SUCCESSION OF BENTHIC HARD BOTTOM COMMUNITIES IN THE SHALLOW SUBLITTORAL OF COMAU FJORD, CHILE

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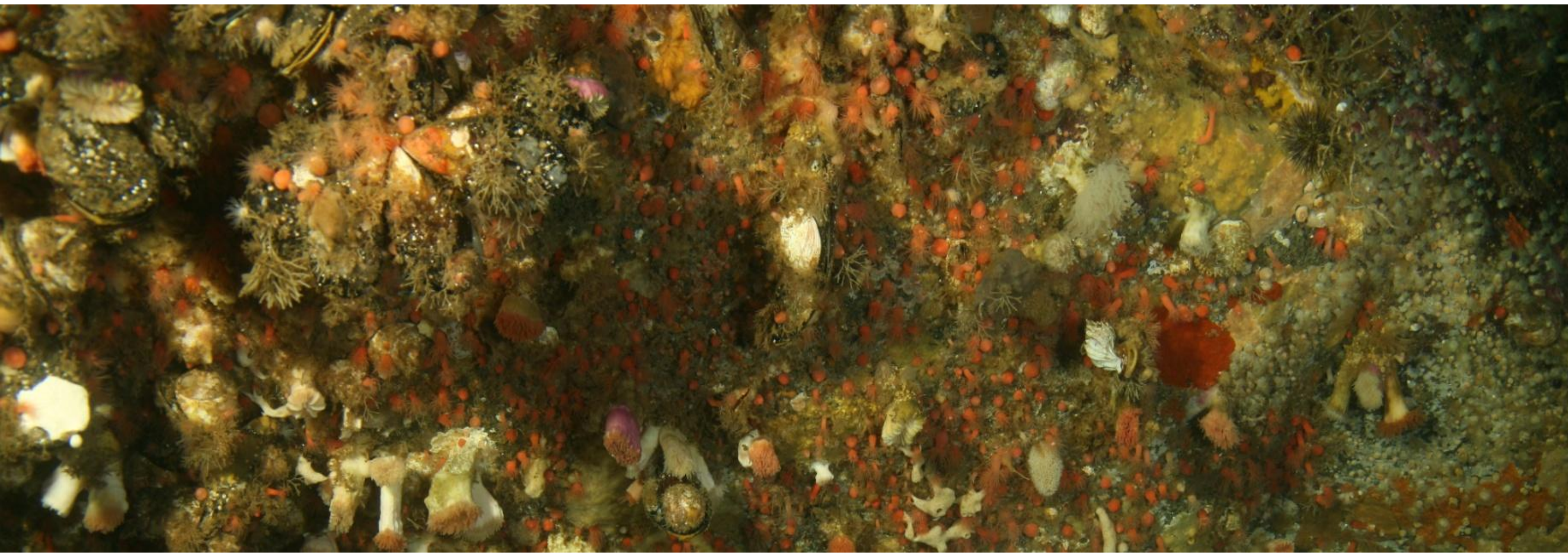

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Structure

Abstract

Succession was already studied over decades. The present thesis investigated the succession on hard substrate at two different study sites within the fjord Comau, Chile. Nine plates were installed at both sites (mouth of fjord and inner fjord) and photographed over three years. Additionally the natural community was recorded and a ground truthing was carried out to verify the analyzed species. Respectively at both sites over 50 different species were detected. Abundance data decreased with only one exception continuously, whereas the percentage cover increased. But the communities on the recruitment plates still did not reach the community structure of the natural environment. The present data indicates that for the hard bottom community in the fjord Comau is best described by the TOLERANCE MODEL (Connell & Slatyer, 1977). An important species of the natural community is the stony coral *Desmophyllum dianthus*, which normally (outside the fjord) grows beneath 1000 m water depth. The the still not reached diversity shows that the mature community is still not reached on the installed recruitment plates.

Zusammenfassung

Die Sukzession von Artengemeinschaften wird bereits seit mehreren Jahrzehnten sowohl auf Hart- als auch Weichböden untersucht. Erste Experimente liefen dazu auch schon im nördlichen, vom Humboldtstrom beeinflussten Chile, jedoch noch nicht in den Fjordsystemen des patagonischen Südens.

In der vorliegenden Studie wurden jeweils neun Fliesen als Besiedlungsplatten (15 x 15 cm) auf 18 m Wassertiefe an zwei verschiedenen Standorten im Comau Fjord Patagoniens installiert. Der Standort Lilliguapy befindet sich am Fjordausgang und zeichnet sich durch eine exponiertere Lage aus, während der Standort Cross Huinay im Inneren des Fjordes liegt und einen besonders niedrigen pH Wert vorweist. Es wurden jährlich Fotos von den Platten und in 2012 auch von der natürlichen Umgebung in direkter Nähe der Fliesen aufgenommen. Hierbei ist anzumerken, dass sich der Versuchsaufbau inmitten einer Korallenbank befindet. Innerhalb derer ist *Desmophyllum dianthus*, eine Steinkoralle, die normalerweise nur unterhalb von

1000 m vorkommt, die meist vertretene Art. Die Besonderheit des Comau Fjordes besteht darin, dass hier die Korallenart bis auf eine Wassertiefe von sieben Metern vorkommt. Die aufgenommenen Bilder wurden mittels Fotoanalyse ausgewertet und die darauf erkennbaren Arten bestimmt. Zur Verifizierung der Artnamen wurde das sogenannte „ground truthing“ durchgeführt, was bedeutet, dass Tiere in der natürlichen Umgebung gesammelt, mit den Fotos abgeglichen und anschließend konserviert und an die jeweiligen Taxonomen zur genauen Bestimmung verschickt wurden.

Die statistische Auswertung der erhobenen Daten ergab, dass an beiden Standorten jeweils über 50 verschiedene Arten gefunden wurden. Die Abundanz der Arten ist über die Zeit des Experiments in Lilliguapy stetig gesunken, während in Cross Huinay zwischen 2010 und 2011 noch ein Anstieg der Gesamtzahl zu verzeichnen war, bevor dann auch diese wiederum abnahm. Für den Bedeckungsgrad ist der Trend genau entgegengesetzt, da hier ein ständiger Anstieg der Werte an beiden Standorten zu beobachten ist. Die Multivariaten Auswertungen zeigten, dass innerhalb der Abundanz nahezu keine statistischen Signifikanzen zwischen den Gemeinschaften der einzelnen Jahre erkennbar waren, jedoch sich die Standorte selbst deutlich unterscheiden. Und auch die natürliche Umgebung unterscheidet sich signifikant sowohl innerhalb der Abundanz als auch des Bedeckungsgrades. Bei letzterem ist darüber hinaus auch ein signifikanter Unterschied zwischen den Gemeinschaften hinsichtlich des Faktors Zeit zu beobachten. Letztlich lässt sich darauf schließen, dass die Lebensgemeinschaft im Comau Fjord dem TOLERANCE MODEL (Connell & Slatyer, 1977) folgt. Die Sukzession scheint jedoch noch nicht abgeschlossen, da sowohl Bedeckungsgrad als auch Abundanzdaten der Besiedlungsplatten noch nicht mit der natürlichen Umgebung übereinstimmen. Die Steinkoralle *Desmophyllum dianthus* ist womöglich einer der Hauptgründe für diesen langen Prozess, da sie einen entscheidenden Hauptbestandteil der natürlichen Besiedlung bildet, ihr Wachstum bis zur vollen Größe jedoch 60 Jahre und mehr betragen kann und von unterschiedlichen pH Werten an den Standorten zusätzlich maßgeblich beeinflusst wird. Die Endgemeinschaft ist bisher nicht erreicht, da die Diversität auf den Platten eindeutig noch nicht mit jener der natürlichen Umgebung übereinstimmt.

1 Introduction

1.1 Succession

The term succession was introduced by Thoreau (1860) to describe changes in forest communities in which, after the deforestation of pinewood, squirrels brought back the first pine cones and new pines were re-established by seed drifting. Many studies on succession have since been carried out.

Biological succession follows a disturbance when new space becomes available (Noël et al., 2009). The first complete model was introduced by Clement (1916), who named six different stages of succession: Nudation, which refers to the creation of free space through disturbance; Migration, ecesis and competition, which describe the arrival, establishment and interaction of organisms at the site; Reaction, which refers to a site modification by organisms, thereby changing the species' relative abilities to establish and survive. Finally, stabilization describes the development of a stable climax. Thus, succession can be defined as a directional, permanent and gradual process of changing species occurrence within a community over time.

A distinction is made between primary and secondary succession. Primary succession takes place in localities that have never previously been settled. These empty substrates are left exposed after devastating disturbances such as landslides, the melting of glaciers or sand drifts through strong air or water movements (Smith & Smith, 2009). Secondary succession occurs after minor disturbance events that have left the substrate unimpaired but that have completely eliminated the existing community (Campbell & Reece, 2003). The scraping of commercially used mussels from the hard substrate is an example of such a disturbance.

Apart from the level of disturbance, its frequency is an important factor for the process of succession (Valdivia et al., 2005): the higher the disturbance frequency, the more the community structure will change. Clement (1936) described the result of this successional progress as a climax community that was generated according to the surrounding climate. The start of the succession is always influenced by different climatic conditions, so that even minor disturbances can lead to major differences in later climax community structures.

The complex process of succession already starts when an experimental panel with a smooth surface is submerged in seawater. At first, macromolecules are taken up by the empty surface (Dexter & Lucas, 1985), before bacteria are adhere as well (Wicken, 1985; Costeron et al., 1978). Afterwards, a fully primary biofilm of bacteria, diatoms and protozoa is built up; later macrophytes and epifaunal organisms attach to the substrate (Davis et al., 1989; Mitchell, 1978). Based on recruitment, predation, nutrient availability and disturbances, succession can reach different levels and results at the end in a mature community. Pioneer species with a fast reproductive rate settle on new substrates first; these are later replaced by slow-growing and long-living species. Community structure changes over time due to interactions between species and their competition for space. The community changes from an early stage with mostly solitary species to later stages with mainly colonial species, which overgrow earlier communities (Teixeidó et al., 2002; Witman & Dayton, 2001). The question as to which species will settle first on a bare substrate is strongly influenced by water movement, larvae occurrence and the seasonal starting point (Valiela, 1995). Currents transport propagules to the solid substrate, on which they can attach and expand.

Clement's (1916) succession model was the only one available for a long time; however, it could not explain all processes of species composition. This gap was filled by Cornell and Slatyer (1977), who developed three models of succession (Fig. 1). The first one was termed FACILITATION; it correlates with the model by Clements (1916) and states that only particularly suitable early pioneer species settle first and that they are necessary for subsequent successional stages. Thereby the first species to colonize the available substrate modify their environment in a way that allows the invasion by - and growth of - late colonizers. INHIBITION means that early colonization stages block later settlers. Due to this, later colonizing species can only exist if the pioneer species are damaged or killed (Connell & Slatyer, 1977). Early and late settlers can be the same type of colonizers and are only selected by their first settling on the available substratum. The TOLERANCE MODEL describes neither positive nor negative effects between successional stages and depends on the individual life-history characteristics of species composition, i.e. if they are early or late settlers and short- or long-living species. First settling short-living species neither inhibit nor facilitate the growth and success of later settling species. This means that almost the same species inventory exists at an early and late stage of the succession and that changes are not obvious in abundance but rather in species size depending on the different life-history characteristics. Directional mechanisms need to be involved in the FACILITATION and TOLERANCE MODEL, but not in the INHIBITION MODEL.

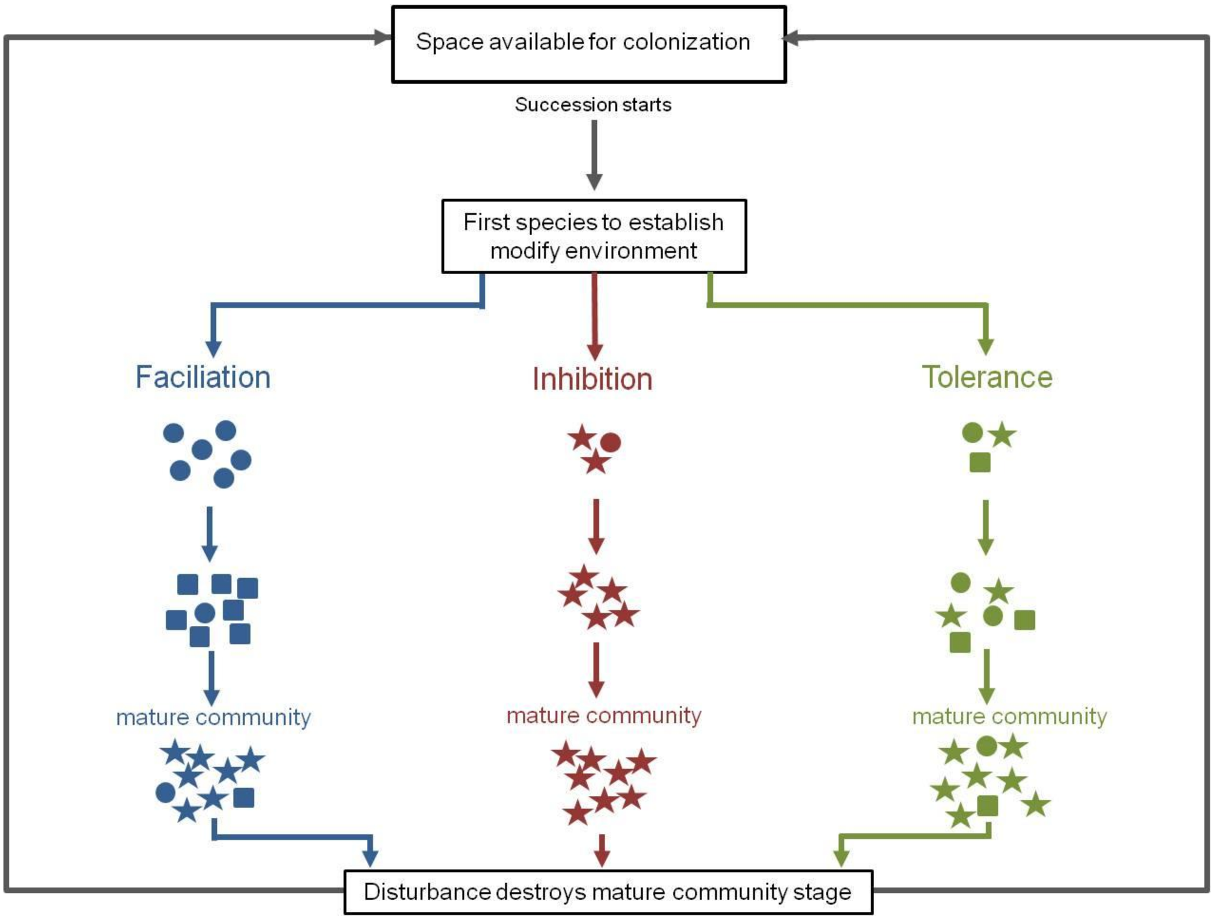

Fig. 1: The three models of succession by Connell and Slatyer (1977) modified after http://sky.scnu.edu.cn/life/class/ecology/chapter/Chapter20.htm. When free space is available succession starts and communities with only early or all kinds of species begin to settle. Established species begin to modify their environment and one of three models begins. Different symbols illustrate different species.

The life history and the age of species is an important precondition for their answer to disturbances and the ongoing succession process as shown by Sousa (1980) working on, succession experiments on algae communities. He demonstrated that young communities were more severely damaged by disturbances but that they also re-established much faster than older communities. Konar (2007) showed that grazing species have a strong effect on the colonization of sessile organisms. The interaction between species can therefore also have a strong impact on succession.

Connell and Slatyer (1977) also pointed out that the intensity of disturbance and the size of a disturbed area influence the successional process. Therefore, smaller sized areas are recolonized faster due to close neighbors that overgrow the free substrate or colonize it with propagules (edge effect). In small areas that are only lightly disturbed, no succession takes place and gaps are only refilled by the growth of surrounding adults. The strongest impact results from an extreme disturbance on a large area, whereby no survivors exist and all colonizers have to arrive from outside. The INTERMEDIATE DISTURBANCE HYPOTHESIS generated by Hutchinson (1953) and Horn (1975) states that the highest diversity is maintained at an intermediate scale of disturbances. Due to the recurrent upcoming disturbances, species have to settle again and need a moderate time-span to build up a new community structure and reach a mature community. Species have to tolerate disturbing effects and compete fast with other species for space and limiting factors as light and nutrients (Roxburgh et al., 2004; Collins et al., 1995).

1.2 Hard bottom communities

Hard substrate is influenced by currents and disturbances and harbors mainly a sessile and encrusting but also a partially mobile community (Lake, 1990; Tait & Dipper, 1998). It occurs in all zones of water depth. In the subtidal zone, three types of hard bottom exist: 1) mineral hard bottom, which originates from natural rock or dead biogenic (e.g. coralline) material, 2) artificial surfaces of anthropogenic origin such as submerged ships or piers, and finally 3) living biogenic surfaces such as mussel beds (Davis, 2009). Svane and Petersen (2001) defined artificial substrates as submerged man-made structures that are susceptible to fouling.

Experimental panels are artificial surfaces; they can, however, imitate a mineral hard bottom, for example in the case of ceramic plates that have a consistent structure and even roughness. Texture, rugosity and orientation of the substrate are strong determining factors for settlement processes and the following succession (Wahl & Hoppe, 2002). The hard bottom surface has a heterogeneous structure and pronounced slopes and overhangs that are responsible for the variability in several abiotic environmental parameters such as light intensity, nutrient availability by currents and sediment exposure. When sufficient light reaches the hard bottom, primarily all major microalgae groups are present within the community (Wahl, 2009). However, when light is absent or not that intense due to water depth or overhangs, all other animal classes compete with macroalgae and are able to occupy the available space. Different case studies suggest that highest species richness occurs in the tropics and decreases pole wards, resulting in a global latitudinal gradient for hard bottom communities (Canning-Clode, 2009). Nevertheless, as described before, sufficient available resources can lead to the establishment of highly complex communities in any environmental setting: Many rocky shores, for example, are densely populated because of the steady supply of well-oxygenated and nutrient-rich water (Tait & Dipper, 1998). Large and diverse sponge communities were found in Antarctic waters (Janussen, 2009), and bryozoans colonize large rocky areas of the Arctic Kongsfjorden (Schwalfenberg, 2012).

Space is one of the most limiting resources on hard substrate and subject to much competition amongst solitary and colonial species. Jackson (1977) demonstrated that solitary species often settle first on available space and are later outcompeted by colonial species such as bryozoans. In their experiment in the Pacific Northwest, however, Greene et al. (1983) revealed that solitary animals such as anemones, mussels and barnacles inhibit the growth of colonies of other species and have the highest abundances. According to Pacheco (2009), several community structures, all heavily structured by influencing variables such as severity of disturbance, colonizing patch size and biological interactions, can be observed on hard bottom surfaces. Pacheco (2011) also showed that the level of light exposure of a rocky wall influences the succession: On each surface, exposed and hidden, a temporal change of community structure was detectable, but the communities between both treatments differed considerably.

1.3 Characteristics of fjord systems

Fjord systems developed geologically in postglacial times. They can be defined as long, deep, high-latitude estuaries, which have been excavated or modified by land-based ice. The process of fjord formation can still be ongoing (Syvitski et al., 1987). Fjords are the deepest of all estuaries and found all over the world. Most fjords occur along the North and South American coasts, in Arctic archipelagos, along the southwest coast of New Zealand as well as in northern Europe, for example in Norway. Fjords are characterized by environmental gradients between the open ocean with fully marine and saline water (mouth side) and the freshwater inflow of rivers and melting glaciers (head side) (Freeland et al., 1979). Fjords are covered by a freshwater layer that can embrace up to 11 m (Freeland et al., 1979), which is responsible for a stable biological zonation (Müller, 2012).

European fjords have been studied for over 150 years (e.g. Hansen, 2002; Rosenberg et al., 2002) but Chilean fjord systems have only been poorly investigated. The hard bottom structure below the water surface is very similar to the structure on land. The Chilean Comau Fjord is characterized by steep, hard rock walls with various slopes and overhangs. The fjord’s pH value is particularly low (Jantzen et al., 2011). Due to the high acidity, the fjord has been used as a model for an actual “future ocean scenario” with falling pH values and therefore a challenging system for all calcifying species. Consequently, the discovery of thriving coral populations (*Desmophyllum dianthus* and *Caryophyllia huinayensis*) was quite remarkable, considering that these are deep-sea stony corals; *Desmophyllum dianthus* is known as a cosmopolitan bathyal species (living at 1000 – 4000 m water depth) (Försterra et al., 2005). It was even more peculiar that these species were found in shallow water up to 7 m in Comau Fjord (Fig. 2); sufficient explanations for this unusual range are still lacking (Försterra & Häussermann, 2003).

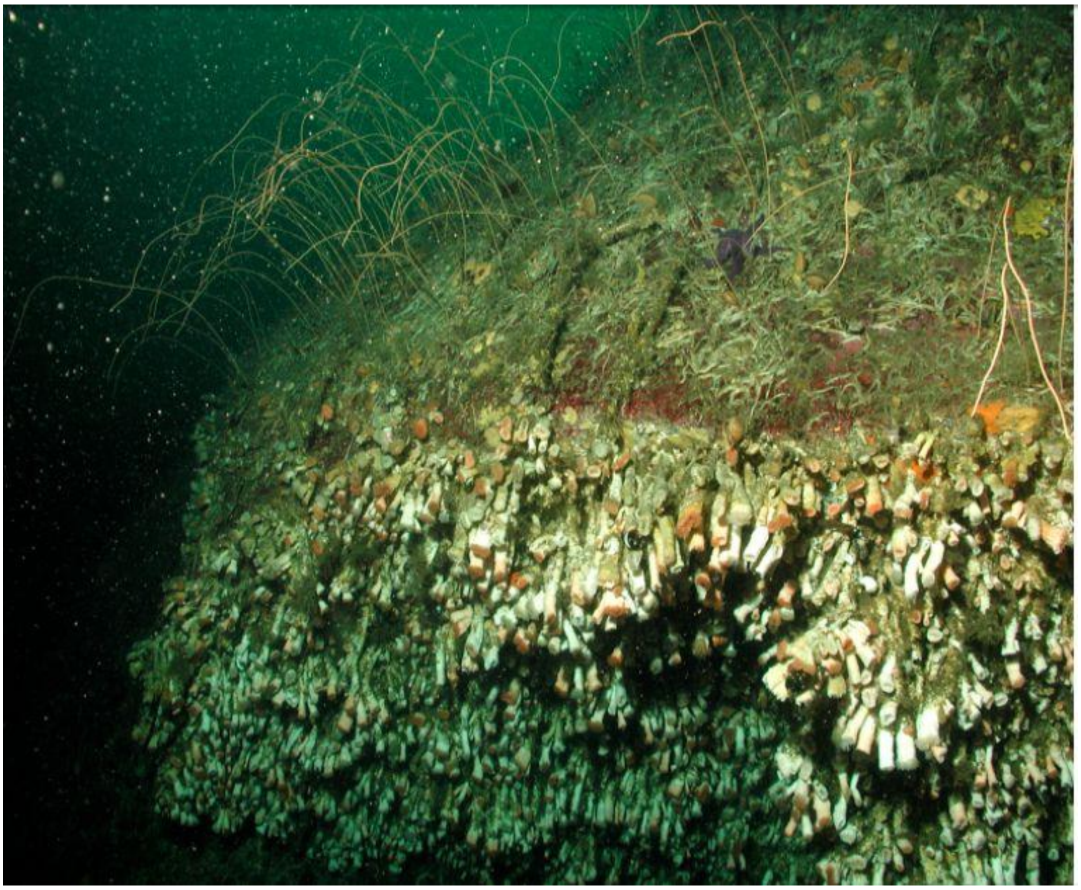

Fig. 2: Overhang in Comau Fjord, Chile, with characteristic, dense *Desmophyllum dianthus* aggregations (Häussermann & Försterra, 2005)

1.4 Aims of study

All types of hard bottom communities have only been poorly studied in South America (Davis, 2009). Especially in the southern part of Chilean Patagonia, no observations of community structures and succession processes have been carried out. Thus, the present study aimed to study the community inventory and structure within the Comau Fjord in southern Chile to get a clue about the ongoing succession processes and compare them to other systems.

The hard substratum in Comau Fjord is characterized by deep walls with only few cracks and caves. An experiment was set up on bare rocks below overhangs to avoid sedimentation of recruitment plates. Pacheco et al. (2010) described significant differences in species composition between hidden and exposed substrates: coralline algae were found only on exposed substrates, while the bryozoan *Membranipora* *isabelleana* was found on hidden treatment surfaces – as the first and last settling species, not being outcompeted by later settlers. Additionally, different temporal community compositions were discernible on the exposed area (Pacheco et al., 2010). Based on this results, it was assumed for the present study that, due to the exposed location of the plates and the same cold temperated system, a staged process would occur and that the potential influence of installation angles would need to be considered. But the Humboldt Current system provides a nutrient-rich surrounding, whereas in the fjord system an oligotrophic environment dominates that could be responsible for a lower species inventory and a down slowed succession.

Considering the reduced light intensity at a water depth of 18 m and beneath the overhangs, where the sampling took place, it was assumed that no macroalgae would be found (Wahl, 2009). The Chilean species identification guide from Häussermann and Försterra (2009) gives an insight into the great diversity of the fjord systems. Therefore, a very diverse community was anticipated to be found. As mentioned before, high abundances of living deep-sea corals can be found in shallow waters of Comau Fjord. Normally, outside the Chilean fjords, these *Desmophyllum dianthus* and *Caryophyllia huinayensis* coral beds are really rare, so that the experiment was carried out in the direct vicinity of one of these dense beds. It was assumed that the stony corals would continuously produce a bare substrate. So far, no information about the reproduction of these two species has been gained; however, first studies have been undertaken to investigate the growth rates of *Desmophyllum dianthus* (Hassenrück, et al., 2012). It is not clear yet, however, how long it takes for the coral to be fully grown, especially when considering that no natural influences such as space competition and species interactions have been tested before. So it is of interest, whether the corals will settle on the recruitment plates and how long they need to grow to mature size and maybe again to such dense aggregations.

The question remains how long it takes till a mature community is reached. The community structure of the Chilean cold-water system of the Humboldt Current is disturbed nearly every four years, so that a quite fast succession for resettlement is needed. In the fjord Comau disturbance events are not that often, so that the succession has more time to develop. Vance (1988) found that his experimental community, near to the Santa Catalina Island (California) in 15 m water depth, needed exactly three years to establish and to be comparable to its reference community. This community, however, was mainly composed of bryozoans, sponges and red algae – and not of corals. Therefore, no concrete evidence for the needed time of succession in the tested system exists. A time period of succession, however, is always influenced by the surrounding abiotic and biotic factors and by the species inventory itself. According to Pacheco (2009), successional sequences can be variable and need a time period of between two and eight years to reach a mature stage, whereas it is not definitely clear if a final stage is attainable.

Consequently, the following four research questions shall be answered:

(i) How is the species inventory described?

(ii) Are different successional stages discernible?

(iii) What kind of succession model describes the community development best?

(iv) How long is the resilience time of the benthic hard-bottom community?

2 Material and Methods

2.1 Study site

The Chilean fjord region extends from 41°30' S to 56° S and is mostly characterized by hard substratum. The fjord Comau is located in its northernmost part, near the island Chiloé (Fig. 3; 42°10' to 42°50' N and 72°40' to 72°60' W). It extends over 40 km from the south to the north and empties into the Gulf of Ancud, which is directly connected to the Pacific Ocean, through the Comau channel. Comau Fjord is characterized by steep slopes of rocky granite substratum, both under and above the water line and reaches an average depth of 250 m and a maximum depth of 490 m. The fjord receives freshwater from precipitation and river influxes during winter and early spring (September – October). Thus, a low salinity layer of 0.5 m (summer) to 10 m (winter) exists with salinity as low as 2, whereas below 18 m the salinity is constant at 32. Diurnal tidal amplitudes of up to 7 m characterize Comau Fjord (Galea et al., 2007). The experiment was carried out at two study sites: in front of the entrance of the fjord at Isla Lilliguapy (42°09’43’’S; 72°35’27’’W) and in its centre at Cross Huinay (42°23’29’S; 72°26’6’’W) (Fig. 3C)

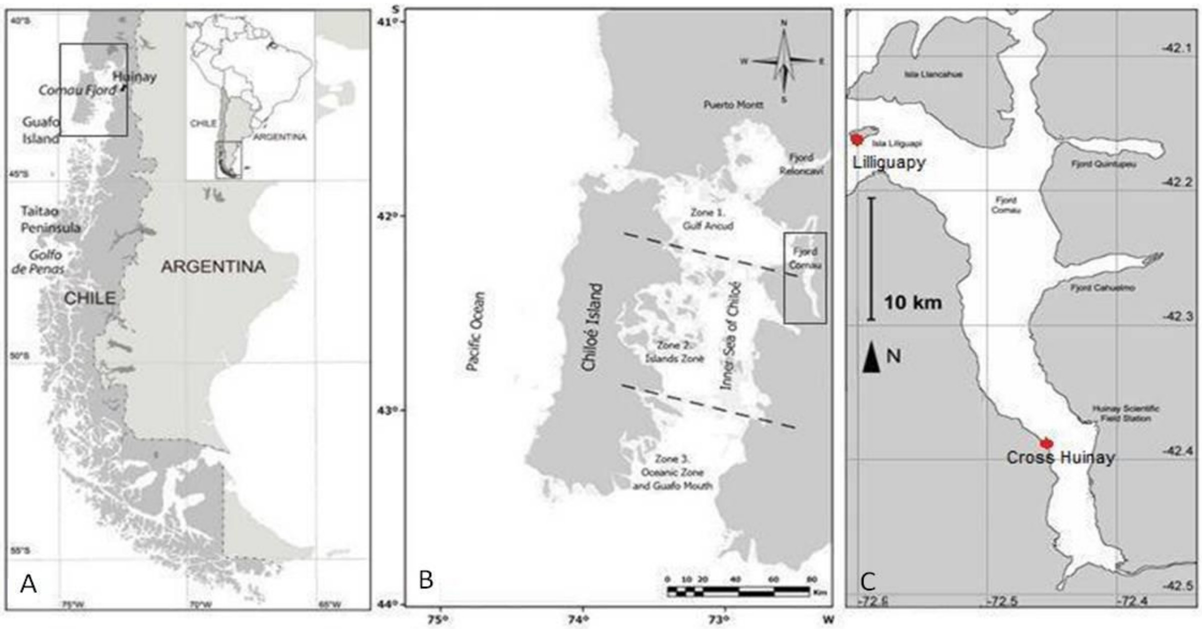

Fig. 3: Location of the study site Comau Fjord in the Chilean fjord region. A: Southern Chile (Försterra et al, 2005) B: Gulf of Ancud (Lara et al., 2010) C: Comau Fjord with both study sites: Lilliguapy and Cross Huinay (modified after Galea et al., 2010).

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2.2 Abiotic environmental characteristics

In 2011 and 2012 temperature loggers were brought out at both sites to measure the data for the next year. At both study sites temperature ranges between 10°C in winter and 16°C in summer (Fig. 4). For Cross Huinay the average temperature of the whole year is 11.1 °C and for Lilliguapy 11.4 °C.

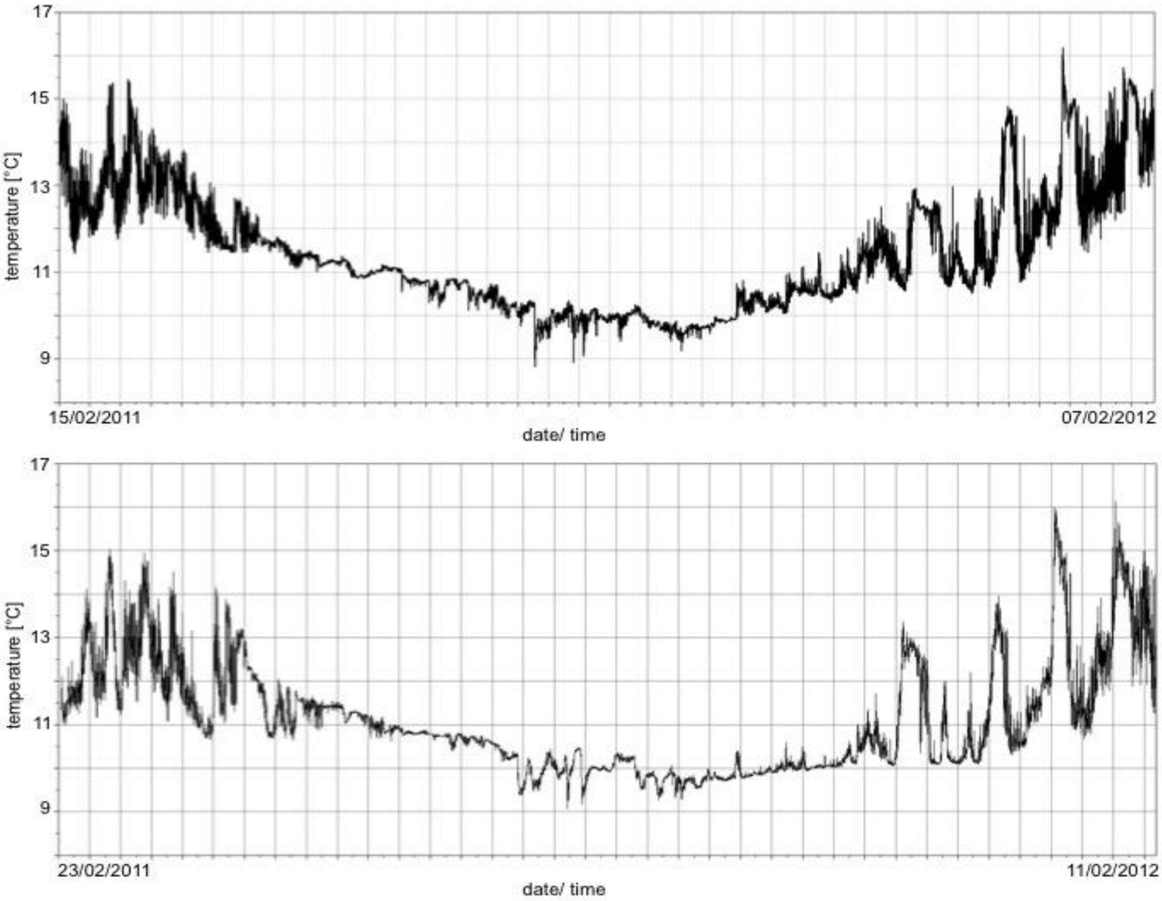

Fig. 4: Temperature at the two study sites Lilliguapy (A) and Cross Huinay (B) from 2011 (Data kindly provided by S. Baumgarten).

In January/February 2011 as well as in January/February 2012 CTD (Seabird SBE 19plus V2 SeaCAT, Sea-Bird Electronics, Bellevue (Washington), USA) casts were carried out to measure salinity, pH-values and temperatures in order to characterize the two sites. Results for 2011 were plotted and extrapolated for the whole fjord from its mouth to the inner part. Both study sites are characterized by a salinity of ca. 32 in the deeper waters. Furthermore they have a low salinity layer (25 - 28) in common, which represents the high rates of freshwater input in this area (Fig. 5).

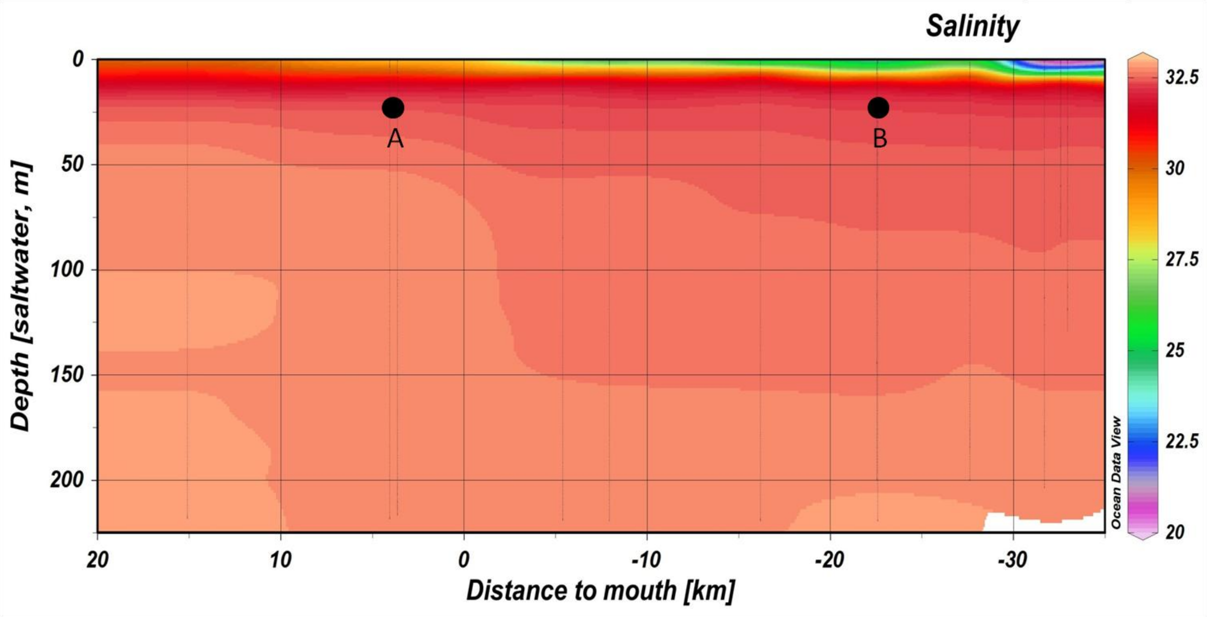

Fig. 5: Hydrographical section indicating the salinity along the axis of Comau Fjord in 2011. Bright grey vertical lines show taken profiles of the water column (Data kindly provided by S. Baumgarten). A: Study site Lilliguapy. B: Study site Cross Huinay. Both sites are located at around 18 m water depth.

Additionally, pH-values were recorded at both sites. In Lilliguapy slightly higher values from 7.9 to 8 were found, whereas Cross Huinay showed values of 7.7 to 7.9. The pH-value of the surface layer is influenced by freshwater from precipitation and river run-off, which leads to values up to 8.3 (Fig. 6).

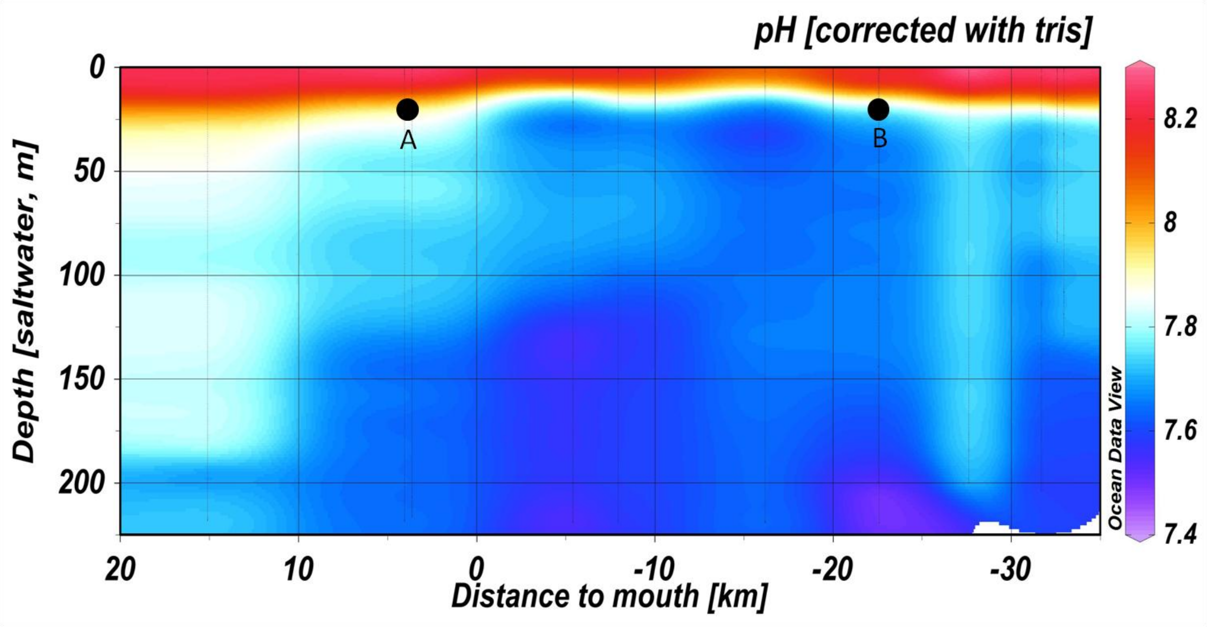

Fig. 6: pH-values of Comau fjord 2011 extrapolated for the distance from fjord mouth. Bright grey vertical lines show taken profiles of the water column (Data kindly provided by S. Baumgarten). A: Study site Lilliguapy. B: Study site Cross Huinay.

2.2 Experimental Set-up

The backside of common tiles was selected as substrate. Advantages of these tiles are that they offer a suitable hard surface with a quite roughness and could easily be installed in the natural environment. The tiles were 15 x 15 cm (225 cm^2) and were fixed with two screws and washers to a PVC frame (Fig. 7). The latter is connected to the wall with a bolt. A square pattern on the tiles allows easy analysis of the percentage cover of species. This pattern has a size of 1.75 cm between the middle of adjacent ridges (Fig. 7).

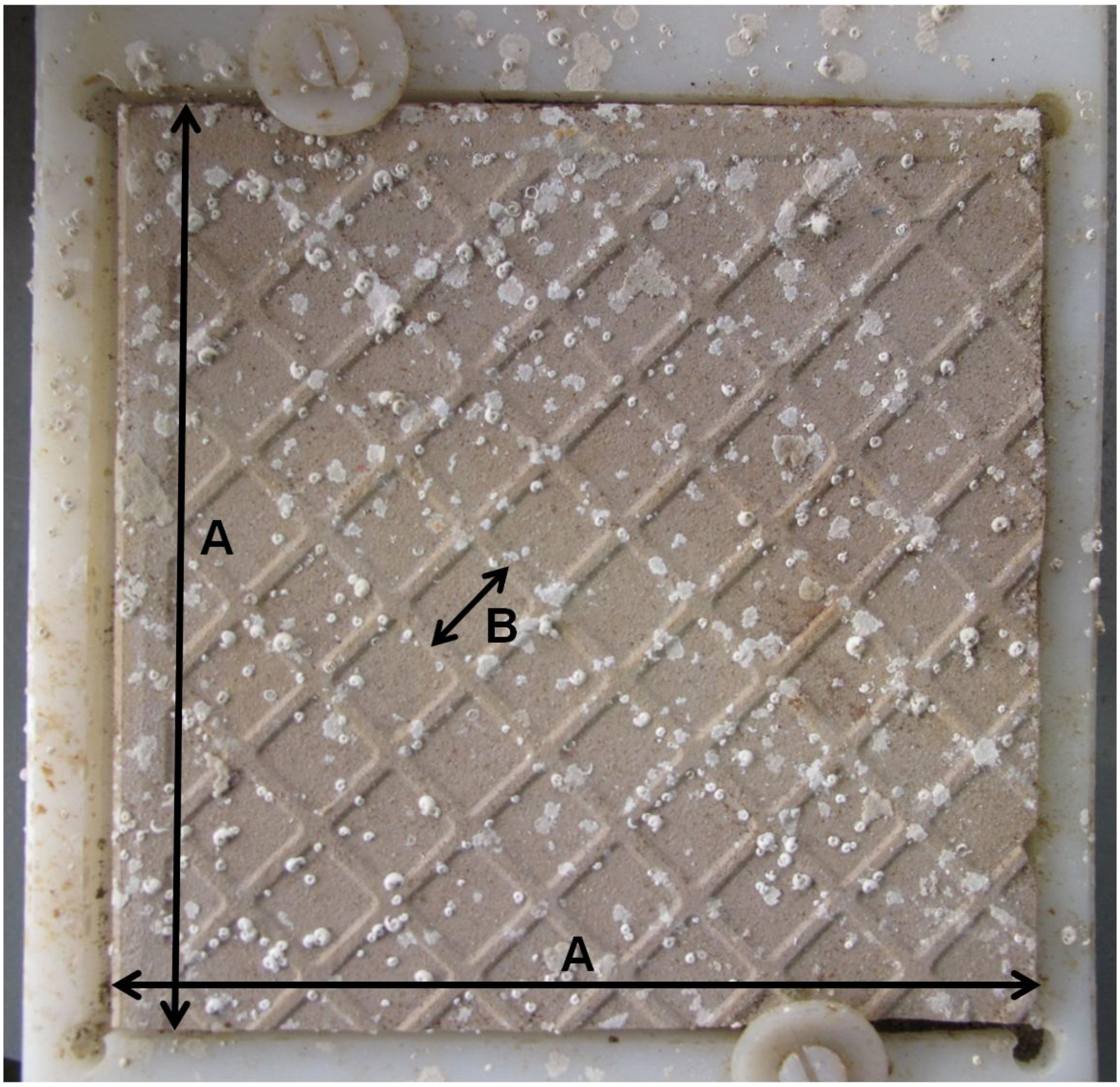

Fig. 7: Backside of a tile in a PVC frame fixed by two screws and washers. A: Dimensions of the plate 15 x 15 cm B: 1.75 cm from middle to middle of divider.

Growth of settling species may be influenced by environmental factors such as depth, sedimentation, the topography and exposure to light. From the ten plates installed initially in January 2009, nine remained to be analyzed consistently at each site. Frames of recruitment plates were marked with numbers for easy identification under water. In each case all plates were attached by scientific SCUBA divers with a pneumatic driller and heavy duty bolts to a rock wall with overhangs to get replicates of the same area (Fig. 8). Corresponding to the depth of hard coral banks of *Desmophyllum dianthus* as a typical local hard bottom community and the mean water level, they are located in Lilliguapy at 18 m water depth and in Cross Huinay at 19 m. Due to this subtidal position, the samples are exposed to a stable fully marine environment. Due to the fact that the natural surrounding hard substratum is characterized by overhangs and slopes plates were installed at angles between 11° and 62°. To detect a possible influence from angles on the establishing community structure, the installation angles of the plates were measured by scientific SCUBA divers.

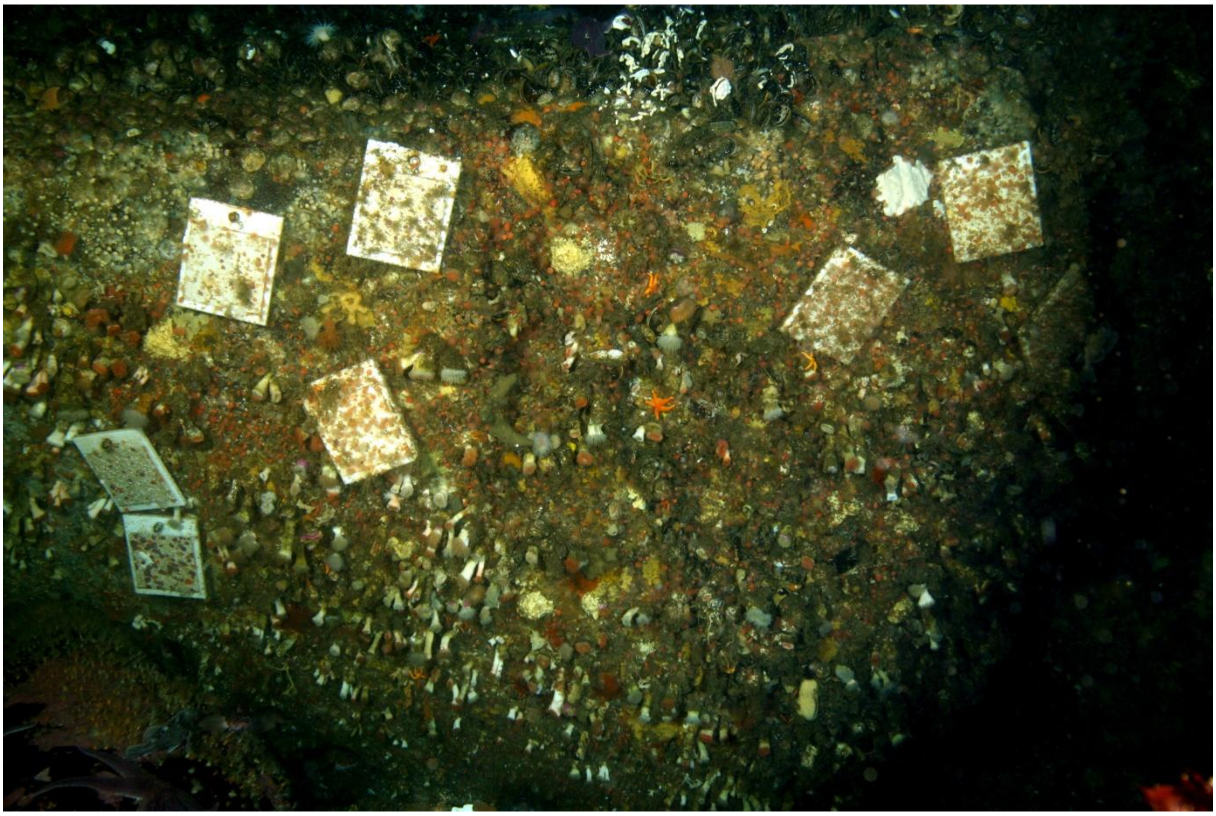

Fig. 8: Study site Lilliguapy: Recruitment plates installed at 18 m water depth at an overhang of a rock wall colonized by a typical hard bottom community of the fjord Comau (note the abundant scleractinian *Desmophyllum dianthus*).

2.3 Photo documentation, sampling and analyses

Since the beginning of the experiment all plates at both sites were photographed (Canon EOS 5D Mark II (Canon, Krefeld, Germany) with a 50 close-up lense and two flashes, resolution of 12 MB) several times for a chronological comparison (Table 1). In 2011 additionally one tile from Cross Huinay was removed, photographed in detail in the laboratory and re-installed. Small sub-samples of some bryozoans were taken and fixed in 99% alcohol for further analysis.

Table 1 Dates of analyzed photographic documentation at study sites Cross Huinay and Lilliguapy.

Cross Huinay	Lilliguapy
28. Apr 2010	26. May 2010
24. Feb 2011	26. Feb 2011
27. Jan 2012	31. Jan 2012

All generated data about species occurrence on recruitment plates were organized in a presence-absence-list for an overview. Supplementary data can be found in Reichel and Laudien (2012). Unknown or unidentifiable species were marked on photos for later identification. One plate in Lilliguapy and two plates in Cross Huinay were selected due to their species richness and variation for removal and later detailed analysis in the laboratory (Fig. 9). After photo documentation the dimensions of large species such as brachiopods, mussels, corals and anemones were measured with calipers. Furthermore, small parts of species that were difficult to identify were taken from the plates and sent to taxonomists for further analysis. Bryozoans, for example, were cut off with an electric grinder (Dremel 8200 with a diamante cutting disc (3.2 mm thickness), DREMEL Europe, Breda, Netherlands) from the rim of the plate. “Ground-truthing” was carried out by sampling individuals of the unknown species (colonizing the tiles) from the surrounding natural environment in order not to disturb the successional colonization on the plates. Attention was paid not to take samples in the direct vicinity of the plates to avoid the destruction of possible parental generations. Sampled species were conserved in 99% alcohol and ascidians in formaldehyde, identified at least to family level, prepared for further identification and then also given to taxonomists for further analysis.

Fig. 9: Recruitment plate N° 2 from Cross Huinay photographed in the laboratory (note *Magellanium venosa*, *Aplidium fugiense*, *Didemnum studeri*, *Figularia sp.*, *Smittina sp.*, *Rhodelinda gardineri*, *Clavularia magelhaenica* and *Desmophyllum dianthus*).

Image analysis was conducted using Adobe Photoshop CS5.1 (Adobe Systems, München, Germany). Species were identified to the lowest level possible at least to species level, counted and archived in the World Data Centre For Marine Environmental Sciences and its database PANGAEA. Abundance of species was determined with the Counting-tool of Adobe Photoshop using different colors for distinct taxa (Fig. 10). As the size of the tiles is known a measurement scale was set. Areas covered by individuals were marked using the Lasso-tool of Adobe Photoshop and the percentage cover recorded (Fig. 10). Species were measured as seen, so that parts that were covered by other specimens couldn't be recorded. Furthermore, they were gauged in their actual position on the photos (e.g. brachiopod, individual 5 versus individual 6, Fig. 10), because if bigger animals cover parts of the plate, it's not possible for species below them to gain the same food supply as free living species, so that animal position and their cover are characteristic.

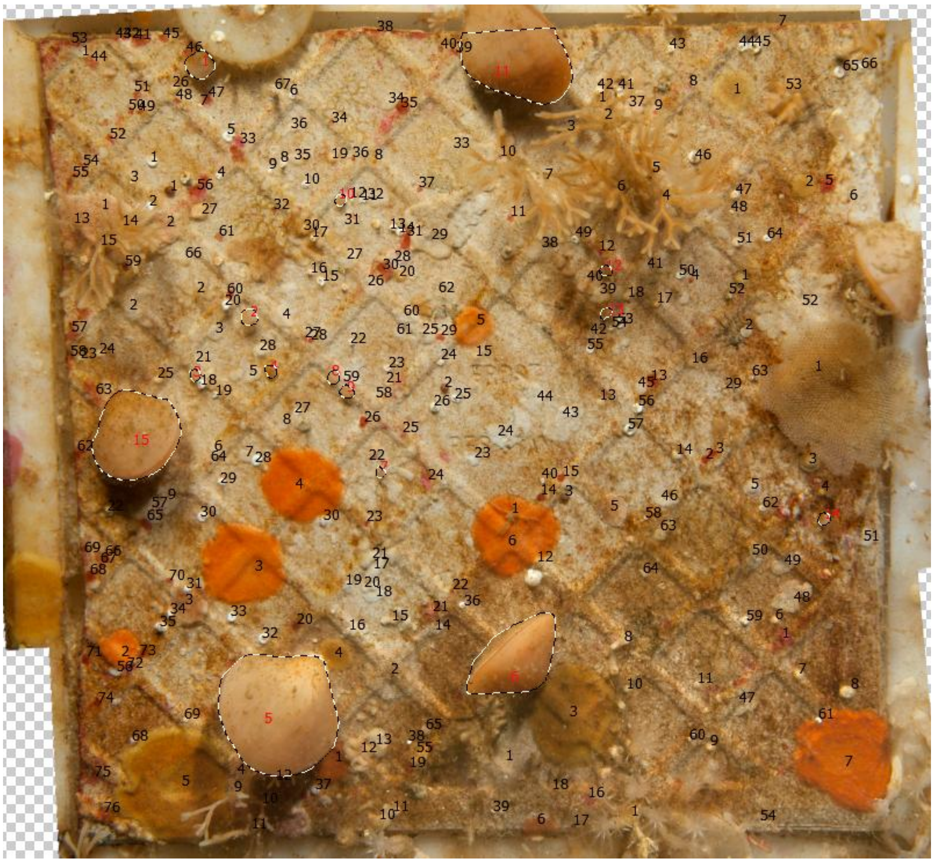

Fig. 10: Recruitment plate N^o 4 from Cross Huinay. Species are marked using the Counting-tool of Adobe Photoshop CS5.1, e.g. the brachiopods *Magellania vonosa* are numbered in red and marked for measuring the percentage cover.

2.4 Statistical analysis

Three datasets of the identified taxa form the basis for all statistical analysis: the presence-absence, the abundances, and the percentage substrate cover. For each plate and photo of the natural environment, organism counts were standardized to one square meter. Abundance and percentage cover data were used for several descriptive analyses to compare the community structure of both study sites as well as the changes of total and individual species numbers throughout the experimental time. The Shannon–Wiener diversity index (*H'*, Log *e*), species richness (d) and

Pielou’s evenness (J’) (Pielou, 1975) were determined for each sample and analyzed in R statistics for possible significances between the communities of the study sites and years.

For multivariate community analyses, presence-absence data and abundance data were used. These data were square-root transformed to avoid an influence of rare species, without excluding them. For these analyses only data of presence-absence and percentage cover were used. Mainly coincidence is responsible, if mobile species such as starfish, sea urchins or gastropods can be seen on the photos or not. Because of that only sessile species were included in the analyses. Multivariate analysis were employed utilizing the PRIMER 6 & PERMANOVA+ package (Clarke and Warwick 2001; Clarke & Gorley, 2006) to detect patterns in community composition at both study sites over time. Using group average linkage, sample classifications were archived and thereafter samples related to each other identified based on the resulting dendrogram. Due to the huge dataset of species, which are quite unequally distributed, it is not advisable to compare single species. Instead, plates with their species inventory were compared within the two sites and as well between them. Therefore, the Bray-Curtis coefficient and the method GROUP AVERAGE were used.

To verify the cluster analysis a MDS statistic (non-metric Multi-Dimensional Scaling) was calculated (Kruskal & Wish, 1978). This ordination technique is based only on the similarity matrix between samples and needs no requirements for distribution and linearity (Clarke, 1993; Clarke & Warwick, 1994). Within MDS scatter plots similarities of the species composition between plates and the control variable NATURAL ENVIRONMENT are represented by the proximity of points. The closer two points of community structure are arranged together, the more similar they are. For each MDS statistic a stress value is provided to indicate the statistical quality; a value of ≤ 0.1 means a good reliability with a minor potential of misinterpretation, a value between 0.1 and 0.2 indicates an ordination, which is still useful for interpretations whereas a value ≥ 0.2 shows that the results need to be used quite carefully more verifying analyses need to be conducted (Clarke & Warwick, 1994).

For the identification of statistical significances a two-factorial design with PERMANOVA was used. PERMANOVA is a routine for testing the simultaneous response of one or more variables to one or more factors in an analysis of variance (ANOVA) experimental design on the basis of any resemblance measure, using permutation methods, rather than by reference to an assumed distribution. It was applied to create a pairwise-test to check for possible significant influence of the time progress and the study sites on the respective community structures on the recruitment plates as replicates. P-value ≤ 0.05 were assumed to indicate significant differences between the community structures.

When significant differences between recruitment plates and the natural environment were detected, SIMPER analysis was used to identify the relevant species and their contribution (Clarke & Gorley, 2006).

Additionally environmental data (pH value, temperature and salinity) of both study sites were used to drive a BIOENV analysis in PRIMER to find a possible correlation. To prove if the community structure is modulated by low pH values newly settled individuals of the calcifying scleractinian *Desmophyllum dianthus* (Esper, 1794) were investigated. Diameters of corallites were measured on all available photos between 2010 and 2012 from successive pictures using Photoshop CS5.1. Gathered data were set in comparison between sites.

2.5 Species identification

Species were identified from highly magnified photos (Fig. 11) and the comparison with sampled individuals, as well as the identification guide of Häussermann and Försterra (2009).

The phylum Cnidaria exists of several classes, which can also be found in the fjord Comau. From the class Scleractinia only three species are known in this region, which can easily be identified by their massive calcareous exoskeletons. Thus identification only from photos is mostly possible as long as the tentacles are more or less retracted.

For the class of Octocorallia, Rhodelinda gardineri could be easy identified by its red color, whereas the other specimens had to be identified under a stereo microscope and later compared from their outer forms with the taken pictures.

The three Actinarian species, colonizing the tiles, have clear external features as their tentacles, column, oral disc and a characteristic coloring for a definite identification.

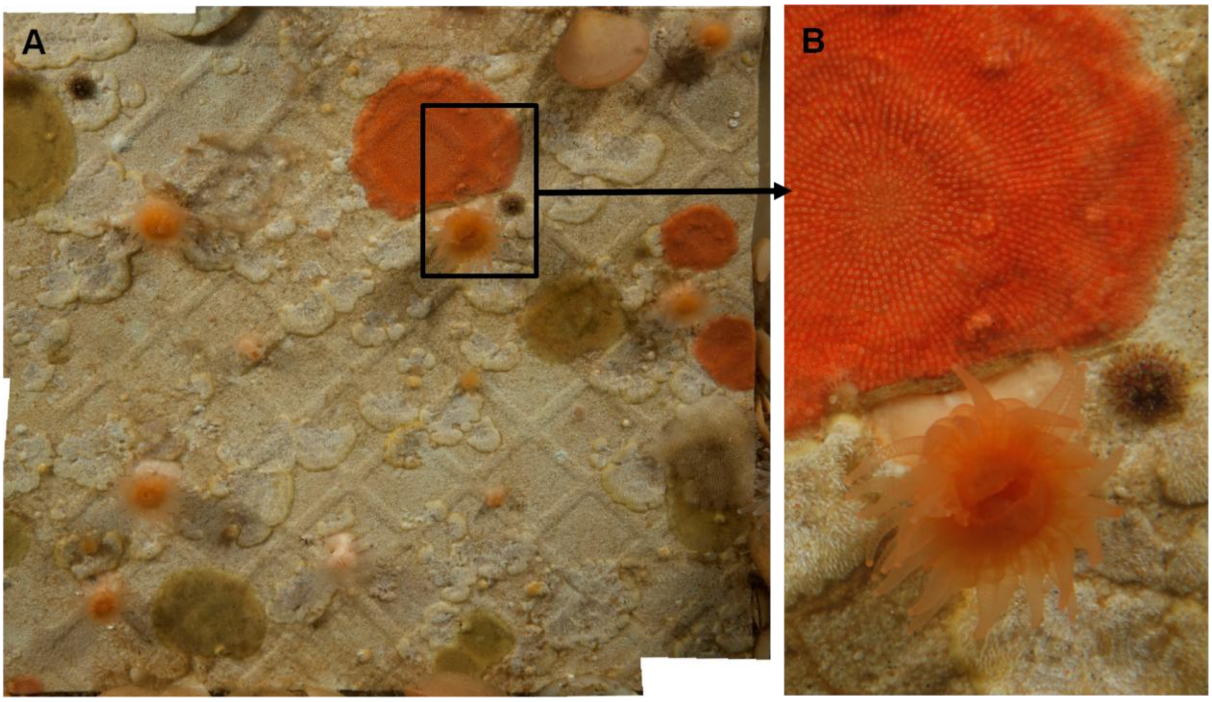

Fig. 11: Photo with 12 MB from the recruitment plate N° 1 from Cross Huinay (A) with a detailed clipping in high resolution (note *Smittina* sp., *Arbacia dufresnii*, *Desmophyllum dianthus* and cf *Plagioecia* sp.).

Based on their small size Hydrozoans are not easy to identify from the pictures. Therefore, microscopic pictures from sampled specimens from different plates directly in situ were taken and sent to the taxonomist Horia Galea (Hydrozoan Research Laboratory, Tourves, France).

From Bivalves only a few species exist in the fjord Comau. The water depth of around 18 m from the plates excludes the bivalve *Mytilus chilensis*, which exists only in the intertidal zone. Due to this, identification could be done without taking samples and only by pictures because of the characteric external features.

From Polyplacophora, Pycnogonidae as well as Gastropoda only a few animals could be sampled in the field and then identified by using a binocular. All others were analyzed by comparing their typical superficies with the taxonomic guide (Häussermann & Försterra, 2009).

From Brachiopods only two species are known in Chilean Patagonia and could be easily distinguished on photos by their external form of the shell.

For sea urchins, Echinoidea, the length of spines is regarded as a main characteristic for the found species, which can be detected without any problems on the photos for precise identification.

Currently approximately 200 sponge species are known from Chilean waters and they are not easy to be identified. The sponge taxonomist Daniela Henkel (Integrated School of Ocean Science (ISOS), Christian-Albrechts University, Kiel, Germany) helped with the identification. The preparation of the sections followed the technique described by Vacelet (2006) and included dehydration, embedding in epoxy resin and cutting using a precision saw with diamond wavering blade. Spicules were prepared by dissolution of the soft tissue of sponge fragments in nitric acid and studied by light microscopy after mounting in Canada balsam on slides. The classification of the sponges followed mostly the guidelines in *Systema Porifera* (Hooper & van Soest 2002).

Polychaets were also sampled in the field and later analyzed by Andreas Bick (University Rostock, Germany). These polychaet samples were afterwards cataloged at the University of Rostock.

Ascidian samples were photographed and send to Marcos Tatián (Universidad Nacional de Córdoba, Córdoba, Argentina).

Bryozoans grow mostly in bigger colonies, which were sampled in the fjord and later cleaned with distilled water and a brush to get rid of detritus. Afterwards, specimens were bleached in a 10 % sodium hypochlorite solution for two hours and then again washed with distilled water and dried at room temperature overnight. Dried colonies were then glued on a stick and thereafter coated with gold for scanning electron microscopy (SEM). Photos were analyzed by Julia Caceres (University of Vienna, Wien, Austria) for species identification.

3 Results

3.1 Species inventory

Due to the high quality and resolution of the photographs, most individuals present on the tiles could be identified to species level. Only a few animals could not be allocated to family level. As described previously (Chapter 2.5) it was necessary to take SEM pictures from bryozoan colonies for taxonomical classification. Bryozoan species were identified by morphological characteristics such as the shape of the operculum and/or ascopore (Fig. 12). In the three consecutive years of this study more than 50 different species were identified and detected, both from the recruitment plates and from the surrounding natural habitat (Table 2). Whereas the total number of species was similar at Lilliguapy and Cross Huinay, species composition differed distinctly. In the following chapters, species are summarized to family level and abundances are provided for each study site to homogenize the data and give a better overview.

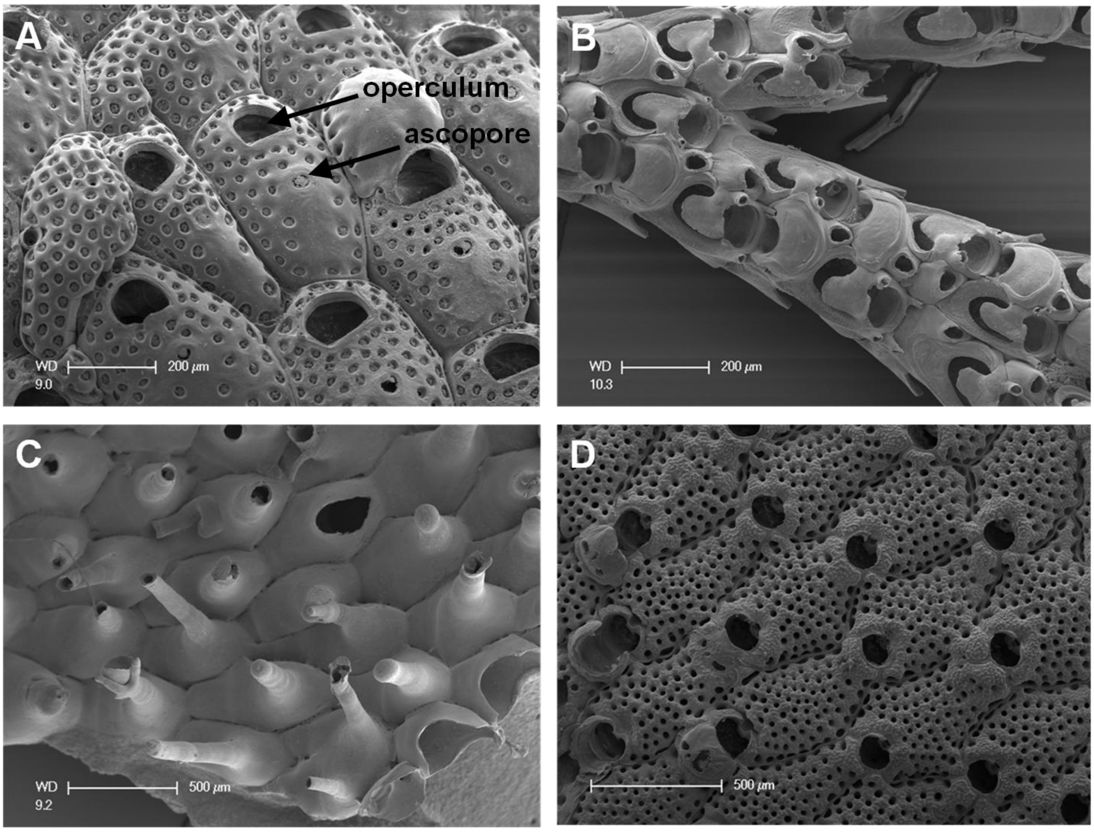

Fig. 12: SEM photographs of bryozoan colonies from the fjord Comau. A: *Fenestrulina* cf *specca* B: *Caberea darwinii* C: *Chaperiopsis* sp. D: *Smittina* sp..

Table 2: Mean abundance (Individuals per m^2) of organisms identified at both study sites. Species are organized to orders. At both sites, data were revealed in 2010, 2011 and 2012 and additionally organisms from the natural surrounding (Nature) were counted as a reference community.

	Lilliguapy				Cross Huinay			
	2010	2011	2012	Nature	2010	2011	2012	Nature
Porifera								
Axynissa sp.	0	6	5	10	0	0	0	0
Clathrina cf *antofagastensis*	28	133	217	41	0	20	15	7
Esperiopsis sp.	17	39	10	0	0	0	5	0
Haliclona (Reiniera) sp.	6	0	74	32	5	0	0	0
Unidentified sp.	189	111	148	234	10	35	30	59
Octocorallia								
Clavularia magelhaenica	0	6	0	0	15	30	74	214
Rhodelinda gardineri	0	0	5	0	0	10	35	0
Unidentified sp.	0	0	0	0	0	0	5	0
Actinaria								
Gonactinia prolifera	11	56	0	0	15	25	49	21
Halcurias pilatus	2456	1706	2128	1999	0	5	0	0
Hormathia pectinata	0	0	15	13	5	15	5	0
Unidentified sp.	0	0	0	0	0	0	0	52
Corallimorpha								
Corinactis sp.	0	0	0	267	0	0	0	20
Scleractinia								
Caryophyllia huinayensis	89	122	138	0	69	168	227	140
Desmophyllum dianthus	6	6	5	105	0	35	30	276
Unidentified *C. huinayensis* or *D.dianthus*	0	0	5	0	0	0	0	205
Polyplacophora								
Callochiton puniceus	0	0	0	6	0	0	5	0
Unidentified sp.	0	0	0	0	0	5	10	0
Bivalvia								
Aulacomya atra	0	2794	844	0	5	5	25	0
Gastropoda								
cf *Crepidula dilatata*	0	0	0	0	0	0	0	0
cf *Fissurella oriens*	6	0	0	0	0	0	0	53
Nacella sp.	0	0	5	0	5	30	20	4
cf Patellidae	0	0	0	14	0	0	0	59
Opisthobranchia								
Unidentified sp.	0	0	0	12	0	10	0	0
Polychaeta								
cf *Hypsicomus phaeotaenia*	0	0	0	706	0	0	0	642
Perkinsiana littoralis	0	0	0	0	0	0	5	26
Pileolaria sp.	4822	1461	2015	128	2825	2909	1600	18

Unidentified sp.	0	6	15	0	0	0	0	4
Pycnogonidae								
Achelia assimilis	0	6	10	0	5	15	5	0
Callipallene margarita	0	0	0	0	10	0	0	0
Balanidae								
cf *Notobalanus flosculus*	0	0	0	0	0	0	0	0
Bryozoa								
Beania cf *magellanica*	244	317	25	13	291	5	69	22
Bugula sp.	11	256	5	60	0	0	0	0
Caberea darwini	0	239	0	325	15	15	10	53
Cellaria malvinensis	506	956	257	175	163	519	356	33
Chaperiopsis sp.	39	83	44	11	0	0	0	30
Disporella cf *octoradiata*	406	311	331	46	1175	1560	983	0
Fenestrulina cf *specca*	311	194	262	237	138	217	202	60
Figularia sp.	44	11	10	0	193	222	242	205
cf *Plagioecia* sp.	150	33	35	112	647	1358	1067	7
Smittina sp. I	11	11	30	53	109	153	173	59
Smittina sp. II	378	467	721	6	227	286	237	0
Smittina sp. III	1222	828	746	350	0	5	5	214
Brachiopoda								
Magellania venosa	0	6	20	0	173	222	277	0
Asteroidea								
Unidentified sp.	0	0	0	4	5	0	0	4
Echinoidae								
Arbacia dufresnii	6	6	20	0	0	5	44	253
Loxechinus albus	0	0	0	4	0	0	20	27
Pseudechinus magellanicus	6	0	44	0	15	10	138	0
Holothuroidea								
Heterococumis godeffrroy	0	0	0	0	0	0	0	8
Ascidiacea								
cf *Aplidium fugiense*	0	6	20	150	0	5	5	13
cf *Aplidium magellanicum*	28	50	54	0	0	0	0	0
cf *Aplidium variable*	6	0	0	0	0	0	0	0
cf *Cnemidocarpa nordenskjoldi*	6	0	5	0	5	49	20	0
Corella eumyota	11	6	5	8	0	5	0	43
Didemnum studeri	50	61	553	4	0	10	40	0
cf Styelidae	11	11	0	0	0	0	0	0
Unidentified sp.	72	61	109	0	0	5	0	0
Gnathostomata								
Helcogrammoides cunninghami	0	6	0	0	0	0	0	0
Rhodophyta								
Unidentified sp. I (encrusted)	0	0	0	10	183	963	770	0

Unidentified sp. II (feathery)	0	0	0	0	15	0	0	0

3.2 Descriptive analysis

In Lilliguapy the total number of organisms found in 2010 on the recruitment plates and the environmental surrounding as a reference community was 11,144 per m^2 and decreased constantly to 8,933 per m^2 in 2012, whereas the natural surroundings were covered by only 5,135 larger organisms per m^2 (Fig. 13 A). Polychaets comprised 14 to 48 %, Actinians 18 % to 40 %, Bryozoans around 30 %, Porifera three to six percent and Ascidians between two and nine percent of the 50 known species and additional 4 families not further identified. Bivalves and Scleractinians were occasionally detected. Comparing the communities of the recruitment plates from 2010 with the colonizing community in 2012 and the surrounding community as a reference community, no differences within the dominating groups are discernible, although the group of ‘others’ (including Polyplacophora, Opisthobranchia, Pycnogonidae, Asteroidea, Balanidae, Echinodermata, Corallimorpharia and Gnathostomata,) increases from almost zero to up to five percent. In the ‘others’ group all species were summarized, that didn’t reach 5 % of the total number of abundance over all years.

In contrast the total number of taxa from study site Cross Huinay did not indicate a clear trend. In total 6,306 individuals per m^2 were observed in the first year. The total number of species then showed a peak with 8,928 in 2011 and decreases to 6,800 organisms in 2012 (Fig. 13 B). The species inventory of the surrounding habitat included only 2,830 individuals. In all three experimental set-ups and the reference community (nature) bryozoans dominated (~ 45 %) on the tiles and 22 % of the total number of organisms in the surrounding community. Polychaets contributed 23 % to 45 % and Scleractinians around 4 % on the recruitment plates and 22 % in the natural environment. Encrusting red algae were found on the tiles, although they were almost absent from the adjacent natural community. Scleractinians and Octocorallia dominate the natural communities, but did not reach high numbers on the tiles.

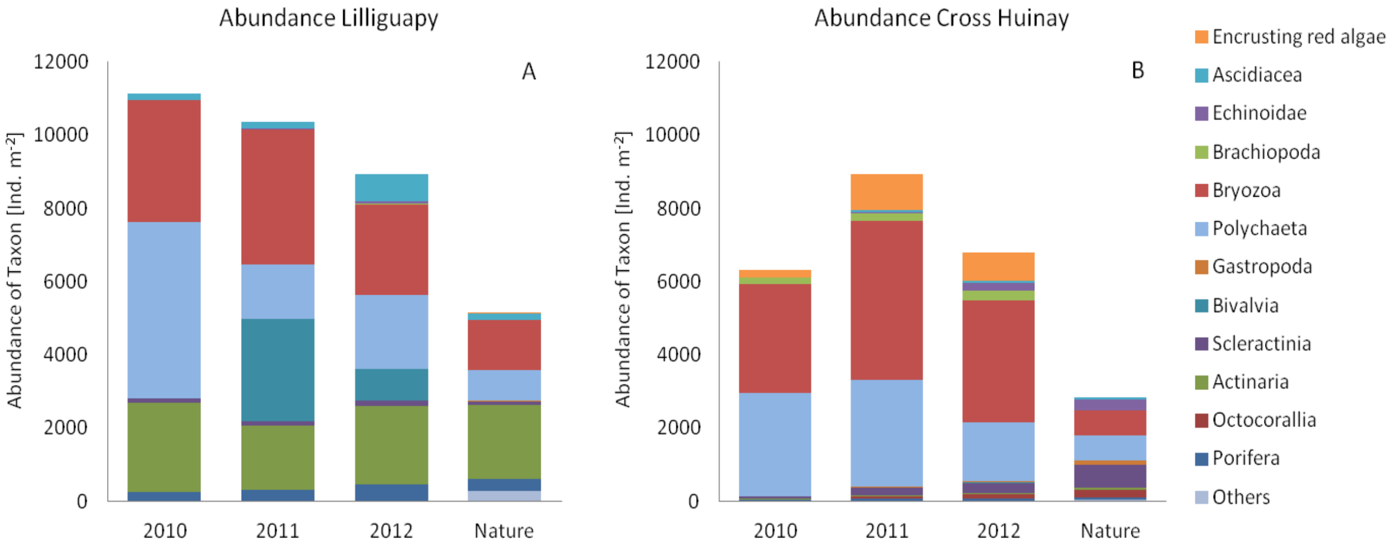

Fig. 13: Abundance (Individuals m^{-2}) of dominating taxa and others (< 5 % of total individual number) for the study sites Lilliguapy (A) and Cross Huinay (B), separated for years. Note that the natural community, photographed in 2012 (Nature) is included for comparisoon. “Others” include Polyplacophora, Opisthobranchia, Pycnogonidae, Asteroidea, Balanidae, Echinodermata, Corallimorpharia and Gnathostomata.

It is important to analyze not only numbers of organisms, because less species with a large size can have as well a high influence on the community. So the percentage cover was measured to set organisms’ size in relation to the size of recruitment plates.

In Lilliguapy the total percentage cover of the recruitment plates (Fig. 14) increased from 37 % in 2010 to 46.1 % in 2012, but did not reach the percentage cover of natural communities (59.2 %). In 2010 two groups of species dominated: bryozoans covered 19.4 % of the plates and actinarians 12.8 %. In 2011 the respective cover was 23.1 % (bryozoans) and 9.7 % (actinarians). Temporal increase in bivalve, sponge and scleractian dominance was also detected, however they remained below the 5 % level. As in the previous years, bryozoans (18.8 %) and actinarians (15.7 %) were the main groups covering the plate surface in 2012. Bivalves reached 5%, whereas scleractinians, hydrozoans and sponges did not attain 5 % cover. In the surrounding natural habitat, actinarians were the major group (18.2 %), followed by sponges (16.3 %) and bryozoans (9.8 %). Scleractinians contributed with 9.1 % whereas hydrozoans covered less than 5 %.

In Cross Huinay the percentage cover of species on the recruitment plates increased from 18.4 % in 2010 to 43.2 % in 2012. However, it did not reach the percentage of the natural surrounding community (54.4 %).

On both sites changes in community structure were recognized throughout the experimental time period. The community composition also differed between both study sites. In 2010, mostly bryozoans covered (12 %) the recruitment plates in Cross Huinay. Additionally 'others', including nine taxonomical groups, reached 5 % of plate coverage. In 2011 bryozoans covered most of the surface (16.5 %). Brachiopods, encrusting red algae and hydrozoans were also detected, but did not reach 5 % cover. Bryozoans attained 24.7 % of cover on recruitment plates in 2012. Hydrozoans (6.6 %) and brachiopods (6.4 %) increased in importance. All other species occupied less than 5 % of the space.

In the surrounding habitat scleractinians covered 17.3 %, red algae 12.7 % and brachiopods 5.7 % of the substrate surface. Octocorallia (4.3 %), bryozoans (4.2 %) and hydrozoans (3.6 %) were also present.

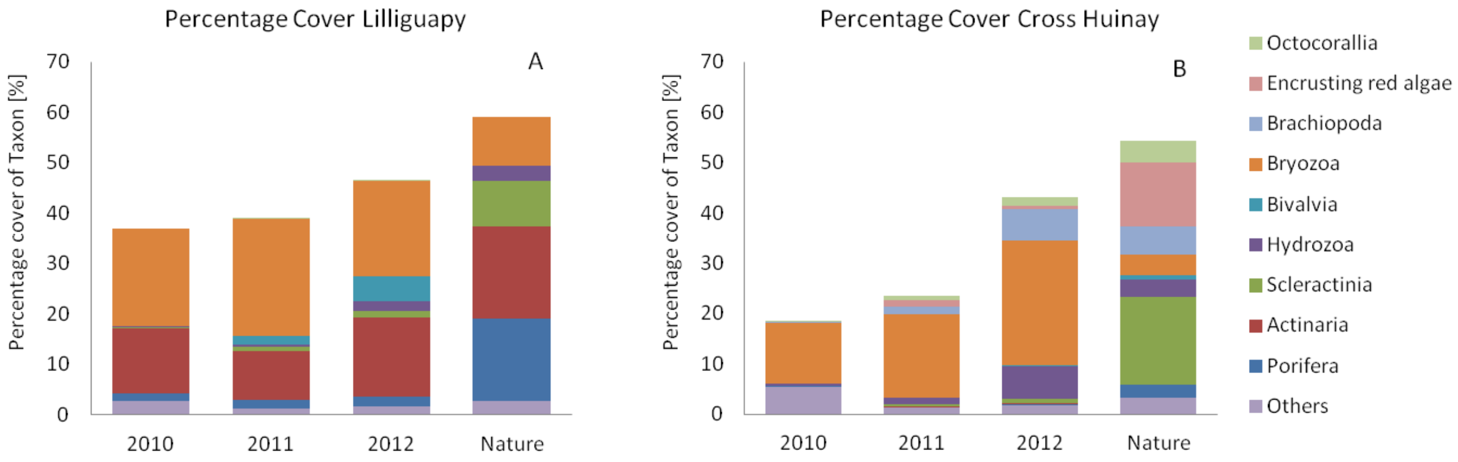

Fig. 14: Percentage cover of dominating taxa and others (< 5 % of total individual number) for the study sites Lilliguapy (A) and Cross Huinay (B), separated for years. Note that the natural community, photographed in 2012 (Nature) is included for comparison 'Others' include Polyplacophora, Echinidae, Gastropoda, Opisthobranchia, Polychaeta, Pycnogonidae, Asteroidea, Ascidiae, Balanidae, Echinodermata, Corallimorpharia and Gnathostomata.

The Margalef Index (*d*), based on abundance data, showed no significant differences (P > 0.05) between the communities of both study sites (Fig. 15). In Cross Huinay species richness was lowest (0.95) in 2010 and reached a maximum (1.45) in 2012

(Fig. 15 A). ANOVA indicated that *d* is significantly different for the factor year (P < 0.01). As a consequence the community structure of the experimental communities at Lilliguapy significantly changed (P < 0.05) over time. Species richness varied between 1.16 and 1.35 (Fig. 15 B).

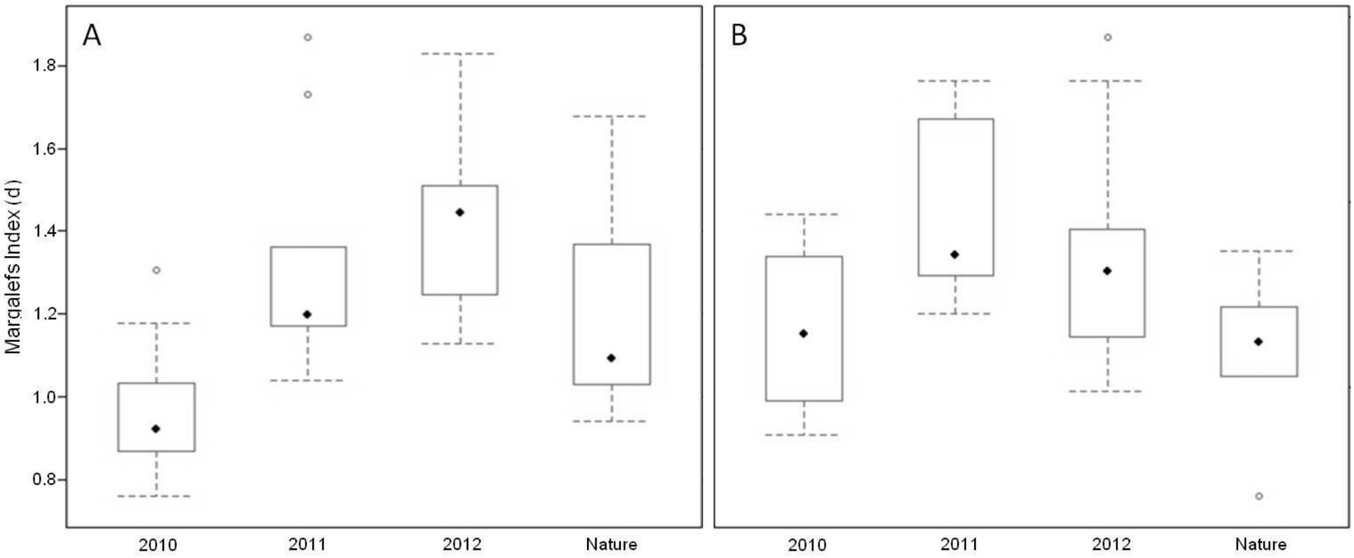

Fig. 15: Species richness (Margalef Index, d) plotted for maturing communities at Cross Huinay (A) and Lilliguapy (B) in comparison to the natural community. Filled circles indicate the median, boxes show the 50 % interval, bars provide the standard deviation and open circles represent outliers.

Pielou's evenness (J') indicates the spatial homogeneity of species. Evenness of the communities from both study sites was not significantly different (P > 0.05). For the maturing communities at Cross Huinay a value of ca. 0.7 was calculated, whereas the natural environment indicated a more even community structure (J' = 0.87) (Fig. 16 A). An ANOVA analysis showed that values were significantly different over time (P < 0.5). In Lilliguapy the evenness is obviously increasing from 0.6 in 2010 to 0.76 in 2012 and is constant in the natural environment (Fig. 16 B). Significance for the evenness of samples for the factor year can also be detected (P < 0.5) for Lilliguapy.

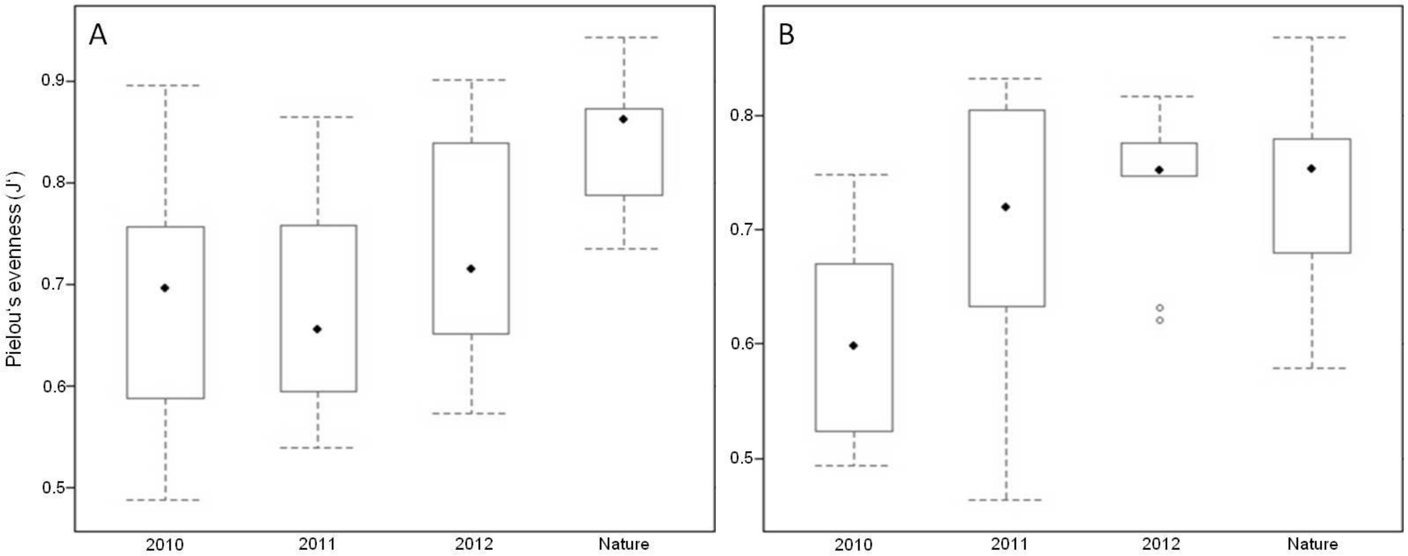

Fig. 16: Pielou's Evenness (J') of the maturing communities at Cross Huinay (A) and Lilliguapy (B) during the experimental period in comparison to the one of the natural community. Filled circles indicate the median, boxes show the 50 % interval, bars provide the standard error and open circles represent the outliers.

The Shannon-Wiener Index of the maturing communities was not significantly different between the two study sites ($P < 0.05$). For Cross Huinay an increase from 1.7 (2010) to 1.9 (2012) was detected, the latter value resembled H' of the natural communities (Fig. 17 A). Significant differences between the diversity of the distinct community stages were not detected ($P > 0.05$). In Lilliguapy the diversity also followed the same trend (1.5 in 2010, 1.9 in 2012), however the maximum exhibited the diversity of the natural communities (1.7) (Fig. 17 B). For these results a significance could be recognized ($P < 0.5$).

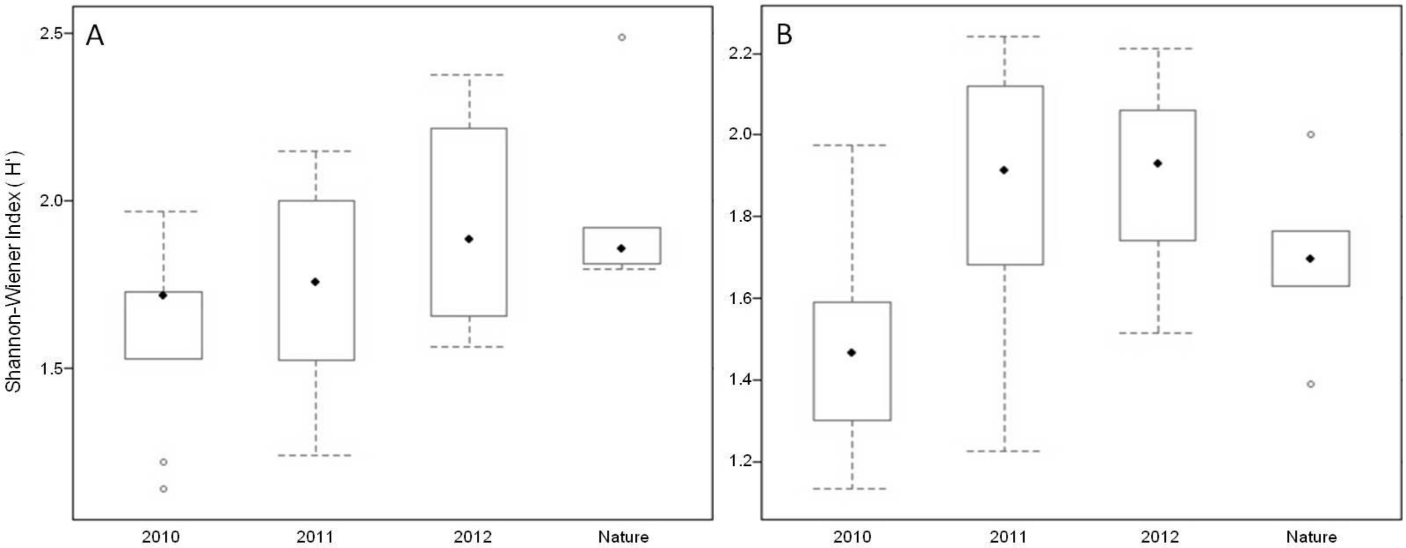

Fig. 17: Shannon-Wiener Index (H') for the maturing communities at Cross Huinay (A) and Lilliguapy (B) during the experimental period in comparison to the one of the natural community. Full circles indicate the median, boxes show the 50 % interval, bars provide the standard error and empty circles represent the outliers.

3.3 Multivariate analysis

Abundance data showed a high significant difference between both study sites ($P < 0.1$). This can be seen as well in the MDS plot (Fig. 18), where sites are grouped with a similarity of 45 %. In Lilliguapy as well as in Cross Huinay the natural community is significantly different from the communities on the recruitment plates ($P < 0.5$), but plate communities were not different between years ($P > 0.5$). In the MDS plot it is obvious that the community of the natural environment in general is different from community structure on the plates and has only a similarity of 30 %.

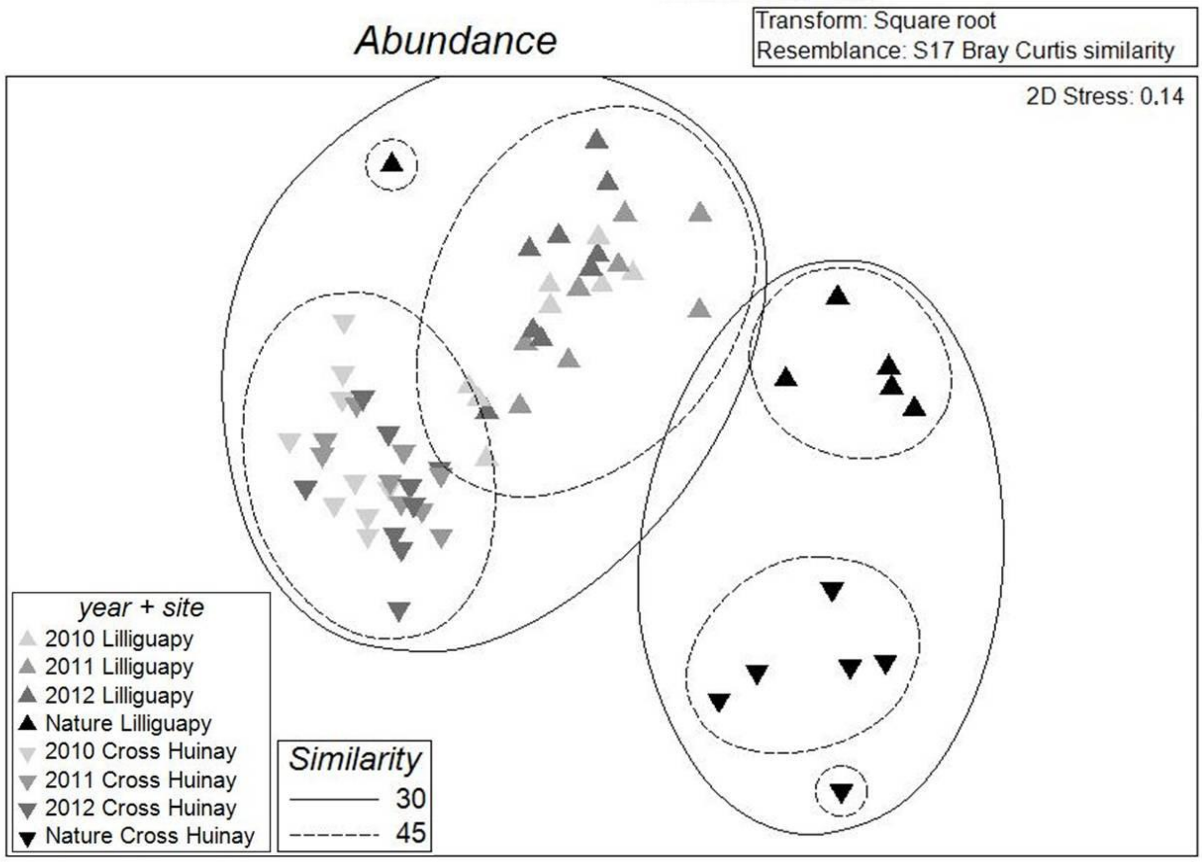

Fig. 18: Non-metric Multi-Dimensional Scaling (MDS) plot of data derived from abundance of the natural communities (Nature,●) and the maturing communities for the years 2010 (●), 2011 (●) and 2012 (●) and both study sites Lilliguapy (▲) and Cross Huinay (▼). Data were square-root transformed and resemblance was measured with a S17 Bray-Curtis similarity analysis, the 2D stress value of this MDS analysis is 0.14.

Based on the dendrogram derived after sample classification of the maturing communities from both study sites a similarity of only 30 % was detected (Fig. 19). Only five samples from Lilliguapy were found within the group of Cross Huinay. Three of them belong to one recruitment plate (plate n° 1, 2010 - 2012) and the remaining two are from the year 2010. The natural communities of Cross Huinay indicated a similarity of only 20 % with all other samples. The rest of all samples from Cross Huinay were at least similar to each other with 30 % similarity. Within this group of 30 % three groups are discernible. Two of these groups contain only samples from 2010 (32 % similarity, situated on the left end of group 'Cross Huinay) and from the years 2010 and 2011 (40 % similarity, right end of the group 'Cross Huinay'). Within the third different subgroups can be found, but all include plates from 2011 and 2012 and at least only two plates from the year 2010. Only the community of one plate (2010) from Cross Huinay is an outlier and has 82% dissimilarity to all other samples. This dissimilarity is due to the occurrence of filamentous red algae, which thrived only on this plate and covered a surface area of 41 %. All in all, it is obvious that quite a separation exists between the plates from the year 2010/2011 and 2011/2012.

An outlier was also detected for the natural communities of Lilliguapy. SIMPER analysis indicated that this difference was caused by the numerically minor occurrence of unidentified sponges and the absence of the scleractinian *Desmophyllum dianthus*. All other natural communities of Lilliguapy were grouped (similarity of 41%).

The main group of the maturing communities showed no obvious temporal trend. Only one group of five samples was grouped with the samples from Cross Huinay.

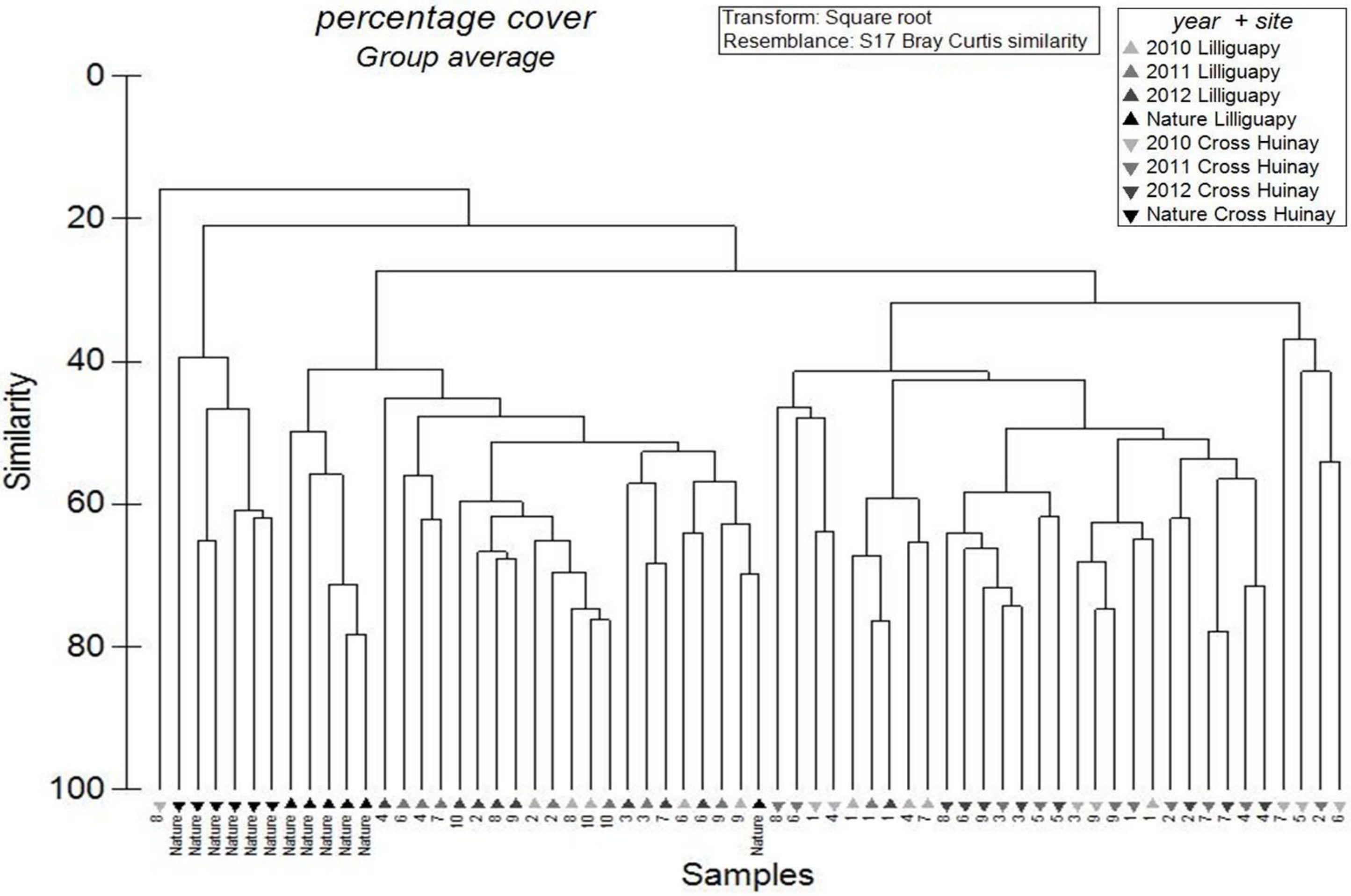

Fig. 19: Dendrogram of CLUSTER analysis of the percentage cover of maturing communities on recruitment plates (2010(●), 2011(●) and 2012(●)) in comparison to natural communities (●) from Lilliguapy (▲) and Cross Huinay (▼). The Y-Axis indicates the percentage of similarities between samples. Numbers of samples represent recruitment plates of both sites. Data were square-root transformed and resemblance was measured with a S17 Bray-Curtis similarity analysis.

The stress value of the Multi-Dimensional scaling plot was 0.19 indicating that the plot can still be interpreted (Fig. 20). Regarding the percentage cover derived from the maturing communities two groups reflecting the study site are clearly separated from each other. The maturing process from 2010 (lower zone of the plot) towards the natural community (upper zone of the plot) is apparent. Only one outlier (already identified in the dendrogram) from 2010 is visible (Fig. 20).

For the experimental communities of Lilliguapy this maturing process is not as obvious. For 2011, 2012 and the natural community this trend is apparent, but the samples from 2010 are not supporting this clear pattern. Again this was in line with the dendrogram (Fig. 20).

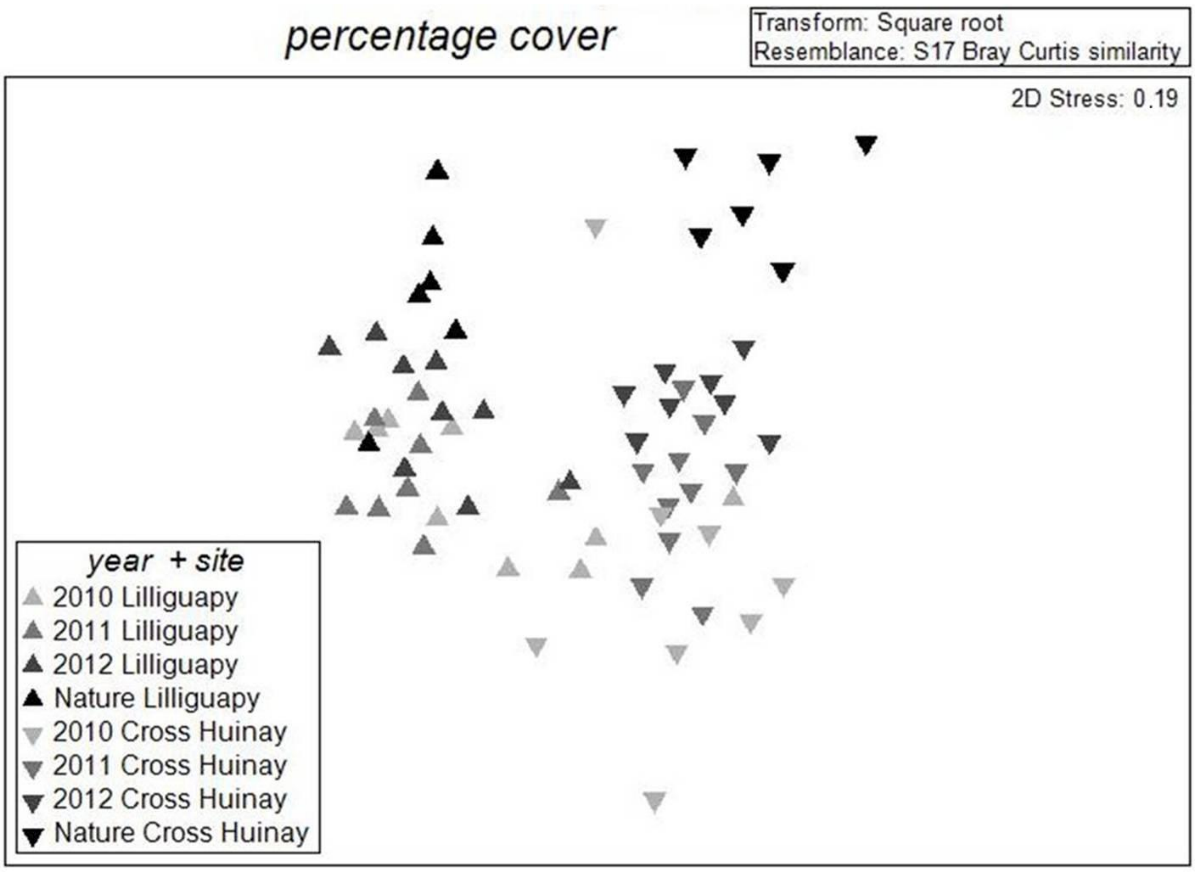

Fig. 20: Non-metric Multi-Dimensional Scaling (MDS) plot of data derived from percentage cover of the natural communities (Nature,●) and the maturing communities for the years 2010 (●), 2011 (●) and 2012 (●) and both study sites Lilliguapy (▲) and Cross Huinay (▼). Data were square-root transformed and resemblance was measured with a S17 Bray-Curtis similarity analysis, the 2D stress value of this MDS analysis is 0.19.

PERMANOVA revealed that the percentage cover of all samples from Lilliguapy and Cross Huinay was significantly different (factors tested: YEAR, SITE and YEAR X SITE; $P < 0.001$). Within Cross Huinay all maturing communities are highly significantly different ($P < 0.01$) from the natural community as well from each other. The years 2011 and 2012 constitute the only exception on that. In Lilliguapy the natural community was high significantly different from all maturing communities ($P \leq 0.005$), and as well the maturing communities were significantly different from each other. Only the communities colonizing recruitment plates from 2010 and 2011 are not significantly different ($P > 0.05$). Results of the PERMANOVA of the presence-absence data are in line with these findings.

SIMPER analysis of abundance data indicated that due to their massive occurrence *Pileolaria* sp. and *Disporella* cf *octoradiata* were the main groups throughout the experimental time (Table 3). However, SIMPER analysis of percentage cover indicated a more diverse spectrum: In Cross Huinay the average similarity of the communities on recruitment plates increased over the years from 38.73 % to 52.28 %, whereas the different recorded samples of the natural community showed a similarity of only 49.83 %. The two species colonizing the largest area are shown in Table for each year and the natural community. Results were ordered by the contribution of species cover to the total percentage cover. The average percentage cover for all samples is also listed. The main groups changed over time. Only *Smittina* sp. II (Norman, 1903) represents a more constant species (important in 2011 and 2012). Contributions of the respective key species increased irregularly, but the average percentage covers were constantly rising. The total percentage cover also increased continuously.

Table 3 Results of SIMPER analysis for the study site Cross Huinay. Only the two species covering the largest area for each year (2010 - 2012) and the natural community are shown with their average percentages of cover (av. pc) within all samples and the contributions (contr.) to the total percentage cover.

	Cross Huinay							
	2010		2011		2012		Nature	
	av. pc [%]	contr. [%]	av. pc [%]	contr. [%]	av. pc [%]	contr. [%]	av. pc [%]	contr. [%]
Pileolaria sp.	0.74	16.52						
Disporella cf *octoradiata*	0.62	14.04						
Fenestrulina cf *specca*			1.94	22.67				
Smittina sp. II			1.65	17.69	2.04	15.64		
Magellania venosa					2.34	15.59		
Encrusting red algae							3.30	23.06
Desmophyllum dianthus							3.05	20.56

By comparing the maturing communities of the different years and the natural communities among themselves SIMPER analysis revealed that the communities in 2010 were less similar from 2012 (33.50 %) than from 2011 (40.28 %). A maturation of the newly settled communities towards the natural communities is recognizable; The similarity increased between 2010 (19.29 %) to 2012 (32.80 %).

At Lilliguapy the average similarity of all maturing communities increased from 38.37 % (2010) to 52.28 % (2012). The natural communities had an average similarity of only 49.83 %. The anemone *Halcurias pilatus* (McMurrich, 1893) contributed most to the average percentage throughout the experimental time (Table 4). Only the second most important species (mostly bryozoans) concerning coverage changed over time. The species' average percentage cover and contribution constantly increased. In comparison to Cross Huinay a higher maximum contribution and a higher average percentage cover was noticeable.

Table 4 Results of the SIMPER analysis for the study site Lilliguapy. Only both main covering species for each year (2010 – 2012) and the natural environment are shown with their average percentage cover (av. pc) within all samples and the contribution (contr.) to the total percentage cover.

	Lilliguapy							
	2010		2011		2012		Nature	
	av. pc [%]	contr. [%]	av. pc [%]	contr. [%]	av. pc [%]	contr. [%]	av. pc [%]	contr. [%]
Halcurias pilatus	2.78	18.24	3.00	21.95	3.72	29.18	4.07	30.51
Smittina sp. III	2.29	17.76						
Cellaria malvinensis			2.04	15.13				
Smittina sp. II					2.73	19.37		
Unidentified sponges							3.43	24.12

As shown for the maturing communities at Cross Huinay, the assemblages at Lilliguapy also indicated a directed trend towards the natural communities (difference between 2010 and 2011: 59.72 %, between 2010 and 2012: 66.50 %). In 2010 the dissimilarity between the experimental and natural communities was 80.71 %, which decreased to 67.20 % in 2012.

3.4 Angles and abiotic parameters

Angles of the recruitment plates (Table 5) were classified for further analyses into the following groups: 10°, 10° to ≤ 20°, >20° to ≤ 30° and so forth. Recruitment plates showing an inclination angle of 10° to 20° only occur at Cross Huinay, whereas the group of 20° to 30° only exists at Lilliguapy.

Table 5 Angles of inclination of the recruitment plates at the study sites Cross Huinay and Lilliguapy.

Cross Huinay		Lilliguapy	
Plate number	Angle [°]	Plate number	Angle [°]
1	49	1	48
2	37	2	27
3	61	3	52
4	33	4	62

5	19	6	32
6	41	7	54
7	11	8	50
8	35	9	37
9	58	10	42

No clear pattern concerning the percentage cover of all species within one community in relation to the substrate inclination was obvious (Fig. 21); Cross Huinay PERMNOVA, P > 0.05). For the maturing communities at Lilliguapy only the group of 30° - 40° is significantly different from the groups 20° - 30° and 60° - 70°, but not different from the four other groups.

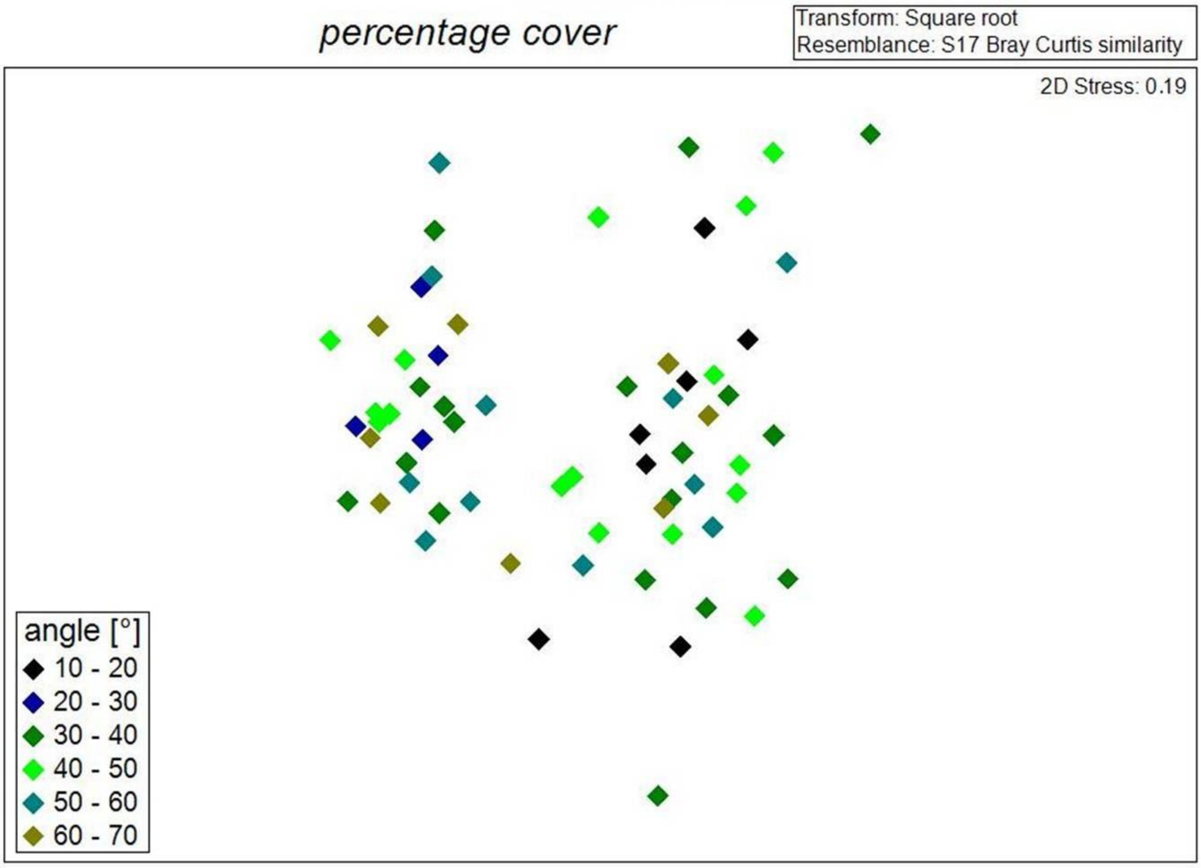

Fig. 21: Non-metric Multi-Dimensional Scaling (MDS) plot of the percentage cover of all samples related to four groups of substrate inclination angles. Data were square-root transformed and resemblance was measured with a S17 Bray-Curtis similarity analysis. The 2D stress value is 0.19.

A BIOENV analysis was carried out with the mean values of environmental data as pH value, temperature and salinity of both study sites (see Chapter 2.2). The result indicated a correlation of 0.52 between Cross Huinay and Lilliguapy.

A specific view on the growth of the scleractinian *Desmophyllum dianthus* showed that clear variations between both sites exist. It was possible to measure the diameter of seven animals from Lilliguapy and four organisms from Cross Huinay constantly over time; specimens were then averaged for comparison. During the experimental time period individuals of *D. dianthus* from Lilliguapy grew almost twice as much in diameter as those from Cross Huinay (Fig. 22).

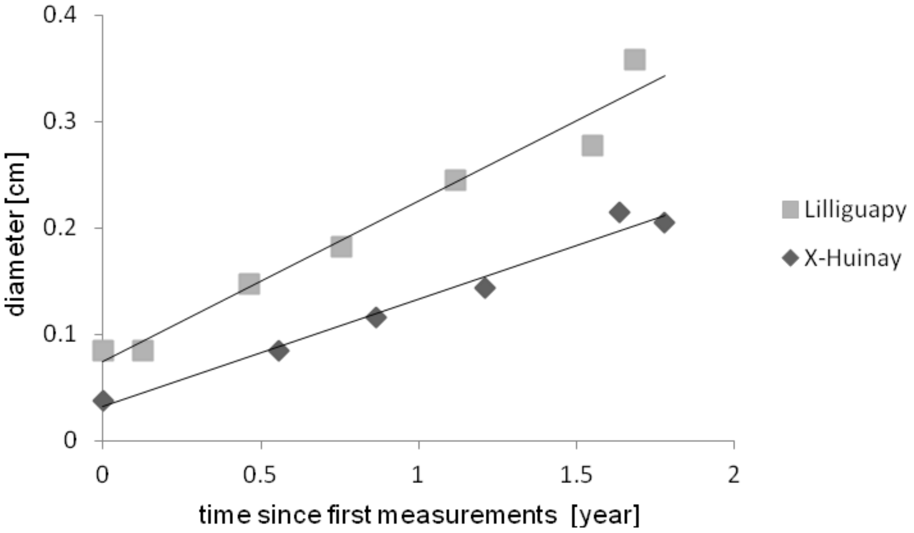

Fig. 22: Averaged diameter growth of *Desmophyllum dianthus* plotted versus time. Data points are separated for the two study sites Lilliguapy and Cross Huinay.

4 Discussion

4.1 Species inventory

The species inventory on the recruitment plates showed a continious decrease of abundances in Lilliguapy, whereas the trend was not that obvious for Cross Huinay. Important to note is that the first data collection took place after the species had already grown on the substrate for one year and that already then high abundances of the species were perceivable. The first settling process of typical pioneer species was therefore not recorded. The abundance data showed a high occurrence of the serpulid *Pileolaria* sp., which is generally known as a pioneer species (Bick, 2006). Worms of this genus live in calcified tubes and, as r-strategists, have a high reproductive rate. They probably settled first as a pioneer species and, later that year, all other species followed. Only a few pictures of recruitment plates from earlier samplings (11.12.2009) exist (e.g. Fig. 1) and support this hypothesis; however, only a few pictures could be inspected because of their low resolution. But these photos were not analyzed, because many areas were recognizable, where it was not obvious if animals settled or only a shadow was seen on the plates, so that no species were detectable.

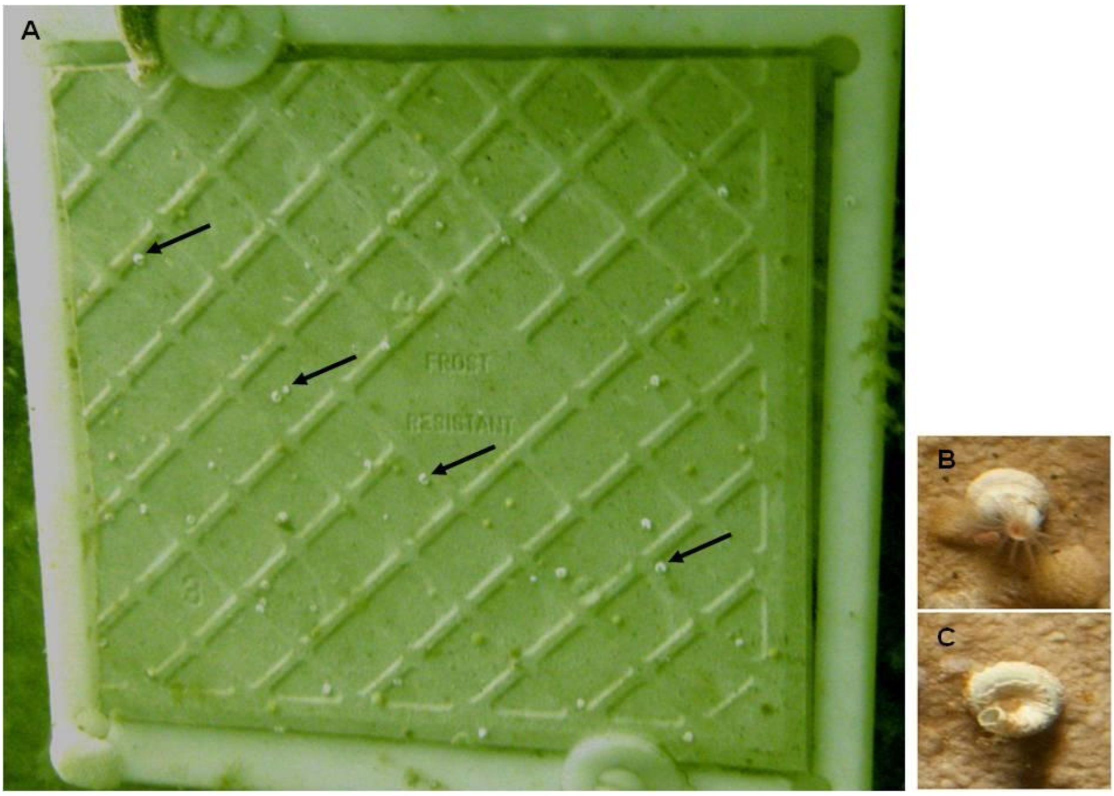

Fig. 23: A: Recruitment plate n° 4 from Cross Huinay, photographed on 11th of December 2009, 11 month after installation. Arrows mark *Pileolaria* sp. on the plate. *Pileolaria* sp. with visible (B) and non-visible (C) radioles in a calcified tube.

A typical directional succession consists of a first stage with fast growing pioneer species that cover the newly available substrate. The abundance of species strongly increases until a plateau is reached (Bernhardt & Poschlod, 1993), when free space becomes the limiting factor. In the following transitional period slower growing species occur and replace the pioneers (Clement, 1936). In the end the best adapted species will dominate the mature community (Remmert, 1989; Smith & Smith, 2009).

In Cross Huinay the abundance shows an increasing trend, with a raising number of serpulids, supporting the hypothesis that the latter species are important pioneers (Fig. 24).

Bryozoans also occured in high abundances on the newly exposed substrate, but no specific species could be detected. So it was not only a single species that always settles first, but rather a group of bryozoans. One of the first settlers seemed to be *Disporella* cf *octoradiata*, but as well all *Smittina* sp. species and *Fenestrulina specca* were often and numerous detectable. Therefore, bryozoans appear to be important early settlers (Brey et al., 1999; Potthoff et al., 2006).

In Lilliguapy, the total number of species did not increase in the early years of observation, which may be due to the fact that the interval between the sampling was too long to detect in-between settlers; a more frequent photocensus would have probably been helpful to identify early stages of succession.

The percentage cover of the pooled data of species from the recruitment plates continuously increased up to 46 % in 2012 and the trend seems to be in line with the natural environment as the reference community, which reached a cover of approx. 60 %. The comparably low values of percentage cover of the latter may be explained by a metological bias: Some areas of the pictures could not be analyzed because of the sedimentation including detritus. Due to that it was not identifiable, if animals or only sedimentation was seen on photos. Similarly, the percentage cover of filamentous hydrozoans was difficult to dermine quantitatively. Another factor may be biological interaction. For example, the direct surrounding of *Desmophyllum dianthus* was hardly ever colonized, indicating that this scleractinian may inhibit other species in their very close vicinity (Jackson & Buss, 1975; Rittschof et al., 1985; Gunthorpe &

Cameron, 1990). Bryozoans did not show any signs of mutual inhibition, but they overgrew sometimes their neighbor bryozoans.

In Cross Huinay species cover of only 18.4 % was detected in 2010, while the plates in Lilliguapy were covered by 37 % in 2010. In comparison the percentage cover of species on the recruitment plates in Cross Huinay doubled over the three experimental years, whereas in Lilliguapy an increase of only 9 % was detected. It can be assumed that the succession starts delayed or proceeds more slowly in Cross Huinay. This leads to the conclusion that succession processes proceed not simultaneously at both study sites.

This non-simultaneous succession may be caused by different abiotic (Kunde, 2004) and biotic factors (Zajac et al., 1998). No direct biotic interactions were detected, and the picture analyses revealed that the same predators, such like sea urchins and sea stars, were present in similarly high numbers at both sites. Key predators, besides macroinvertebrate grazers, may greatly influence the community composition (Breitburg, 1985). Unfortunately there is almost no information available for other important factors for the Chilean Comau fjord region such as larval occurrence, recruitment and grazing (Robles, 1981; Wolf, 1973). Therefore, no statement about the specific biotic pressure on the community and its influence on the differing structure at the study sites can be made.

Water depth and temperature were nearly the same in all experimental runs and did not show high variability over time. Due to the very little differences between the environmental conditions at both study sites (see Chapter 2.2), no influence of these abiotic parameters between sites was apparent within the BIOENV analysis, but that could be caused by the little abiotic data and not by the parameters themselves. However, as the pH value is measured on a logarithmic scale, low numerical differences may have a huge impact on the fauna (e.g. calcifiers) (Dupont, et al., 2010; Mingliang, et al., 2011; Veron, 2011). The pH value at Cross Huinay was around 7.7, whereas at Lilliguapy a pH value of 7.9 was measured in 2011. This may have an influence on the growth rate of calcifying species. For the stony coral *Desmophyllum dianthus* (Fig. 24E) different growth rates on both sites were detected and support results of shown in chapter 4.3 and were already proved by Jantzen et al. (2012a). The pH value has a strong impact on any species with a calcium carbonate skeleton (Jantzen et al., 2012b).

The pioneer species *Pileolaria* sp. as well as the bryozoans and the stony corals are all calcifiers that are depending on the surrounding pH value. If the trend of a faster growth rate at a higher pH, such as seen in *D. dianthus* at Lilliguapy*,* is transferable to other species, the pH value could be a reason for a less abundant occurrence of the calcifying organisms at the study site Cross Huinay. But for the brachiopod Magellania venosa no influence of pH value was obvious. So single species may be continuously measured in short time intervals in future studies to further investigate pH influences on community structure in the fjord Comau. The best way to do this would be *in situ* or again with photo-analysis this time with the aim of a more precise look at the perceptibility of species.

The substrate angle may strongly influence the community structure. Jørgensen and Gulliksen (2001) detected larger species heterogeneity of the respective hard–bottom communities on horizontal surfaces as compared to vertical ones. The authors explained the variability by differences in the impact of sedimentation. Connell (1999) also tested the influence of substrate orientation on epibiotic organisms and found strong effects on the community structure: mainly the algal community reflected the angle and taxa such as *Cladophorales* were more abundant and diverse on vertical surfaces. In the present study no significances between the developing communities colonizing plates installed in different angles were recognized. Here angles in different gradations between 10° and 60° were tested, while the former studies compared complete horizontal (0°) or vertical (90°) surfaces. Only one angle group (30° - 40°) in Lilliguapy differed from two other groups. These were mainly caused by a high occurrence of the bivalve *Aulacomya atra* (Molina, 1782). This mussel has a high reproduction rate (Griffith, 1977) and two peaking spawning seasons a year – from August till September and from October till November (Avendaño & Cantillánez, 2012). So it can be assumed that spawning took place in October until November and larvae settled on two recruitment plates in Lilliguapy in 2010 and grew up till the photo documentation in 2011 was conducted. Over 200 mussels were observed on these two plates (n° 6 and n° 9), which explains the difference in structure with communities from plates installed in different angles. Maybe the settlement of

Aulacomya atra is dependent on the angle of substrate, because they settle on the only both plates within that angle group, but that fact is still not investigated. Both effected plates were installed directly next to each other, so it is as well possible that water movement brought the larvae to that area by accident.

Key species discriminating between the community structure (detected with SIMPER) differed between sites. In Cross Huinay the brachiopod *Magellania venosa* (Solander, 1789) (Fig. 24D) and encrusting red algae are notable, whereas these species are rare on recruitment plates of Lilliguapy. The appearance of the brachiopod can be explained by the close vicinity of the plates to a big stone with a mature brachiopod population typical for the central Comau Fjord (Baumgarten, 2012). Due to the reproduction strategy of brachiopods, a high density of animals is important for successful propagation (Horstmann, 2001). Larvae drift with water currents and adjacent areas of hard substrate provide a suitable settling substrate. In Lilliguapy no high abundances of *M. venosa* were detected in the close vicinity.

A reason for the one-sided occurrence of the red corallines was not identified. No ecological information on cold-water corallines is available till today (Adey et al., 2005).

In Lilliguapy the bryozoan *Smittina* sp. III (Fig. 24C) and the actinian *Halcurias pilatus* (Fig. 24A) are notable, because they are exclusively occurring here. The genus *Smittina* is covering over 110 direct taxa (WORMS, 2012). It exists all over the world in a depth between 10 m and 21 m. The bryozoan is calcified, in line with the bulk of the Magellanic bryozoan fauna (Moyano, 1982). It may grow up to 50 cm in diameter thrives on several substrates such as rocks or polychaete tubes (Häussermann & Försterra, 2009). Calcified bryozoans in general prefer a stable salinity, minor sedimentation and low water currents (Kaselowsky, 2004). The latter may be a distinguishing characteristic, because of the exposed position of the island Lilliguapy, where the recruitment plates are installed. But which bryozoan species is affected to which extend was not identified. Most of them are also very plane in their morphology, so that currents have nearly no perpendicular surface to interact with. Due to the high number of species within the genus, no exact identification was realizable, so that no differences of the bryozoan *Smittina* sp. II (Fig. 24B), which occurs in Lilliguapy as well as in Cross Huinay, were detectable.

The actinaria *Halcurias pilatus* occurs from shallow waters down to depths exceeding 500 m (Levin & Gooday, 2003). Unfortunately no information on its ecophysiology is available. However, a study on the related anemone *Actinia equin showed an* optimum of hemolysis at a pH value between 8.5 and 8.8 and a minimum of activity below pH value of 6.5 (Maček & Lebez, 1981; Belmonte et al., 1993). If this holds generally true, *Halcurias pilatus* may grow better in the pH Milieu of Lilliguapy compared to the acidified environment of Cross Huinay.

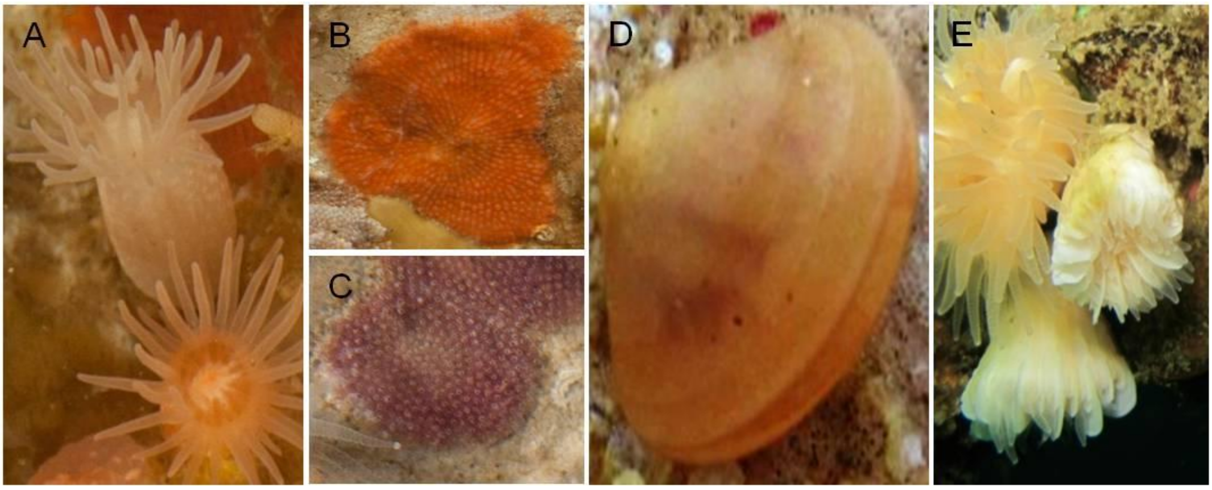

Fig. 24: Key species of the recruitment plates and the natural environment from Lilliguapy and Cross Huinay: A: Anemone *Halcurias pilatus* B: Bryozoans *Smittina* sp. II C: *Smittina* sp. III D: Brachiopod *Magellania venosa* E: Scleractinian *Desmophyllum dianthus*.

4.2 Ecological indices

As expected the Margalef index shows the same trend as the abundance data, because it is another way of express species richness. It does not differ significantly between sites due to the similar number of species and the same pioneers such as serpulids and bryozoans.

An identical pattern is notable for Pielou’s evenness. In the latter also no differences between sites were detectable, but within the sites significant differences between years and also between the experimental and the natural reference community were detected. The temporal difference in evenness can be caused by the successional process (Medina et al., 2005; Sanders, 1968). Numbers of species, as well as the species and the community composition changed with time.

The biodiversity expressed via the Shannon-Wiener index was not different between the two sites. In Cross Huinay and Lilliguapy the value varied between 1.5 and 1.9. It is a matter of conjecture that only the same way of succession at both sites causes the similarity between the communities, although important and dense covering key species exist again respectively only at one study site. To support the hypothesis future work may ground truth the visual monitoring (photocensus) by harvesting the communities. But it already has been found that no high differences have to occur between photo analysis and the ground truthing (Medina, et al., 2005).

The significant difference between the biodiversity of the developing communities (2012) compared to the ripe community indicates that the natural community is not yet reached. Thus it is assumed that the communities on the recruitment plates are still developing and have not yet reached any visible plateau (Clement, 1936).

4.3 Succession patterns

To gauge the resilience time of the community structure on the recruitment plates the abundance as well as the percentage cover of species has to be analyzed in more detail. Both data sets are important for the analysis, because the number and the size of specimens have a determining influence on their ecological importance; High occurrences from serpulids or mussels for instance build, despite their small size, a high biomass and provide the basis for the settling and feeding of other species (Fernandez et al., 2000; Müller, 2012). On the other hand, single larger species such as framework-building corals have a high ecological relevance for the associated fauna (Sale, 1978; Benayahu & Loya, 1981; Veron, 1995).

Abundance data showed significances between sites but not always between years. The difference of sites was caused by the different species inventory, such as bryozoans *Smittina* sp. III, the anemone *Halcurias pilatus* and *Fenestrulina specca*. In Cross Huinay the community was not significantly different between years due to the constantly high presence of the serpulid *Pileolaria* sp. and similar numbers of bryozoans. This may be explained by growth over time, and the lack of newly settled specimens that grow to bigger colonies. Only the natural community differed significantly, because of the lower number of species, particularly polychaets and bryozoans. The same holds true for the surrounding community of the plates from Lilliguapy. In line with Cross Huinay the community of the year 2012 differed significantly from all other plates, because of the high abundance of *Halcurias pilatus* and the decreasing number of *Pileolaria* sp. This again leads to the assumption that the succession process is more progressed in Lilliguapy compared to Cross Huinay. There is possibly a change of successional stage in Lilliguapy between 2010/2011 and 2012, whereas in Cross Huinay the community does not make that change, but reaches already the first stage after the increase of total number of species.

The MDS plots comparing percentage cover of the communities showed a clear horizontal layered pattern. Only in Cross Huinay the communities of the years 2011 and 2012 and in Lilliguapy of the years 2010 and 2011 overlap. The difference within the communities (2010/2011 and 2012) from Lilliguapy may be explained by the high abundance and the high percentage cover of the violet bryozoan *Smittina* sp. III. The proximity of similarity between the group from Lilliguapy and the samples of Cross Huinay is due to the presence of the bryozoans *Smittina* sp. II and *Fenestrulina* cf *specca*. In Cross Huinay the scleractinian *Desmophyllum dianthus* increasingly covered the artificial substrate but occupies most of the space in the natural community as expected. This pattern can be explained by the average age of ~60 years (Försterra, et al., 2005) or more (Adkins, et al., 2004) of the specimens. The total percentage cover increases constantly, whereas the species with the highest proportion change over time. In 2012 *D. dianthus* is the most important species in Cross Huinay and it can also be found in Lilliguapy on the third place after the anemone *Halcurias pilatus* and unidentified sponges. From the present analyses of abundance and the data of percentage cover, the TOLERANCE MODEL (Connell and Slatyer, 1977) is most appropriate: The abundances of species are not changing extremely. Differences are only produced by changes of numbers of species but not by changes of the species inventory. But this result is only valid for the present study with the chosen points of time for photo documentation – early succession within the first year was not investigated and should be considered in further studies. In general the hypothesis is supported by the increasing percentage cover and the dominance of large species such as *D. dianthus*. The TOLERANCE MODEL is characterized by a stable community inventory as observed here and a slow-growing settler (here *D. dianthus*), which becomes dominant in the developing community.

In contrast, hard-bottom community succession is commonly best described by the INHIBITION MODEL, whereas from soft-bottom communities the FACILITATION MODEL is mostly known (Connell & Slatyer, 1977; Lake, 2006). But the FACILITATION MODEL also describes the community development of some hard substrates (e.g. Arkema et al. 2009). The authors found that giant kelp forests modify the surrounding environment in a way that many new invertebrates can settle. The same trend occurred in the Mediterranean Sea, where serpulids were replaced by mussels, in turn the latter were replaced in a third phase by a polychaete community (Gravina et al., 1989). Lissner et al. (1991) presented a description on deep-water hard substrate communities, where the FACILITATION MODEL as well as the TOLERANCE MODEL may be applicable. In contrast to soft-bottom communities (Pacheco et al., 2010; Gallagher, et al., 1983), no study existed yet stating that a hard-bottom community development is best described by the tolerance model.

5. Outlook

In a future experiment in the fjord Comau, recruitment plates could be installed in different points of time to investigate a possible influence of seasonality on the succession process. Due to abiotic effects such as temperature and storm events as well as due to different larvae drifts, succession can take various ways of progress. Therefore another classification of succession was made by Berlow (1997), who characterized succession as CANALIZED, EXTERNALLY DRIVEN or CONTINGENT. When it is CANALIZED, specific succession process proceeds, no matter when a disturbance occurs, resulting in a community, that is self-determined. That means that the process of succession follows fixed patterns and is not influenced by surrounding events. When EXTERNALLY DRIVEN the succession is influenced by extrinsic effects and development starts due to a specific moment of time of disturbance. So abiotic factors for example extremely influence the succession process and when a disturbance occurs in winter time another process of colonization takes place than in summer time. In contrast, a CONTINGENT process is only induced by external factors. Depending on the start of succession and natural context the proceeding will be different at any point of time. Precise requirements such as environmental conditions or recruitment events and specific interactions between species lead to unrepeatable patterns of succession.

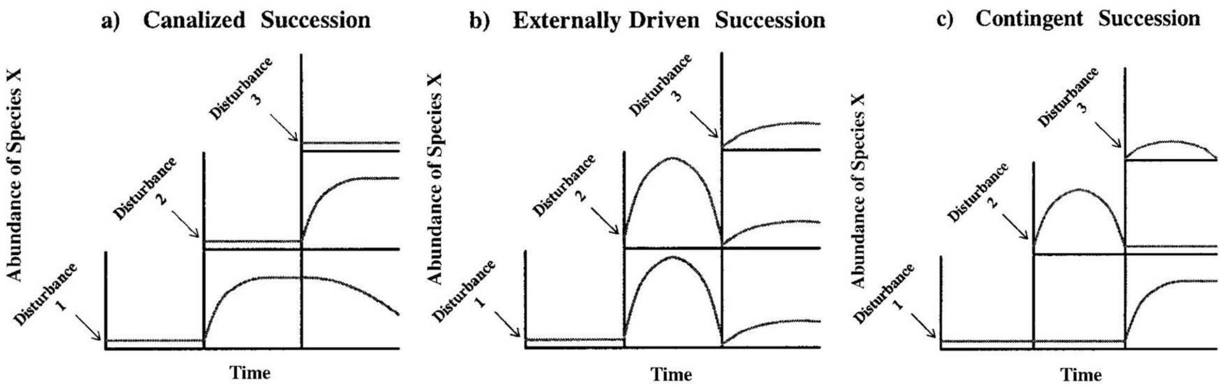

Fig. 25: Succession model by Berlow (1997) with three different possibilities of succession progress as answers on disturbances at different points of time.

When Pacheco et al. (2010b) investigated the influence of seasonality on hard-bottom community succession, they found no evident effect on the succession. Tait and Dipper (1998) suggest seasonal and annual fluctuations within short time periods, but a constant community in longtime investigations. To proof this hypothesis for the fjord system longtime observations of the natural community have to be done, to see if the community is stable or various over time. Furthermore a comparison for communities in different water depths could be carried out. Laudien and Orchard (2012) found a similar hard-bottom species inventory in depths between 30 m and 200 m in Kongsfjorden, but dominances shifted with depth. A comparison between depths would be interesting, especially due to the characteristic deep rock walls of fjords such as the fjord Comau.

6 Conclusion

Summarized, the community structure of the Chilean Comau fjord is very diverse. Both study sites host over 50 different species. Due to the stable abundance data and increasing percentage cover, the TOLERANCE MODEL from Connell and Slatyer (1977) pertains for the succession on the recruitment plates. One of the most abundant species in the natural environment as the reference community, the scleractinian *Desmophyllum dianthus* could be found. Perhaps the different pH value is responsible for the faster growth of calcifying species in Lilliguapy. In further investigations the community structure as a function of seasonality and depth could be analyzed.

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9 Selbstständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.
Die eingereichte schriftliche Fassung der Arbeit entspricht der auf dem elektronischen Speichermedium.

Weiterhin versichere ich, dass diese Arbeit noch nicht als Abschlussarbeit an anderer Stelle vorgelegen hat.

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