



## Variability at multiple spatial scales in intertidal and subtidal macrobenthic communities in a fjord with glaciers, Magellanic Subantarctic ecoregion, Chile

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### ARTICLE INFO

#### Keywords:

Macrobenthic communities  
Spatial scales  
Environmental heterogeneity  
Glacial influence  
Macroalgae  
Marine invertebrates

### ABSTRACT

It has been observed in high-latitude marine environments of the Southern Hemisphere that the variability in the ecological patterns of macrobenthic communities show variations at different spatial scales (*i.e.* cm to km), mainly influenced by environmental stress gradients. We examined macrobenthic communities of intertidal and subtidal habitats in a glacial fjord using taxonomic, ecological and oceanographic approaches, estimating vertical and horizontal variation using a nested design with different spatial scales ranging from centimeters to kilometers (quadrats, patches, shore and sites respectively). We found that vertical patterns in taxon richness and community structure were significant in both habitats. These patterns also showed horizontal variability at different spatial scales, becoming more pronounced at smaller scales (quadrats). The dominant taxa in the intertidal (macroalga) and subtidal (macroinvertebrate) communities also exhibited a scale-dependent distribution pattern, indicating that the greatest horizontal variation occurs at small spatial scales. Annual and opportunistic green algae such as *Ulva intestinalis* and *Cladophora flexuosa* were dominant in the intertidal, while the dominant taxa in the subtidal were the filter-feeding bivalve *Aulacomya atra* and the suspensivorous hydrozoan *Symplectoscyphus marionensis*. The results were related to biological interactions and local abiotic factors characteristic of an estuarine system influenced by glaciers, with lower salinity and temperature and higher turbidity in sites close to glaciers. The information generated on diversity patterns is very relevant and can serve as a baseline in the evaluation of ecological patterns of shallow macrobenthic communities in environmental gradients influenced by glaciers in the Magellanic Subantarctic ecoregion.

### 1. Introduction

The study of patterns of ecological variation such as diversity, composition and structure along environmental gradients has increased

during the last three decades, being fundamental to understand and predict ecological changes in communities (Underwood and Chapman, 1998, Fraschetti et al., 2005, Paine et al., 2018). The observation of these patterns of ecological variation has contributed to the

**Abbreviations:** ANOVA, Analysis of variance; AP, Antarctic Peninsula; BG, Bernal Glacier; cm, centimeters; CTD, Conductivity, Temperature and Depth probe; EW, Estuarine water; FMO, Fjord of the Mountains; FNU, Formazin Nephelometric Unit; GG, German Glacier; *i.e.*, in other words; IJ, Jaime Island; km, kilometers; LEMAS, Laboratory of Antarctic and Subantarctic Marine Ecosystems; LI, Long Island; m, meters; MDS, Multidimensional scaling; MS, Mean Square; MSAW, Modified Subantarctic Water; ODV, Ocean Data View; PERMANOVA, Permutational multivariate analysis of variance; SP, Summer Passage; PSU, Practical Salinity Units; PVC, Pseudo-variance components; SIMPER, Similarity Percentages; US, Union Sound; VC, Variance components.

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<https://doi.org/10.1016/j.pocean.2022.102879>

Available online 30 August 2022

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development of several vertical zonation models (Stephenson and Stephenson, 1949, Araújo et al., 2005). However, vertical zonation itself does not explain all the variability in biodiversity distribution patterns in coastal ecosystems (Menconi et al., 1999, Zamprogno et al., 2012). Understanding the relationships between spatial patterns of biodiversity in relation to physical factors (*i.e.* wave exposure, substrate heterogeneity, shore slope) and biological processes (*i.e.* predation, competition, herbivory and recruitment) may provide a better understanding of the influence of these factors on the distribution of intertidal and subtidal organisms (Menge and Sutherland 1976, Benedetti-Cecchi et al., 2000, Dethier and Schoch, 2005, Diez et al., 2009). Scales of observation are very relevant since zonation patterns can be very dependent on the horizontal scale of spatial observation (*i.e.* km, m, cm) (Ojeda et al., 2014, Valdivia et al., 2014, Rodríguez et al., 2021).

Intertidal and shallow subtidal habitats allow the identification and measurement of vertical zonation patterns and horizontal variability at different scales (Benedetti-Cecchi, 2001, Coleman, 2002, Benedetti-Cecchi et al., 2003, Catalán et al., 2020, Frascchetti et al., 2005). Particularly, intertidal habitats exhibit patterns of vertical variation due to the constant pressure of abiotic stressors (*e.g.* increased air exposure, constant temperature changes, differences in wave action and shoreline topography) (Stephenson and Stephenson, 1949, Crowe et al., 2000). The subtidal habitat also has important abiotic and biotic factors that generate different vertical zonation patterns: attenuation of solar radiation, water movements, currents, turbidity, predation, competition (Valdivia et al., 2014). Horizontal variation can also be influenced by a combination of abiotic stressors and biological processes. (Underwood and Chapman, 1998, Benedetti-Cecchi et al., 1999, Benedetti-Cecchi, 2000, Díaz and McQuaid, 2011). Evidence suggests that both local ecological processes and micro-scale abiotic factors (*e.g.* substratum, aspect of slope) generate fine-scale horizontal variability (from centimeters to a few meters) (Frascchetti et al., 2005, Valdivia et al., 2011, 2014, Rodríguez et al., 2021), while regional-scale abiotic processes (*e.g.* surface water temperature, precipitation and photoperiod) would be responsible for high vertical variability (Ojeda et al., 2019, Catalan et al., 2020).

The archipelago region of the Magellanic Subantarctic ecoregion (MSE) located between 48° and 56°S was modeled during the Pleistocene by the advance and retreat of ice during glaciations (McCulloch et al., 2005, Fraser et al., 2009). These ice movements generated a dismembered and complex coastline formed by fjords and channels (Araya-Vergara, 2006; Iriarte, 2018). Ice recession after the Last Glacial Maximum (LGM), generated a complex mosaic of marine habitats, which were colonized by different taxa that structured the different assemblages along the different marine habitats of the MSE (Fraser et al., 2012). Within the MSE it has been described that small-scale environmental variability is an important driver that shapes the composition, structure and diversity of benthic marine communities (Rozzi et al., 2007, Mansilla et al., 2013, Ojeda et al., 2014, 2017, Villalobos et al., 2021). Due to these characteristics, the MSE is a truly ideal natural laboratory to study the effect of abiotic environmental variations on the distribution of benthic communities (McGovern et al., 2020, Villalobos et al., 2021).

Within the MSE there are several fjords with glaciers that are vestiges of the last glaciation (Segovia and Videla, 2017), which represent a unique ecosystem (Rozzi et al., 2012). The effect of climate change is becoming increasingly evident and it is reported that in the last two decades glaciers have lost about -23 Gt per year, showing a negative mass balance since 2009 (Dussailant et al., 2019). Melting of glaciers within a fjord causes an increase in the inflow of lower density freshwater into the marine systems, resulting in a decrease in salinity and stratification of the seawater column (Iriarte, 2018). Glacier melt has local effects at scales < 100 km, which causes changes in light availability due to high turbidity in fjord surface waters caused by sediment transport in drainage systems and resuspension of fine sediments (Dowdeswell and Vásquez, 2013, Marshall et al., 2021). Therefore,

benthic marine communities inhabiting these fjords are exposed to different environmental stress gradients (*i.e.* changes in salinity, temperature, turbidity, nutrients and oxygen) (Syvitski and Shaw, 1995, Mansilla et al., 2013, Gasbarro et al., 2018). These environmental gradients can generate local physiological barriers that would inhibit the dispersal, survival, growth and reproduction of many benthic species (Tilman et al., 2012, Becheler et al., 2022). Recent research on the Antarctic coast has suggested that glacier melt may have significant effects on the diversity and structure of benthic marine communities (Valdivia et al., 2015, 2020, 2021). It has also been suggested that small-scale processes are very relevant for structuring and maintaining local communities in these environments highly disturbed by physical factors (Valdivia et al., 2011, 2014, 2020, Rodríguez et al., 2021).

The evaluation of spatial variability patterns of benthic diversity at different scales can help us to understand the functioning and stability of fragile ecosystems under different climate change scenarios. This study aims to evaluate the distribution patterns of benthic marine communities along a fjord with the presence of glaciers at different spatial scales.

## 2. Materials and methods

### 2.1. Study area

The study was conducted during a cruise in the summer of 2020 between the Fjord of the Mountains (FMO) and Summer Passage, Magellanic Subantarctic ecoregion, Chile (51°S; 73°W) (Fig. 1, Suppl. Table 1). The fjord is about 60 km long and 2 km wide. The geomorphology of the FMO creates a south-north axis of environmental variability with contributions of fresh water from five marine-terminating glaciers that emerge from the Cordillera Sarmiento, producing the oceanographic conditions of FMO. The fjord mouth connects the FMO with Union Sound, and subsequently with Summer Passage approximately 70 km to the southwest.

The study sites were selected according to the environmental variability of the area. Therefore, two sites were chosen in the FMO: German Glacier (GG) and Bernal Glacier (BG). The first, due to glacier retreat, presents a fluvio-glacial channel of 3 km with respect to the fjord, while the second has terminal moraines with an extension of 500 m with respect to the fjord (Fig. 1). The Union Sound study site was Jaime Island (JI), without glacier presence, with estuarine and oceanic influence (Fig. 1, Suppl. Table 1). Long Island (LI), without glacier presence was used in the Summer Passage. It is located in a more exposed area, with greater exposure to the influence of ocean waters (Fig. 1, Suppl. Table 1).

### 2.2. Oceanographic characterization

Temperature and salinity profiles were measured with the CTD SBE 19 V2 plus equipment. The measurements were performed at a maximum depth of 30 m in a transect from north to south from GG to LI, with distances among hauls that varied from 5 to 10 km, except for the measurement of LI that was >60 km (Fig. 1, Suppl. Table 2). Turbidity measurements were made at a maximum depth of 10 m at each study site using a HANNA HI 9829 Portable Multiparameter. The vertical profiles of the environmental variables were represented with the Ocean Data View v5.2.0 software (ODV) (Schlitzer, 2021).

### 2.3. Biodiversity sampling design

The macrobenthic communities were characterized through manual collection of biological samples of macroinvertebrates and macroalgae (>1 cm) in each intertidal level (high, mid and low), and SCUBA diving in two subtidal depths (5 and 10 m). Percent coverage of the taxa was recorded using photo-quadrants (50 × 50 cm) at a fixed height of 1 m from the substrate, using an Olympus TG-6 camera (Ojeda et al., 2017,

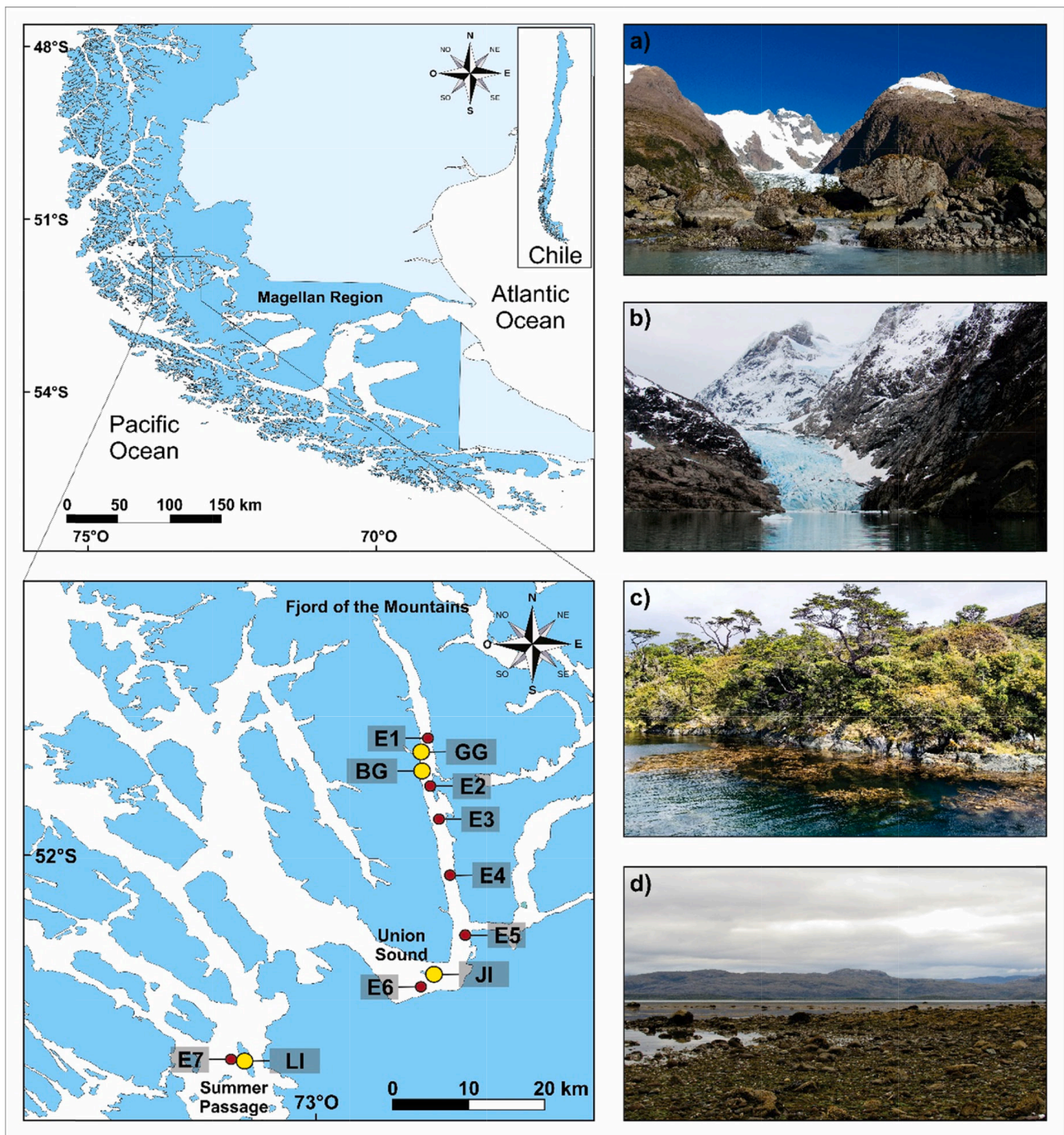


Fig. 1. Map of the Magellanic Subantarctic ecoregion, showing study sites (yellow circles) and CTD salinity and temperature measurement stations (red circles). From north to south: GG: German Glacier (a); BG: Bernal Glacier (b); JI: Jaime Island (c); LI: Larga Island (d).

Rodríguez et al., 2021). The biological samples collected were frozen for transport to the Laboratory of Antarctic and Subantarctic Marine Ecosystems (LEMAS) of the Universidad de Magallanes. Seaweeds and invertebrates were classified to the lowest possible taxonomic level (family, genus or species) with the support of specialized literature for macroalgae (Hoffmann and Santelices, 1997, Ramírez and Santelices, 1991, Mendoza and Nizovoy, 2000, Boraso et al., 2003) and macroinvertebrates (Reid and Osorio, 2000, Linse, 2002, Aldea et al., 2011, Rosenfeld et al., 2015). They were also classified according to their functional attributes: mobility (sessile or mobile), and trophic habits (filter feeder, suspensivore, herbivore, omnivore, carnivore and

scavenger) (Ojeda et al., 2014). The morphological habit was used for macroalgae (filamentous, corticated filamentous, tubular, foliated, corticated foliated, corticated terete, crustose, leathery) (Steneck and Dethier, 1994, Bates, 2009, Rosenfeld et al., 2018). The macroalga samples were herborized using the methodology of Ramírez (1995) and deposited in the cryptogamic herbarium of the LEMAS (<https://sweetgum.nybg.org/science/ih/herbarium-details/?irn=258932>) at the Universidad de Magallanes.

Photo-quadrants were taken in the four study sites (GG, BG, JI and LI) for the intertidal and subtidal habitats, separated by a distance >10 km (Suppl. Fig. 1). Two separate shores with a distance of about 1 km

between them were chosen randomly in each study site (Suppl. Fig. 1). In each shore, three patches with a separation of <100 m were randomly selected. Three photo-quadrants were obtained per intertidal coastal elevation level (high, mid and low) for each site and for each subtidal depth (5–10 m depth) (Suppl. Fig. 1). In summary, the intertidal sampling design was  $4$  (sites - random)  $\times$   $2$  (shores - random)  $\times$   $3$  (patches - random)  $\times$   $3$  (intertidal levels - fixed)  $\times$   $3$  (quadrants - random) = 216 quadrants. The subtidal sampling design was  $4$  (sites - random)  $\times$   $2$  (shores - random)  $\times$   $3$  (patches - random)  $\times$   $2$  (subtidal levels - fixed)  $\times$   $3$  (quadrants - random) = 144 quadrants. Finally, according to the fit of the model and according to García (2007), the following spatial scales of observation were defined: sites, large scale; shores, mid-scale; patches and quadrants, small scale.

#### 2.4. Biological data analysis

Photographic quadrats were analyzed with PhotoQuad v1.4 software (Trygonis and Sini, 2012). The quadrat boundary was defined manually for each image with a digital border, and stratified random markers ( $n = 100$ ) were used to obtain the measure of relative abundance of taxa (*i.e.* percent cover). For quantification, taxa present within each photo-quadrat were considered, focusing on primary spaces (*i.e.* basal species). When overlapping organisms occurred, we included secondary space holders (sessile species attached to primary space holders) and associated mobile species (Villalobos et al., 2021).

Variations of intertidal and subtidal macrobenthic marine communities with respect to different spatial scales were determined using taxon richness as the total number of taxa identified in each photo-quadrat, and community structure through calculation of the Bray-Curtis dissimilarity distance between pairs of observations (Bray and Curtis, 1957), using coverage values transformed to proportions.

A univariate mixed model (ANOVA) was used for taxon richness using R v3.5.3. software (R Development Core Team, 2020), and a multivariate mixed model (PERMANOVA) for the Bray-Curtis dissimilarities calculated from the coverage percentages of the community structure using the PRIMER 6 v6.1.13 software with the complement PERMANOVA + v1.0.3 (Clarke and Goley, 2005) (PRIMER-E, Ltd. Plymouth, UK). Prior to the ANOVA analysis with the average taxon richness, the variable was transformed to  $\ln(x + 1)$  to fulfill the normality assumptions. The random factors in the models were sites, shores (nested within sites) and patches (nested within shores), and as a fixed factor the intertidal and subtidal coastal elevation level. Homogeneity of variances of the ANOVA model was evaluated using residual-vs-fit and normal Q-Q plots, a method considered the most appropriate for large samples (Suppl. Figs. 2, 3) (Wilk and Gnanadesikan, 1968). This was done with R.

The relationships between the benthic assemblage structure (taxon cover) and environmental variables (temperature, salinity and turbidity) were investigated using a canonical correspondence analysis (CCA) (Ter Braak, 1986) using the vegan package in R. Rare species are often positioned as outliers in correspondence analysis ordinations (Greenacre, 2013) and statistical estimation problems are posed by multicollinearity (Ter Braak, 1986). Rare taxa were omitted from analysis prior to conducting CCA (Zubia et al., 2018). A Monte-Carlo randomization test (1000 permutations) was used to assess the probability of the observed pattern being due to chance (McCune and Grace, 2002).

The contribution of each taxon to the variation of the community structure was determined through the analysis of similarity percentage (SIMPER) routines (Clarke, 1993). This procedure was used to determine the species that contribute to the similarity of a group (typifying species), and to know the species that contribute to the differentiation of the different groups (discriminating species) (Clarke, 1993). The average dissimilarity among groups was separated and expressed as the average abundance of each taxon, applying the contribution cutoff of each taxon at 90 %. This analysis was performed in PRIMER 6 v6.1.13 software with the PERMANOVA + v1.0.3 plugin (Clarke and Goley,

2005, PRIMER-E, Ltd. Plymouth, UK).

The patterns of spatial variation in taxon richness, community structure and the most abundant taxa in the intertidal and subtidal assemblages were evaluated with the method proposed by Valdivia et al. (2011, 2014). In this procedure, the variance component (VC) and pseudo-variance component (PVC) obtained through the ANOVA and PERMANOVA analyses for the random factors were calculated. For each random factor, VC and PVC were estimated as the difference between its mean square (MS) and the MS of the term immediately below in the nested hierarchy. They were evaluated with the VCA package in R (Valdivia et al., 2014). Negative variance components were set to zero (Valdivia et al., 2014).

### 3. Results

#### 3.1. Oceanographic characterization

Salinity and temperature profiles showed Estuarine Water (EW) in the surface layer (0–20 m depth), which was accentuated in the sections near the study sites of the GG and BG due to melting. Their salinities varied between 18 and 20 PSU and temperatures up to 9.50 °C (Fig. 2a, 2b). EW is present throughout the entire FMO. Salinity and temperature increased towards LI, where salinity varied between 23 and 25 PSU and temperature reached 12.3 °C (Fig. 2a, 2b). An intermediate water mass (20–30 m depth) was recorded flowing throughout the FMO and homogenizing towards the LI study site as a result of mixing between the shallow and deep water masses in LI (Fig. 2a, 2b). Modified Subantarctic Water (MSAW) was observed below the intermediate mixing circulation (>30 m depth). Salinity >30 PSU (30 PSU) and temperatures lower than 9.50 °C were recorded in LI (Fig. 2a, 2b).

Turbidity was variable between study sites; in the GG and GB sites in the FMO the turbidity presented high values in the most superficial zone (<2 m, Fig. 1c). Towards the fjord mouth of the FMO, in JI the turbidity showed high values as depth increased (>6 m, Fig. 1c). There was no turbidity in LI, outside the fjord. The site with the highest average turbidity was in the GG; 152.7 FNU was recorded; the lowest average turbidity was found in LI with 0 FNU (Fig. 2c).

#### 3.2. Richness and composition of macrobenthic communities

The richness of the benthic communities was represented by 29 taxa in the intertidal habitat (Suppl. Table 3) and 62 taxa in the subtidal habitat (Suppl. Table 4). Macroalgae (86 %) were the most frequent in the intertidal habitat ( $S = 25$  spp.), while, macroinvertebrates (55 %) were more frequent in the subtidal habitat ( $S = 34$  spp.). Eleven functional groups were identified in the intertidal and 13 in the subtidal. In the intertidal the species of corticate, foliose and filamentous terete algae were featured (21 % each), while sessile filter feeders were prominent in the subtidal (24 %).

#### 3.3. Patterns of spatial variability in macrobenthic communities

Taxon richness was highest for the intertidal habitat at sites GG and LI and lowest at sites BG and JI (Suppl. Fig. 4a). In the subtidal habitat, taxa richness was higher at sites far from the glaciers (JI and LI) and lower at sites with glaciers (GG and BG) (Suppl. Fig. 4b).

Local patterns of intertidal and subtidal taxon richness in the intertidal habitat showed vertical and horizontal variability (Figs. 3, 4). It was observed that the sites near the glaciers did not show an increase in average richness (from high to the low intertidal), except for sites JI and LI. These patterns, however, varied between scales of observations, as shores showed differences in taxon richness but patches did not (Fig. 3). Accordingly, ANOVA indicated a significant interaction effect of level by shore scale on taxon richness (Table 1). The vertical zonation in taxon richness was less clear for the subtidal habitat than for the intertidal, nevertheless, horizontal variation was important in the subtidal. Taxon

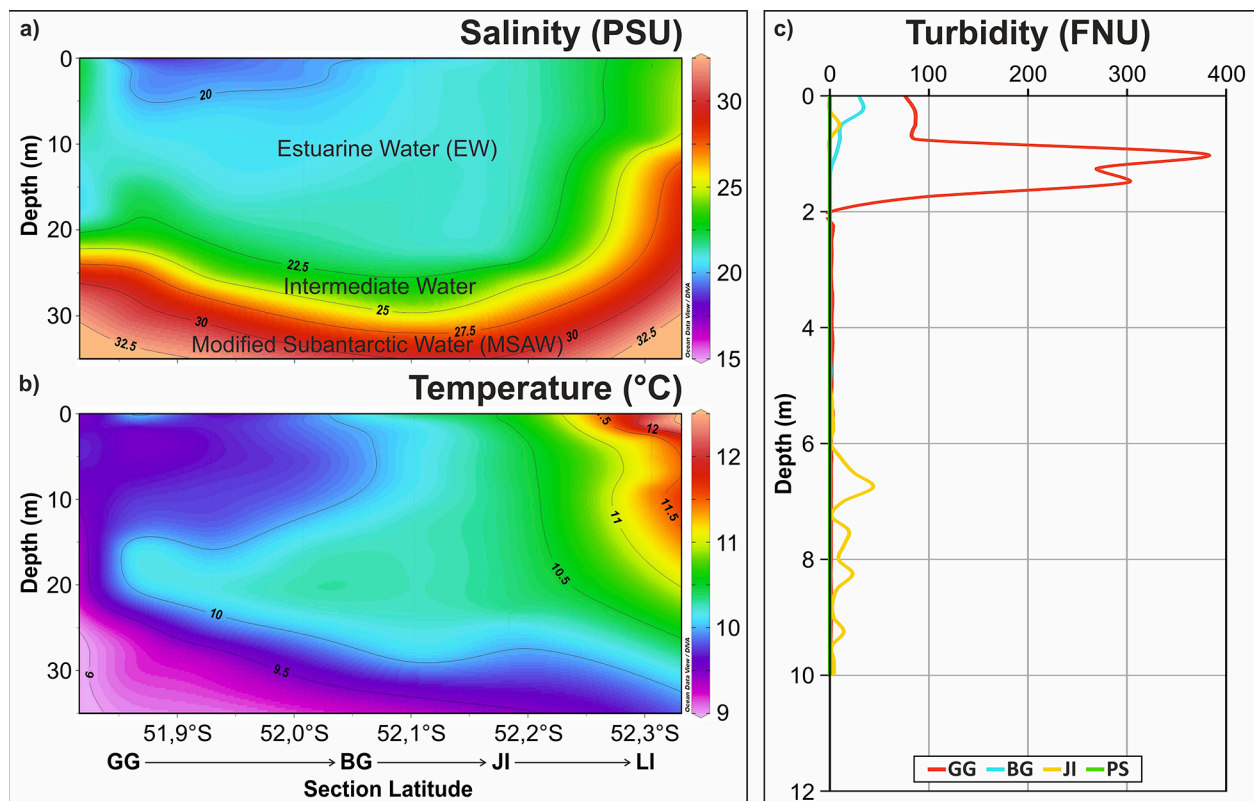


Fig. 2. Vertical sections (0–30 m) of salinity (a) and temperature (b), and profiles (0–10 m) of turbidity (c) obtained during summer 2020 between fjord of the Mountains and Summer passage, Magellanic Subantarctic ecoregion, Chile.

richness tended to increase from 5 to 10 m at, LI, but showed an inverse trend in BG and JI (Fig. 4). The ANOVA results supported these patterns, as a significant interaction between depth and patch scale was detected (Table 1).

The CCA analysis revealed a strong correspondence between these environmental factors and the presence of two groups of species (Fig. 5). For the intertidal habitat, the assemblages that were associated with more estuarine conditions and higher turbidity (negatively correlated with higher salinity and temperature) had higher frequency and coverage of *R. tortuosum*, *U. intestinalis* and *C. flexuosa* (Fig. 5a). Assemblages that were associated with more marine conditions and less turbidity (positively correlated with higher salinity) had higher frequency and coverage of *S. lomentaria*, *A. arcta*, *N. fastigiata* and *Porphyra/Pyropia* sp1. (Fig. 5a). The horizontal variation in community structure was more marked for the subtidal habitat than in the intertidal habitat (Fig. 5b). The assemblages that were associated with more estuarine conditions and higher turbidity had higher frequency and coverage of *A. atra*, *S. marionensis*, *B. laevis* and *U. lactuca* (Fig. 5b). Assemblages that were associated with more marine conditions and less turbidity had higher frequency and coverage of *Porphyra/Pyropia* sp2., *Chaetopterus* sp., *Rhodymenia* sp2., *P. magellanica*, *S. condensata*, *H. berkeleyi*, *C. virgatum*, *L. flavicans*, *S. skottsbergii*, *M. chilensis* and *D. ligulata* (Fig. 5b). The PERMANOVA results supported the influence of the spatial variability on the effects of the horizontal and vertical stress gradients on community structure, as the interactive effect of both factors was significant in different scales (Table 1).

The variance component (VC) of intertidal and subtidal taxon richness showed a general pattern of horizontal variance; the higher variance components were those observed at the smallest scale, except for the low intertidal level (Fig. 6a, 6b). Pseudo-variance components (PVC) in the intertidal and subtidal community structure also showed high spatial scale-dependent variability. The highest values of the PVC in the intertidal and subtidal were found at small spatial scales (Fig. 6c, 6d).

SIMPER analysis showed that the intertidal community structure is composed of 10 taxa that explain 90 % of the dissimilarity between the high and mid-levels, as well as between the mid and low levels (Table 2). The taxa that contribute most to intertidal dissimilarity (>50 %) were the foliose algae *U. intestinalis* and *Porphyra/Pyropia* sp1., tubular *A. utricularis* and filamentous *C. flexuosa* (Table 2). Twenty-three taxa explain 90 % of the dissimilarity of the subtidal community structure between 5 and 10 m depth (Table 3). The taxa that most contributed to the dissimilarity (>50 %) were the sessile filter feeder *Aulacomya atra* and sessile suspensivores *S. marionensis* and *B. laevis* (Table 3).

The VC of the taxa with the highest contributions to dissimilarity based on SIMPER analyses showed the highest variances at the smallest scales of observation, i.e. patches and quadrants (Fig. 7). The VC of the representative macroalgae in the different spatial scales fluctuated according to the intertidal level. The VC of *U. intestinalis* at the lowest level was similar to those of shores and quadrants, while at the mid-level it was greater in shores, and at the lowest level in quadrants (Fig. 7a). The highest VC of *C. flexuosa* in the high and mid intertidal occurred among quadrants, while in the low intertidal it was among shores (Fig. 7b). In the subtidal, the VC of the taxa with the highest contribution to the dissimilarity based on the SIMPER analyses also showed the highest variability at small scales, particularly among quadrants at both subtidal depths (Fig. 7c, 7d).

#### 4. Discussion

The results showed an environmental gradient in the Fjord of the Mountains (FMO), since study sites GG and BG inside FMO are near to glaciers comprise an estuarine system, with an increase in salinity and temperature towards study sites JI and LI outside FMO. Turbidity was higher at study sites GG and BG inside FMO due to the direct influence of glaciers. The results also showed that the horizontal and vertical variations in richness and community structure of the intertidal and subtidal

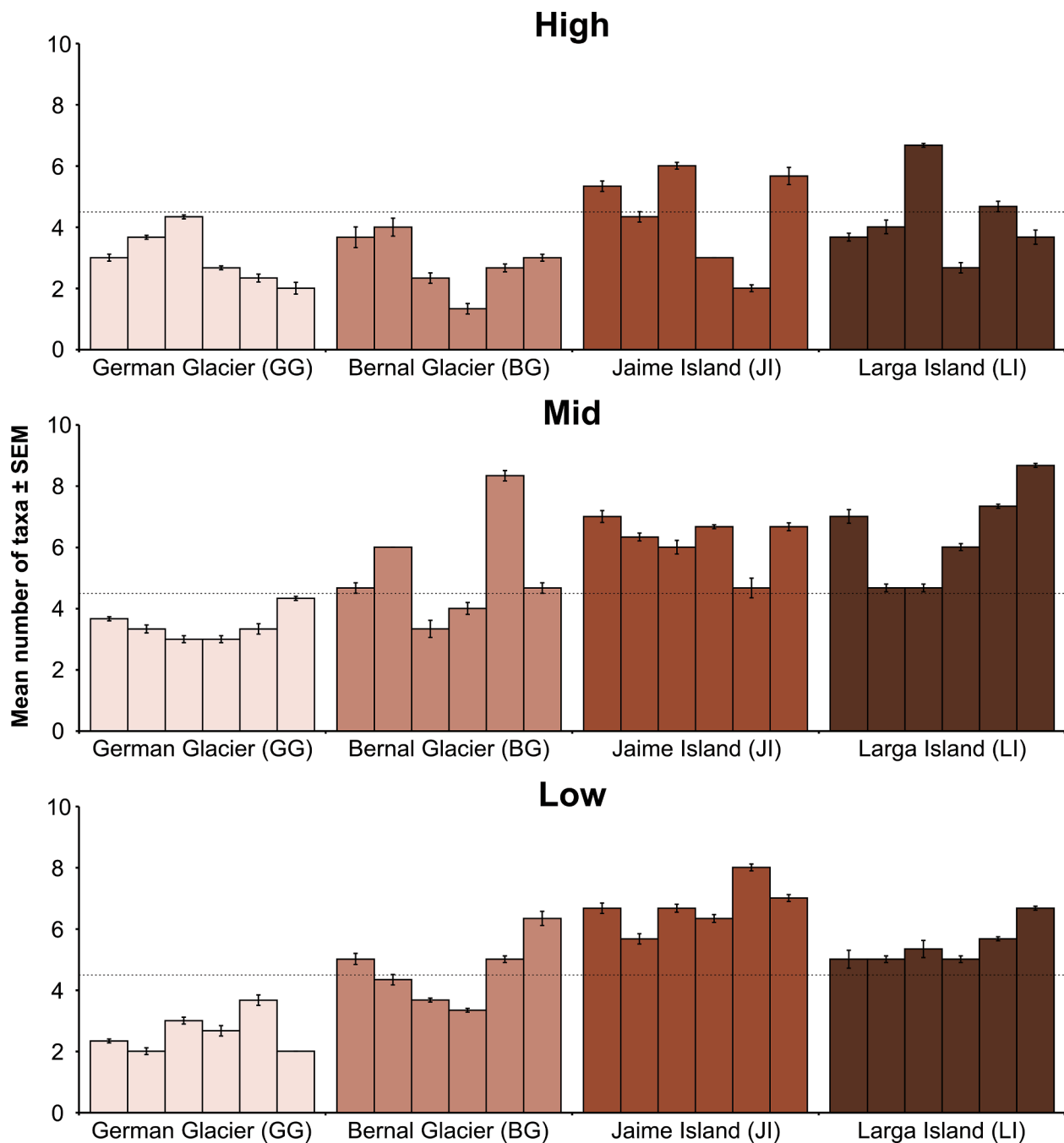


Fig. 3. Scale of local patterns of average taxon richness for each site, coast, patch and intertidal level (high, mid and low), Magellanic Subantarctic ecoregion, Chile. Each bar represents approximately 21.5 m width of each site shore and patch ( $\pm$ standard error,  $n = 5$ ). The first three bars of each site correspond to one shore, and the second three to the other shore, each bar is a patch within the shore and the site. Dashed line indicates mean intertidal taxon richness.

habitats were significant at different spatial scales. The dominant taxa in the intertidal and subtidal assemblages also exhibited a scale-dependent distribution pattern. The VC and PVC supported this, indicating that the largest patterns of horizontal variation generally occurred at small scales. Therefore, the results supported the prediction that univariate and multivariate analyses would show significant differences and larger VC and PVC at small spatial scales. We will discuss the characteristics of the assemblages and possible processes that could explain this high small-scale spatial variability along an environmental gradient in a fjord in the MSE.

#### 4.1. Hydrological features

The decrease in salinity and temperature within the FMO is influenced by glacial melt and freshwater discharge in GG and BG (Mansilla, 2022). An estuarine system with marked vertical and horizontal gradients is generated, as in other fjords of the MSE (Valle-Levinson et al., 2006, Iriarte et al., 2014, Pérez-Santos et al., 2014). This estuarine system varied from inside the FMO to outside, as glacially modified waters are exchanged in the JI and LI with upwelling coastal oceanic water intrusions (Damme et al., 2005, Straneo and Cenedese, 2015, Beird et al., 2015). Our results coincide with those described by Silva and Calvete (2002), who had already recorded the horizontal gradient (head-mouth) in FMO two decades ago. It is important to mention that

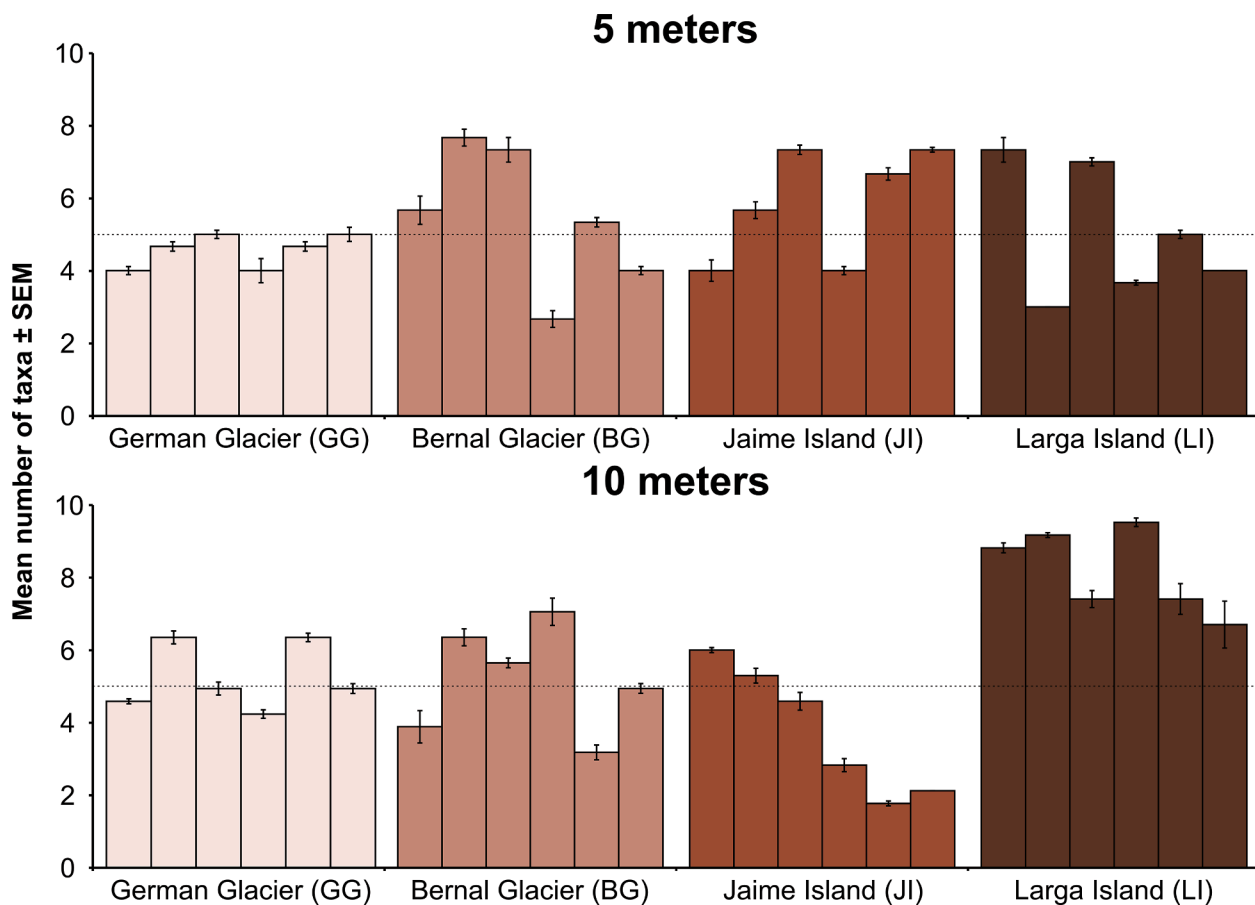
**Table 1**

Analysis of variance of spatial scale-dependent patterns of taxon richness (ANOVA) and community structure (PERMANOVA) in the intertidal and subtidal of the study sites, Magellanic Subantarctic ecoregion, Chile. Abbreviations: LE, Level; DE, Depth, SI, Site; SH, Shore; PA, Patch.

Source of variation	Taxon richness					Community structure		
	df	MS	F	P	MS	Pseudo-F	P	
Intertidal	LE	3	2.94	33.80	***	34,007	2.24	*
	SI	2	1.99	22.96	***	37,107	1.96	
	SH(SI)	4	0.09	1.12		18,916	4.62	***
	LExSI	6	0.27	3.11	**	15,227	1.96	*
	PA(SH(SI))	16	0.16	1.95	*	4099	3.09	***
	LExSH(SI)	8	0.23	2.76	**	7764	2.50	***
	LExPA(SH(SI))	32	0.09	1.09		3107	2.34	***
	Res	143	0.09					
	Subtidal	DE	3	0.51	6.15	**	14,131	1.43
SI		1	0.07	0.02		29,768	2.84	*
SH(SI)		4	0.37	2.99	*	10,480	3.45	**
DExSI		3	0.92	10.40	***	9855	1.66	
PA(SH(SI))		16	0.15	1.05		3039	1.73	***
DExSH(SI)		4	0.39	2.75	*	5933	1.90	**
DExPA(SH(SI))		16	0.22	1.76	*	3115	1.78	***
Res		96	0.12					

Df, Degrees of freedom; MS, Mean squares; F, F-ratio; P, P-values

\*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001



**Fig. 4.** Scale of local patterns of mean taxon richness for each site, shore, patch and subtidal depth (5 and 10 m), Magellanic Subantarctic ecoregion, Chile. Each bar represents approximately 21.5 m width of each site, shore and patch ( $\pm$ standard error, n = 5). Three bars correspond to a shore within the site, and each bar is a patch within the shore and the site. Dashed line indicates mean intertidal taxon richness.

what was observed in FMO is not a general pattern in all fjords of the MSE; similar (e.g. Seno Ballena) and different (e.g. Puyuhuapi Fjord) gradients have been recorded (Valle-Levinson et al., 2006, Betti et al., 2017).

Freshwater discharges from glaciers in GG and BG exhibited increased turbidity at shallow depths. In estuarine systems, this is a

consequence of glacier melting and re-suspension of fine sediments (Włodarska-Kowalczyk et al., 2005, Chu et al., 2012, Tait, 2019). By contrast, higher turbidity was recorded with increasing depth in the JI, while no turbidity was recorded in LI. Therefore, JI is affected by sediment transport from the head of the FMO as a result of fjord circulation (Silva and Calvete, 2002). Turbidity decreases with increasing distance

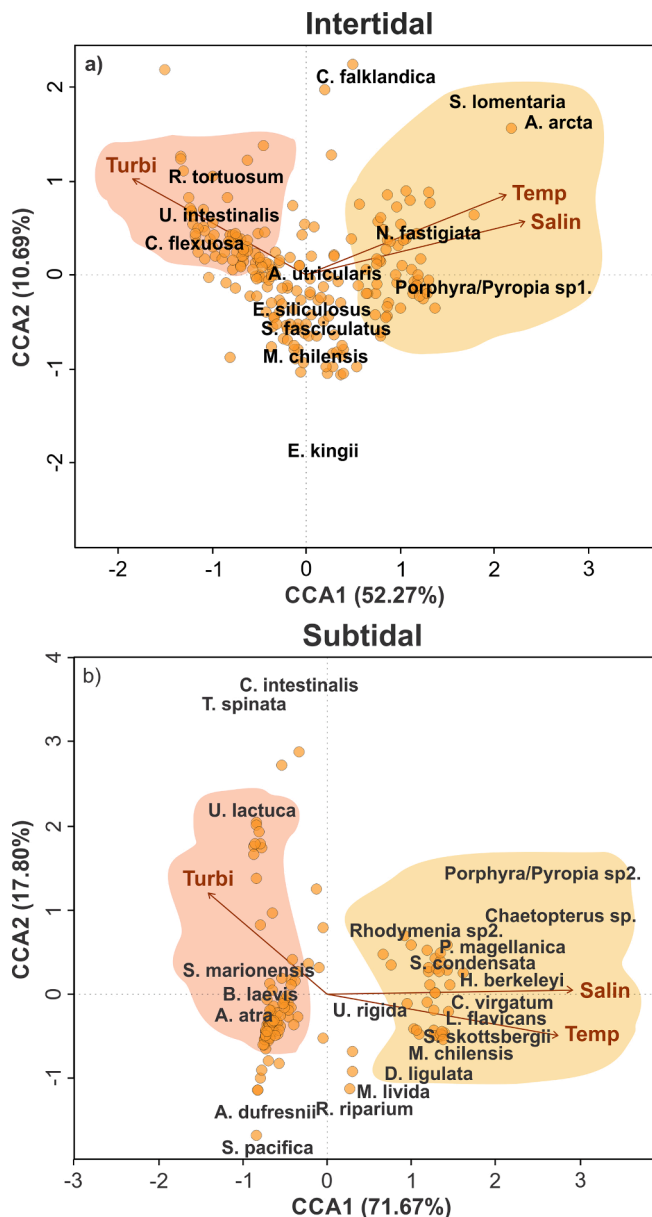


Fig. 5. Canonical correspondence analysis (CCA) biplot for the ecological correlations between the intertidal taxon cover (a) and subtidal taxon cover (b) and the oceanographic variables of the study sites, Magellanic Subantarctic ecoregion, Chile.

from the mouth of the fjord (Murray et al., 2015). These results are related to measurements in Arctic fjords, where > 100 FNU has been recorded as a result of sediment input from glacial melt, which mainly occurs in the coastal zone near glaciers (Klein et al., 2019). High turbidity dependent on proximity to glaciers has also been recorded in areas with the presence of glaciers in the Antarctic Peninsula (Valdivia et al., 2020). However, these gradients in high latitude fjords may vary seasonally and spatially (Schneider et al., 2014, Saldias et al., 2016). Therefore, in the future it would be important to characterize the fjord oceanographically seasonally, to determine the variability in the stratification of water masses and the variation of sediment discharge due to glacial melting.

#### 4.2. Vertical and horizontal variability of benthic communities

Vertical patterns of taxon richness were dependent upon location within the fjord, mainly in the two sites close to the glacier (GG and BG);

no increase in richness was observed towards the lower level of the intertidal, contrary to what has been reported in other intertidal studies of the MSE (Ojeda et al., 2014, 2019). The high environmental disturbance along the GG and BG sites caused by low salinity and high turbidity would be driving a less diverse and more vertically homogeneous intertidal habitat, as occurs in Arctic intertidal shores (Peck et al., 2006, Kuklinski, 2009) and Antarctic shallow glacial environments (Valdivia et al., 2020). For the subtidal environment only the LI site presented an increase in richness with depth, while the JI site, despite being farther from the glaciers than GG and BG, presented its highest richness at 5 m depth. Below 8 m depth at this site there was a lot of particulate material on the bottom, thus reducing the rocky substrate cover. These types of small-scale factors such as the nature and cover of the substrate also contribute to changes in the composition and diversity of benthic assemblages along a vertical and horizontal gradient (Gutt et al., 1999, Aldea and Rosenfeld, 2011, Ojeda et al., 2014, Valdivia et al., 2014). This absence of a marked pattern of vertical and horizontal diversity along the FMO is in agreement with that reported by Villalobos et al. (2021) for another estuarine system of the Magellan province, the Comau Fjord, where the highest values of taxon diversity were also found at different depths along the fjord. Therefore, in both cases the typical pattern of estuarine systems, a decrease in diversity from the head to the mouth of the estuarine ecosystems, was not found (Meire et al., 2005, Beuchel et al., 2006, Villalobos et al., 2021). Hence, the horizontal patterns of macrobenthic organisms are context- and taxonomic group-dependent (Brattegard, 1966, Rosenberg and Möller, 1979, Hansen and Ingólfsson, 1993, Villalobos et al., 2021). As reported by Villalobos et al. (2021), the absence of a linear pattern of richness along the FMO agrees with the hypothesis of sub-habitat dependence (Scrosati et al., 2020), which predicts that a geographic pattern of biodiversity in a given region will differ among different sub-habitats. This model assumes that the main abiotic drivers of sessile species distributions vary among sub-habitat types (Scrosati et al., 2020, Villalobos et al., 2021).

In high latitude intertidal habitats of the Southern Hemisphere, particularly the rocky shores of the MSE and AP, grazing gastropods of the genus *Nacella* are common and dominant species among the macroinvertebrate assemblages (Guzmán, 1978, Ríos and Gerdes, 1997, González-Wevar et al., 2011, Ojeda et al., 2014, Rosenfeld et al., 2018, Valdivia et al., 2018). *Nacella* species have been described as forcing the richness and abundance of algae, as well as structuring the intertidal macro and microalgal communities (Aguilera, 2011, Valdivia et al., 2014, Valdivia et al., 2018). However, in our study *N. magellanica* was present with minimal abundances in the FMO, rejecting herbivory as an ecological process that is structuring and modifying the spatial patterns of algal communities along the FMO (Rosenfeld et al., 2018, Valdivia et al., 2018). Therefore, our results differ from those found by Valdivia et al. (2014) where the high abundance of the grazer *N. concinna* would be forcing the structuring and formation of vertical and horizontal patterns of spatial variability at small scales in the intertidal communities of King George Island, Antarctica. Valdivia et al. (2018) reported that grazing by *N. magellanica* on rocky shores of the Strait of Magellan generates significant modifications in periphyton and filamentous algae. Therefore, the absence of dominant grazers on the shores of the FMO may favor the intertidal dominance of annual macroalgae and an opportunistic life strategy such as that of *U. intestinalis* and *C. flexuosa* (Daly and Mathieson, 1977, Sousa, 1984, Mathieson et al., 1991), species that also possess functional attributes which allow them to proliferate in ecosystems with different levels of environmental disturbance (Littler and Littler, 1980, Steneck and Dethier, 1994, Fong et al., 1996, Martins and Marques, 2002, Larsen and Sand-Jensen, 2006).

The particularities in the intertidal of the FMO indicate that vertical and horizontal variations at small spatial scales could be determined by other biological processes (i.e. competition and recruitment), local abiotic factors (i.e. salinity and turbidity) and habitat complexity (i.e. substrate heterogeneity, presence of glaciers) (Ørberg et al., 2018, Valdivia et al., 2020). For example, our results highlight the low abundance



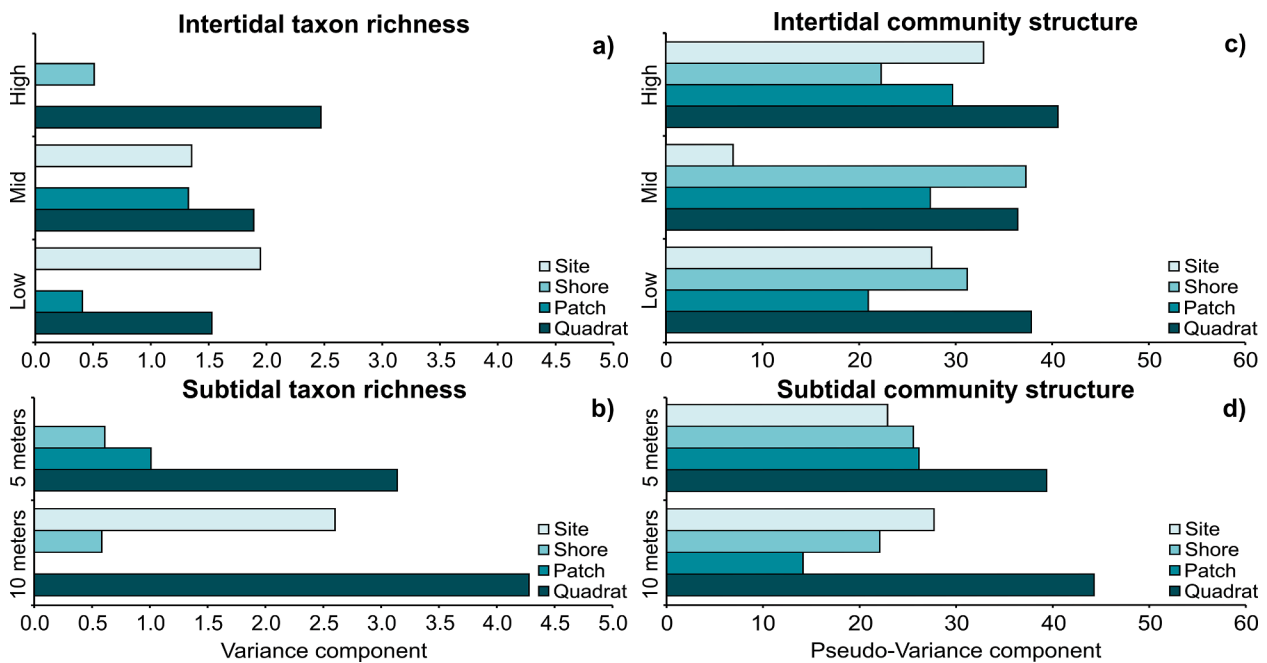


Fig. 6. Spatial scale-dependent variance components (VC) of taxa richness for intertidal (a) and subtidal (b) habitat and spatial scale-dependent pseudo-variance components (PVC) of community structure for the intertidal (c) and subtidal (d) habitats of the study sites, Magellanic Subantarctic ecoregion, Chile.

Table 2

Similarity percentage analysis (SIMPER) of taxa in the intertidal habitat of the study sites, Magellanic Subantarctic ecoregion, Chile.

Taxa	Mean abundance		Accumulative contribution
	High	Mid	
<i>Ulva intestinalis</i>	0.17	0.19	27.19
<i>Porphyra/Pyropia</i> sp1.	0.13	0.02	42.01
<i>Nothogenia fastigiata</i>	0.04	0.08	53.93
<i>Cladophora flexuosa</i>	0.04	0.06	62.95
<i>Ectocarpus siliculosus</i>	0.03	0.06	71.21
<i>Adenocystis utricularis</i>	0.01	0.06	77.80
<i>Scytothamnus fasciculatus</i>	0.02	0.03	82.05
<i>Mytilus chilensis</i>	0.01	0.03	86.04
<i>Acrosiphonia arcta</i>	0.00	0.03	89.12
<i>Elminius kingii</i>	0.00	0.01	91.37
	<b>Mid</b>	<b>Low</b>	
<i>Ulva intestinalis</i>	0.19	0.04	19.34
<i>Cladophora flexuosa</i>	0.06	0.11	33.07
<i>Adenocystis utricularis</i>	0.06	0.09	44.48
<i>Ectocarpus siliculosus</i>	0.06	0.08	55.18
<i>Nothogenia fastigiata</i>	0.08	0.00	65.21
<i>Mytilus chilensis</i>	0.03	0.07	73.97
<i>Acrosiphonia arcta</i>	0.03	0.02	78.90
<i>Elminius kingii</i>	0.01	0.03	82.80
<i>Scytothamnus fasciculatus</i>	0.03	0.02	86.54
<i>Cladophora falklandica</i>	0.02	0.02	90.19

and fragmented distribution of the filter-feeding bivalve *Mytilus chilensis*, a species that historically has been described as an abundant organism that forms dense matrices on rocky shores along the MSE (Guzmán and Ríos, 1981, Ojeda et al., 2014, Molinet et al., 2015). Considering the absence of intertidal carnivores (Hunt and Scheibling 1995, 1996, Curelovich et al., 2016, Ojeda et al., 2017), a better explanation to describe this horizontal distribution pattern in *M. chilensis* would be the local abiotic factors mentioned earlier. Therefore, the high heterogeneity in the abiotic factors and the identity of the species that compose the assemblages along the FMO would explain the high variability that we found at different spatial scales (Scrosati et al., 2011, Ojeda et al., 2017, Curelovich et al., 2018).

The filter-feeding bivalve *Aulacomya atra* is a conspicuous species of shallow subtidal habitats in high latitudes of the Southern Hemisphere,

Table 3

Similarity percentage analysis (SIMPER) of taxa in the subtidal habitat of the study sites, Magellanic Subantarctic ecoregion, Chile.

Taxa	Mean abundance		Accumulative contribution
	5 m	10 m	
<i>Aulacomya atra</i>	0.20	0.16	24.19
<i>Symplectoscyphus marionensis</i>	0.06	0.07	34.71
<i>Balanus laevis</i>	0.06	0.05	43.53
<i>Mytilus chilensis</i>	0.08	0.01	51.70
<i>Ulva lactuca</i>	0.05	0.00	57.22
<i>Sarcopeltis skottsbergii</i>	0.03	0.01	60.57
<i>Spongomorpha pacifica</i>	0.02	0.00	63.83
<i>Heterosiphonia berkeleyi</i>	0.01	0.02	66.94
<i>Myriogramme livida</i>	0.02	0.01	69.98
<i>Ceramium virgatum</i>	0.01	0.01	73.01
<i>Ptilonia magellanica</i>	0.00	0.03	75.28
<i>Ulva rigida</i>	0.01	0.00	77.37
<i>Arbacia dufresnii</i>	0.01	0.01	78.98
<i>Porphyra/Pyropia</i> sp2.	0.00	0.01	80.38
<i>Desmarestia ligulata</i>	0.01	0.00	81.76
<i>Macrocystis pyrifera</i>	0.00	0.01	83.13
<i>Ciona intestinalis</i>	0.01	0.00	84.30
<i>Schizoseris condensata</i>	0.00	0.01	85.45
<i>Lessonia flavicans</i>	0.01	0.00	86.59
<i>Chaetopterus</i> sp.	0.00	0.01	87.68
<i>Rhodymenia</i> sp2.	0.00	0.01	88.70
<i>Tedania spinata</i>	0.00	0.01	89.54
<i>Rhizoclonium riparium</i>	0.01	0.00	90.34

forming extensive matrices in both hard substrates and coarse-grained sediments (Reid and Osorio, 2000, Sepúlveda et al., 2016, Betti et al., 2017, Betti et al., 2021). They also play a relevant role as ecosystem engineers by providing habitat complexity and three-dimensionality (Jones et al., 1994, Ojeda et al., 2014). Particularly, *A. atra* was dominant along the subtidal of the FMO, however, it had a fragmented (patchy) distribution in the BG, GG, and JI and a dense (matrix) distribution in the LI. The absence of dominant predators that selectively eliminate species such as the asteroid *C. livida* in the subtidal of the FMO could not explain the fragmented structure and distribution, as described in previous studies (Gaymer et al., 2001, Gaymer and Himmelman, 2002, Gil and Zaixso, 2008, Lamare et al., 2009). Therefore,

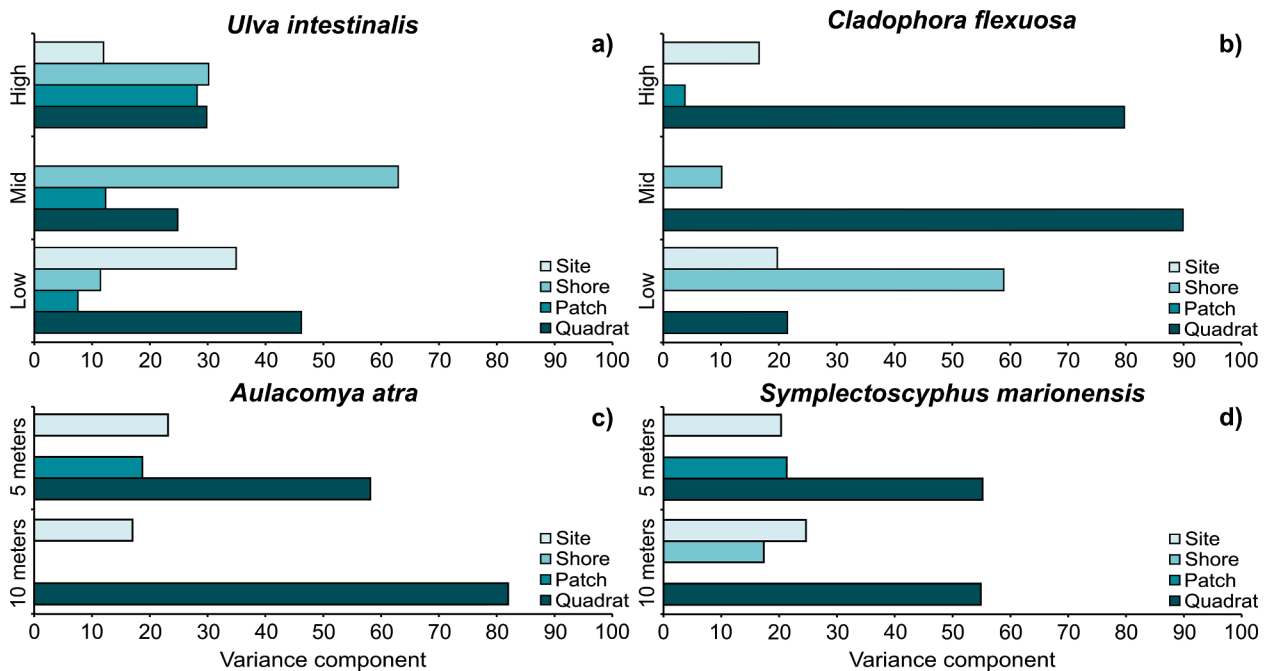


Fig. 7. Variance components (VC) of the most representative taxa in the intertidal: *Ulva intestinalis* (a) and *Cladophora flexuosa* (b), and in the subtidal: *Aulacomya atra* (c) and *Symplectoscyphus marionensis* (d) through horizontal scales of spatial variability in the study sites, Magellanic Subantarctic ecoregion, Chile.

these patterns observed in the structure could be related to local abiotic factors of FMO such as the negative consequences caused by the reduction in salinity on the growth of mussels near the GG and BG glaciers (Navarro, 1988). It has also been described that physical disturbances such as turbidity and consequent sedimentation could decrease the presence of hard substrates for benthic recruitment, generating biological interactions such as interspecific competition (Noda 1999, Hamilton 2000, Thiel and Ullrich, 2002, Navarrete et al., 2010). Therefore, it is important to mention that in the GG and BG glaciers *A. atra* co-inhabits with other sessile species such as *S. marionensis* and *B. laevis*. *A. atra* does form dense matrices in the subtidal of the LI, thus emphasizing that local abiotic factors could explain the high variability we found in the distribution and structure of the assemblages.

These singularities in local FMO factors could also explain the low abundance of macroalgae in the subtidal compared to other studies in the MSE (i.e. Marambio et al., 2016, Ojeda et al., 2019), where the degree of sedimentation and light regime define the lower limit of algal distribution (Wlodarska-Kowalczyk et al., 2005). Salinity is a determining factor in the proportion of red and brown algae in the first meters of estuarine systems (i.e. Munda, 1978, Schubert et al., 2011), since red algae appear to be more sensitive to variations in salinity than brown algae (Cole and Sheath, 1990). This is related to our results, explaining the absence of algae of the order Corallinacea in FMO, which are common in the sublittoral rocky shores of the MSE (Newcombe and Cárdenas, 2011, Cárdenas and Montiel, 2015). In contrast, outside the fjord in LI, lower turbidity and higher salinity allow for greater stability and thus a change in the composition and structure of the macroalgae (Aumack et al., 2007, Filbee-Dexter et al., 2018). We recorded the appearance of the large perennial macroalgae *Durvillaea antarctica*, *Sarcopeltis skottsbergii* and *Lessonia flavicans* (Marambio et al., 2017, Velasco-Charpentier et al., 2021) indicating greater environmental stability and more oceanic conditions, since these species do not tolerate water masses with low salinity and high turbidity (Mansilla et al., 2014, Marambio et al., 2017, Méndez et al., 2017).

## 5. Conclusion

The study sites in the MSE generally had their own local factors that generate extreme environmental conditions during the summer season typical of an estuarine system influenced by glaciers (variations in salinity, temperature, turbidity, sedimentation and substrate heterogeneity), influencing diversity patterns and ecological processes at different spatial scales. The local abiotic factors mentioned above were possibly the most determinant in generating patterns of variation in taxon richness and community structure, with greater variability at smaller spatial scales. The information generated on diversity patterns is very relevant and is a baseline for the evaluation of ecological processes considering spatial scales in shallow macrobenthic communities within environmental gradients influenced by glaciers in the MSE. This provides further evidence on the effects of glacial retreat and influence on shallow macrobenthic communities in the complex scenarios promoted by global changes. Finally, we suggest that it would be important to have a larger number of samples over a longer time, to verify if what is observed can vary over time. In addition, it would be important to replicate this nested design with different spatial scales in other sites with glacial influence, to verify if the observed pattern is a pattern that only occurs in the Mountains fjord or is common to other places within the MSE.

## Funding

FONDECYT Regular 1180433, Grant ANID ACE210006, Technological Centers of Excellence with Basal Financing ANID-Chile to the Cape Horn International Center (CHIC- ANID PIA/BASAL PFB210018) and ANID – Millennium Science Initiative Program – ICN2021\_002.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The authors do not have permission to share data.

## Acknowledgements

Funding was obtained from Fondecyt Regular 1180433 to AM, FB, SR, AM, JPR, FM and KG would like to thank Project ANID/BASAL FB210018. SR, KG and ZL would like to thanks the Project ANID–Millennium Science Initiative Program–ICN2021.002. The authors also wish to thank Dr. Danilo Bustamante, Dra. Martha Calderón and Dr Maximo Frangópulos for their constructive suggestions, which considerably improved the quality of the paper. In addition, we want to thanks Dr. Aldo Barreiro for his help and suggestions with the design and statistical analysis. We especially thank Lafayette Eaton for English revision and editing and to Jose Luis Iriarte and two anonymous reviewer for their helpful comments.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2022.102879>.

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