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Seasonal benthic patterns in a glacial Patagonian fjord: the role of suspended sediment and terrestrial organic matter

Eduardo Quiroga1,2,*, Paula Ortiz3,4, Rodrigo González-Saldías2,5,6, Brian Reid3, Fabián J. Tapia2,6, Iván Pérez-Santos2,7, Lorena Rebolledo2,8,9, Rodrigo Mansilla2, Carlos Pineda4, Ilia Cari4, Nicole Salinas1, Américo Montiel10, Dieter Gerdes11

1Pontificia Universidad Católica de Valparaíso (PUCV), Escuela de Ciencias del Mar, Valparaíso, Chile
2COPAS Sur-Austral, Universidad de Concepción, Concepción, Chile
3Centro de Investigación en Ecosistemas de la Patagonia (CIEP), Coyhaique, Chile
4Programa de Magister en Oceanografía, Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso (PUCV), Valparaíso, Chile
5Unidad de Biotecnología Marina, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Chile
6Departamento de Oceanografía, Universidad de Concepción, Chile
7Centro I-Mar, Universidad de Los Lagos, Puerto Montt, Chile
8Instituto Antártico Chileno (INACH), Punta Arenas, Chile
9Centro FONDAP de Investigación de Ecosistemas de Altas Latitudes (IDEAL), Universidad Austral de Chile, Valdivia, Chile
10Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile
11Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, 27568 Bremerhaven, Germany

ABSTRACT: Complex marine–terrestrial interactions characterize Chilean fjords, where benthic communities influence the distribution of organic matter (OM). We examined spatial and seasonal changes in the hydrography, sediment conditions and soft-bottom macrobenthic, meiofaunal, and total microbial biomass in a glacial Patagonian fjord (Martinez Channel, Chile). The transport of a high load of glacial mineral and particulate OM to the fjord in the austral summer coincided with low total live benthic biomass. Multivariate analysis evidenced temporal-related macrofaunal groups influenced by the different environments produced by the advection of sediment transport and terrestrial OM from the Baker River, Chile. The relationships between density/biomass and respiration versus body size varied considerably with distance from major riverine inputs, but the slopes of density size spectra and normalized biomass size spectra were less negative in summer than in winter. Occasional large-scale advective processes in the water column affected sediment conditions and removed surface macrofauna, influencing the slope and intercept of the regression models. In the outer fjord, lateral advection and subsequent sedimentation of terrestrial OM contributed a significant fraction to total OM sediments (14.76%). Stable carbon isotopes measured in benthic organisms suggest that benthic communities in the inner fjord may assimilate a significant fraction of terrestrial OM via heterotrophic bacteria in contrast to the minor input of terrestrial OM in the outer fjord.

KEY WORDS: Macrofauna · Meiofauna · Total microbial biomass · Stable isotopes · Trophic structure

INTRODUCTION

The fjords of Chilean Patagonia are characterized by complex marine–terrestrial interactions between freshwater sources and adjacent coastal systems that make for highly dynamic estuarine ecosystems (Silva et al. 2011). Low nitrate and phosphate in freshwater discharges from continental runoff, rivers and glacial
tributaries contrast with high silicic acid concentration (Torres et al. 2014). Below the pycnocline, however, the influence of oceanic sub-Antarctic waters (SAAW) elevates nutrient concentrations in Patagonian fjords, resulting in strong vertical and horizontal hydrographic gradients, with characteristics that fluctuate depending on the volume and dominant source of freshwater input (Aiken 2012). Different sources of freshwater modulate primary production (PP) and the contribution of terrestrial organic matter (OM) (Lafon et al. 2014). In addition, tidal and wind-driven currents locally enhance mixing and water mass exchanges, promoting dynamic abiotic and biotic variables in fjords (Ross et al. 2014). In fact, variations in advective transport along the coast and between the open coastal zone and adjacent fjords influence seasonal differences in benthic community structure, larval transport, suspended material and vertical OM fluxes (Reigstad & Wassmann 1996, Elahi et al. 2014, Sørensen et al. 2015).

Strong coupling of benthic and pelagic systems occurs in fjords (Nøji et al. 1993, Reigstad & Wassmann 1996, Dunton et al. 2005, Carroll & Ambrose 2012, González et al. 2013, Provost et al. 2013). In Chilean Patagonian fjords, highly seasonal PP results in the efficient export of organic carbon (OC) to sediments in spring–summer, thus enhancing OM flux to the benthic system (González et al. 2013, Jacob et al. 2014). Many studies have demonstrated that the benthos is an excellent indicator of both local and advective processes (Dunton et al. 2005). In addition, benthic communities play an important role in the functioning of fjord and estuarine ecosystems by affecting rates and pathways of OM exchange and transformation (Graf 1992, Jørgensen 1996, Raffaelli et al. 2003, Sørensen et al. 2015). Multiple studies have highlighted the quality and magnitude of OM depositions as primary regulators of benthic community structure, from bacteria to megafauna (e.g. Dunton et al. 2005, Evrard et al. 2012, Macdonald et al. 2012, Quiroga et al. 2012, Grange & Smith 2013, Bell et al. 2016). In fjord systems, particulate organic matter (POM) of terrestrial origin or from the adjacent continental shelf augments the vertical rain of autochthonous POM reaching the benthos (McLeod & Wing 2009, Lafon et al. 2014, Bell et al. 2016). Persistent invertebrate–chemoautotroph symbioses in the temperate forests of New Zealand demonstrate strong coupling between terrestrial and marine ecosystems in fjords, particularly in shallow habitats (McLeod & Wing 2009, McLeod et al. 2010). However, the roles of chemosynthetic bacteria and terrestrial POM as potential food sources for most benthic feeders in Patagonian fjords remain unclear (Mayr et al. 2011, Zapata-Hernández et al. 2014), and there have been few studies of the trophic structure of benthic communities in Chilean fjords (Zapata-Hernández et al. 2014).

Analysis of body-size distribution is an important tool for describing and comparing community structure and OC flux in marine and freshwater ecosystems (Peters 1983, Stead et al. 2005) and as an indicator of ecosystem functioning (Kerr & Dickie 2001). Recurring patterns of size structure (e.g. Quiñones et al. 2003, Marquet et al. 2005) and in biomass size distribution in benthic ecosystems (e.g. Schwinghamer 1985, Drgas et al. 1998, Quiroga et al. 2005, 2012) have been reported in pelagic ecosystems. In general, the energy equivalence hypothesis, i.e. the regression of animal abundance/biomass over body size on a log scale, predicts a relatively constant slope of ~0.75 across different communities, indicating equal rates of resource utilization by differently sized organisms (Peters 1983, Cyr et al. 1997, Stead et al. 2005). However, environmental fluctuations alter species composition as well as density, biomass, and body size distribution of benthic communities, which influences spatial–temporal patterns in size spectra, which suggests a lack of equilibrium (Stead et al. 2005, Akoumaniaki et al. 2006, Quiroga et al. 2012). We hypothesize that variations in advective transport along the coast and between the open coastal zone and adjacent fjords, in turn, cause variations in total microbial benthic biomass, macro- and meiofaunal biomass, and parameters of the density/biomass size spectra representing reliable process indicators (Rakocinski 2012). The aims of the present study were: (1) to describe spatial (inner, middle and outer fjord) and temporal (summer and winter) variations in bacterial and macro- and meiobenthic biomass in relation to gradients in hydrographic (salinity and turbidity) and sediment (quantity and quality of sediment-bound OM); and (2) to assess the importance of OM from different origins for benthic distribution patterns in an ocean-inner fjord gradient. Based on the AZTI marine biotic index (AMBI), an ecological indicator for managing estuarine and coastal waters worldwide (Borja et al. 2008), Quiroga et al. (2013) classified the health status of the benthic community in the inner fjord as high quality but unbalanced diversity (i.e. high number of species but dominated by small-bodied organisms), possibly related to high levels of freshwater input from glacial river discharges. Quiroga et al. (2013) also highlighted the effects of local physical and environmental conditions on the health status of a fjord system, in
this case the effects of freshwater discharge into semi-confined fjord ecosystems. Local conditions, and thus the ecological impact on the benthic realm, vary seasonally, but climate change scenarios also predict future change. Macrobenthos represent a size group particularly rich in species that integrates environmental history over longer time scales than do rapidly changing plankton because of their relative site fidelity (Arntz et al. 2005). The retreat of glaciers in the coming decades will increase turbidity and reduce PP in the euphotic zone (although the longer-term disappearance of glaciers might massively reduce turbidity). This will, in turn, change the chemistry of inshore waters and influence benthic community patterns. However, there is no simple way to predict such future impacts on the Patagonian fjord biota, especially given the limited data from these systems. In this context, the comprehensive set of observations presented in this study contributes considerably to understanding these systems and provides an appropriate baseline for comparative studies under the scenario of climate change in Chilean Patagonia.

MATERIALS AND METHODS

Study area

In general, sediment delivery from turbid meltwater dominates the fjords of southern Chile, widely distributing fine-grained debris and producing zones of well-sorted sediments and a predominantly smooth seafloor (Dowdeswell & Vásquez 2013). Three major rivers (the Baker, Bravo, and Pascua) influence the marine ecosystem of the Baker Basin (i.e. the Baker Channel and the Martinez Channel), delivering a total supply of $5.1 \times 10^4$ km$^3$ yr$^{-1}$ of freshwater to the Martinez and Baker Channels (Quiroga et al. 2012). These rivers exhibit strong seasonality, with maximum flow rates in summer and a spring minimum, corresponding to the periods of maximum and minimum ice-melt, respectively. In fact, summer discharges from the Baker River represent 45.2% of the annual discharge (Lara et al. 2015). The Baker River accounts for about 1000 m$^3$ s$^{-1}$ of the total input into the study area and is the major source of fine sediment, organic matter and some macronutrients (Quiroga et al. 2012, Marin et al. 2013). The total annual load of fine suspended sediment into the Martinez Channel is approximately $5.3 \times 10^6$ t yr$^{-1}$, which includes fine suspended particles, mostly silt and clay (Quiroga et al. 2012).

Sampling

In order to characterize ecological processes in the Martinez Channel, we obtained environmental data from 11 stations between the Baker River mouth and the Gulf of Penas on the Pacific Ocean shelf (Fig. 1, Table 1). We determined hydrographic conditions, including turbidity and fluorescence, from a set of CTD profiles (SBE-25, Seabird Electronics, and XR Series multi-channel loggers, RBR) taken in August 2014 and January 2015 (Table 1). Water samples were collected in Niskin bottles to measure chlorophyll a (Chla), phaeopigments (Phaeo), and total suspended particulate matter (SPM) at the surface and at 5, 10, 20 and 30 m depth. Duplicate Chla and Phaeo samples were filtered (GF/F glass fibre filters) and frozen ($–20^\circ$C) prior to analysis by fluorometry (Turner design TD-700) following Holm-Hansen et al. (1965). Duplicate suspended particulate total matter samples were vacuum-filtered from 200 ml water on pre-weighed Whatman glass microfibre filters GF/F (0.7 mm pore size) and rinsed with distilled water (Zajączkowski & Włodarska-Kowalczyk 2007). We observed sections along the channel using Ocean Data View (Schlitzer 2012) to compare among seasons. In addition, we characterized the SPM and particulate organic carbon (POC) in 2010, 2014 and 2015 based on water samples collected seasonally from the Baker River. A mooring with an acoustic Doppler current profiler (WorkHorse Sentinel ADCP, 307.7 KHz) was installed close to the Steffen Fjord mouth (47° 46.06′ S, 73° 41.295′ W, Fig. 1) at ~100 m pointing upwardly to collect data during the austral summers of 2014 and 2015. We set hourly temporal resolution with an average of 250 pings and a vertical resolution of 1 m, producing a standard velocity deviation of 0.86 cm s$^{-1}$. A symmetric Lanczos-cosine low-pass filter with a cutoff frequency of 0.6 cycles per day (Walters & Heston 1982, Pizarro 1991, Emery & Thompson 1998) was used to remove the tidal component. Sediment samples were collected at 17 stations from independent replicates using a gravity corer (50 mm diameter). The samples were kept frozen ($–20^\circ$C) prior to analyses of total organic matter (TOM), total organic carbon (TOC), C/N ratio, Chla and Phaeo. Grain sizes were analysed on wet sediments at the Laboratory of Sedimentology of the University of Chile, Santiago, using a Malvern Mastersizer 2000 equipped with a Hydro-G. We obtained TOM using the calcination method and a muffle furnace (Luczak et al. 1997). Sediment-bound Chla and Phaeo were extracted from duplicate subsamples of wet sediment (ca. 1 g) using 90% acetone. After 24 h
Fig. 1. Study area and sampling stations along the Martinez Channel, Chile. (a) Benthic sampling stations for July–August 2014 and January 2015. (b) Benthic sampling stations for January and August 2010. Black dots: sediment and water column samples; white dots: water column stations.

Table 1. List of stations, locations, and variables measured during the study

<table>
<thead>
<tr>
<th>Stn</th>
<th>Location</th>
<th>Date</th>
<th>Season</th>
<th>Latitude (°S)</th>
<th>Longitude (°W)</th>
<th>Fjord section</th>
<th>Depth (m)</th>
<th>Data measured</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Baker River mouth</td>
<td>Mar 25, 2014</td>
<td>Late summer</td>
<td>47°53.19'</td>
<td>74°21.19'</td>
<td>Inner</td>
<td>50</td>
<td>Hydrographic/Sediment</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jul 25, 2014</td>
<td>Winter</td>
<td>47°47.33'</td>
<td>73°35.15'</td>
<td>Inner</td>
<td>60</td>
<td>Hydrographic/Sediment/Sediment trap</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jan 29, 2015</td>
<td>Summer</td>
<td>47°47.17'</td>
<td>73°35.05'</td>
<td>Inner</td>
<td>43</td>
<td>Sediment</td>
</tr>
<tr>
<td>2</td>
<td>Isla Berta</td>
<td>Jul 25, 2014</td>
<td>Winter</td>
<td>47°50.13'</td>
<td>73°53.35'</td>
<td>Middle</td>
<td>100</td>
<td>Hydrographic</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jan 26, 2015</td>
<td>Summer</td>
<td>47°50.13'</td>
<td>73°53.35'</td>
<td>Middle</td>
<td>100</td>
<td>Hydrographic</td>
</tr>
<tr>
<td>3</td>
<td>Merino Jarpa</td>
<td>Jul 26, 2014</td>
<td>Winter</td>
<td>47°46.29'</td>
<td>74°01.20'</td>
<td>Middle</td>
<td>50</td>
<td>Hydrographic/Sediment/Sediment trap</td>
</tr>
<tr>
<td>4</td>
<td>Martinez Channel</td>
<td>Aug 4, 2014</td>
<td>Winter</td>
<td>47°46.29'</td>
<td>73°35.15'</td>
<td>Middle</td>
<td>50</td>
<td>Hydrographic</td>
</tr>
<tr>
<td>5</td>
<td>Estero Lara</td>
<td>Mar 27, 2014</td>
<td>Late summer</td>
<td>47°50.13'</td>
<td>73°53.35'</td>
<td>Middle</td>
<td>24</td>
<td>Hydrographic/Sediment</td>
</tr>
<tr>
<td>6</td>
<td>Punta Baker</td>
<td>Aug 5, 2014</td>
<td>Winter</td>
<td>47°52.01'</td>
<td>74°26.32'</td>
<td>Outer</td>
<td>50</td>
<td>Hydrographic/Sediment/Sediment trap</td>
</tr>
<tr>
<td>7</td>
<td>Islas Porcias</td>
<td>Aug 1, 2014</td>
<td>Winter</td>
<td>47°53.20'</td>
<td>74°40.22'</td>
<td>Outer</td>
<td>50</td>
<td>Hydrographic/Sediment</td>
</tr>
<tr>
<td>8</td>
<td>Baker River mouth</td>
<td>Jan 23, 2010</td>
<td>Summer</td>
<td>47°47.53'</td>
<td>73°35.05'</td>
<td>Inner</td>
<td>50</td>
<td>Sediment</td>
</tr>
<tr>
<td>9</td>
<td>Baker River mouth</td>
<td>Aug 3, 2010</td>
<td>Winter</td>
<td>47°47.53'</td>
<td>73°35.05'</td>
<td>Inner</td>
<td>50</td>
<td>Sediment</td>
</tr>
<tr>
<td>10</td>
<td>Punta Raul</td>
<td>Jan 21, 2010</td>
<td>Summer</td>
<td>47°46.27'</td>
<td>73°39.15'</td>
<td>Inner</td>
<td>60</td>
<td>Sediment</td>
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<td></td>
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<td>Aug 3, 2010</td>
<td>Winter</td>
<td>47°46.27'</td>
<td>73°39.15'</td>
<td>Inner</td>
<td>60</td>
<td>Sediment</td>
</tr>
<tr>
<td>11</td>
<td>Canal Montalva</td>
<td>Jan 21, 2010</td>
<td>Summer</td>
<td>47°49.53'</td>
<td>73°30.41'</td>
<td>Inner</td>
<td>40</td>
<td>Sediment</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aug 5, 2010</td>
<td>Winter</td>
<td>47°49.53'</td>
<td>73°30.41'</td>
<td>Inner</td>
<td>40</td>
<td>Sediment</td>
</tr>
</tbody>
</table>
of darkness at 4°C, we sonicated the samples for 5 min, centrifuged at 3000 rpm (1000 × g) for 10 min, and analysed extracts fluorometrically for Chla and Phaeo content. Photosynthetic pigment values were obtained before and after acidification with 1 N HCl, following Lorenzen (1967), as described in Parsons et al. (1984), substituting the dry weight (DW) of the sediment in grams per volume of water. After drying duplicate sediment subsamples (ca. 1 g) at 105°C for 20 h, we expressed values as μg Chla g−1 DW after correcting for porosity obtained from the water content. The sum of Chla and Phaeo, referred to as the chloroplastic pigment equivalent (CPE), provides an indicator of phytodetrital input to sediments (Pfannkuche & Soltwedel 1998). We measured the sediment redox potential (ORP) for the 0−2 cm surface sediment layer using a platinum standard combination electrode with a calomel internal reference (SG™, Mettler-Toledo). TOC content, C/N and carbon stable isotope ratios (δ13C) of the surface sediments were analysed at the Laboratory of Biogeochemistry and Applied Stable Isotopes (LABASI, PUC), Chile. We evaluated the contribution of allochthonous (i.e. of terrestrial source) organic matter (AOM) to sediments by applying a 2-source mixing model (Bianchi 2007), obtaining the end-members from river and marine sediments from Silva et al. (2011). Surface-tethered double cylindrical sediment traps with a length/diameter ratio of 7:1 (Salcedo-Castro et al. 2015) evaluated the vertical flux of POC. Sediment traps were deployed at 20 m water depth at Stns 1, 3 and 6 in August 2014 for periods of 1−3 d. Samples were analysed for POC using 0.5 l of seawater filtered through pre-combusted Micro Filtration System (MFS) filters and stored frozen until later analysis.

We collected 2−6 replicate macrofaunal samples with a 0.052 m² van Veen grab sampler, excluding faunal groups not sampled quantitatively by this method (e.g. nematodes, foraminifers). Sediment samples were sieved through a 500 μm-mesh screen prior to fixing biological material in a 10%-buffered formaldehyde−seawater solution. Additionally, we collected triplicate subsamples (35 mm diameter) from the centre of each gravity core for meiofauna. For this study, we define metazoan meiofauna as organisms passing through a 500 μm screen but retained on a 63 μm sieve. After sectioning the sub-cores (0−50 and 50−100 mm), we measured meiofaunal biomass as ATP (Raghukumar et al. 2001) and then extracted meiofauna from the remaining sediment by centrifugation with a sugar solution as the flotation medium (Giere 2009). We repeated centrifugation 3 times at 3000 rpm (136 × g) for 5 min each, decanting and rinsing the floating matter after each centrifugation. All of the organic material remained in the supernatant, requiring filter out particles of macroalgal detritus and terrestrial OM.

We assessed total microbial biomass (TMB), comprised of bacteria and nano-fauna (i.e. fungi, yeasts and protozoans), within the 0−2 and 2−4 cm layers of sediment samples through a series of biochemical procedures (Fabiano & Danovaro 1998). Immediately after sampling, we extracted triplicate subsamples in a buffer solution. ATP was quantified using the bioluminescence assay (Holm-Hansen & Booth 1966, Karl 1993) and a Turner Design Model TD 20/20 ATP meter. Internal standards corrected for losses of extractable ATP, and we converted ATP concentrations to carbon equivalents using a 250 mg of C mg−1 factor for TMB (Fabiano & Danovaro 1998). For meiofauna, we used an average ATP concentration of 1.35 mg ATP g−1 wet weight (Giere 2009).

**Data analysis**

We standardized the density and biomass data from each grab sample by area prior to determining the means and standard deviations per station. We then compared community parameters statistically using the Kruskal-Wallis non-parametric test (Zar 1999). Additionally, we estimated mean individual weight (W) as total macrofauna community biomass divided by total macrofauna community density. To identify spatial and temporal variations in community size structure, we used 3 body size distribution models: (1) density size structure (DSS), (2) normalized biomass size spectra (NBSS) and (3) estimated oxygen uptake (EOU). We constructed DSS at each station/time by plotting total density and biomass in each size class across taxa (Cyr et al. 1997), and constructed NBSS as described by Platt & Denman (1978). The intercept of NBSS indicates total biomass at a given system and time (Sprules & Munawar 1986). EOU (i.e. individual respiration in μl h−1) was determined following Banse (1982), using log10EOU = 1.29 + 0.74 log10W, where W (in mg) denotes mean individual body mass expressed as ash-free DW estimated from standard conversion factors for each taxon (Brey 2001). We corrected EOU at 10°C using the Arrhenius equation (Brey 2010) and then plotted mean density and EOU of each taxon and size class against mean body size per size class at each station.

We tested for temporal differences in the slopes of all regressions using an ANCOVA F-test (Zar 1999). In instances of homogeneous regression slopes
(i.e. no significant temporal differences), we compared the intercepts. In addition, we used a 1-way ANCOVA in order to distinguish the effects of freshwater river inputs in the fjord (i.e. fjord section) given that such inputs can obscure otherwise strong trends between the parametric regressions and environmental covariates (Quiroga et al. 2013). The ANCOVAs were carried out using PAST software (Hammer et al. 2001).

The species abundance data matrix was transformed according to \( y = \sqrt{x} \) for the ordination method non-metric multidimensional scaling (nMDS) analysis (Clarke & Gorley 2006). We then tested for significant differences among stations and sampling dates using 2-way permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). Ordination analysis was carried out using PRIMER v5 statistical software (Clarke & Gorley 2006). We explored variability among fjord sections and seasons, based on environmental settings using principal coordinate analysis of non-transformed data with a correlation matrix (Jongman et al. 1987). We also correlated biological variables (i.e. macrofaunal density and biomass, meiofaunal biomass, total microbial biomass, slopes of NBSS, DSS and EOU) and environmental variables (i.e. sand and clay content, ORP, TOC, C/N ratio, sediment-bounded pigments, AOM) using Pearson’s correlation after log\(_{10}(x+1)\) transforming biological and environmental variables except for percentage values, which we transformed as arcsin \( (\sqrt{x/100}) \), as suggested by Zar (1999). Expectation maximization was used to calculate missing values in the correlation matrix (Dempster et al. 1977). All data are reported as mean ± SD.

RESULTS

Environmental conditions

Hourly total suspended solids and input of POC in the study area were highest in summer. Based on the river discharges from 2012, 2014 and 2015 (www.dga.cl, Fig. 2a), the maximum and minimum averages of suspended sediment loads varied between 0.5 kg h\(^{-1}\) (±0.01) in January and 0.04 kg h\(^{-1}\) (±0.001) in September and showed strong interannual variations. The maximum and minimum average POC contribution varied between 4.8 g h\(^{-1}\) (±0.085) in January and 0.5 g h\(^{-1}\) (±0.004) in September, based on river discharges from 2012, 2014 and 2015 (Fig. 2b). These concentrations were estimated taking into consideration what are termed glacial-lake outburst floods, which occur several times a year and produce considerable short-term increases in the quantity of POM and particulate inorganic matter delivered to the inner fjord.

In winter 2014 (July–August), thermal stratification occurred throughout the Martinez Channel, with an approximately 10 m-thick surface layer at <8°C overlying a warmer layer (>9°C). Surface salinity exhibited a longitudinal gradient and varied from 0 PSU near the river mouth to 30 PSU at the seaward end (Fig. 3a). Salinity levels >30 PSU were found below 10 m throughout the entire transect. A weak surface turbidity signal was detected in the first 20 km of the inner fjord (Fig. 3b). Chlorophyll fluorescence was higher close to the surface almost half way up the Martinez Channel (50 km), with maximum values of 0.4 mg m\(^{-3}\) (Fig. 3c). Very different conditions were found in the
Martinez Channel in summer 2015 (January). There was a warmer surface layer (>12°C) in the upper 10 m, accompanied by lower surface salinity measured over the entire channel from the inner to the outer fjord (Fig. 3e). High surface turbidity (>60 NTU) was detected up to 20 km from the river mouth, decreasing to about 20 NTU at about 55 km from the mouth (Fig. 3f). Chlorophyll fluorescence concentrations were high (>1 mg m⁻³) at the seaward end, while concentrations were close to zero in the inner fjord (Fig. 3g).

Current velocity and direction at 50 m depth obtained from acoustic Doppler current profiler (ADCP) measurements were generally higher during the austral winter (Fig. 4a–c). Winter currents were directed mainly NW, but to some extent also E and SE, with velocities ranging from ca. 0 to 3 cm s⁻¹. During summer (Fig. 4d–f), water currents at this depth were directed mainly NW, and velocities were distinctly lower (max. 1.5 cm s⁻¹) than in winter.

Fifteen environmental parameters were used to analyse relationships between biological and environmental patterns. These variables were measured in different seasons and sections of the Martinez Channel. The results are summarized in Table 2. Among the variables, the percentage of sand and clay content, δ¹³C and AOM displayed clear seasonal and/or spatial patterns (Table 2). The sediment conditions showed marked differences from the inner to the outer fjord and among seasons (Table 2). The surface sediment (0–4 cm) showed lower clay content in winter (2.6–6.8%) than in summer (68.9–83.3%). Spatially, clay content in the middle fjord (6.8%) was almost 3 times as high as that in the inner and outer fjords. The sand content also exhibited differences between sampling periods, with higher values in winter (20.5–66.4%) than in late summer (10.2–28.0%). Defined spatial patterns in the fjord also became obvious in the percentages of δ¹³C (indicator of AOM) and Chla in sediments, presumably a reflection of the relative contributions of terrigenous versus phytoplankton derived carbon. In fact, in our study area, lower values of δ¹³C (−27.16 to −28.39‰) were measured in the inner fjord than in the outer fjord (−21.77 to −21.81‰). In summer, Chla concentrations in sedi-
ments were higher in the outer fjord (7.48 µg g\(^{-1}\)) than in the inner fjord (2.32 µg g\(^{-1}\)), while in winter, Chla concentrations in sediments varied between 0.84 µg g\(^{-1}\) in the inner fjord and 1.33 µg g\(^{-1}\) in the outer fjord. OC fluxes estimated in winter 2014 showed a ca. 40-fold increase from the inner (13.28 mg OC m\(^{-2}\) d\(^{-1}\)) to the outer fjord (559.13 mg OC m\(^{-2}\) d\(^{-1}\)).

**Benthic standing stock and size spectra**

A total of 120 taxa of macrofauna were recorded in the study area. Mean total densities varied from 288 ± 151 ind. m\(^{-2}\) (middle fjord, summer 2015) to a maximum of 5391 ± 1567 ind. m\(^{-2}\) in the inner fjord (late summer 2014, Fig. 5a). The respective macrofauna biomasses varied between 159.1 ± 72.9 mg OC m\(^{-2}\) (inner fjord, winter 2014) and 431.0 ± 165.8 mg OC m\(^{-2}\) in the inner fjord (summe, r2015, Fig. 5b). Although there were significant differences in macrofaunal density and biomass among sampling periods (Kruskal-Wallis tests, corrected value, density \(H_c = 17.95, p = 0.001\), biomass \(H_c = 26.28, p = 0.0001\)), no significant differences were found among locations (i.e. inner, middle and outer fjords) (Kruskal-Wallis tests, density \(H_e = 3.77, p = 0.15\), biomass \(H_e = 0.66, p = 0.72\)). Total microbial biomass in the study area varied between 0.02 ± 0.01 µg OC g\(^{-1}\) (middle fjord, summer
and 0.93 ± 0.16 µg OC g⁻¹ in the inner fjord (winter 2014). The differences in biomass among locations were not significant (Kruskal-Wallis test, $H_c = 1.69, p = 0.43$, Fig. 5c). Meiofaunal biomass oscillated between 0.44 ± 0.44 (inner fjord, summer 2010) and 3.49 ± 1.74 mg OC g⁻¹ in the outer fjord (winter 2014), with no significant differences among locations (Kruskal-Wallis test, $H_c = 3.23, p = 0.20$, Fig. 5d). However, TMB and meiofaunal biomass showed significant differences (Kruskal-Wallis tests, TMB $H_c = 74.29, p = 0.0001$, meiofauna $H_c = 37.24, p = 0.0001$) among sampling periods, with lower values of biomass in summer and higher in winter (Fig. 5c,d).

The nMDS analysis based on taxon density data revealed significant differences in community structure among sampling periods and locations (PERMANOVA test, $F_{2,48} = 10.525, p = 0.0001$, Fig. 6a, Table 3).

The DSS of the macrobenthic communities obtained at all 3 locations in the different sampling periods showed significant relationships between wet weight and density ($p < 0.05$, Fig. 7a–c). The slopes of the regression model varied between −0.80 (±0.08) and −1.01 (±0.09) for the inner fjord, −0.30 (±0.08) and −0.65 (±0.09) for the middle fjord and −0.65 (±0.07) and −0.92 (±0.12) for the outer fjord. The intercepts ranged between 7.18 and 12.13 in summer 2015 (Fig. 7a–c). Significant temporal variation was observed in the outer fjord (ANCOVA test, $F_{1,104} = 4.743, p = 0.032$, Table 4). According to the NBSS analysis, the relationship between size classes and normalized biomass was statistically significant ($p < 0.05$, Fig. 7d–f), with slopes ranging from −0.83 (±0.05) to −1.03 (±0.15) for the inner fjord. The slopes for the middle fjord were lower and varied between −0.31 (±0.03) and −0.76 (±0.08), and the slopes for the outer fjord varied between −0.70 (±0.07) and −0.82 (±0.11). Significant temporal variation was observed in the middle fjord (ANCOVA test, $F_{2,16} = 4.056, p = 0.045$, Table 4). Notably, more negative slopes indicate a macrobenthic community dominated by small-bodied organisms. The EOU showed an increase of respiration rates with body size and all regression models were significant ($p < 0.05$, Fig. 7g–i). The slopes of the regression model varied between 0.25 (±0.05) and 0.34 (±0.08) for the inner fjord, 0.28 (±0.07) and 0.51 (±0.09) for the middle fjord and 0.36 (±0.06) and 0.41 (±0.07) for the outer fjord (Fig. 7g–i). No significant temporal differences in the EOU slopes were found (ANCOVA, $p > 0.05$, Table 4). Additionally, the slopes of DSS, NBSS and EOU models appear to be influenced by freshwater river input in the different fjord sections, which is consistent with the environmental data (ANCOVA, DSS: $F_{3,167} = 4.904, p = 0.003$; NBSS: $F_{3,33} = 4.027, p = 0.011$; EOU: $F_{2,136} = 3.207, p = 0.043$, Table 4).

### Relationships between environmental and biological data

The results of the PCA ordination based on 7 environmental variables (TOC, C/N ratio, AOM, and $\delta^{13}$C and $\delta^{15}$N) were used to explain the variability in macrobenthic community structure. The first two axes explained 58.5% of the total variance, with the inner fjord showing the highest values for the first axis and the outer fjord showing the highest values for the second axis. The outer fjord also showed significant differences in community structure among sampling periods and locations (PERMANOVA test, $F_{2,48} = 10.525, p = 0.0001$, Fig. 6a, Table 3).
Chla, CPE, Chla/Phaeo and ORP) are presented in Fig. 6b. The first 2 PCA axes accounted for 65.2% of the total variance. The environmental variables related to the degree of oxidation (i.e. redox potential) and the quality of OM (Chla/Phaeo and AOM) accounted for most of the differences among the inner, middle and outer fjord. In fact, the highest AOM and C/N values were found at inner fjord stations. In contrast, the Chla/Phaeo ratio (which is a measure of recently settled algal detritus), CPE and Chla exhibited a better association with middle and outer fjord stations, characterized by higher values of fresh OM derived from PP, especially in summer. ORP values were higher at the middle and outer fjord stations during winter conditions (Fig. 6b). Significant correlations ($p < 0.05$) were found between ORP and total density of macrofauna, the NBSS slope and intercept and the DSS and EOU slopes (Table 5). TOC related negatively to the EOU slope, whereas Chla/Phaeo correlated with the NBSS slope and intercept and total macrofauna density (Table 5).
Stable carbon and nitrogen isotopes, which are efficient means for tracing carbon flows and trophic positions in food webs, were used to analyze samples of 9 benthic invertebrate taxa and the conger *Genypterus blacodes*, covering mega- and macrofauna species. The stable carbon isotope composition ($\delta^{13}C$) varied between $-17.82‰$ for *Terebellidae* sp. (Polychaeta) and $-24.98‰$ for *Chilina chilensis* (Mollusca), which is a common freshwater gastropod in the Baker River delta (Fig. 8a). The stable nitrogen isotope composition ($\delta^{15}N$) in the samples varied between $2.01‰$ for *C. chilensis* and $14.66‰$ for *G. blacodes*. Among decapods, $\delta^{13}C$ values ranged from $-22.64‰$ (*Peltarium spinosulum*) to $-22.98‰$ (*Libidoclaea granaria*). The galatheid *Munida gregaria* had higher $\delta^{13}C$ values ($-19.34 \pm 10.95‰$) than those of other decapods. In contrast, $\delta^{13}C$ values of peracarid crustaceans ranged from $-20.17‰$ (*Amphipoda* sp. A) to $-21.46‰$ (*Cirrolana* sp.). POM from the Baker River showed negative $\delta^{13}C$ values ($-27.21 \pm 0.96‰$), and suspended POM from the water column and sediment from the inner fjord showed values of $-28.40 \pm 0.34‰$ and $-26.27 \pm 4.55‰$, respectively (Fig. 8a, Table S1 in the Supplement at www.int-res.com/articles/suppl/m561p031_supp.pdf). Comparing the stable C and N isotope data to those from the Comau Fjord, without glacio-fluvial influence but with a similar benthic fauna (e.g. crustaceans, molluscs, nemerteans and fish), showed lower and less variable $\delta^{13}C$ values (Fig. 8b, Table S2 in the Supplement). The gastropod *Nacella deaurata* from the Comau Fjord (Mayr et al. 2011, Zapata-Hernández et al. 2014) was the only organism with higher values ($-26.5‰ \delta^{13}C$ and $8‰ \delta^{15}N$) than those found in our study. In fact, stable isotope values recorded in our study area are different from those observed in the Comau Fjord ($-20$ to $15‰ \delta^{13}C$), suggesting a trophic subsidy associated with the input of terrestrial OM.

**DISCUSSION**

**Temporal variability**

Fluvial discharges significantly change environmental conditions in the Martínez Channel in ways that modify the biogeochemical properties of the water column and sediments and shape spatial and temporal benthic patterns. Oceanic SAW mixes with freshwater discharged into the fjords, generating sharp vertical and horizontal gradients (Dávila et al. 2002, Schneider et al. 2014). The freshwater inputs
Fig. 7. Seasonally averaged normalized biomass size spectra for the (a–c) macrofaunal community, (d–f) density size spectra and (g–i) estimated oxygen uptake at 3 locations in the Martinez Channel.
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are major drivers for circulation, hydrographic structure and productivity patterns in fjord systems, affecting plankton and benthos alike. The hydrographic conditions in the Martinez Channel showed such well-defined gradients throughout the fjord in both August 2014 (winter) and January 2015 (summer). As a response to higher meltwater discharge in summer, the temperature of the surface water layer was high and salinity was low, with pronounced stratification along the entire fjord, whereas the conditions in winter were the opposite, with colder surface water overlying warmer water beneath. Turbidity is a key factor

Table 4. Results of 1-way ANCOVA for testing differences in density size structure (DSS), normalized biomass size spectra (NBSS), and estimated oxygen uptake (EOU) parameters (slope and intercept) of the regression model for 3 locations in the fjord. \( a = \) intercept. **Bold**: significant at \( p < 0.05 \)

<table>
<thead>
<tr>
<th>Model</th>
<th>Fjord section</th>
<th>Comparison between season</th>
<th>Slope (mean ±SD)</th>
<th>( a )</th>
<th>( r^2 )</th>
<th>( p )</th>
<th>ANCOVA</th>
<th>Homogeneity of slopes</th>
<th>Equal intercepts</th>
</tr>
</thead>
<tbody>
<tr>
<td>DSS</td>
<td>Inner</td>
<td>Late summer 2014</td>
<td>-0.93 ± 0.09</td>
<td>12.09</td>
<td>0.77</td>
<td>0.0001</td>
<td>( F_{a,96} )</td>
<td>0.891</td>
<td>5.839</td>
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<tr>
<td></td>
<td></td>
<td>Winter 2014</td>
<td>-1.01 ± 0.09</td>
<td>12.13</td>
<td>0.83</td>
<td>0.0001</td>
<td>p</td>
<td>0.414</td>
<td><strong>0.004</strong></td>
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<tr>
<td></td>
<td></td>
<td>Summer 2015</td>
<td>-0.80 ± 0.08</td>
<td>11.30</td>
<td>0.74</td>
<td>0.0001</td>
<td>p</td>
<td>0.066</td>
<td>0.879</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>Late summer 2014</td>
<td>-0.65 ± 0.09</td>
<td>9.87</td>
<td>0.55</td>
<td>0.0001</td>
<td>( F_{2,108} )</td>
<td>2.795</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Winter 2014</td>
<td>-0.60 ± 0.10</td>
<td>9.46</td>
<td>0.49</td>
<td>0.0001</td>
<td>p</td>
<td>0.066</td>
<td>0.879</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Summer 2015</td>
<td>-0.30 ± 0.08</td>
<td>7.18</td>
<td>0.36</td>
<td>0.0001</td>
<td>p</td>
<td>0.066</td>
<td>0.879</td>
</tr>
<tr>
<td></td>
<td>Outer</td>
<td>Winter 2014</td>
<td>-0.92 ± 0.12</td>
<td>11.60</td>
<td>0.69</td>
<td>0.0001</td>
<td>( F_{1,104} )</td>
<td>4.743</td>
<td>0.654</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Summer 2015</td>
<td>-0.65 ± 0.07</td>
<td>10.08</td>
<td>0.64</td>
<td>0.0001</td>
<td>p</td>
<td>0.032</td>
<td>0.421</td>
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<tr>
<td>NBSS</td>
<td>Inner</td>
<td>Late summer 2014</td>
<td>-1.01 ± 0.09</td>
<td>3.98</td>
<td>0.95</td>
<td>0.0002</td>
<td>( F_{2,18} )</td>
<td>0.900</td>
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<tr>
<td></td>
<td></td>
<td>Winter 2014</td>
<td>-1.03 ± 0.15</td>
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<td>0.92</td>
<td>0.004</td>
<td>p</td>
<td>0.429</td>
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<tr>
<td></td>
<td></td>
<td>Summer 2015</td>
<td>-0.83 ± 0.05</td>
<td>2.70</td>
<td>0.98</td>
<td>0.002</td>
<td>p</td>
<td>0.429</td>
<td>0.071</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>Late summer 2014</td>
<td>-0.76 ± 0.08</td>
<td>1.94</td>
<td>0.95</td>
<td>0.0001</td>
<td>( F_{5,167} )</td>
<td>4.056</td>
<td>0.996</td>
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<tr>
<td></td>
<td></td>
<td>Winter 2014</td>
<td>-0.73 ± 0.14</td>
<td>1.54</td>
<td>0.85</td>
<td>0.002</td>
<td>p</td>
<td>0.445</td>
<td>0.394</td>
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<td></td>
<td></td>
<td>Summer 2015</td>
<td>-0.31 ± 0.03</td>
<td>-1.97</td>
<td>0.97</td>
<td>0.0001</td>
<td>p</td>
<td>0.445</td>
<td>0.394</td>
</tr>
<tr>
<td></td>
<td>Outer</td>
<td>Winter 2014</td>
<td>-0.82 ± 0.11</td>
<td>3.14</td>
<td>0.92</td>
<td>0.0004</td>
<td>( F_{1,13} )</td>
<td>1.898</td>
<td>1.626</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Summer 2015</td>
<td>-0.70 ± 0.07</td>
<td>1.49</td>
<td>0.95</td>
<td>0.001</td>
<td>p</td>
<td>0.196</td>
<td>0.226</td>
</tr>
<tr>
<td>EOU</td>
<td>Inner</td>
<td>Late summer 2014</td>
<td>0.25 ± 0.05</td>
<td>6.60</td>
<td>0.46</td>
<td>0.0001</td>
<td>( F_{96} )</td>
<td>0.643</td>
<td>2.365</td>
</tr>
<tr>
<td></td>
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<td>Winter 2014</td>
<td>0.34 ± 0.08</td>
<td>5.83</td>
<td>0.43</td>
<td>0.0003</td>
<td>p</td>
<td>0.528</td>
<td>0.099</td>
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<td></td>
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<td>Summer 2015</td>
<td>0.32 ± 0.06</td>
<td>6.29</td>
<td>0.45</td>
<td>0.0001</td>
<td>p</td>
<td>0.528</td>
<td>0.099</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>Late summer 2014</td>
<td>0.47 ± 0.06</td>
<td>4.99</td>
<td>0.60</td>
<td>0.0001</td>
<td>( F_{2,108} )</td>
<td>2.615</td>
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<td></td>
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<td>Winter 2014</td>
<td>0.28 ± 0.07</td>
<td>6.38</td>
<td>0.28</td>
<td>0.0006</td>
<td>p</td>
<td>0.078</td>
<td>0.535</td>
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<td>Summer 2015</td>
<td>0.51 ± 0.09</td>
<td>4.54</td>
<td>0.60</td>
<td>0.0001</td>
<td>p</td>
<td>0.078</td>
<td>0.535</td>
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<tr>
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<td>0.41 ± 0.07</td>
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<td>0.49</td>
<td>0.0001</td>
<td>( F_{1,84} )</td>
<td>0.167</td>
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<td>0.36 ± 0.06</td>
<td>5.69</td>
<td>0.45</td>
<td>0.0001</td>
<td>p</td>
<td>0.683</td>
<td>0.874</td>
</tr>
</tbody>
</table>

Table 5. Pearson correlation matrix with the abiotic and biotic variables. **Bold**: significant at \( p < 0.05 \). ORP: redox potential; TOC: total organic carbon; C/N: carbon and nitrogen ratio; Chla: chlorophyll a-bounded sediment; CPE: chloroplast pigment equivalent; Chla/Phaeo: chlorophyll a and phaeopigment ratio; AOM: autochthonous organic matter; NBSS: normalized biomass size spectra; DSS: density size structure; EOU: estimated oxygen uptake

<table>
<thead>
<tr>
<th>Model</th>
<th>Comparison between</th>
<th>ANCOVA</th>
<th>Test for equal intercepts</th>
<th>Homogeneity (equality) of slopes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>df</td>
<td>( F )</td>
<td>( p )</td>
</tr>
<tr>
<td>DSS</td>
<td>Fjord section</td>
<td>3,167</td>
<td>0.748</td>
<td>0.524</td>
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<td>NBSS</td>
<td>Fjord section</td>
<td>4,33</td>
<td>1.137</td>
<td>0.359</td>
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<tr>
<td>EOU</td>
<td>Fjord section</td>
<td>2,136</td>
<td>1.005</td>
<td>0.37</td>
</tr>
</tbody>
</table>

Macrofaunal density -0.09 0.04 0.84 -0.13 -0.14 -0.46 0.00 0.86 0.15
Macrofaunal biomass 0.55 -0.23 0.36 -0.41 0.03 0.20 0.50 0.32 0.15
Meiofaunal biomass -0.06 0.39 0.47 -0.11 -0.62 -0.06 0.27 0.33 0.52
Total microbial biomass -0.38 0.47 0.28 0.24 -0.48 -0.36 -0.15 0.56 0.51
NBSS Slope 0.06 0.02 -0.88 0.41 -0.14 0.65 0.29 -0.78 0.31
NBSS Intercept -0.03 -0.03 0.91 -0.32 0.11 -0.62 -0.21 0.83 -0.18
DSS Slope 0.26 -0.13 -0.83 0.32 -0.08 0.54 0.21 -0.69 0.20
EOU Slope 0.04 0.00 0.82 -0.74 0.15 -0.37 -0.08 0.53 -0.54
High turbidity is known to limit PP and thus also OC flux to sediments. The turbidity patterns in the study area were consistent with those recorded by Marin et al. (2013) and Meerhoff et al. (2014), with maximum concentrations of suspended solids in the inner fjord associated with the glacial origin of suspended sediments (Dussaillant et al. 2010, Quiroga et al. 2012). Such constraints for benthic–pelagic coupling and the role of environmental factors have been investigated previously in Arctic and Norwegian fjord systems (Reigstad & Wassmann 1996, Oug 2000, Dunton et al. 2005, Zajaczkowski & Wlodarska-Kowalczuk 2007, Serensen et al. 2015), but comparable investigations in Chilean fjords are still limited. Most of these studies have concluded that variations in benthic faunal biomass is not related to differences in sediment granulometry, but rather to enhanced local flux of particulate OC. In Arctic fjords, the high standing stock of benthic communities is related to food availability rather than to grain-size distribution (Reigstad & Wassmann 1996, Zajaczkowski & Wlodarska-Kowalczuk 2007). As is the case of the Martinez Channel, the Chilean fjords are dominated by sediments originating from turbid meltwater produced by ice-surface ablation and snowmelt. These sediments enter marine waters via tidewater glaciers and glacialfluvial systems and distribute fine-grained debris widely over the adjacent fjord systems, causing high turbidity locally (Dowdeswell & Vásquez 2013). High turbidity prevents PP in the euphotic zone, and Chla concentrations in the Martinez Channel were lower than those in other Patagonian fjords (Jacob et al. 2014). In fact, PP along the Chilean Patagonian coastline tends to decrease from north to south and is particularly low around areas influenced by glacier derived freshwater input (Jacob et al. 2014).

In terms of composition, density and biomass, the macrobenthic communities in this study were typical of those living on soft-bottoms in Chilean fjords (Montiel et al. 2011, Quiroga et al. 2012). Quiroga et al. (2012) described benthic trophic types in the study area, which were dominated by detritus and suspen-
sion feeders. Considering all macrobenthic species in the fjord in our study, *Scoloplos* sp., *Aphelochaeta cf. marioni*, Ophelliidae sp. A, Dorvilleidae sp. A, *Aricidea antarctica, Capitella* sp., *Thyasira patagonica*, and *Leanira quattrefagesii* accounted for more than 50.9% of the total density in the middle fjord, while the polychaetes *L. antarctica, Capitella* sp., *Prionospio (Minuspio) chilensis* and *A. antarctica* accounted for more than 43.4% of total density in the inner fjord. This difference may be due to the higher sedimentation rates in the inner fjord, dominated by small surface-dwelling pioneering species (Włodarska-Kowalczyk et al. 2016). The nMDS and PERMANOVA analyses evidenced temporal-related groups influenced by the different environments resulting from the advection of sediment transport and terrestrial OM from the Baker River during the summer. This has a strong regulating effect on the standing stock of these communities.

There are only a few studies of seasonal benthic communities in Chilean fjords (Quiroga et al. 2012) and no studies of meiobenthic and microbial communities in this region. In contrast, Arctic tidal glaciers are among the most heavily studied ecosystems in the northern hemisphere (e.g. Gorlich et al. 1987, Conlan et al. 1998, Włodarska-Kowalczyk et al. 2005, 2012, Renaud et al. 2007, Węsławski et al. 2011). In general, benthic communities in Arctic tidal glaciers are exposed to chronic physical disturbances that are often accompanied by changes in live benthic biomass, feeding modes and diversity patterns along the gradient of glacier-induced disturbance (Włodarska-Kowalczyk et al. 2005, 2007, Węsławski et al. 2011). In our study area, we found significant differences between summer and winter in the live biomass of all benthic groups (i.e. TMB, macro- and meiofauna), with lower biomass in the austral summer, which is related to the instability of bottom sediments associated with discharges from the Baker River. This pattern is similar to those reported for Arctic fjords, where the highest levels of benthic fauna biomass and richness occur in the spring after phytoplankton blooms, while in summer, when a high load of glacial mineral material is transported to fjords, the number of both meio- and macrobenthic individuals decreases remarkably (Pawłowska et al. 2011). Sediment stability and sedimentation are the most important factors influencing the distribution of benthic fauna in subtidal sediments (Włodarska-Kowalczyk et al. 2005, 2007, 2016). In our study area, granulometry exhibited a very heterogeneous pattern throughout the fjord, probably related to river discharges carrying sediment and suspended material. Salinity fluctuations here appear unimportant since the freshwater input from the Baker River is relatively high and constant over time, and the salinity in deeper water layers remains similar to that of the adjacent coast (Aiken 2012). In addition, phytoplankton production is restricted to the upper meters of the water column in both summer and winter, but Chla concentration and resulting OM sedimentation is influenced by the distribution of suspended materials in the upper water column rather than by the thickness of the freshwater layer (González et al. 2013). Therefore, the high sedimentation rate associated with the Baker River is important for benthic fauna because it alters sediment texture and stability, preventing animals from maintaining an optimum position in the sediments, thus affecting their standing stock (Zając-kowski & Włodarska-Kowalczyk 2007, Pawłowska et al. 2011, Włodarska-Kowalczyk et al. 2016).

**Size spectra**

The relationships between density/biomass and oxygen uptake versus body size exhibited considerable variation throughout the fjord. This pattern is also related to turbid meltwater from Baker River discharge, which is much higher in summer (Quiroga et al. 2012). In fact, we found temporal differences in the DSS and NBSS slopes in summer in the outer and middle fjord, respectively. The slopes of the regression models can be used to detect gradual changes in biomass distribution across the macrofaunal size spectra in the middle fjord, which is a transitional area with oxidized sediment and fresh (labile) OM derived from PP. The DSS slope in our study is in the range of those reported for other benthic systems, which were close to −0.75, supporting the hypothesis of energy equivalence (Cyr et al. 1997, Stead et al. 2005, Akoumianaki et al. 2006). We found a less negative slope in the middle fjord in summer 2015, indicating a macrobenthic community dominated by large and intermediate-sized organisms with sporadic occurrence of small-bodied organisms (Akoumianaki et al. 2006). In this transitional zone, advection in the water column occurs at large scales affecting sediment conditions and removing surface macrofauna, thus limiting the abundance of small surface organisms. This selective disturbance may have modified community size structure, influencing the slope and intercept of the regression models.

Sprules & Munawar (1986) proposed the NBSS intercept as an indicator of total biomass in the system. We found lower intercept values with less
negative slopes in summer in the middle fjord (see Table 4), suggesting a decrease in macrobenthic community biomass accompanied by the disappearance of small organisms. The long-term effects of disturbances on macrofaunal succession are not significant in our study area because the macrobenthic communities are dominated by small-bodied polychaetes (Paraonidae, Capitellidae and Cirratulidae) with continuous year-round breeding, short life spans, and fast turnover rates (Quiroga et al. 2012).

The NBSS slopes can be used as indicators of the influence of environmental fluctuations on the productivity of aquatic communities (Kerr & Dickie 2001). In our study area, we found slopes ranging from −0.31 (±0.03) in the middle fjord to −1.03 (±0.15) in the inner fjord, suggesting that biomass size structure in the fjord varies. The NBSS slopes for the inner and outer fjord were not significantly different, but the slope for the middle fjord was much lower in summer (see Table 4). The intercepts of the present study were much higher than those obtained by other authors studying other marine regions, which was probably related to fresh and terrestrial OM supplies in the study area (Saiz-Salinas & Ramos 1999, Quiroga et al. 2005, 2012, 2014, Hua et al. 2013). Patagonian glacial fjords are highly productive seasonally, which may explain our higher intercept values. In fact, Chla sediment concentrations in our study area ranged from 2.28 to 7.48 µg g⁻¹ in summer, which are similar to those recorded in Artic fjords (Drewnik et al. 2016).

The EOU slopes in our study were similar to those reported by Akoumianaki et al. (2006). No oxygen uptake–body size regression slopes close to 0.75 were observed at any of the locations and in either of the seasons, suggesting that sediment transport and freshwater discharges by the Baker River are the most likely sources for the highly positive regression slopes. In summary, the size-spectrum approach provides a more dynamic interpretation of an ecosystem, because the slope and intercept of the biomass size spectra is related to the energy use of the entire community (Sprules & Munawar 1986). In our study area, we found NBSS slopes in the range of those reported for other benthic ecosystems (Quiroga et al. 2014). The NBSS slope showed marked changes in the middle fjord in summer, suggesting a selective disturbance for small organisms. This is probably associated with sediment transport that can be destructive to benthic fauna owing to changes in sediment texture and stability, thus impeding animals from maintaining an optimum position in the sediment. In contrast, the intercepts are more related to terrestrial OM input. Ecological processes operate at a variety of temporal and spatial scales that are also related to body size. Therefore, the NBSS is useful for obtaining averages for the short-term spatially localized dynamics of marine coastal ecosystems with marked seasonal changes in environmental conditions.

**Trophic structure**

Marine–terrestrial interactions in Chilean fjords are complex, and benthic communities play an important role in the distribution of OM. Understanding OM exchange from different origins (from PP and/or terrestrial) is key to making more detailed predictions about productivity, diversity and food web dynamics, which are closely related to temporal and spatial OM flows. In this context, the Baker River transports large quantities of suspended sediment with coarse and fine POC of vascular plant origin, producing changes in the physical and chemical conditions of the water column and sediments (Quiroga et al. 2012). This pattern is similar to that in other fjord regions (e.g. New Zealand), where substantial rainfall and dense forests constantly deliver large amounts of dissolved AOM to fjord waters (McLeod & Wing 2009, Yamashita et al. 2015).

In our study, we found that terrestrial OM (AOM and δ¹³C) exhibited a well-defined gradient in the sediments from the inner to outer fjords (Table 3). Silva et al. (2011) pointed out that the seaward extension of the influence of terrestrial OM from the inner fjord to the adjacent ocean is reflected in δ¹³C and the C/N ratio, indicating that sediments in the inner and middle fjords are associated with terrestrial input, whereas the outer fjord is less influenced by terrestrial OM. However, the lateral advection of terrestrial POM in a semi-closed fjord like the Martinez Channel contributes a significant fraction of AOM in the sediments (<14.76%), in particular in winter due to higher current velocities. Vargas et al. (2011) suggest that changes in the isotopic δ¹³C composition of zooplankton is a response to POM advection by dominant currents in the study area.

The influence of terrestrial carbon sources on benthic communities in Chilean fjords has been considered relatively weak (Zapata-Hernández et al. 2014), but this view may be partly due to a paucity of studies conducted in the region. Field observations and carbon stable isotopes measured in benthic organisms in our study indicate that benthic communities in the inner fjord assimilate via heterotrophic bacteria. Carbon isotope POM values from the river were
markedly lower than sediments and suspended POM in the Baker River mouth. In addition, we found the snail *Chilina chilensis*, a freshwater grazer that assimilates via methanotrophic or chemosynthetic bacteria is important in fjord food webs associated with river discharges (McLeod & Wing 2009). In addition, previous studies have shown the importance of methanotrophic and sulfur bacteria in reducing environments (clay and organic-rich sediments) as food sources for freshwater macroinvertebrates (see Doi et al. 2006 and references cited therein). We found low δ¹³C values in the decapods *Peltarium spinosulum* (−22.64 ‰), *Libidoclaea granaria* (−22.98 ‰) and *Munida gregaria* (−19.34 ‰), indicating incorporation of chemosynthetic biomass. Thus, chemosynthetic bacteria are important in the fjord food webs associated with river discharges (McLeod & Wing 2009). It is important to note that terrestrial OM enters the benthic food web directly via pelagic pathways or as detritus assimilated through heterotrophic bacteria (McLeod & Wing 2009, Vargas et al. 2011, Zapata-Hernández et al. 2014). This terrestrial OM may explain the high macrofaunal density values in the inner fjord (14 034 to 17 800 ind. m⁻², Quiroga et al. 2012). However, the presence of diverse microbial and fungal communities that are well adapted to the cold low salinity waters of proglacial fjords (Gutiérrez et al. 2015) may constitute another pathway for the degradation of the terrestrial OM and therefore an alternative to incorporating this form of OM into the food web. Further research in this area is needed given that microbial reworking of terrestrial OM constitutes a main source of humic-like enriched dissolved organic carbon (DOC) in some fjords (Yamashita et al. 2015), which may result in significant OC burial in fjord sediments (Smith et al. 2015). In the context of climate change, seawater becomes more acidic (i.e. lower pH) as CO₂ is absorbed from the atmosphere, stimulating microbial degradation of dissolved organic matter (Piontek et al. 2010). This in turn affects the reconstitution of POC from DOC and our understanding of energy transfer through terrestrial OM associated with the microbial loop in the water column (Bell et al. 2016).

Perhaps the most important result of this study is the fact that benthos biomass spectra conformed to a common pattern in spite of differences in habitat and community structure among fjord sections. This supports the view that biomass spectra can be a sensitive descriptor of constraints imposed on the benthic community in a highly stratified fjord, where environmental conditions are intimately linked to instability of sediment conditions and different OM sources (from PP and terrestrial OM). In the present study, the relationships between biomass spectra (as process indicators sensu Rakocinski 2012) and environmental conditions can be used to assess changes in the community structure and the food web of highly sensitive Patagonian fjord ecosystems. These results help us understand the impact of human activities on fjord ecosystems already exposed to climate change-induced temperatures increases and ice-cover reduction, with unpredictable effects on biodiversity and ecosystem functions.

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