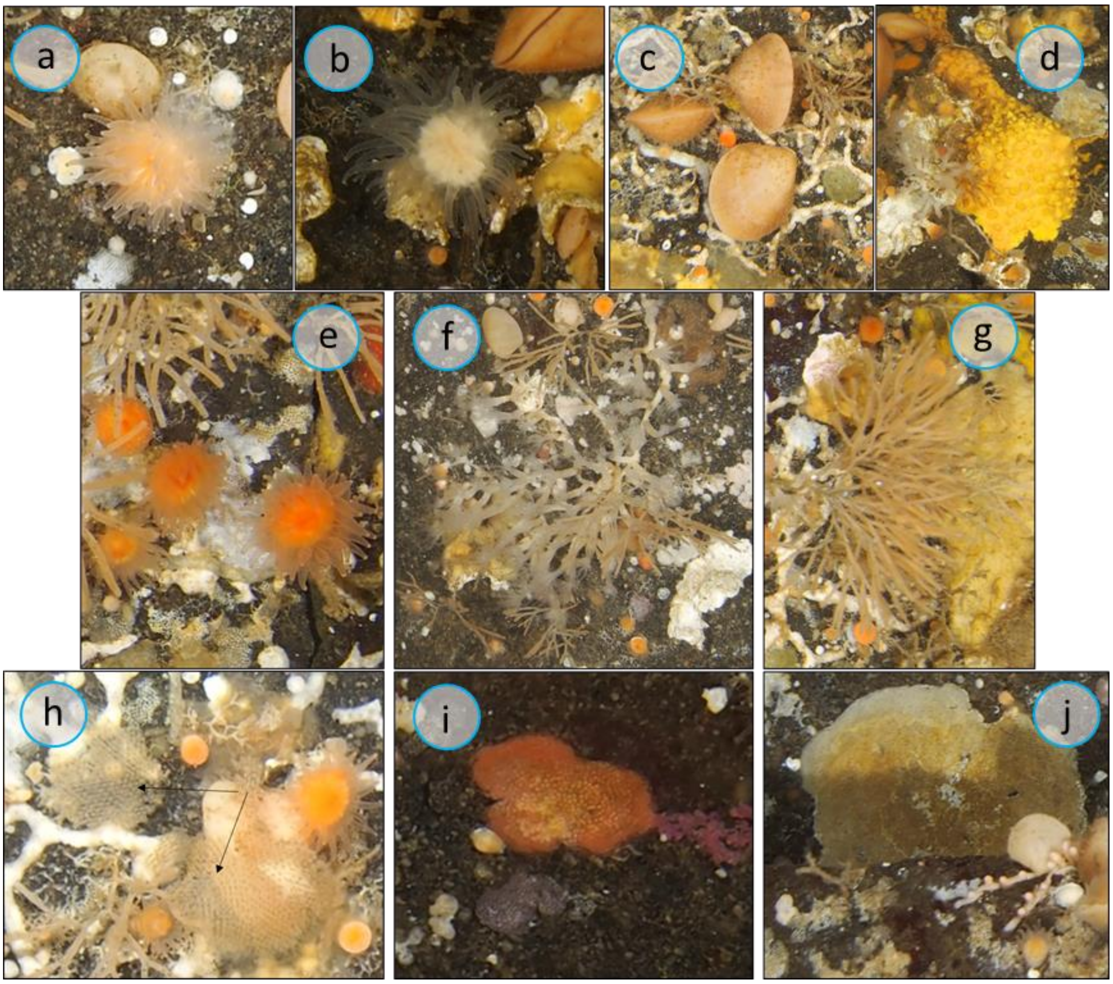

Figure 9: Underwater pictures of some abundant taxa occurring at XHN and SO. a) and b) scleractinian coral *Desmophyllum dianthus*, c) brachiopod *Magellania venosa*, d) poriferan *Cliona chilensis*, e) scleractinian coral *Caryophyllia huinayensis*, f) octocoral Cf. "*Clavularia*" *magelhaenica*, g) erect-branching bryozoan *Cellaria* sp., h) sheet-like bryozoan *Beania* sp., i) encrusting bryozoan Cf. *Smittina* spp., j) encrusting bryozoan Cf. *Smittina* sp.

A list of species and genera which were included in the coarser taxonomic groups is given in Table 3. The identification is solely based on picture analysis, uncertainties are marked by cf. For descriptive and statistical analyses only the 17 clearly identified taxa were considered (indicated in bold). Mobile species, besides Actiniaria, were not considered for the analysis.

Table 3 List of sessile benthic hard-bottom species encountered at the stations XHN, SO and LG from 2014 to 2016 (based on image analysis). Taxa which resemble species, but where no taxonomic identification was possible, are indicated by cf. Taxa included in the analysis are formatted in bold.

Porifera

- Demospongiae
    - *Cliona chilensis* Thiele, 1905
    - Cf. *Tethya papillosa* Thiele, 1905
    - Cf. *Axinella crinita* Thiele, 1905
    - Cf. *Scopalina* sp.
    - Various yellow encrusting sponges
    - Encrusting red sponge

Anthozoa

- **Actiniaria**
    - *Halcurias pilatus* McMurrich, 1893
    - *Acontiaria* sp. (brown)
- Scleractinia
    - ***Desmophyllum dianthus*** Esper, 1794
    - ***Caryophyllia huinayensis*** Cairns, Häussermann & Försterra, 2005
    - ***Tethocyathus endesa*** Cairns, Häussermann & Försterra, 2005
- Corallimorpharia
    - Corynactis sp.
- **Octocorallia**
    - *Rhodelinda gardineri*
    - Cf. *„Clavularia" magelhaenica* Studer, 1878
    - Cf. *Incrustatus comauensis* van Ofwegen, Häussermann and Försterra, 2007
    - *Primnoella chilensis* Phillipi, 1894

Hydrozoa

Polychaeta

- Spionida
    - Cf. *Spiochaetopterus* sp.
- Serpulida spp.
- Sabellida
    - Cf. *Apomatus* sp.

Mollusca

- Gastropoda
    - ***Crepidula dilatata*** (Lamarck, 1822)
- Bivalvia
    - ***Aulacomya atra*** Molina, 1782

Brachiopoda

- ***Magellania venosa*** Dixon, 1789
- ***Novocrania lecointei*** Joubin, 1901

Crustacea

- **Cirripedia**
    - *Notobalanus floscus* Darwin 1854

Bryozoa

- **Erect-branching**
    - *Cellaria* sp.
    - Cf. *Caberea* sp.
- **Encrusting**
    - Cf. *Smittina* spp.
    - *Membranipora isabelleana* d'Orbigny, 1842
    - *Disporella* sp.
- **Sheet-like**
    - *Beania* sp.
    - *Microporella* sp.

Ascidia

- ***Didemnum studeri*** Hartmeyer, 1911

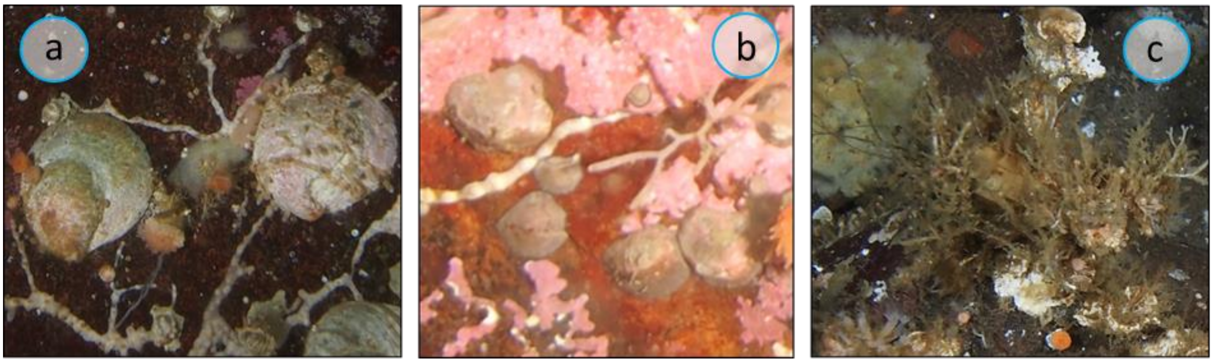

Figure 10: Pictures of some abundant taxa occurring at XHN and SO. a) *C. dilatata*, b) *N. lecointei*, c) Hydrozoa covering *Cellaria* sp.

3.2.2 Comparison between the stations XHN and SO

The benthic communities at the stations XHN and SO were significantly different in terms of abundance [ind m^{-2}] of individual taxa (PERMANOVA F = 15.38, p = 0.0001) as well as percentage cover (PERMANOVA F = 25.78, p = 0.0001) in all three monitored years. This difference between stations is independent of differences between years, as revealed by PERMANOVA testing of the correlation between the factors station and year (abundance: F = 0.61, p = 0.82; cover F = 0.26, p = 0.96).

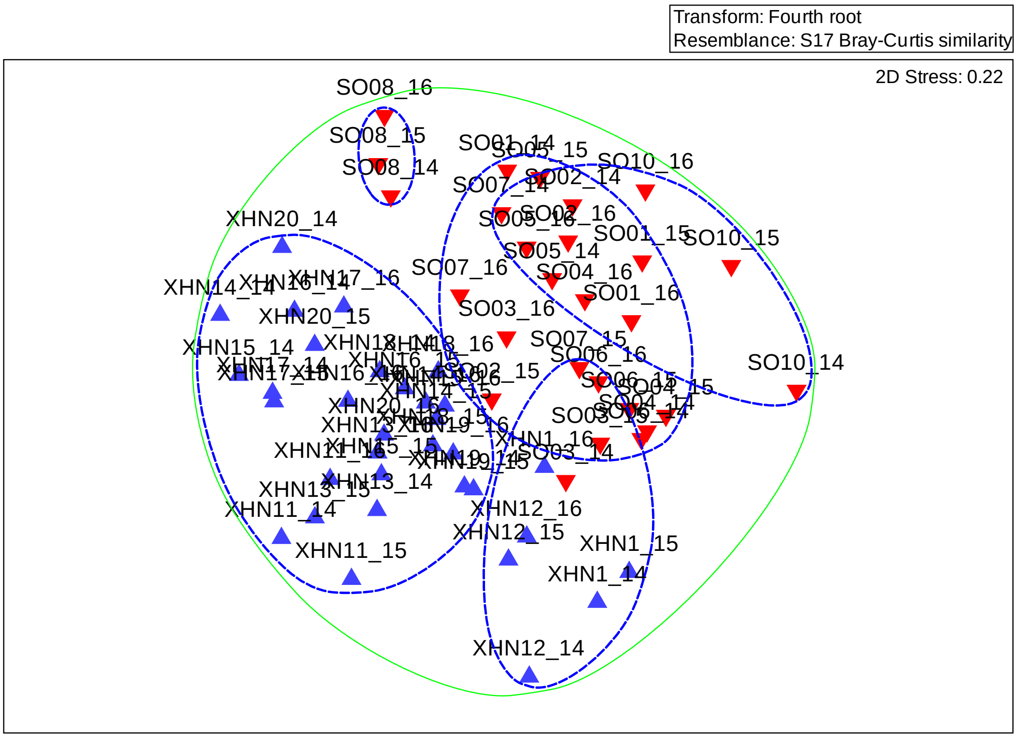

Figure 11: nMDS plot of taxon abundance [ind m^{-2}] from 2014 to 2016 separated by station: XHN (blue triangle) and SO (red triangle). The Bray-Curtis similarity (%) is given in two levels: 75 (green line), 80 (blue line).

The taxon abundance, displayed in a nMDS plot (Figure 11), can be coarsly separated into XHN (blue) and SO (red). At a similarity level of 80 %, some areas of the two stations are clustered together. Taxa contributing most to the separation (SIMPER average dissimilarity XHN/SO = 22.79 %) were the brachiopod species *N. lecointei* and *M. venosa*, the gastropod *C. dilatata* and sheet-like bryozoans with ~ 10 % contribution respectively, as indicated by SIMPER analysis. The brachiopod *N. lecointei* was more abundant in XHN, whereas *M. venosa* showed greater numbers in SO. Between both stations all analyzed areas from 2014 to 2016 showed a similarity of >75 %, as indicated by cluster analysis (Figure 11). At a 80 % similarity level, one area (SO 10, 2014-2016) deviates from the other areas in SO. In comparison, it showed a relatively low abundance of *C. huinayensis* and high abundance of encrusting bryozoans. Additionally, it was one of the few monitored sites inhabited by the cirriped *N. floscus*. These characteristics may cause the reduced similarity to the other areas in SO. At this similarity level (80 %) five clusters could be discerned. Areas in XHN were mainly grouped in two clusters, which were classed as one in SIMPROF analysis, showing statistical validity. In terms of percentage cover, the stations shared a similarity of 75 %, beyond which they formed two distinct station-specific clusters, apart from area SO_03 in 2014 and 2015 (Figure 12). A single cluster was formed by one area in SO (SO_10) in 2014, where hydrozoans covered less than 1 % of the area, which was a unique occurrence. Only taxa contributing with more than 1 % of cover were included in the statistical analysis, creating this distinct cluster.

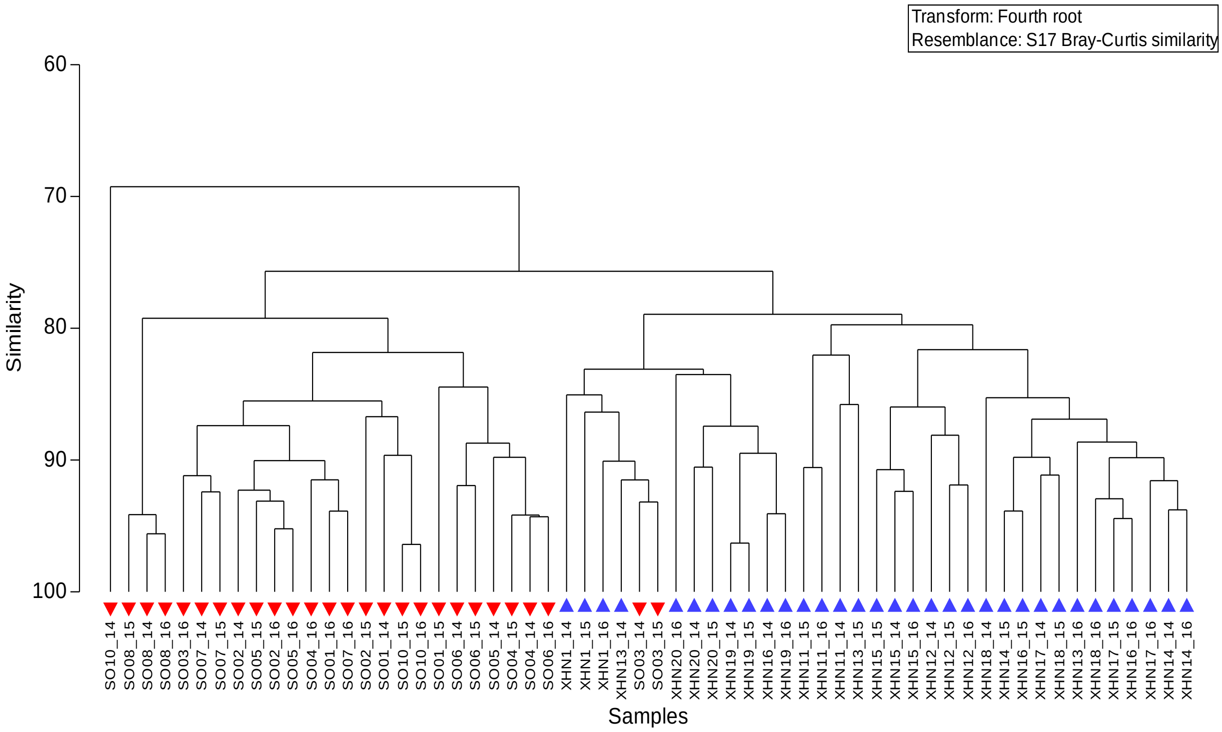

Figure 12: Dendrogram showing similarity between percentage cover of taxa at XHN (blue triangle) and SO (red triangle) from 2014 to 2016. The data are grouped in clusters based on Bray-Curtis similarity [%] and SIMPROF testing.

The same area deviated in terms of abundance as well (SO 10, 2014-2016). Taxa which contributed most to the percentage cover dissimilarity (average dissimilarity XHN/SO = 23.77 %) between XHN and SO were *C. dilatata* (contribution = 21 %), *M. venosa* (14 %), Crustose Red Algae (14 %) and Hydrozoa (12 %), as revealed by SIMPER analysis. The benthic community of SO contained less individuals of *C. dilatata* than XHN, but generally had higher percentage cover of the other three taxa. The difference between XHN and SO is reflected in comparisons of total abundance [ind m^{-2}] as well as total covered area [%], both for which SO generally displayed higher values over the analyzed time span. Despite similar patterns in abundance and cover, a RELATE test showed no major correlation of these two factors (ϱ = 0.622). Statistical results and conclusions drawn from analysis of abundance data cannot be transferred on percentage cover and vice versa.

3.2.3 Comparison of the benthic community between years

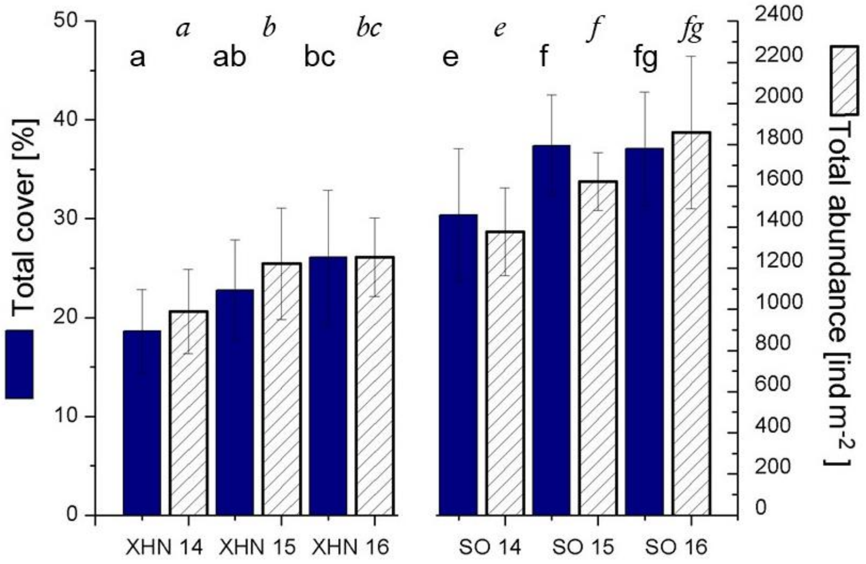

Figure 13: Comparison of mean total cover [%] (left axis) and mean total abundance [ind m^{-2}] (right axis) of counted organisms at the affected stations XHN (left) and SO (right) in the years 2014 to 2016. Letters above the bars indicate significantly different values (cover: print, abundance: italics). Error bars indicate SD; note the different scales for cover and abundance.

Mean total cover [%] and abundance [ind m^{-2}] increased continuously at both stations over the analyzed time span (Figure 13). From 2014 to 2016, increase in cover was significant at both stations (t-Test XHN $p = 0.008$; SO $p = 0.048$) with ~7 % at XHN and SO respectively. Mean total cover was lower in XHN in all years, but the mean increase of percentage cover from 2014 to 2016 was higher (35 %) than in SO (22 %). The increase in cover over one year was only significant in SO from 2014 to 2015 ($p = 0.032$, Figure 13). At both stations, total abundance increased significantly between 2014 and 2015 (XHN $p = 0.041$, SO $p = 0.015$). It plateaued in the following year in XHN and showed an increasing trend in SO, which was not statistically significant. In XHN, total abundance increased by an average of 265 ind m^{-2}, which is an increase of 27% in two years. In comparison, SO showed a higher absolute (496 ind m^{-2}) and relative increase (37 %) in terms of abundance from 2014 to 2016. The most abundant taxa in the benthic community at XHN and SO were Porifera, Octocorallia, the stony coral *C. huinayensis*, Hydrozoa and erect-branching and encrusting bryozoans (Figure 14). The dynamics of abundance over the analyzed period were very species specific. Taxa increasing continuously in abundance from 2014 to 2016 were the scleractinans *C. huinayensis*, *D. dianthus*, hydrozoans and polychaetes. The steepest increase was visible in *C. huinayensis*, which doubled in mean abundance in XHN and almost tripled in SO over the analyzed time span and *D. dianthus*, which showed a ~ 500 % increase in two years from 5.8 to 24.7 ind m^{-2} in XHN and 4.2 to 25.8 ind m^{-2} in SO. Some taxa showed an increase within the first year and a decline in the following year. This was mainly the case for all morphotypes of bryozoans, most prominent in the sheet-like bryozoans. A trend to decline could already be seen in the other two morphotypes. Porifera showed no clear trend, decreasing slightly but returning to initial mean abundance in the second year. The only taxon with an obvious difference in development between the two stations, were octocorals, which showed a steady increase in SO, whereas they varied in XHN. None of the identified species decreased continuously over the analyzed time span.

Only six taxa contributed with more than 1 % cover to the total covered area. These dominant taxa were Porifera, Octocorallia, Hydrozoa, *C. dilatata*, encrusting bryozoans and Red Crustose Algae (Figure 15). As was the case for abundance, the change of cover over time was very taxa specific. Octocorals and hydrozoans increased continuously from 2014 to 2016. Mean area covered by octocorals doubled in XHN (4.6 to 9.4 %) and SO (3.5 to 7.1 %) within two years, hydrozoan cover grew by factor 2.5 at both stations (XHN: 1.2 to 3.5 %, SO: 3.5 to 8.9 %). A continuous decrease was found in area covered by *C. dilatata*. The gastropod was overgrown and used as secondary substrate by other benthic species, as can be tracked in Figure 15. Porifera and encrusting bryozoans show the same pattern in change of percentage cover as in abundance. Sponges decrease in the first year, but regain or exceed their previous percentage cover in 2016. The Crustose Red Algae did not change in percentage cover of the analyzed time span. Across both stations, the communities changed in a comparable pattern. SIMPER analysis revealed that the similarity in taxon abundance and cover within the community (XHN and SO combined) increased from 2014 to 2016 (Table 4). In the first two years, taxa contributing highest to similarity in abundance were Porifera, Octocorallia and encrusting and erect-branching bryozoans. In 2016, the contribution of *C. huinayensis* increased and bryozoans decreased. Looking at percentage cover the same five taxa were responsible for ~80 % of the similarity between the years: Octocorallia, Porifera, Hydrozoa, Red Crustose Algae and encrusting bryozoans.

Table 4 Average similarity [%] of benthic community in terms of abundance and cover within one year (left) and dissimilarity [%] between two years (right) across both stations. Based on results of SIMPER analysis.

Average similarity [%]	*Abundance*	*Cover*
2014	79.83 %	77.69 %
2015	81.81 %	78.98 %
2016	83.05 %	81.06 %

Average dissimilarity [%]	*Abundance*	*Cover*
2014 vs 2015	19.31 %	21.79 %
2015 vs 2016	18.19 %	20.80 %
2014 vs 2016	19.72 %	22.24 %

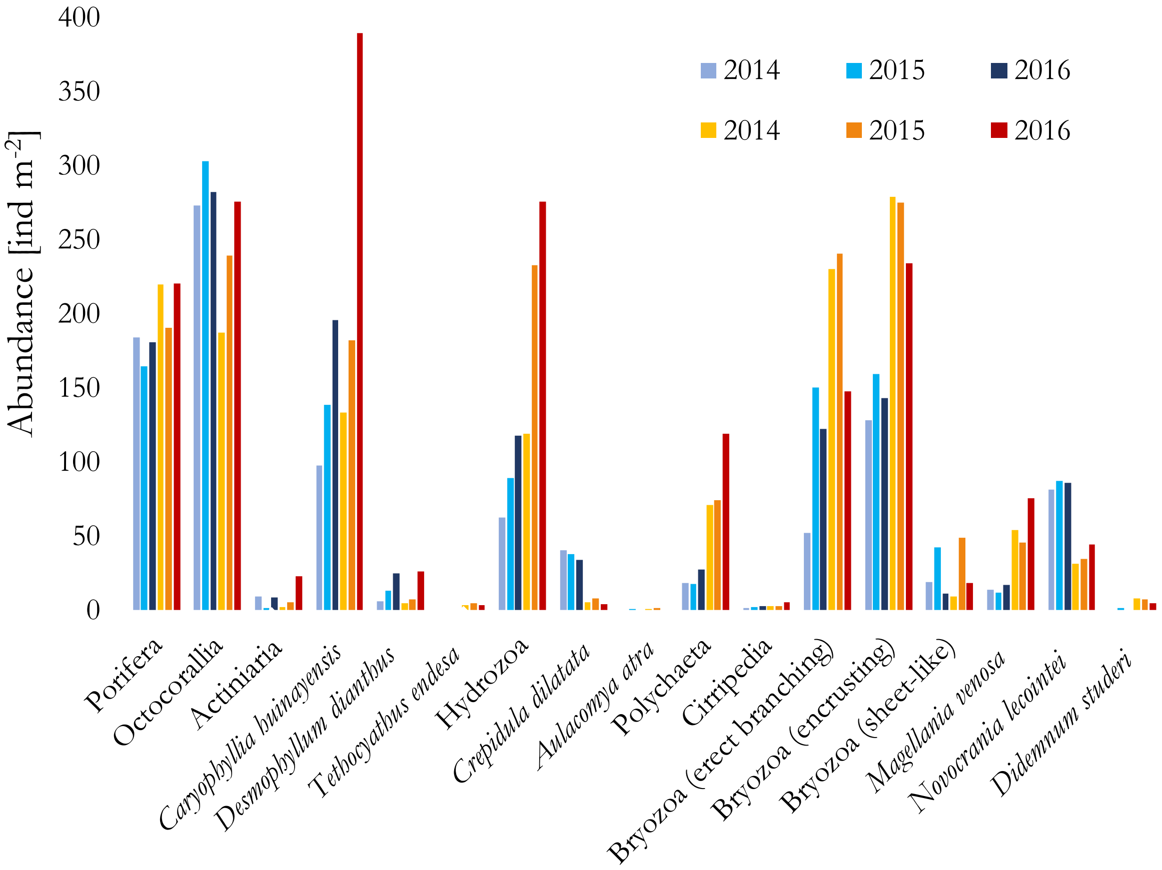

Figure 14: Mean abundance [ind m^{-2}] of all identified sessile benthic taxa at stations XHN (blue) and SO (red) from 2014 to 2016 based on photo analysis, data is tabulated in Appendix 2.

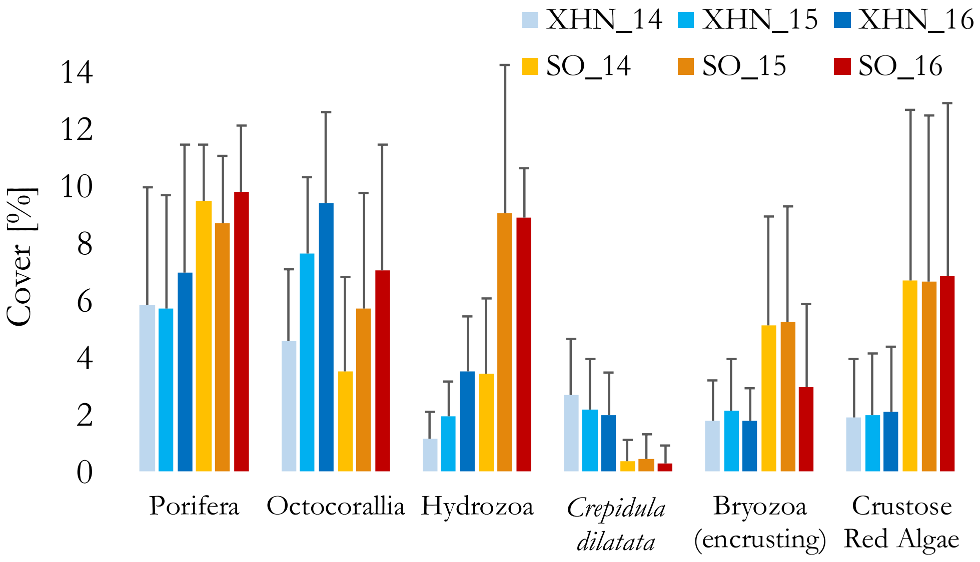

Figure 15: Mean cover [%] of observed taxa at stations XHN (blue) and SO (red) from 2014 to 2016 based on photo analysis, error bars indicate SD. Only taxa contributing with >1 % are displayed, data is tabulated in Appendix 3.

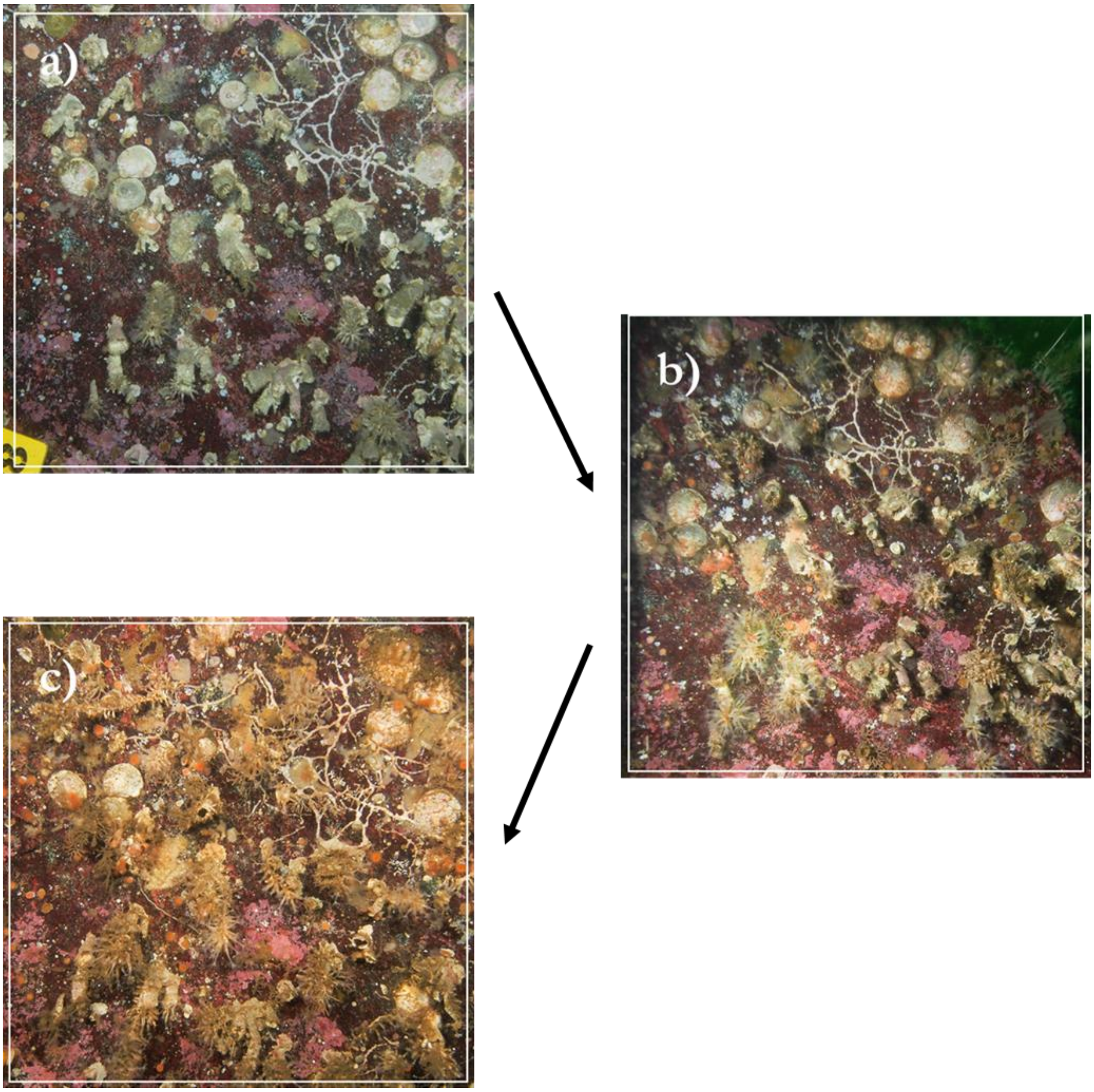

Figure 16: Underwater photographs of a monitored area in XHN (XHN_18), showing the benthic community in a) October 2014, b) January 2015 and c) March 2016.

Taxa contributing most to the dissimilarity in abundance between years were *N. lecointei*, sheet-like bryozoans, *D. dianthus* and *C. dilatata*, with ~ 10 % respectively, as revealed by SIMPER analysis. The dissimilarity in percentage cover was mainly based on the decrease of *C. dilatata* (~ 17 % contribution) and the change in cover of sheet-like bryozoans, Hydrozoa, *M. venosa* and Red Crustose Algae, with contributions of ~ 16 – 10 %.

3.2.4 Dynamics of *D. dianthus*

Individuals of the CWC *D. dianthus* were found at both stations in some areas in 2014 (XHN: 5 areas, SO: 4 areas), in 2016 the scleractinian was part of the monitored community in all areas but one at both stations (XHN: 10 areas, SO: 8 areas). Recruits were found growing on the rocky substrate as well as on old *D. dianthus* skeletons (Figure 17, right).

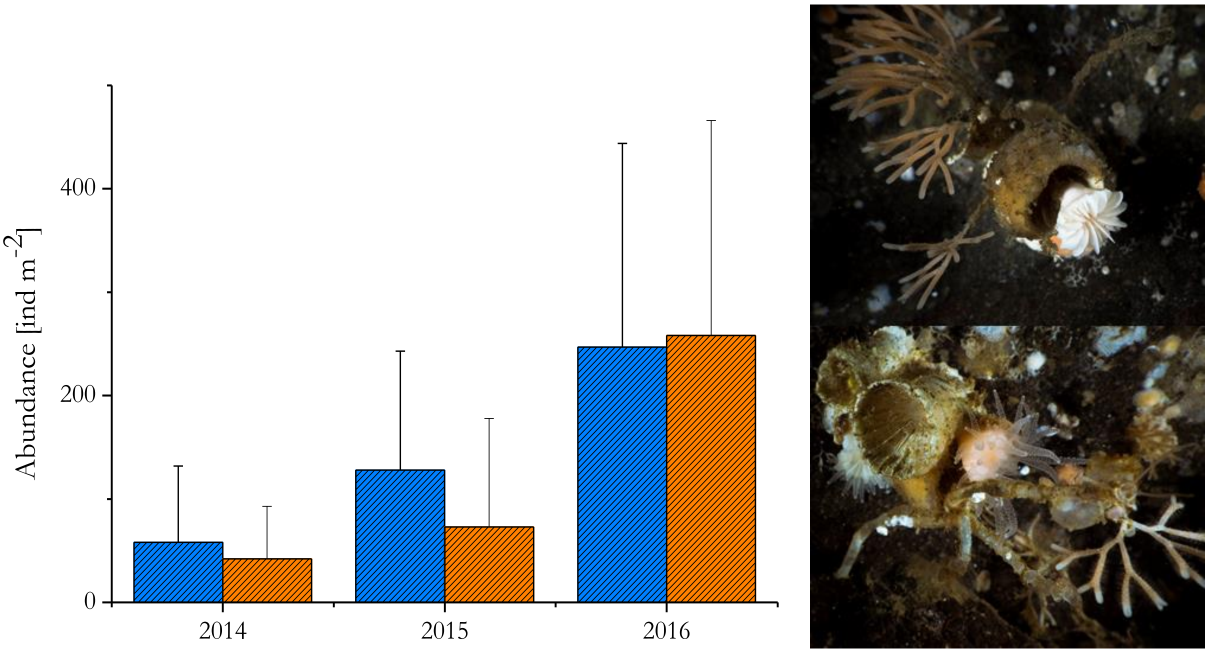

Figure 17: Left: Mean abundance [ind m^{-2}] of *D. dianthus* at the stations XHN (blue) and SO (orange) from 2014 to 2016. Error bars indicate SD, data is based on photo analysis. Right: Pictures of *D. dianthus* recruits and various other taxa growing on coral skeletons at SO (©Felix Butschek, 2017).

The abundance of *D. dianthus* increased significantly over the analyzed time span (Figure 17, left). In XHN, a significant change was found from 2014 to 2016 (Mann-Whitney test U = 0.016) where the mean abundance increased from 5.8 to 24.7 ind m^{-2}. The analyzed areas in SO first displayed a lower mean abundance in 2014 (4.2 ind m^{-2}), but significantly increased from 2015 to 2016 (Mann-Whitney test U = 0.035) to 25.8 ind m^{-2}. There is no significant differenct in the abudance between the stations. Over two years the number of individuals of *D. dianthus* increased by factor four in XHN and in SO by factor six.

Coarse length measurements showed that individuals grew an average of ~2 mm in calyx diameter per year and an average of ~4 mm from 2014 to 2016. The largest individual reached a calyx diameter of 17 mm in 2016, starting with 12 mm in 2014. Average calyx diameter of the measured individuals was 8 mm in 2014 and 11 mm in 2016.

3.3 Succession after coral removal

A total of eight areas were analyzed at the station Liliguapi (LG). Due to lack of images or poor quality, two areas could not be evaluated. Six areas could with certainty be attributed to either control or treatment. Therefore, two areas were excluded from the analysis of a possible treatment effect.

3.3.1 Species inventory

The species inventory at LG deviated from the stations XHN and SO. Differences were found in the presence of *Corynactis* sp. (Corallimorpharia) and at least two species of actinians (*H. pilarus*, *Acontiaria* sp. brown). The bivalve *A. atra* occurred more frequently in the analyzed areas (75 % of all areas). Octocorals and the scleractinian *C. huinayensis* were only found in two areas. The brachiopod species *M. venosa* was completely absent in LG. Single individuals of *N. lecointei* were found in one treatment area, but disappeared by 2016. Cirripedia and the ascidian *D. studeri* were not present in 2015 initially, but were recorded in one control area in 2016.

3.3.2 Treatment versus Control

Cluster analysis revealed two distinct groups (Figure 18), which were in accordance with treatment and control. Different years were not split into separate groups, communities of the same area showed high similarity between 2015 and 2016, especially the control group (Figure 19). In terms of percentage cover, treated areas initially showed a lower mean total cover (~ 35 %) than the control (~ 48 %).

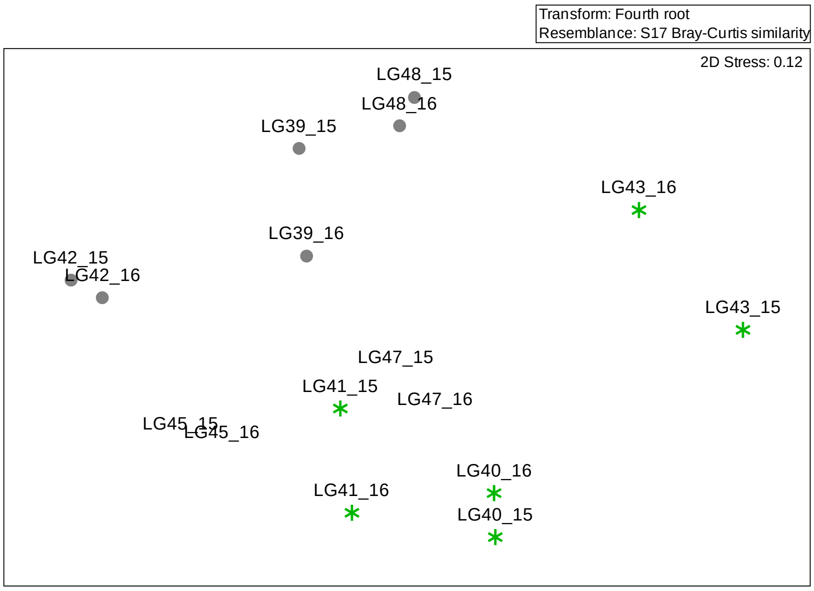

Figure 18: nMDS plot comparing taxon abundance [ind m^{-2}] of treatment (grey circle) and control (green star) group at LG in 2015 and 2016. Areas without symbol could not be clearly matched to treatment or control.

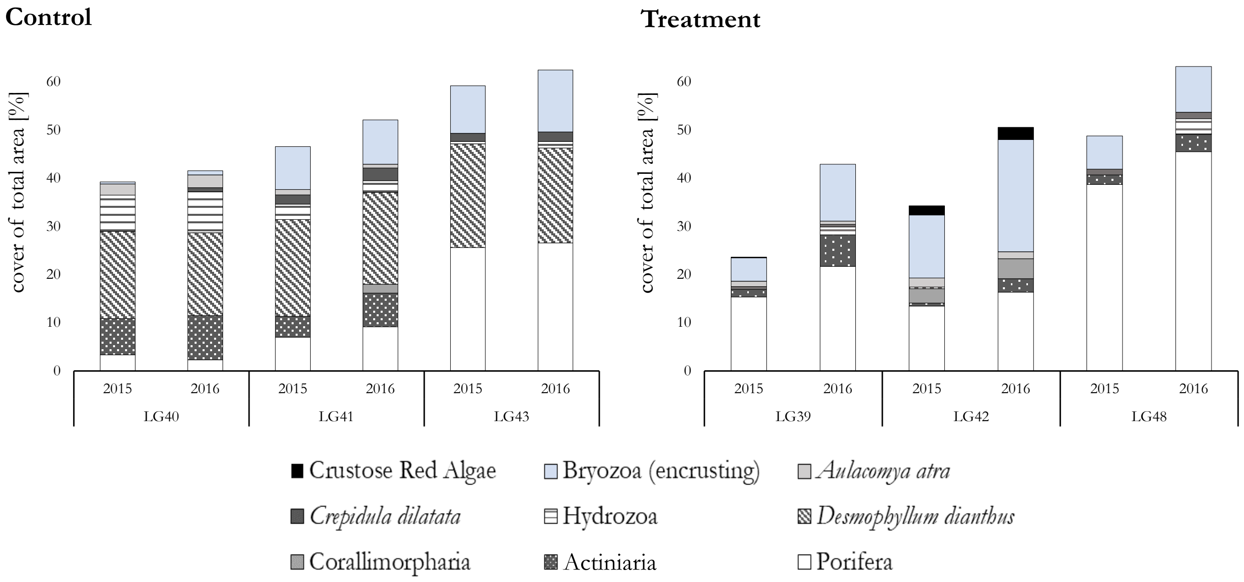

Figure 19: Percentage cover of observed benthic taxa (contributing with >1 %) in control (left, n=3, undisturbed) and treatment areas (right, n=3, *D. dianthus* removed) at the station LG in 2015 and 2016.

By 2016, mean total cover had increased to a comparable value in both groups (~ 52 %), with cover in treated areas increasing ~ 17 %. Different taxa were dominant in percentage cover in the respecitve groups: treated areas were dominated mainly by Porifera (mean ~ 25 %) and encrusting bryozoans (mean ~ 11 %, Figure 19). The control areas showed a higher variability. Dominant taxa were *D. dianthus* (~ 19 %) and, especially in one area, Porifera. Actinians and encrusting bryozoans contributed highly to total percentage cover in two areas, hydrozoans in one. A significant difference was revealed when comparing percentage cover of treated and control areas (PERMANOVA f = 6.87, p = 0.004), but not between 2015 and 2016 (f = 0.547, p = 0.613). Despite there being no significant difference in total cover (t-Test, control p = 0.681, treatment p = 0.151), an increasing trend over the year was visible in all areas. The same difference between treatment and control was found in abundance (PERMANOVA, f = 5.93, p = 0.003), whereas there was no difference between years (f = 0.127, p = 0.949) and no correlation between the factors. A similar pattern in cover and abundance was suspected, as a RELATE test showed good correlation between the data sets ($\varrho = 0.775$).

The treated areas presented lower total abundance (mean 1537 ind m^{-2}) than the control (mean 4830 ind m^{-2}) across both years. Difference in taxon abundance was especially visible in *D. dianthus* (treatment ~ 4 ind m^{-2}, control ~ 300 ind m^{-2} Figure 20). Slightly higher abudance of Porifera and encrusting bryozoans was found in treated areas. There is no significant difference between the years in terms of abundance and no visible trend in total abundance. Variability is high between the areas, as indicated by the SD, especially in the control group (Figure 20).

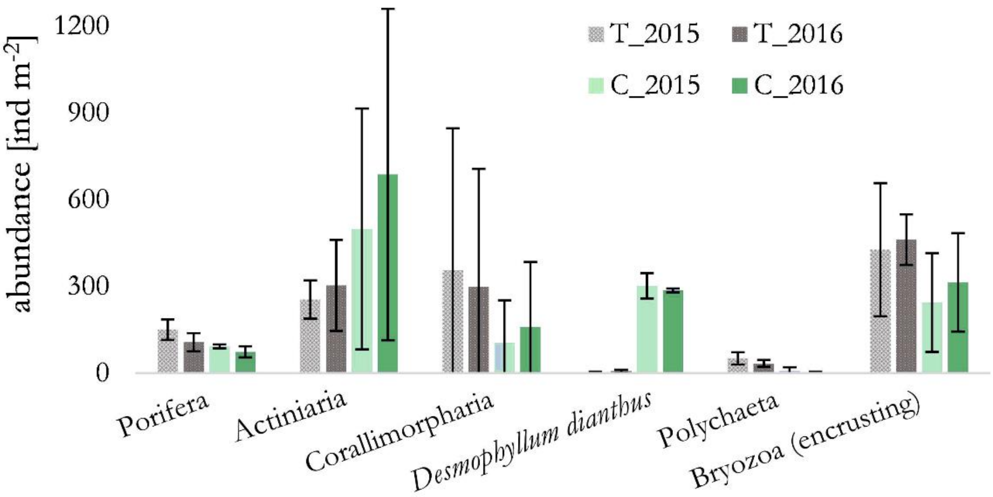

Figure 20: Abundance [ind m^{-2}] and SD (error bars) of the five most abundant taxa at the treatment (grey) and control areas (green) respectively in 2015 and 2016 at the station LG. Note that the error bars of the taxon Corallimorpharia are cut at y=0.

This high variability is reflected in the parameters describing the community diversity (Table 5). In the treated areas, a decrease in *S* from 2015 to 2016 is visible, caused by the disappearance of the ascidian *D. studeri*. Decreasing *H*' and *J*' were attributed to an increase in actinian abundance in some areas, and slight increases and decreases of other taxa. The control group exhibited an increase in *S* with the appearance of polychaetes, actinians and cirripeds, but simultaneous disappearance of erect-branching bryozoans. Values of *H*' and *J*' decrease, as actinians and encrusting bryozoans are increasing, but porifera are decreasing. This results in an overall decrease in homogenity of the community.

Table 5 Comparison of species richness *S* (± SD), Shannon-Wiener diversity *H*' (± SD) and evenness *J*' (± SD) between treatment and control communities in 2015 to 2016 at LG.

Treatment	**S**	**H‘**	**J‘**	***Control***	**S**	**H‘**	**J‘**
2015	8.33 ± 0.47	1.44 ± 0.06	0.68 ± 0.03	*2015*	9.00 ± 1.41	1.46 ± 0.29	0.66 ± 0.09
2016	7.33 ± 0.47	1.31 ± 0.07	0.66 ± 0.01	*2016*	9.67 ± 1.25	1.41 ± 0.38	0.62 ± 0.13

4 Discussion

4.1 Technical considerations

There are some constraints to the monitoring setup that need to be considered. The bolt-and-frame system clearly marks the monitored areas. However, due to visibility, coordination and orientation underwater, the frame was not always attached to the appropriate bolts in the same position. This created a discrepancy when overlaying images of the same area in different years. To compensate this, the 40×40 cm square for analysis was adjusted manually to always cover the same area. Pictures of the year 2016 were used as reference. However, it could not be ensured in all cases that the analyzed area matched exactly. Additionally, due to timing of expeditions, the images were not taken in a uniform time interval and resulting data therefore must be interpreted with consideration, especially when calculating growth rates.

A restraint to image analysis is the quality of the photographs; a limit for identification should be set based on the lowest quality. In this study, 5 mm were set as limit, which was based on empirical judgement. Teixidó *et al.* (2004) set a minimum of 0.5 cm for identifying benthic community recovery after iceberg disturbance in the Antarctic. Small taxa, such as some encrusting bryozoan (*Disporella* sp.) and tube-forming polychaete species (*Pileolaria* sp.), as well as early recruits of all species would be underrepresented in the results. To estimate the loss of information, pictures of higher quality should be taken of some areas and analyzed. Blurriness and particles in the water column impeded the precision of the analysis, especially the calculation of covered area. Without sampling and microscopic examination, taxa such as sponges, octocorals, hydrozoans and bryozoans could not with certainty be identified based on image analysis alone. Jackson (1993) showed that analysis at higher taxonomic levels does not imply loss of information when comparing stations. The aim of this study was not to present a precise species inventory but the change on a community level; this precision of identification is therefore justified. During image analysis, some species-specific constraints arose. As percentage cover data was calculated using 2D image analysis, protruding structures were underestimated in terms of cover. This was especially relevant in the growth of soft corals on dead coral skeletons. Abundance was not an ideal measure to quantify soft corals, as the borders of individuals were not clearly reproducible. A similar issue occurred with hydrozoans, where abundance should not be taken into account, as they are colonial species. Measuring percentage cover of hydrozoans presented a difficulty as the quality of the pictures did not make it possible to discern between substrate, detritus and hydroid cover. In this study, only the top layer was considered when calculating percentage cover. This put an emphasis on taxa overgrowing other species, such as hydrozoans growing on shells of *C. dilatata*, which caused a significant decrease in the gastropod's covered area. Despite this bias, the method of using multi-layered percentage cover was rejected. As soft corals and hydrozoans were densely overgrowing other taxa, it was not possible to define the covered area of the underlying individuals in a reproducible way. Clear outlines of e.g. brachiopods and gastropods were not visible and could therefore not be used in the area analysis. Comparing these challenges with methodical approaches in other studies, the precision of the analysis seems to be in line with published literature. Using the top layer in measuring cover is widely accepted (Teixidó *et al.*, 2002, 2004; Sugden *et al.*, 2007; Beuchel and Gulliksen, 2008) in combination with automated analysis of cover based on specific taxon colors or with grid-point analysis; Valdivia *et al.* (2005) estimated cover in 5 % intervals. In the present study, monitoring at XHN and SO was conducted in multiple replicate areas, which statistically decreases the uncertainty in the measurements.

The monitoring of the benthic communities after the mortality event in XHN and SO was set up February 2014, leaving a gap of two years before the regular photo documentation. The development of the community during that time span can only be inferred from the following years. A direct comparison to the development of an unaffected coral community and associated benthic fauna close to the two stations XHN and SO from 2014 to 2016 is not possible. No monitoring was set up at a site with comparable oceanographic conditions and intact aggregations of *D. dianthus*. Therefore, changes in community composition cannot be explained solely as effects of the disturbance but might be caused by other factors or ongoing changes that were not considered. Scleractinian disturbances of this dimension have never before been reported in Comau Fjord, however occasional patches of dead corals covered by sulfur bacteria were noticed since 2003 (Försterra *et al.*, 2014). Therefore, it has to be considered that this disturbance was not a singular event. Cifuentes *et al.* (2007) showed that temporal variability of disturbance might only have a restricted impact on the development of fouling communities, formed by hydrozoans, bryozoans, barnacles and colonial ascidians. However, this was the case for non-selective disturbances and might not be applicable to benthic communities consisting of non-clonal organisms.

Results of the coral removal experiment are based on the change over one year and can only be considered as preliminary. The low number of replicates per group in a community which exhibited high variability and patchiness (e.g. Corallimorpharia) remains an issue. Statistical analysis based on three replicates but with a high number of variables, up to 17 different species, has insufficient degrees of freedom. However, despite this statistical shortcoming, patterns were seen in the community development that matched observations of the change in the communities affected by the mortality event. The evaluation of the results was impeded as the initial conditions of the treated areas in 2015 were unclear and not uniform. The aim of the experiment was to observe the change in the benthic community after the loss of this dominant structure-providing species and compare it to the control group. Two areas had to be excluded due to image quality. In one of the treated areas, *D. dianthus* was not completely removed, and all treated areas were cleared of benthic organisms to a different degree. Overall, one year of monitoring did not provide enough data for a funded analysis, as the results were very heterogenous. Similarity of an area between the first and the following year was higher than between one group within the same year. The experiment provided results on the biodiversity of the system, which were compared to values measured in previous studies at this site. The experimental setup highlights the need for high replicate numbers when dealing with ecological data sets, to account for high variability or patchiness. However, when conducting invasive and destructive experiments, an ethically justifiable trade-off has to be made between replicate number and preservation of the ecosystem. Continuing photographic sampling of the experiment in the upcoming years might reveal similar patterns in the replicates of the same group. Following the change in percentage cover over more than one year, growth rates can be calculated and then compared between the two groups to show possible differences.

4.2 Patterns of community development after coral mortality

4.2.1 Patterns of single taxa

Disturbances affecting singular or related scleractinian species have been reported frequently in tropic areas (Cheal *et al.*, 2010). Studies on the aftermath and structural change of the ecosystem show cases of recovery as well as phase-shifts, where the community structure developed towards a new state (Norström *et al.*, 2009). A disturbance in Comau fjord in 2012 only affected the scleractinian CWC *D. dianthus*, whereas the rest of the benthic community appeared unharmed. In the years following this mortality, total abundance and cover increased continuously and significantly from 2014 to 2016. The abundance of the scleractinian *C. huinayensis*, associated with *D. dianthus* on overhangs in Comau Fjord (Försterra and Häussermann, 2009) increased significantly over the period of monitoring. As the recording limit for organisms during the picture analyses was set to 5 mm, smaller individuals were not counted, therefore the abundance of this species was even underestimated. Within two years, abundance of *C. huinayensis* doubled at XHN (98 to 196 ind m^{-2}) and tripled at SO (133 to 390 ind m^{-2}, Figure 14). Extrapolating this rate, abundance of this species might exceed previous records for the benthic community in Comau Fjord (Reichel, 2012; Wurz, 2014). *C. huinayensis* is a suspension feeder, catching zooplankton with its tentacles. This process is dependent on current velocity (Wurz, 2014), as too slow currents might limit the offer of prey drifting by. In an intact community, *D. dianthus*, with recorded length of 40 cm (Försterra and Häussermann, 2003), will reach farthest away from the substrate into the current passing the rocky walls. Like the significantly smaller species *C. huinayensis* (< 2 cm height, Wurz, 2014) it is a suspension feeder. Larval mortality as a result of suspension feeding organisms, can be a limiting factor in the recruitment of scleractinians (Fabricius and Metzner, 2004). The disappearance of *D. dianthus* may therefore have relieved pressure on the larval survival causing increasing abundances of *C. huinayensis* in the affected areas. Most of the individuals were growing on the rocky substrate instead of the old coral skeletons (Figure 21), which excludes the availability of free space to settle as the driving factor in the observed change in abundance.

Octocorals showed a steep increase in percentage cover, doubling at both study sites in the fjord within two years (Figure 15). Soft corals are widely recognized as fast colonizers with high growth rates due to asexual propagation (Atrigenio and Alino, 1996). In SO and XHN, soft coral cover increased on rocky substrate, expanding from already existing colonies, indicating asexual propagation. Additionally, they colonized dead skeletons of *D. dianthus* markedly, to a point where the underlying structure was no longer recognizable. Based on this, the availability of free space and possibly food supply appear to be important factors limiting the expansion of soft corals in this benthic community (Karlson *et al.*, 1996).

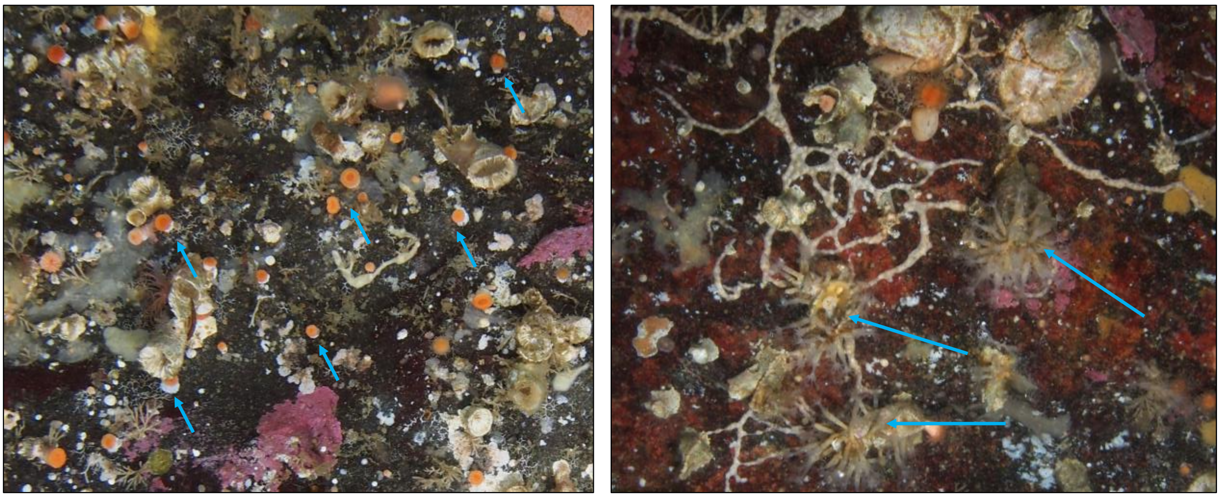

Figure 21: Underwater images taken at SO in 2016. Left: Abundance of *C. huinayensis* (arrows) increased significantly after the mortality event, mainly growing on the rocky substrate. Right: Octocorals exhibit a horizontal growth form on the rocky substrate but a vertical growth form on coral skeletons (arrows).

The naked skeletons form a 3D structure, which increased the potential settlement area in comparison to ground area. Moreover, as the occurring soft corals are suspension feeders (Arntz and Clarke, 2012), growing on the skeletons of *D. dianthus* and away from the substrate into the water current might be an advantage in catching prey drifting by. Octocorals grow in the benthic boundary layer, where vertical growth ensure better access to food (Fréchette *et al.*, 1989) and possibly other fluxes. On the rocky substrate, the prevailing growth form of soft corals were horizontal branching stolons, whereas the skeletons were mainly colonized with stolons reaching away from the substrate (Figure 21). Studies in the tropics have shown that disturbed stony-coral communities can undergo a phase-shift and become dominated by soft corals, inhibiting the growth of scleractinians (Atrigenio and Alino, 1996; Fox *et al.*, 2003). Despite the continuous increase of soft corals, *D. dianthus* recruits could be found in almost all analyzed areas by 2016 (Figure 17). Calyx measurements revealed a growth of ~2 mm in calyx diameter per year, which is in accordance with growth rates measured in situ and in the laboratory for *D. dianthus* in Comau Fjord (Jantzen *et al.*, 2013a). In comparison to soft corals, they exhibit slow growth. However, as proposed by Reichel (2012), they will eventually outcompete other taxa and become dominant in the benthic community. Predictions about the dynamics between soft and stony corals exceed the scope of this data and study. At present there is no indication for a phase-shift in the community towards domination of soft corals.

The percentage cover of hydrozoans increased from 2014 to 2016 at SO as well as XHN, slightly levelling off in the second year at SO. The observed taxa were ephemeral and grew on the rocky substrate, sponges and other animals, as well as covering large parts of the dead exposed coral skeletons (Figure 22). Early colonizing hydrozoans are opportunistic species, characterized by rapid growth and short residence times (Gili and Coma, 1998). As such they play an important role in biofouling communities. Rico *et al.* (2012) described that hydrozoans were rapidly spreading on substrate freed by dislodgement of ascidians in Argentinian Patagonia. The different bryozoan morphotypes showed a successional pattern over the analyzed time span. At XHN and SO, encrusting bryozoans increased in percentage cover within the first year and decreased afterwards (Figure 15), as did erect-branching bryozoans (Figure 14). Matching dynamics were described by Reichel (2012) from Comau Fjord and are similar to the ones reported by Pacheco et al. (2011) from the cold-temperated north-Chilean coastal upwelling system, where the early settling encrusting species *Membranipora isabelleana* expanded after the first year of exposure of artificial substrate to be then replaced by barnacles in the course of the succession. The present study revealed the sheet-like morphotype, here mainly represented by *Beania* sp., increased its abundance from 2014 to 2015 and then disappeared in most areas in 2016. This pattern is in accordance with Reichel (2012), where after a growth surge within the first year, *Beania cf. magellanica* was massively reduced a year later. In general, species settling early during succession will either hinder or facilitate the arrival of later species (Breitburg, 1985). For soft corals, species are known to contain allelochemicals, inhibiting growth of scleractinian species and increasing competitiveness (Atrigenio and Alino, 1996). Later settlers however will in both cases inhibit the already established species, decreasing their abundance or percentage cover (Breitburg, 1985). This creates an increase, a peak and decline of the pioneer taxa abundance, as observed here for *Beania* cf. *magellanica*.

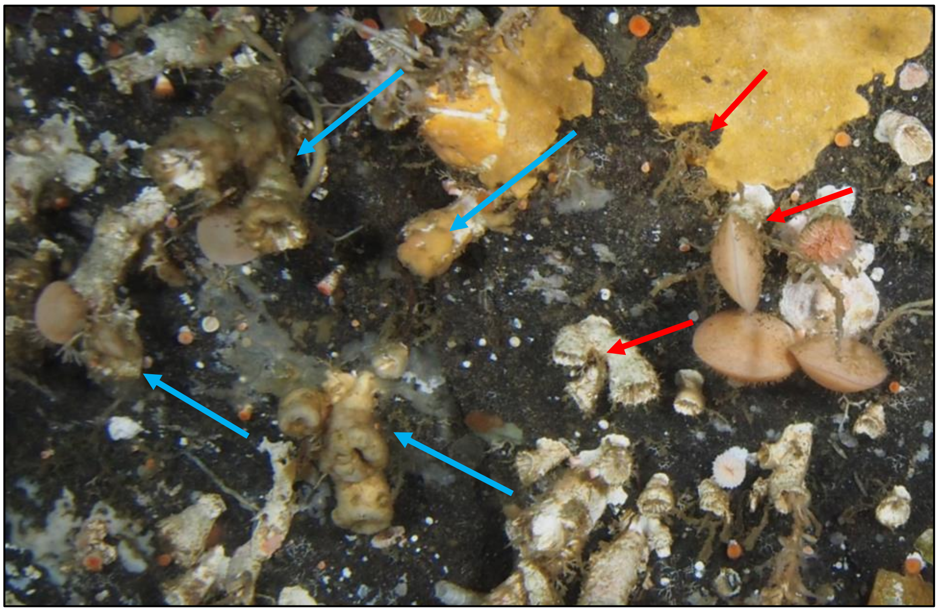

Figure 22: Underwater image taken at XHN in 2016 showing sponges covering dead coral skeletons (blue arrows) and hydrozoans covering the rocky substrate, coral skeletons and brachiopod shells (red arrows).

Poriferans were a dominant group in terms of percentage cover in the analyzed areas, however, no clear trend of expansion or decline following the coral mortality was observed within the study time. The boring sponge *Cliona chilensis* is associated with *D. dianthus*, boring and growing into the coral skeleton (Försterra and Häussermann, 2009). However, it also occurs as sheets and globes on the rocky substrate, like other observed sponge taxa. From the substrate they expanded onto dead coral skeletons (Figure 22). However, this had no significant impact on overall percentage cover yet (Figure 15). Demospongiae exhibit slow growth rates in temperate sublittoral waters, with fast growing species only reaching an estimated diameter of 40 cm in ten years, whereas slow species would only grow to one cm in diameter in the same time span (Ayling, 1983). Therefore, no rapid expansion of poriferans was expected in the affected areas. An interesting aspect to consider is the trophic link between scleractinian corals and sponges. Rix *et al.* (2016) demonstrated that sponges are able to feed on coral mucus, an energy-rich compound, released as dissolved organic matter (DOM, Wild *et al.*, 2009, 2010; Naumann *et al.*, 2011). It is assimilated into the sponge tissue or released as detritus, which was shown to play an important role in nutrient recycling in warm-water as well as CWC reefs (Rix *et al.*, 2016). Additionally, the so-called sponge loop passes the energy contained in coral mucus on to higher trophic levels, thereby retaining energy in the system. There are no records of coral-sponge coupling or estimates of the magnitude of matter and energy transfer for the species occurring in Comau Fjord so far. However, this trophic link should be studied further when investigating the impacts of the disappearance of *D. dianthus*, as it may affect higher trophic levels benefitting from the release and recycling of coral mucus.

4.2.2 Diversity indices

A trend in community development can be described using diversity indices. Species richness S did not significantly increase at either station affected by the coral mortality, but an increasing trend was visible in S_{mean} at either station. It explains the significant increase in H' from 2014 to 2016, as J' did not change over this period. Overall, a rise in number of species with a stable, even distribution will lead to an increase in diversity, reflected in H'. The increasing number of species was caused by the reappearance of *D. dianthus* in most areas and the settlement of barnacles and the brachiopod *N. lecointei* in a few areas, where they had previously not been present. In the analysis of the community succession, the effects of grazers have not yet been considered. Nudibranchs put feeding pressure on hydrozoans, keeping growth and expansion in check (Försterra and Häussermann, 2009). Breitburg (1985) showed that grazing highly impacts the development and succession of benthic communities, favoring some species over others, which might not be as susceptible. Additionally, grazing relieves competition for space, which might be advantageous for some species and causes growth and expansion (Hixon and Brostoff, 1996). In comparison to disturbances affecting and diminishing an entire community, the community in this case is still largely intact, including the macrobenthic grazers. Therefore, grazing might be of higher importance in this study than after large-scale incidents such as defaunation after hypoxic events (Lim *et al.*, 2006). In Comau Fjord, the benthic grazing community was not affected by the disturbance and therefore did not have to recover before exerting pressure on the ecosystem. In future analysis, the frequency of occurrence of macrobenthic grazers should be considered to build a more complete picture of the dynamics affecting the recovery of the ecosystem.

4.2.3 Differences in community change between XHN and SO

The statistical dissimilarity between the community in XHN and SO is attributed to single taxa, particularly the presence of two brachiopod species and the occurrence of the gastropod *C. dilatata*. Statistical analysis revealed it to be independent of changes in the community over time. No difference in the measured abiotic parameters was found, which could potentially explain the slightly different species inventories. Water temperature showed minimal difference between the stations (Figure 7), only slightly increasing in variability in summer. One particularly strong deviation in April 2016 might be explained by the presence of a prevailing warm water mass at XHN in the first half and towards the end of the month (Appendix 1). Despite their proximity, the oceanographic conditions might vary between the stations. SO is located at the tip of a small headland, where the fjord starts to bend, possibly being exposed to stronger currents than XHN, which is slightly more sheltered (Figure 3). Despite the variability in species inventory, higher overall abundance and percentage cover in SO, results from both stations show the same successional pattern of the community, which may thus be considered as site replicates.

4.2.4 Comparison of observed patterns to primary succession

Comparing the observed community development to patterns of primary succession, differences as well as similarities were noticed. Reichel (2012) studied the primary succession of the benthic hard-bottom community in Comau Fjord in ~20 m depth using artificial substrate. The station X-Huinay S (XH) is located closely to XHN (~ 0.5 km distance). Her results showed an initial increase in abundance with subsequent decrease, but continuous increase in percentage cover over three years. This was mainly caused by the rapid colonization of the substrate by calcifying polychaetes. The settlement of encrusting bryozoans as well as the brachiopod *M. venosa* defined the early successional stages and dominated the community (Reichel, 2012). In contrast, in the present study, bryozoans did not form a dominant role in succession. Cifuentes et al. (2010) describes bryozoans as important part of the pioneer community but weak competitors, exploiting the free substrate for short times. They seem to be less important for secondary succession, as stronger competitors subsequently replace them. Based on the model of directional replacement (Platt and Connell, 2003), early successional stages life history and rapid colonization are assumed to be important factors. Pacheco *et al.* (2010) showed this linear replacement and competitive exclusion on hard-bottom substrate off northern Chile with early encrusting bryozoans being replaced by barnacles, followed by erect-branching bryozoans after two years. The linear dynamics do not apply to this study, which highlights the different dynamics between primary and secondary succession. Later in the succession, biotic interaction determines the community structure, favoring species which are more tolerant to competition as well as to abiotic conditions (Cifuentes *et al.*, 2010). This becomes evident in the results of this study, where expansion in cover and abundance was not limited to pioneer species only. Proliferation of *C. huinayensis* may attributed to biotic interaction or the relief of competition. Soft corals thrived on the newly available space but might as well benefit from the disappearance of a competitor in suspension feeding. However, patterns of primary succession are also recognizable, such as the overgrowth of coral skeletons by hydrozoans and a slight initial increase in bryozoan cover, caused by the availability of new substrate.

4.3 Comparison with natural unaffected benthic community

The study on succession by Reichel (2012) presents available data from the year 2012 on the structure and species inventory of a *D. dianthus* dominated benthic community in Comau Fjord prior to the die-off. Therefore, it is used here to compare the results of the present study to a mature pre-mortality community, as the station XH is located just south of XHN. In the natural community at XH, total abundance was calculated as ~2830 ind m^{-2}. Four years after the mass mortality in 2016, the total abundance at XHN (1253 ind m^{-2}) and SO (1860 in m^{-2}) had not reached numbers comparable to the mature community in XH, despite continuous increase and considering the low abundance of *D. dianthus*. It is not clear what size limit and precision Reichel (2012) set for identifying and counting individuals, which must be considered when comparing results. Percentage cover increased to a total of 37 % (SO) and 26 % (XHN) in 2016; in the natural community in XH it was up to 54 %. In some areas at XH prior to the disturbance, *D. dianthus* accounted for up to 20 % cover alone, which matches the difference in percentage cover between the pre-mortality and the affected community.

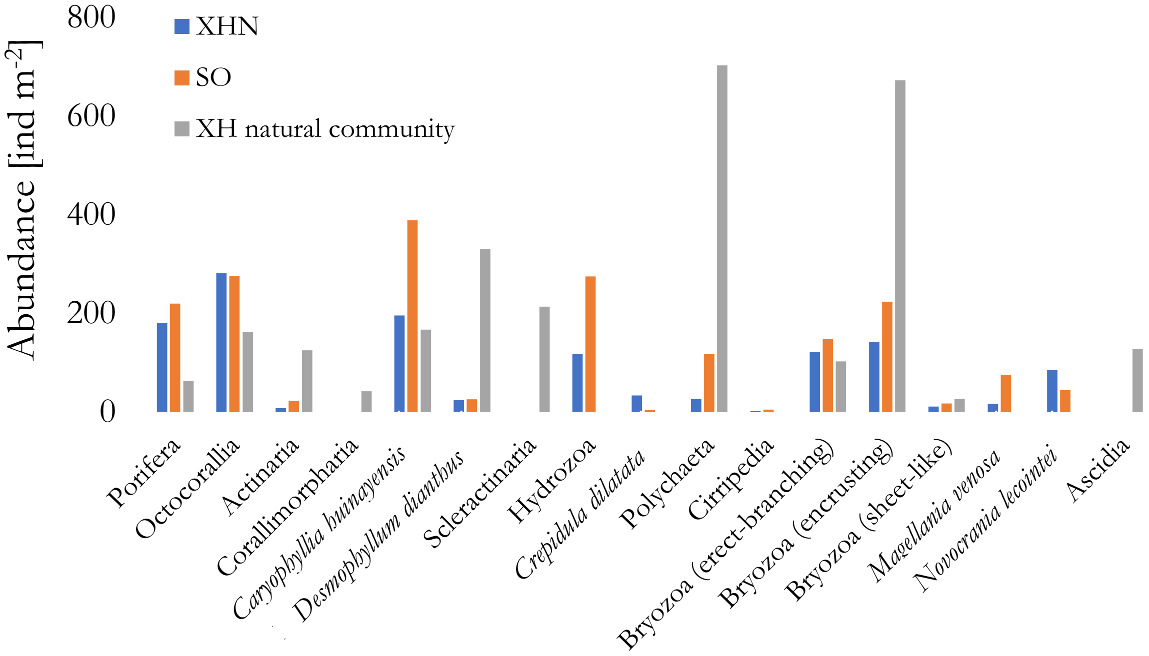

Figure 23: Comparison of abundance [ind m-2] of benthic taxa counted at the affected sites XHN (blue) and SO (orange) in 2016 with the mature pre-mortality community at the site XH in 2012 (grey, data: Reichel, 2012).

When comparing the abundance of single taxa in the community, some differences become apparent. An obvious difference is the abundance of *D. dianthus* itself (Figure 23). However, a steady increase in recruits with maximum abundance of 45 ind m^{-2} after four years was observed (Figure 17). This settlement rate is in accordance with the results of Reichel (2012) from artificial substrate, where after two years an average of 30 ind m^{-2} were counted. In this study, a few individuals already displayed a calyx length of ~12 mm in 2014. The disturbance did not have a lasting effect, which would prohibit the resettlement and recruitment of *D. dianthus*. The discrepancy in polychaete and encrusting bryozoan abundance (Figure 23) can be explained by a methodical approach. The dominant polychaete taxon identified by Reichel (2012) was *Pileoaria* sp., which was not considered in this study due to small size. Comparing abundance of encrusting bryozoans between studies is difficult, as they are colonial species and different approaches to counting might be applied. In the natural community, encrusting bryozoans accounted for 4.2 % of covered area (Reichel, 2012), which is of comparable dimension to XHN and SO. Additionally, living individuals of *D. dianthus* cover a large part of the area (Häussermann and Försterra, 2007), shading other organisms and hiding them from analysis. This probably explains the difference in poriferans (Figure 23), as the present results indicate that they did not significantly increase in percentage cover after the disappearance of *D. dianthus*. Higher abundances of soft corals and the stony coral *C. huinayensis* in the affected community might be an effect of this bias as well. However, the significant increase in these taxa from 2014 to 2016, when *D. dianthus* was already dead, is a real deviation from the natural community structure and linked to the disturbance. The substantial cover of hydrozoans in the affected areas and the absence in the mature community indicates that successional processes are still ongoing.

As the community structure of XHN and SO was shown to be statistically different, the same variability can be inferred when comparing it to the natural community in XH. Using diversity indices, which were similar between stations in this study, a better measure of difference was achieved. Reichel (2012) calculated a Shannon-Wiener diversity *H'* of 1.9 with an evenness *J'* of 0.87. This is in accordance with the 2016 results found in this study: a slightly higher *H'* of 2.0 and slightly lower, unchanging evenness *J'* of ~0.8. The species richness *S* was not compared, as Reichel (2012) sampled organisms and used microscopy to identify taxa to genus and species level. Comparison between the different data sets is still valid, as Jackson (1993) suggests that there is no information loss in identifying benthic communities to familial level or above, when discriminating between sites. Based on these results, the structure of the affected and the natural community seem to be similar. The similarity suggests that the ecosystem has a high resilience and stability, as defined by Holling (1973). A disturbance which eradicated the dominant macrobenthic species did not result in a major shift within the community or a collapse of the system. The system's speed of recovery from the past event seems to be dictated by the growth rate of *D. dianthus*. It can be assumed that the community will return to its previous state as the scleractinians are reaching their previous size. This supports the assignment of the community to the TOLERANCE model, where the community is stable until the most tolerant taxon, which might be a slower growing species, dominates the community. Iriarte *et al.* (2010) describe the Patagonian fjord as a highly vulnerable ecosystem. The present study suggests that the benthic community can absorb the impact of small-scale disturbances and recover from it. This conclusion however cannot be applied to large-scale disturbances, as they might harm the entire ecosystem instead of a single species, as was the case in this study. The Chilean fjord system is a hotspot of biodiversity (Försterra and Häussermann, 2009), which is a crucial property influencing the resilience of an ecosystem (Steneck *et al.*, 2002; Hooper *et al.*, 2005). Functional diversity and different responses of species to changing abiotic conditions have a stabilizing effect on the community (Hooper *et al.*, 2005). In this case, other suspension feeders such as octocorals, poriferans and the scleractinian *C. huinayensis* are filling some functions of *D. dianthus*, compensating the gap in the system. However, the slow growth of benthic organisms in Chilean cold-water system (Pacheco *et al.*, 2011) must be taken into account, as became evident through the present analysis. Considering the growth rate of the scleractinian *D. dianthus*, it may take more than 20 years for individuals to reach calyx lengths of 5 cm (Jantzen *et al.*, 2013a). No predictions on the development of the community within this time span can be made. Some ecosystem properties are initially not affected by species loss, as there may be multiple species that provide a similar functional role (Hooper *et al.*, 2005). This puts the ecosystem in a different perspective, as initial resilience and stability are coupled with long recovery times. It is therefore necessary to continue the monitoring of the community recovery and development. Nyström *et al.* (2000) describe that anthropogenic influence can create additional stress to natural disturbances or even have synergistic effects. Considering the expansion of the salmon aquaculture and tourism in the Chilean fjord region (Niklitschek *et al.*, 2013; Försterra *et al.*, 2016), which increase the anthropogenic pressure on the system, further monitoring of the recovery is strongly recommended. Following a viral outbreak in the salmon aquaculture with devastating losses in 2007, antibiotic use has doubled to 557 tons in 2015 (Tecklin, 2016). Experts predict further growth in Chilean salmon supply, reaching 576,000 t in 2018 (Craze, 2017). Resulting eutrophication and possible hypoxic events put pressure on the system and can cause disturbances with long recovery times for the benthic community.

4.4 Effect of coral removal on benthic community

4.4.1 Change in abundance, percentage cover and biodiversity

The monitored benthic community at LG was characterized by high spatial and low temporal variability. Patchy taxa, such as Corallimorpharia and Actiniaria caused different patterns of abundant groups. *D. dianthus* dominated the control group where only little change in community structure was observed, mainly marked by immigration of actinians and an increase of bryozoan cover. All treated areas increased in percentage cover, reaching comparable values to the control area (Figure 19). The available substrate was colonized by immigrating actinians, expansion of poriferans and encrusting bryozoans. Actinians, here *H. pilarus* and *Acontiaria* sp. (brown), are motile species and migrate into areas, where biotic pressure created by inter- or intraspecific competition is low (Riemann-Zürneck, 1998). The removal of *D. dianthus* and the subsequent opening of a niche for suspension feeders therefore facilitated the settlement of actinians. The expansion of poriferans and bryozoans could primarily be attributed to availability of free substrate, which in the case of bryozoans is in line with patterns of primary succession shown by Reichel (2012). The increase of poriferan cover could be an indication for the proposed sponge-loop (Rix *et al.*, 2016) in this system. However, these are assumptions, which cannot be supported statistically due to high variability and low number of replicates.

Reichel (2012) analyzed the biodiversity of the natural benthic community at LG in 2012 and calculated a H' value of 1.7 and a J' value of 0.76. Results of the present study indicate lower mean values for treated ($H'_{2016} = 1.31 \pm 0.07$, $J'_{2016} = 0.66 \pm 0.01$) as well as control ($H'_{2016} = 1.41 \pm 0.38$, $J'_{2016} = 0.62 \pm 0.13$) areas, which is partially explained by the high SD due to the low replicate number. Maximum values in the control group ($H'_{max} = 1.79$, $J'_{max} = 0.75$) are comparable to Reichel (2012). In treatment areas, all applied biodiversity indices S, H' and J' decrease within the first year. The disappearance of some taxa, such as the ascidian *D. studeri*, the immigration of actinians and the expansion of bryozoans lead to a shift in community structure. The changes are apparently caused by the removal of *D. dianthus*. However, the control group underwent a similar decrease in H' and J', as actinian abundance and bryozoan cover increased, suggesting a general modulation in the benthic community at LG. Again, the low number of replicates does not allow a more substantial analysis and interpretation of the observations.

4.4.2 Comparison of the benthic community at LG with XHN and SO

The benthic community at the opening of the fjord (LG) could be clearly differentiated from the communities inside the fjord (Figure 24). The unharmed community at LG showed a lower S, H' and J' (Table 5) than the benthic fauna at XHN and SO, which did not significantly vary over time or between stations ($S_{mean} \sim 11$, $H'_{mean} \sim 1.9$, $J'_{mean} \sim 0.8$). Corallimorpharia and Actiniaria were more abundant at LG. The bivalve *A. atra* occurred at the monitored areas in LG at 18 m depth, inside the fjord the monitored areas were below the mussel belt (20 m depth). Both identified brachiopod species were only rarely found at LG. The removal of corals at LG had a different effect on the community as the coral mortality, which might be due to the different species inventory. The scleractinian *C. huinayensis* was less abundant at LG at treated and control areas (mean ~ 54 ind m^{-2}) than was previously observed at this site (618 ± 626 ind m^{-2}; Wurz, 2014). Octocorals and hydrozoans, which contributed majorly to the succession of the community inside the fjord, were not present at the treatment areas at LG and did not change in the control group. The only similarity could be found in the expansion of encrusting bryozoans, as a universal pattern of primary succession in Comau Fjord (Reichel, 2012; Gottschlich, 2014).

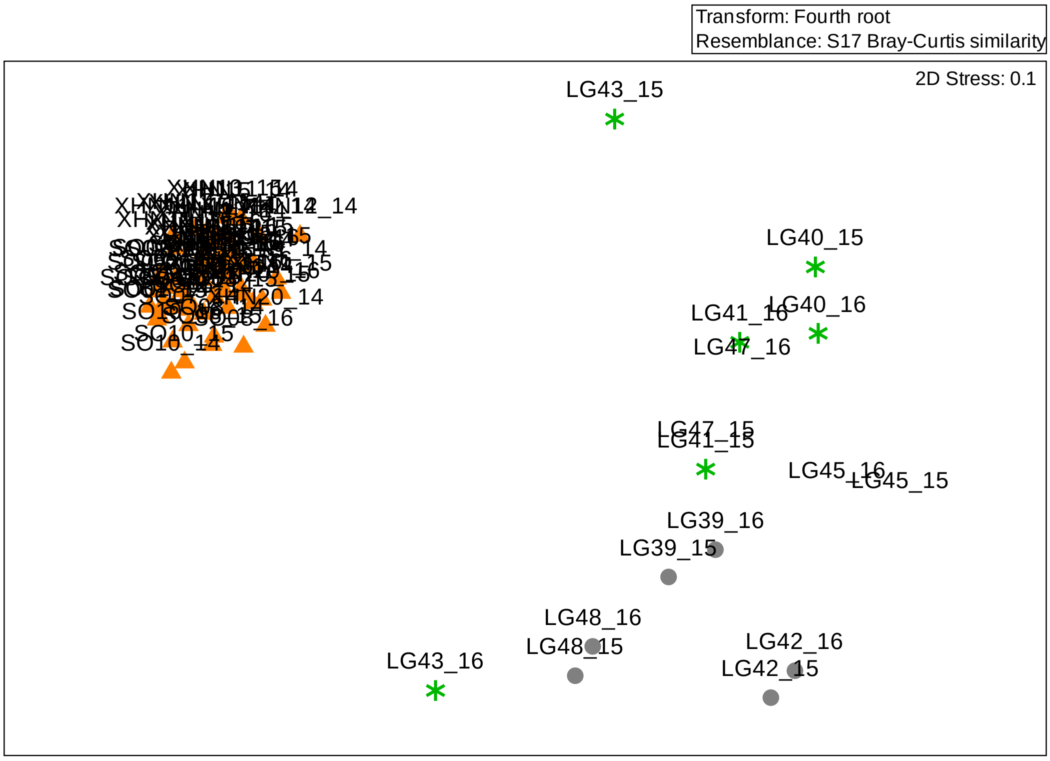

Figure 24: nMDS plot of abundance [ind m^{-2}] of benthic taxa at the stations inside the fjord (XHN, SO; orange triangle), affected by the coral mortality, compared with the community at the opening of the fjord (LG), where *D. dianthus* was actively removed from the community (treatment: grey circles, control: green stars).

Where octocorals and hydrozoans took advantage of the free substrate as opportunistic colonizers at XHN and SO, actinians immigrated into the area of relieved biotic pressure and lowered competition at LG. A general effect of the disappearance or removal of *D. dianthus* from its benthic community might be that other medium-sized suspension feeders take advantage of the open niche (Valdivia *et al.*, 2005).

4.5 The role of *D. dianthus* in the benthic community

In a recent review of habitat-forming taxa in the fjords of Chilean Patagonia, Försterra *et al.* (2016) cdescribe the scleractinian CWC *D. dianthus* as ecosystem engineering species, by forming complex three-dimensional pseudo-colonies. The so-called 'animal forests' (Rossi *et al.*, 2017) are associated with a highly diverse benthic community. As autogenic engineers (Jones *et al.*, 1994), scleractinians create habitats by forming calcified endoskeletons. Different organisms colonize the skeleton of living corals, when tissue retreats due to growth (Försterra *et al.*, 2016), as well as dead skeletons, as observed in octocorals, hydrozoans and poriferans in this study. The naked skeletons remained attached to the rock after the animal died and created free substrate. They were almost completely covered four years later and even formed settlement substrate for *D. dianthus* recruits (Figure 17, right). By diversifying the structure of the habitat, higher abundance might be supported. The growth form of *D. dianthus* creates micro-habitats and enlarges the surface area of the substrate, which is overgrown by various species. However, in comparison to CWC reefs in the North Atlantic, where single colonies of *L. pertusa* can reach a maximum of one meter in height (Freiwald, 2002), in the shallow water in Comau Fjord, pseudo-colonies of *D. dianthus* do not construct the structures of the same scale. As they are growing on steep slopes along the rock walls, dead skeletons fall, excavated by boring sponges, form piles of coral rubble on the sediment and are mostly lost to the community. High sedimentation stress from the surface prohibits growth of corals (Försterra and Häussermann, 2003) and other taxa on the skeletons. This contrasts with horizontal CWC reefs in the Atlantic, where coral rubble further contributes to the reef, morphing patches to thickets and coppices. Due to large depth, sediment stress is lower in these communities. These structures eventually turn into coral banks, comparable to shallow-water reefs (Freiwald, 2002).

As observed in this study, dead skeletons of *D. dianthus* provide substrate for colonizing organisms, but on a much smaller scale. With the present results it was not possible to discern whether the colonization of skeletons was favored over free plane substrate. As the skeletons form a major part of the new free substrate, it is not possible to tell whether they were colonized because they form erect structures or just because they provide free space. Longer monitoring of the experiment at LG, where the structures were removed, could provide insight into this question. Försterra *et al.* (2016) describe that the coral communities serve as refuge and feeding ground for juvenile fish. They observed a decline of fish in the benthic community after the disappearance of *D. dianthus*. Based on the definition of Jones (1994) and review of Jones and Gutierrez (2007) *D. dianthus* can be classed as ecosystem engineer. However, the suggestion that this property supports the high biodiversity of the benthic community could not be supported by the present study. On the level of species richness, the disappearance of *D. dianthus* in Comau Fjord did not have a major impact on the community. The species inventory did not undergo drastic changes, biodiversity indices remained stable and were comparable to the natural benthic community (Reichel, 2012). However, no information about possible changes on species level were collected, but there was no apparent change in ecosystem functioning. No specific functional group showed a decline or disappeared. Based on these findings, apparently not the structural influence of *D. dianthus* but more the biodiversity of the benthic community seems to stabilize the system after the disturbance. Nyström *et al.* (2000) describe resilience as the ability of an ecosystem to resist, re-organize and re-establish following disturbances. The present results show that the system compensates the disappearance of the previously dominant taxon by re-organizing, as other taxa are occupying the niche of *D. dianthus*. Large-scale disturbances ranging over greater distances and depths, caused by El Niño or hypoxic events, might have different implications. The resettlement of *D. dianthus* with normal growth rates show the process of re-establishment. Impacts on the community might be revealed as long-term effects, which cannot be determined based on the current results. No lasting effects of the disturbance can be assumed yet.

4.6 Conclusion and outlook

Following the coral mortality event, the benthic community exhibited an increase in percentage cover and abundance. This supported expectations, as the disappearance of living *D. dianthus* created newly available space (e.g. tissue-free coral skeletons). Rapid colonizers, such as octocorals and hydrozoans, seemed to take advantage of the free substrate. Growth rates of benthic organisms were in accordance with previous publications. The results underlined the role of *D. dianthus* as dominant species, exerting biotic pressure on the community. The changes following the mortality event, e.g. the increase in abundance of the scleractinian *C. huinayensis*, were therefore explained by this pressure being relieved. Individuals of *D. dianthus* resettled and exhibited normal growth rates. Following the TOLERANCE model, it can be assumed that they will recover. They may again outcompete the currently increasing taxa, such as octocorals, returning the system to its pre-disturbance state. Biodiversity was not negatively impacted. The system exhibited a high resilience to the disturbance and is predicted to fully recover. The areas at LG, where corals were removed, presented the same pattern of relieved biotic competition and subsequent occupation of the open niche by other suspension feeders, such as actinians.

Based on observed growth rates of *D. dianthus*, a full recovery of the system is expected on a scale of decades. In the short term, the community showed high resilience, facilitated by the high biodiversity. However, this might not apply to the long term and larger-scale disturbances. Therefore, monitoring of the recovering community should be continued. Using taxonomical sampling, a better estimation of the species richness would be possible and might underline the results in higher resolution. Further studies on possible competition between the different scleractinian species might explain the increase in *C. huinayensis* in the affected communities. In Central Patagonia, the hydrocoral *Errina antarctica* Gray, 1872, a major habitat-forming species supporting high biodiversity (Winkler, 2013), was affected by a mass die-off around 2009 (Häussermann and Försterra, 2014). Investigating the recovery of this system and comparing it to the present study might give further insight into how disturbances of habitat-forming species impact benthic communities in Chilean fjords and on chances of recovery. Despite the vulnerability of the scleractinian *D. dianthus* in this mortality event, the benthic community inside Comau Fjord exhibited high resilience and stability. However, due to slow growth rates, long recovery times are expected until the community returns to the pre-disturbance structure. Expanding aquaculture, infrastructure and tourism might in the future create more frequent disturbances, threatening the marine life. Protection measures should address the unique occurrence of the shallow CWC communities under consideration of the long recovery times and increased likelihood of such disturbances due to multiple anthropogenic and climatic stressors.

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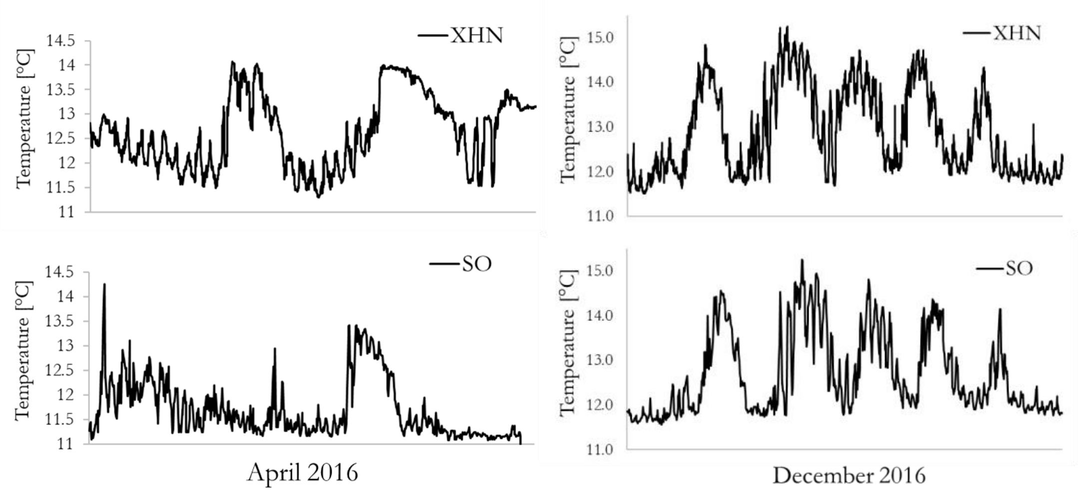
Appendix

Appendix 1: Water temperature [°C] in April and December 2016 at the stations XHN and SO in 20 m depth.



Appendix 2: Total and mean abundance [ind m^{-2} ± SD] of taxa identified at XHN (left) and SO (right) from 2014 to 2016.

	XHN			SO		
	2014	2015	2016	2014	2015	2016
Total abundance [ind m^{-2}]	988.3 ± 204.9	1221.8 ± 270.5	1252.8 ± 187.9	1377.7 ± 209.1	1621.9 ± 135.0	1859.2 ± 362.9
Porifera	183.9 ± 78.4	164.1 ± 57.4	180.6 ± 79.6	219.5 ± 72.2	190.6 ± 54.9	220.1 ± 66.1
Octocorallia	272.9 ± 200.1	303.2 ± 198.4	282.0 ± 105.4	187.4 ± 145.9	239.4 ± 179.4	275.7 ± 146.9
Actiniaria	8.7 ± 27.5	1.1 ± 3.6	8.0 ± 25.3	1.7 ± 4.8	4.8 ± 11.5	22.9 ± 64.8
Corallimorpharia	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Caryophyllia huinayensis	97.6 ± 62.3	138.5 ± 69.6	195.7 ± 73.8	133.1 ± 62.6	181.7 ± 76.5	389.5 ± 160.7
Desmophyllum dianthus	5.8 ± 7.4	12.8 ± 11.5	24.7 ± 19.7	4.2 ± 5.1	7.3 ± 10.5	25.8 ± 20.8
Tethocyathus endesa	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	2.8 ± 8.0	4.4 ± 12.3	2.8 ± 8.0
Hydrozoa	62.6 ± 31.7	89.1 ± 34.4	117.5 ± 48.3	118.6 ± 56.8	233.0 ± 91.2	275.4 ± 74.0
Crepidula dilatata	40.4 ± 30.0	37.3 ± 29.3	33.7 ± 24.2	4.8 ± 7.8	7.6 ± 9.9	3.9 ± 5.8
Aulacomya atra	0.0 ± 0.0	0.6 ± 1.8	0.0 ± 0.0	0.7 ± 2.0	1.4 ± 3.9	0.0 ± 0.0
Polychaeta	18.3 ± 13.2	17.4 ± 13.9	27.0 ± 17.4	70.8 ± 46.6	73.9 ± 38.8	118.6 ± 57.8
Cirripedia	1.2 ± 3.7	1.8 ± 3.9	2.3 ± 4.1	2.3 ± 3.3	2.3 ± 3.2	5.3 ± 7.9
Bryozoa (erect branching)	51.8 ± 31.5	150.3 ± 67.8	122.1 ± 33.0	230.2 ± 94.1	240.3 ± 66.2	147.5 ± 60.0
Bryozoa (encrusting)	128.1 ± 69.6	159.3 ± 90.7	142.7 ± 74.0	278.9 ± 127.6	275.1 ± 147.1	233.7 ± 147.1
Bryozoa (sheet-like)	18.5 ± 24.4	42.4 ± 30.7	10.9 ± 8.6	9.1 ± 10.3	48.3 ± 51.8	17.8 ± 7.7
Magellania venosa	13.4 ± 14.1	11.7 ± 13.2	16.5 ± 14.4	54.1 ± 32.4	45.2 ± 28.2	75.6 ± 47.6
Novocrania lecointei	81.3 ± 63.3	87.1 ± 69.0	85.8 ± 66.3	31.2 ± 59.1	34.5 ± 79.7	44.3 ± 86.6
Didemnum studeri	0.0 ± 0.0	1.1 ± 3.6	0.0 ± 0.0	7.4 ± 12.3	6.7 ± 8.0	4.7 ± 9.6

Appendix 3: Mean total cover [% ± SD] and covered area [% ± SD] of taxa contributing with >1 % in the years 2014 to 2016 at the stations XHN (left) and SO (right) derived from photo analysis.

	XHN			**SO**		
	2014	2015	2016	2014	2015	2016
Total cover [%]	18.6 ± 4.2	22.8 ± 5.1	26.1 ± 6.8	30.4 ± 6.7	37.4 ± 5.1	37.1 ± 7.8
Porifera	5.9 ± 4.1	5.8 ± 4.0	7.0 ± 4.5	9.5 ± 2.0	8.7 ± 2.4	9.8 ± 2.3
Octocorallia	4.6 ± 2.5	7.6 ± 2.7	9.4 ± 3.2	3.5 ± 3.3	5.7 ± 4.1	7.1 ± 4.4
Hydrozoa	1.2 ± 1.0	1.9 ± 1.2	3.5 ± 1.9	3.5 ± 2.6	9.1 ± 5.2	8.9 ± 1.7
Crepidula dilatata	2.7 ± 2.0	2.2 ± 1.8	2.0 ± 1.5	0.4 ± 0.7	0.5 ± 0.9	0.3 ± 0.6
Bryozoa (encrusting)	2.8 ± 1.4	2.1 ± 1.8	1.8 ± 1.2	5.1 ± 3.8	5.2 ± 4.1	3.0 ± 2.9
Crustose Red Algae	1.9 ± 2.1	2.0 ± 2.1	2.1 ± 2.3	6.7 ± 6.0	6.7 ± 5.8	6.9 ± 6.1