

1 **Turbulence and hypoxia contribute to dense zooplankton scattering layers**
2 **in Patagonian Fjord System.**

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34 **Abstract**

35 The aggregation of plankton species along fjords can be linked to physical properties
36 and processes such as stratification, turbulence and oxygen concentration. The goal of this
37 study is to determine how water column properties and turbulent mixing affect the horizontal
38 and vertical distributions of zooplankton along the only north Patagonian Fjord known to date
39 where hypoxic conditions occur in the water column. Acoustic Doppler Current Profiler
40 moorings, scientific echo-sounder transects, and *in-situ* plankton abundance measurements
41 were used to study zooplankton assemblages and migration patterns along Puyuhuapi Fjord
42 and Jacaf Channel in Chilean Patagonia. The dissipation of turbulent kinetic energy was
43 quantified through vertical microstructure profiles collected throughout time in areas with
44 high zooplankton concentrations. The acoustic records and *in-situ* zooplankton data revealed
45 diel vertical migrations (DVM) of siphonophores, chaetognaths, euphausiids and copepods. In
46 particular, a dense layer of zooplankton was observed along Puyuhuapi Fjord between the
47 surface and the top of the hypoxic boundary layer (~100 m), which limited the vertical
48 distribution of most zooplankton and their DVM, generating a significant reduction of habitat.
49 Aggregations of zooplankton and fishes were most abundant around a submarine sill in Jacaf
50 Channel. In this location zooplankton were distributed throughout the water column (0 to
51 ~200 m), with no evidence of a shallower hypoxic boundary due to the intense mixing near
52 the sill. In particular, turbulence measurements taken near the sill indicated high dissipation
53 rates of turbulent kinetic energy ($\epsilon \sim 10^{-5} \text{ W kg}^{-1}$) and vertical diapycnal eddy diffusivity (K_ρ
54 $\sim 10^{-3} \text{ m}^2 \text{ s}^{-1}$) values. The elevated vertical mixing ensures that the water column is well
55 oxygenated (3-6 mL L⁻¹, 60-80 % saturation), creating a suitable environment for zooplankton
56 and fish aggregations. Turbulence induced by tidal flow over the sill apparently enhances the
57 interchange of nutrients, oxygen concentrations, and creates a fruitful environment for many
58 marine species, where prey-predator relationships might be favored.

59

60 **Keywords:** turbulence, hypoxia, Acoustic data, zooplankton, scientific echo-sounder,
61 Patagonian fjords, sill exchange.

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64

65 **1 Introduction**

66 Spatial and temporal variability of plankton assemblages have been linked to oceanographic
67 features and processes such as water column stratification, tidal mixing and turbulence,
68 frontal structures, advection, and secondary circulation in estuaries and fjords (Govoni et al.,
69 1989; Timothy et al., 1998 Rodriguez et al., 1999; Lee et al., 2005; Lough and Manning,
70 2001; Munk et al., 2002; Meerhoff et al., 2013; Meerhoff et al., 2015). In fjords, residual
71 flows resemble typical estuarine gravitational circulation with landward flow at depth and
72 seaward flow at the surface. It has been found that residual flows in fjords can retain
73 planktonic larvae inside the system (Dyer, 1997; North & Houde, 2001, 2004; Meerhoff et al.,
74 2015), affecting the community composition, biomass, productivity and distribution of
75 zooplankton in the fjord (Basedow et al., 2004). Moreover, horizontal mixing between
76 interfacial density layers has been shown to induce lateral circulation (Farmer and Feeland,
77 1983), which in turn affects larval distributions in fjord systems (Meerhoff et al., 2015).

78 Recent studies have investigated how tidally induced mixing, and therefore variations
79 in stratification, affects ichthyoplankton and zooplankton assemblages (Perez et al., 1977;
80 Nixon et al. 1979; Oviatt, 1981, Lee et al., 2005). Lee et al., (2005) found that variations in
81 stratification throughout a tidal cycle affected both overall abundance and species
82 composition of zooplankton in the Irish Sea. However they did not have the tools to relate the
83 hydrodynamic and hydrographic variability of this region with vertical and horizontal
84 distributions of fish larvae and zooplankton. Oviatt (1981) found that zooplankton
85 concentrations were lower in laboratory tanks than in nature (Narragansett Bay). Since this
86 was not due to the physical action of mixing (induced by paddles in the tank), they
87 hypothesized that tank confinement and turbulence had broken down vertical segregation
88 between adults and juveniles, resulting in increased cannibalism. While vertical segregation of
89 zooplankton groups, probably related to different trophic guilds, has been confirmed by
90 several studies (e.g. Haury et al., 1990), this segregation can be reduced by turbulent
91 processes enhancing contact between preys and predators (Visser and Stips 2002; Visser et
92 al., 2009). For instance, available theoretical models predict optimal prey consumption at
93 dissipation rates of turbulent kinetic energy (ϵ) between 10^{-6} and 10^{-4} W kg⁻¹ (Lewis and
94 Pedley, 2001). In fjords, topographic conditions are extremely irregular (Inall and Gillibrand,
95 2010), inducing high turbulence and enhanced vertical mixing, particularly at sills (Klymak
96 and Gregg 2004; Whitney et al., 2014). However, enhanced productivity, oxygenation, and/or
97 local retention may occur at these same highly turbulent areas. Therefore, additional field

98 studies are needed to inform our understanding of the relationship between mixing-inducing
99 physical forcings, such as wind or advection, and vertical abundance patterns and species
100 composition in fjords and other estuarine systems.

101 Hypoxia is known to have a significant impact on plankton distribution and
102 development, hence on the health of the ecosystem as a whole (Ekau et al., 2010). Some
103 species can tolerate hypoxic water, e.g., smaller species, euphausiids and jellyfish can live in
104 under 30% oxygen saturation and dissolved oxygen of 1.6 mL L⁻¹. Others taxa, such as some
105 copepods and fishes, may be more sensitive to hypoxia and have preference for oxygen
106 saturations of 50-100% and DO concentrations of 2.6-5.2 mL L⁻¹ (Ekau et al., 2010). The
107 sensitivity of species to tolerate different oxygen concentrations, however, may vary among
108 organisms from different environments. In particular, in coastal upwelling zones along Chile,
109 while some copepods seem to be limited to depth ranges with waters well oxygenated, others
110 seem to be well adapted for residence at depths with minimum oxygen depth (Castro et al.,
111 2007). Hypoxic conditions (< 2 mL L⁻¹) have been detected in four regions of Patagonian
112 (Puyuhuapi Fjord, Jacaf Channel, Aysén Fjord and the Almirante Montt Gulf), and in each
113 region the oxygen depleted zones are mainly located at the fjords heads and down to 100 m
114 depth (Silva and Vargas, 2014; Schneider et al., 2014), but no relationship was made with the
115 zooplankton species that inhabit this ecosystem. This study will therefore focus on how
116 hypoxic conditions affect the distribution and aggregation of zooplankton in Puyuhuapi Fjord
117 and Jacaf Channel, two of the four hypoxic systems in Patagonia.

118 In Patagonian fjords, a comprehensive description of zooplankton distribution patterns
119 has been provided by Palma (2008), considering a total of 220 *in-situ* plankton samples, from
120 a number of depth strata between the surface and ~200 m. Main zooplankton groups included
121 siphonophores, chaetognaths, cladocerans, copepods and euphausiids. Although a positive
122 north to south gradient in the abundance of major zooplankton species was found, potential
123 relationships between the vertical distributions and environmental variables were not deeply
124 assessed. Later on, Landaeta et al., (2013) studied the vertical distribution of
125 microzooplankton and fish larvae in Steffen fjord (47.4° S) at four depth strata (200-50 m, 50-
126 25 m, 25-10 m and 10-0 m depth) during November 2008. Copepod nauplii and copepodites
127 of *Acartia tonsa* together with *Maurolicus parvipinnis* fish larvae were observed around the
128 pycnocline region, suggesting that the vertical structure of the water column might play a role
129 in larval fish distribution. More recently, studies on zoo- and ichthyo-plankton vertical
130 distributions in Reloncaví Fjord revealed that DVM timing might be modified by the tidal

131 regime which is particularly strong in this area (Castro et al., 2014). However, none of these
132 studies provided explicit assessments of the relationships between vertical distribution of
133 zooplankton and turbulence or water column properties.

134 Most studies carried out in Chilean coastal waters, including those mentioned above,
135 have relied on plankton nets and other collecting devices (pumps) deployed in single locations
136 (fixed stations). An alternate approach is to use acoustic techniques, which can provide high
137 resolution data on zooplankton DVM patterns (Valle-Levinson et al., 2014) and segregation
138 patterns throughout the water column (Sato 2013; Sato et al., 2016). For instance, DVM
139 patterns of dense krill aggregations have been detected using Acoustic Doppler Current
140 profilers (ADCP) moored around the Antarctic Peninsula, the Kattegat Channel and off Funka
141 Bay, Japan (Buchholz et al., 1995; Lee et al., 2004; Zhou and Dorland 2004; Brierley et al.,
142 2006). In Chilean fjords, ADCPs have been used to identify changes in vertical distribution
143 and DVM patterns of zooplankton (e.g., from normal diel to twilight vertical migrations) over
144 several months in Reloncaví Fjord (Valle-Levinson et al., 2014). These studies, although
145 novel at describing temporal variations in zooplankton patterns, focused mainly on the
146 behavior of particular species, but failed to consider how the vertical distribution of
147 zooplankton is modified by water column conditions (e.g., temperature, salinity, oxygen and
148 turbulence).

149 Compared to ADCPs, scientific echo-sounders are characterized by narrower beam
150 angles, lower frequencies and longer ranges. They have also been used to provide valuable
151 qualitative and quantitative information on various aquatic species and communities, from
152 zooplankton to large predators (Ballón et al., 2011). Overall, macrozooplankton can be
153 acoustically identified and virtually separated from other organisms, such as fish, by
154 considering their acoustic properties (Kloser et al., 2002; Logerwell and Wilson, 2004;
155 Mosteiro et al., 2004; Simmonds and MacLennan, 2005). Although the use of several
156 frequencies does not necessarily increase precision (Horne and Jech, 1999), the use of at least
157 two frequencies (38 and 120 kHz) is currently a standard practice in zooplankton studies as
158 identification methods developed by Ballón et al., (2011) and others can be utilized.

159 The present study aims to evaluate the effects of water column properties, such as
160 dissolved oxygen and turbulent mixing, on the horizontal and vertical distributions of
161 dominant zooplankton groups along a Patagonian Fjord system. To achieve this goal ADCP
162 and scientific echo-sounder data are combined with biological observations from *in-situ*
163 stratified zooplankton samples and water column measurements from microstructure profilers

164 and conductivity-temperature-depth-oxygen (CTDO) profilers. The remainder of this article
165 will include a detailed description of the study area in section 2 followed by an explanation of
166 the data collected and the data analysis methodology in section 3. The results will be
167 presented in section 4 with a discussion, focusing on differences between two Patagonian
168 fjords, presented in section 5. The main conclusions of the study will be presented in section
169 6.

170

171 **2 Study Area**

172 Patagonian fjords extend from 41° S to 56° S, and are typically deep and narrow as a result of
173 their formation during glacial progression. Their hydrography is characterized by two vertical
174 layers, consisting of a low salinity surface layer in the first ten meters of the water column
175 (resulting from rainfall and glacial melt) that overlays a subsurface salty layer originated in
176 the Pacific Ocean (Silva and Calvete, 2002; Pérez-Santos et al., 2014). Fjord systems play an
177 important role in primary production and carbon cycling by providing a zone where energy
178 and particulate material are exchanged between land and marine ecosystems (Gattuso et al.,
179 1998). The principal nutrient (nitrate) is supplied to these fjords by oceanic transport, and
180 particularly through the intrusion of Sub Antarctic water (SAAW), a water mass that may also
181 transport some species of zooplankton (González et al., 2011).

182 Puyuhuapi Fjord and Jacaf Channel form an atypical example of a Patagonian fjord
183 system, where Puyuhuapi Fjord meets oceanic waters via its southern mouth and Jacaf
184 Channel near its head (Fig.1). Jacaf Channel is known for its extreme depth (> 400 m at the
185 mouth) and a shallow sill located near its head (Fig. 1). Seasonal hydrographic measurements
186 along Puyuhuapi Fjord have shown a stratified water column except in late winter, when the
187 water column became partially mixed due to a reduction in freshwater supply from rainfall
188 and glacial melting (Schneider et al., 2014). Hypoxic conditions have been detected in
189 Puyuhuapi Fjord below 100 m depth, where oxygen concentrations were found to be as low as
190 1-2 mL L⁻¹ (Schneider et al., 2014; Pérez-Santos, 2017). This observed oxygen depletion
191 could be caused by limited ventilation due to shallow sills, or by the input of low-oxygen
192 Equatorial Subsurface Water into the fjord (Silva and Vargas, 2014; Schneider et al., 2014).
193 The Puyuhuapi Fjord is the only northwestern Patagonian fjord known to experience such
194 extreme hypoxic conditions. At the same time, it is an area where intense aquaculture
195 activities have been recently developed, which reinforces the need of this study.

196

197 **3 Data and methodology**

198 **3.1 Water column properties**

199 Although hydrographic surveys have been conducted from 1995 to 2016 in Puyuhuapi Fjord
200 and Jacaf Channel, only the most recently data, from 2016, is presented in figure 2 to illustrate
201 overall hydrographic background and permanent hypoxic conditions in Puyuhuapi Fjord.
202 These profiles were obtained with a Seabird 25 CTDO, sampling at 8 Hz with a descent rate
203 of $\sim 1 \text{ m s}^{-1}$. The data collected, whose nominal vertical resolution was $\sim 12 \text{ cm}$, were averaged
204 into 1 m bins, following Seabird recommendations. The conservative temperature ($^{\circ}\text{C}$) and
205 absolute salinity (g kg^{-1}) were calculated according to the Thermodynamic Equation of
206 Seawater 2010 (COI et al., 2010). To validate CTDO oxygen measurements, *in-situ* oxygen
207 samples were analyzed using the Winkler method (Strickland and Parsons, 1968), carried out
208 using a Metrohm burette (Dosimat plus 865) and an automatic visual end-point detection
209 (AULOX Measurement System).

210 Microstructure measurements were collected using a Vertical Microstructure Profiler
211 (VMP-250, Rockland Scientific, Inc.). The VMP-250 was equipped with two airfoil shear
212 probes and two fast response FP07 thermistors, which allowed for data recording at 512 Hz
213 with a descending free fall speed of $\sim 0.7 \text{ m s}^{-1}$. The micro-shear measurements permitted the
214 calculation of the dissipation rate of turbulent kinetic energy (ε) for isotropic turbulence,
215 according to Lueck et al., (2002), Eq. (1),

$$216 \quad \varepsilon = 7.5 \nu \overline{\left(\frac{\partial u'}{\partial z}\right)^2} \quad (1)$$

217 where, ν is the kinematic viscosity, u is the horizontal velocity, z is the vertical coordinate axis
218 and therefore $\overline{\left(\frac{\partial u'}{\partial z}\right)^2}$ is the shear variance.

219 Using the values of ε , the diapycnal eddy diffusivity (K_{ρ}) was calculated. The most
220 used formulation was proposed by Osborn (1980),

$$221 \quad K_{\rho} = \Gamma \frac{\varepsilon}{N^2}, \quad (2)$$

222 where Γ is the mixing efficiency, generally set to 0.2 (Thorpe 2005), and N is the buoyancy
223 frequency. Shih et al. (2005) noted that when the ratio $\varepsilon / \nu N^2$ is greater than 100, Eq. (2)
224 results in an overestimation. Therefore, they proposed a new parameterization for this case
225 given by:

$$226 \quad K_{\rho} = 2\nu \left(\frac{\varepsilon}{\nu N^2}\right)^{1/2}. \quad (3)$$

227 More recently, Cuypers et al. (2011) used Eq. (3) when $\varepsilon / \nu N^2 > 100$, Eq. (2) when 7
228 $< \varepsilon / \nu N^2 < 100$, and considered null eddy diffusivity when $\varepsilon / \nu N^2 < 7$. This approach was
229 followed in this study. The correlation between the dissipation rate of turbulent kinetic
230 energy and the abundance of major zooplankton groups throughout the water column was
231 accomplished by using a quadratic polynomial curve fit between these data sets (explained in
232 detail in section 4.6). These analyses were only applied to measurement collected at the fixed
233 station in Puyuhuapi Fjord, because the VMP-250 was not available during the measurement
234 campaign in Jacaf Channel.

235

236 **3.2 Acoustic data**

237 Acoustic measurements were obtained with two 307.7 kHz Teledyne RDI Workhorse ADCPs,
238 moored upwards at depths of ~50 m (ADCP-1) and ~100 m (ADCP-2) in north-central
239 Puyuhuapi Fjord (Table 1, Fig. 1, ADCPs moored at the same location). Data were collected
240 hourly with a vertical bin size of 1 m, over periods of austral autumn (ADCP-1: May, 2013)
241 and spring-summer (ADCP-2: January 2014). During the final ADCP-2 mooring deployment,
242 acoustic data were also collected along Puyuhuapi Fjord using a SIMRAD EK60 scientific
243 echo-sounder running a single frequency 38 kHz transducer (ES38B), during daytime and
244 nighttime hours from January 22-25, 2014 (black line in Fig. 1). *In-situ* zooplankton sampling
245 (see section 3.3 for details) was carried out on January 23-24, 2014, at a fixed station close to
246 the ADCP mooring location over a period of 36 hours (Fig. 1) in order to validate acoustic
247 measurements.

248 In August 2014, a second scientific echo-sounder survey was conducted. During this
249 measurement campaign coverage was extended to eastern Jacaf Channel (Fig. 1, red line) and
250 a second 120 kHz transducer (ES120-7C) was added to the 38 kHz transducer used in the first
251 survey. Several day/night transects were completed from Puyuhuapi Fjord into Jacaf Channel
252 with special attention paid to Jacaf sill. To determine the statistical relationship (R^2) between
253 acoustic data from the 38 kHz echo-sounder with hydrographic properties of the fjords
254 (temperature, salinity and dissolved oxygen), a quadratic polynomial curve was also applied
255 between these data sets. During this experiment two RDI Workhorse ADCP were installed in
256 the vicinity of the Jacaf sill: one 307.7 kHz ADCP was moored close to the bottom (~100 m)
257 and another 614.4 kHz one (referenced as ADCP-3) at ~30 m. Unfortunately, only data from
258 ADCP-3 was recovered.

259 Vessel speed during both echo-sounder surveys was maintained between 8-10 knots.
260 Echo-sounders were operated using a variable ping rate 0.3-2.0 ping s⁻¹, a pulse duration of
261 1.024 milliseconds and output powers of 2 kW and 0.5 kW for 38 and 120 kHz, respectively.
262 Calibration was made using proper copper spheres and standard procedures (Foote et al.,
263 1987).

264

265 **3.2.1 Echo-sounder data analysis**

266 Post-processing of echo-sounder data was performed in Echoview (Myriax inc, Tasmania,
267 <https://www.echoview.com/>), using the open access version ("FishZpkPeru38&120.evi") of
268 Ballón et al., (2010)'s algorithm, which combines mean volume backscattering (MVBS) from
269 38 and 120 kHz, using both $\Delta MVBS$ (differences) and $\Sigma MVBS$ (summations) to discriminate
270 and quantify the abundance of macrozooplankton. This algorithm separates raw data into
271 three different virtual echograms: fish and two macrozooplankton groups (macrozooplankton
272 or "fluid-like" and gelatinous or "blue noise" organisms). The fluid-like group follows a
273 sphere model (Holliday & Pieper, 1995) considered appropriate to represent cylindrical and
274 spherical shapes, including euphausiids and large copepods, which are dominant
275 macrozooplankton groups off Peru and Chile (Ayon et al., 2008). The algorithm is considered
276 to be useful for 38 and 120 kHz data from targets whose radius is ≥ 0.5 mm and has a dB
277 difference of 2-19 dB (Ballón et al., 2010 and 2011). As implemented, the post-processing file
278 FishZpkPeru38&120.evi is also designed to remove blind areas, near field, background noise
279 and rainbow phenomenons.

280 Given physical limitations imposed by sound absorption of selected frequencies (38
281 and 120 kHz) across the water column, an effective sampling of the water column up to 250
282 m was expected. Absorption is greater for 120 kHz, which exhibits the shortest range, but has
283 a greater vertical resolution than 38 kHz. The 38 kHz frequency, on the other hand, exhibits a
284 longer range, but limited resolution affecting small zooplankton (e.g. small copepods)
285 detection. Nonetheless, this is the most commonly used frequency, which has proven to be
286 efficient for studying macrozooplankton groups such as siphonophores, chaetognaths and
287 euphausiids (Mair et al., 2005; Cade and Benoit-Bird, 2015; Ariza et al., 2016).

288 Volume backscattering strength (S_v , dB re 1 m⁻¹) values were integrated using a grid of
289 20 m (depth) by 50 m (distance), and re-scaled into the customary index "nautical area
290 scattering coefficient" (NASC, in units of m² n mi²). Since NASC lies on the linear domain, it

291 can be considered proportional to and suitable for indexing zooplankton abundance (Ballón et
292 al., 2011).

293

294 3.2.2 Acoustic data analysis from ADCPs

295 ADCP echo intensity was converted to mean volume backscattering strength (S_v , dB re 1 m⁻¹),
296 as done for scientific echo-sounder data, following the conversion formula:

$$297 \quad S_v = C + 10 \log[(Tx + 273.16)R^2] - L_{DBW} - P_{DBW} + 2\alpha R + K_c(E - E_r) \quad (4)$$

298 where, C is a sonar-configuration scaling factor (-148.2 dB for the Workhorse Sentinel), T_x is
299 the temperature at the transducer (°C), L_{DBW} is log₁₀(transmit-pulse length, $L=8.13$ m), P_{DBW}
300 is log₁₀(output power, 15.5 W), α is the absorption coefficient (dB m⁻¹), K_c is a beam-specific
301 sensitivity coefficient (supplied by the manufacturer as 0.45), E is the recorded AGC
302 (automatic gain control), and E_r is the minimum AGC recorded (40 dB for ADCP-1 and 41
303 dB for ADCP-2). The beam-average of the AGC for the 4 transducers was used to obtain
304 optimal results following the procedure in Brierley et al. (2006). Finally, R is the slant range
305 to the sample bin (m), which uses the vertical depth as a correction (Lee et al., (2004)).
306 Therefore, R is expressed as,

$$307 \quad R = \frac{b + \frac{L+d}{2} + ((n-1)d) + (d/4)}{\cos \zeta} \frac{\bar{c}}{c_I} \quad (5)$$

308 where b is the blanking distance (3.23 m), L is the transmit pulse length (8.13 m), d is the
309 length of the depth cell (1 m), n is the depth cell number of the particular scattering layer
310 being measured, ζ is the beam angle (20°), \bar{c} is the average sound speed from the transducer
311 to the depth cell (1453 m s⁻¹) and c_I is the nominal sound speed used by the instrument (1454
312 m s⁻¹).

313

314 3.3 Zooplankton sampling

315 In situ mesozooplankton samples were collected with a WP2 net (60 cm diameter mouth
316 opening, 300 μm mesh, flow meter mounted in the net frame) towed vertically from 50 m to
317 the surface in May 2013, and with a Tucker trawl (1 m² mouth opening, 300 μm mesh with
318 flow meter) used to obtain stratified oblique tows in January 2014 and August 2014 (Table 1).
319 All samples were preserved in a 5% formaldehyde solution. Zooplankton abundances were
320 standardized to individuals per m³ of filtered seawater. WP2 vertical tows consisted of 5 depth
321 intervals from surface to 50 m, every 10 m (0-10, 10-20, 20-30, 30-40, 40-50 m).

322 Stratified Tucker tows considered four depth strata: 0-10 m, 10-20 m, 20-50 m, 50-100
323 m in the Puyuhuapi Fjord, and also 100-150 m depth in the Jacaf Channel. Sampling occurred
324 during a 36-h period every 3 h from January 22-24, 2014 (Puyuhuapi Fjord) and every 5-6 h
325 from August 18-19, 2016 (Jacaf Channel) (Fig. 1, red dots). At all sites and dates, all
326 zooplankters were identified, sorted into functional groups, measured (length) and classified
327 into size-classes using a 5 mm length threshold. Copepods, the most abundant group, were
328 further classified into <1 mm, 1-5 mm and >5 mm prosome length groups. To determine the
329 correlation (R^2) between the S_v records from the 38 kHz transducer and the major zooplankton
330 groups, a quadratic polynomial curve was applied between these data sets (further details in
331 section 4.3).

332

333 **3.4 Tidal harmonic analysis**

334 The tidal constituents were computed using HOBO U20 water level loggers and the pressure
335 sensor from ADCP-3 (Table 1-2, Fig. 1). A tidal harmonic analysis was applied to the sea
336 level time series according to Pawlowicz et al., (2002), which considers the algorithms of
337 Godin (1972, 1988) and Foreman (1977, 1978). We classified tides by the dominant period of
338 the observed tide based on the form factor (F), defined by the ratio between the sum of the
339 amplitudes of the two main diurnal constituents (larger lunar declinational, O_1 and luni-solar
340 declinational, K_1) and the sum of the amplitudes of the two main semi-diurnal constituents
341 (principal lunar, M_2 and principal solar, S_2), $F = (O_1 + K_1) / (M_2 + S_2)$ (Bearman, 1989; where, F
342 < 0.25 semi-diurnal, $0.25 < F < 1.5$ Mixed semi-diurnal and $F > 3.0$ diurnal).

343

344 **4. Results**

345 **4.1 Hydrographic features**

346 The most recent hydrographic surveys carried out in Puyuhuapi Fjord (June 2016) showed
347 hypoxic conditions (dissolved oxygen <2 mL L⁻¹) below 120 m depth coherent along the
348 channel (Fig. 2d). The lowest DO values were detected at the head of the fjord (35-50.5 km)
349 with ~1.5 mL L⁻¹ and 25% of oxygen saturation (Fig. 2d and 2e). The hypoxic layer was
350 located at the depth range of the Equatorial Subsurface Water (ESSW), (Fig. 2c). Ventilated
351 water (3-6 mL L⁻¹) was observed at depths occupied by Modified Sub-Antarctic water
352 (MSAAW) and Sub-Antarctic Water (SAAW), characterized by a salinity range from 31 to 33
353 g kg⁻¹, colder water temperature and a weaker temperature gradient (Fig. 2b).

354

355 **4.2 ADCP Acoustic data and *in-situ* zooplankton samples**

356 Volume backscatter from the ADCP-1 (50 m depth, May 2013) showed large variability,
357 ranging from high (-90 to -75 dB re 1 m⁻¹) to low (-115 to -100 dB re 1 m⁻¹) S_v values (Fig.
358 3a). The highest S_v values (>-90 dB re 1 m⁻¹) were recorded during the night hours (~18:00 h
359 to ~07:00 h), while minimum S_v values were observed at daytime (~07:00 h to ~18:00 h)
360 suggesting the incorporation of vertically migrating organisms from deeper layers (below
361 ADCP-1 mooring depth of 50 m). From the *in-situ* measurements of zooplankton collected at
362 various depth strata in May 2013, the most abundant zooplankton groups were copepods (<5
363 mm), siphonophores, chaetognaths and medusae (Fig. 3c-d). A marked change in vertical
364 distribution and in total abundance of the zooplankton groups in the water column was
365 observed from the first sampling hour (late afternoon, ~17 h, not shown) to the first night
366 sampling time (~18 h), revealing the start of the nocturnal migration to the surface coincident
367 with a DVM pattern as seen in the ADCP-1 backscatter data (Fig. 3a-b).

368 Data from the ADCP-2 mooring (positioned deeper but at the same location as ADCP-
369 1) from January 22-24, 2014 also showed a strong zooplankton DVM pattern, which extended
370 down to ~100 m depth (Fig. 4a). During daylight hours (8-18 h), dense zooplankton
371 aggregations were observed between 80-100 m depth, which started to ascend from 18:00 to
372 21:00 h, concentrated close to the surface at night, and began to descend at ~06:00 h. *In-situ*
373 stratified sampling showed the most abundant mesozooplankton groups were copepods,
374 euphausiids, siphonophores, chaetognaths, decapods and medusae (Fig. 4 b-d). Euphausiids
375 and siphonophores showed higher abundance close to surface layer (10-20 m) during night
376 hours (Fig. 4c) and at deeper layers during the daytime (Fig. 4d). However, euphausiids
377 showed the clearest diel vertical migration with maximum abundance at the 10-20 m layer
378 during night hours, and at 20-50 during the daytime (Fig. 4c-d).

379

380 **4.3 Acoustic data from scientific echo-sounder**

381 **4.3.1 Summertime surveys**

382 Summer daytime S_v values along the Puyuhuapi Fjord averaged -89.1 ± 7 dB re 1 m⁻¹ and
383 ranged between -110 and -77.3 dB re 1 m⁻¹, from the mouth to the head of the fjord (Fig. 5a).
384 Most of the backscatter was concentrated in the first 100 m of the water column, matching
385 ADCP results (Fig. 3 and 4). At the ADCP-2 mooring location (black dot in Fig. 5a), higher
386 backscatter signals were found between 50-100 m depth, showing good agreement between
387 echo-sounder and ADCP-2 data (Fig. 3, 4 and 5). Average NASC profiles for zooplankton

388 showed higher values between 50-100 m (above the hypoxic layer) both during day and night
389 (Fig. 5b and e). Although some NASC values were observed within the hypoxic layer (below
390 ~120 m depth), all dense aggregations were observed above it (Fig. 5g). Daytime S_v signals
391 attributed to fishes were typically detected at ~50 m depth, being much higher (<-60 dB re 1
392 m^{-1} ; Fig. 5c) than S_v signals attributed to zooplankton.

393 Summer nighttime S_v values along the Puyuhuapi Fjord (Fig. 5d-f) showed maximum
394 S_v and NASC values near the surface (Fig. 5d and 5f), suggesting an ascending vertical
395 migration of both zooplankton and fishes (Fig. 5a vs. 5d and Fig. 5c vs. 5f). The depth of fish
396 aggregations in the daytime at the head of the fjord (between 50-100 m depth; Fig. 5c)
397 compared with the depth of fish aggregations near the head at nighttime (~25 m depth; Fig.
398 5f), shows a distinct vertical migration pattern. NASC data also show an increase in
399 zooplankton abundance in the surface layers (0-60 m) at night (Fig. 5b and 5e). Although the
400 water column depth extended to ~300 m, dense backscatter was observed above 100 m depth
401 during both day and night time hours (Fig. 5a and d). As DO concentrations typically decrease
402 from 2 $mL L^{-1}$ to 1 $mL L^{-1}$ below 100 m depth, zooplankton in Puyuhuapi Fjord appear to
403 prefer water with a higher oxygen concentration (3-7 mLL^{-1}), (Fig. 5). The correlation
404 between *in-situ* zooplankton samples (species > 5mm) and the S_v records was high with
405 $R^2=0.5$ for S_v vs. siphonophores, $R^2=0.64$ for S_v vs. chaetognaths, and $R^2=0.78$ for S_v vs.
406 euphausiids. A much weaker relationship ($R^2=0.22$) was found between S_v and copepods >1
407 mm.

408 **4.3.2 Wintertime Surveys**

409 Wintertime surveys, carried out along Puyuhuapi Fjord and Jacaf Channel (~35 km
410 total transect length, Fig. 1) using two frequencies (38 and 120 kHz), allowed separation of
411 total backscatter into Fluid like (FL) and Blue noise (BN) groups (Fig. 6a-b). Total S_v in
412 Puyuhuapi Fjord (0-18 km) reached higher values in the first 100 m of the water column, but
413 at slightly deeper locations (50-100 m) than in summer (Fig. 5), possibly due to bad weather
414 conditions encountered on the sampling day. Greater S_v values (-80 to -60 dB re 1 m^{-1}) were
415 observed in Jacaf Channel (18-32 km), particularly around the submarine sill, which is 6 km
416 long and occurs between km 22 to 27, with the shallowest point (50 m depth) occurring at ~24
417 km (Fig. 6). At this site $S_v > -110$ was found up to ~200 m depth. Particularly high intensities
418 were attributed to the blue-noise (Fig. 6b) and the fish groups (Fig. 6c) around the Jacaf sill.

419 Continuous acoustic sampling repeated over the Jacaf Channel sill confirmed the
420 presence of intense backscatter signals (Fig. 6 and 7), and the presence of two backscattering

421 layers: one denser layer between 100-150 m and a second, less dense layer from 200 to 250 m
422 (Fig. 7a). The *in-situ* zooplankton sampling at the fixed station located in Jacaf Channel
423 detected DVM patterns (Fig. 8). The depth integrated abundance of zooplankton >5 mm
424 showed increased values during night time hours (23 h and 22 h in Fig 8a, in particular for
425 euphausiids). Further, the elevated abundance of zooplankton groups (euphausiids and
426 chaetognaths) were found in the 100-150 m layer particularly at day time (Fig. 8b-f), which
427 matched well with acoustic data for the fluid-like group (Fig. 7a).

428 A correlation was found between the *in-situ* zooplankton sampling (species >5mm)
429 and the 38 kHz S_v values from Jacaf Channel. In particular, a positive correlation was again
430 obtained, with $R^2=0.42$ for S_v vs. chaetognaths, $R^2=0.41$ for S_v vs. euphausiids and $R^2=0.65$ for
431 S_v vs. copepods (species >1 mm).

432

433 **4.4 Relationships between acoustic records and water column properties**

434 To examine relationships between zooplankton behavior and water column properties,
435 continuous 38 kHz S_v values obtained in summer and winter at Puyuhuapi Fjord and Jacaf
436 Channel, respectively, were matched to the consecutive time at which CTD and DO data
437 were captured. The relationship between water temperature and S_v values showed a rather
438 weak correlation during summer ($R^2=0.30$) and winter ($R^2=0.41$), predicting maximum S_v
439 values to occur between 8 and 10°C (Fig. 9a and 9b). Also, a positive but rather weak
440 correlation, was found between S_v and salinity in Puyuhuapi ($R^2=0.29$, Fig. 9c) and Jacaf (R
441 $^2=0.35$, Fig. 9d), with higher S_v values predicted in more oceanic waters (salinity >31,
442 MSAAW and SAAW). Both in Puyuhuapi Fjord and Jacaf Channel S_v and both DO and
443 oxygen saturation showed the highest R^2 values of the series ($R^2\sim 0.6$, Fig. 9e-h). Hence, only
444 20.4% of total $S_v > -110$ dB re 1 m^{-1} were located in the hypoxic layer of Puyuhuapi Fjord,
445 while just 1.2 % were located in the hypoxic layer in Jacaf Channel (Fig. 9e-h).

446

447 **4.5 Tidal regime**

448 The harmonic analysis carried out with the sea level time series obtained in Puyuhuapi Fjord
449 and Jacaf Channel, denoted the dominance (in terms of amplitude) of the semi-diurnal
450 constituents (M_2 and S_2 ; Table 2). Diurnal constituents (O_1 and K_1) were also important,
451 specifically at the Jacaf ADCP-3 station located close to the Jacaf sill region (Table 2 and Fig
452 1). The contribution of diurnal constituents added the mixed character to the tidal regimen in
453 the study area. The spectral analysis implemented at all sea level stations showed maximum

454 energy in the semi-diurnal band (Table 2), with the highest spectral energy ($57.29 \text{ m}^2 \text{ cph}^{-1}$)
455 at Jacaf sill (Jacaf ADCP-3 station), which could be due to the extreme convergence of the
456 channel at this location accelerating the tidal flows.

457

458 **4.6 Mixing process**

459 Turbulence measurements collected with the VMP-250 microprofiler showed high dissipation
460 rates of turbulent kinetic energy (ε) in the first 20 m depth of the water column in Puyuhuapi
461 Fjord and Jacaf Channel (Fig. 10). In this layer ε ranged from 10^{-7} to $10^{-5} \text{ W kg}^{-1}$. However,
462 below this surface layer (<20 m depth) the highest values were obtained around the Jacaf sill
463 region ($\varepsilon=1.2 \times 10^{-7} \text{ W kg}^{-1}$), as shown on 21 November 2013 at 140 m depth (Fig. 10 a). In
464 Puyuhuapi Fjord the shear estimates obtained between 20-180 m were less intense and
465 therefore ε was weak (10^{-10} to $10^{-7} \text{ W kg}^{-1}$), (Fig. 10c and 10e). The dissipation rates of
466 turbulent kinetic energy are obtained by integrating the velocity shear spectrum at each
467 respective depth bin up to the noise limit. The noise limit is determined by comparing the
468 measured spectra to the theoretical Naysmyth Spectra and determining where the
469 measurements begin to deviate from theory. To display how the estimates of ε were obtained
470 at the Jacaf sill depth, the shear spectra are shown for VMP profiles collected at the Jacaf sill
471 region (21 November 2013 at 140 m depth; Fig. 10b), and in Puyuhuapi Fjord on 22
472 November 2013 (at 140 m depth; Fig. 10d) and on 23 January 2014 (at 140 m depth; Fig.
473 10f).

474 In Puyuhuapi Fjord the correlation between ε and zooplankton S_v data (38 kHz, fixed
475 station, January 2014) was high ($R^2=0.65$). In the same campaign, the *in-situ* zooplankton
476 density (>5 mm) was also positively correlated with ε values ($R^2=0.79$ for ε vs.
477 siphonophores, $R^2=0.66$ for ε vs. chaetognaths, and $R^2=0.77$ for ε vs. euphausiids).
478 Unfortunately, VMP data was not collected in Jacaf Channel in wintertime. In order to
479 confirm the relationship between ε and various zooplankton species, additional turbulence
480 measurements were collected in November 2013 along the Jacaf sill (Fig. 11a). Results
481 showed strong velocity shear (Fig. 11b) accompanied by high ε values (10^{-7} to $10^{-5} \text{ W kg}^{-1}$;
482 Fig. 10c). Maximum ε was measured in the Jacaf-Puyuhuapi confluence (10 km along
483 transect) at ~63 m depth where $\varepsilon=1.9 \times 10^{-5} \text{ W kg}^{-1}$, (Fig. 11b; St. 164). The diapycnal eddy
484 diffusivity (K_ρ) was also high in the same area with values of 10^{-4} to $10^{-3} \text{ m}^2 \text{ s}^{-1}$ (Fig. 11c).

485

486

487 **5 Discussion**

488 This study represents one of the first attempts to combine measurements of acoustics,
489 stratified plankton sampling, microstructure profiles, and standard hydrographic profiles to
490 investigate both the vertical distribution patterns of zooplankton and why these patterns exist
491 in northwest Patagonian Fjords and other subantarctic latitudes. Three main findings resulted
492 from this effort. First, DVM patterns of zooplankton became evident from all methodological
493 approaches, at all study periods: May 2013, January 2014 and August 2014 (Fig. 3-8).
494 Second, strong evidence arose showing zooplankton avoidance of hypoxic layers. And, third,
495 a clear increment of zooplankton and fish aggregations around the Jacaf sill could be related
496 to increased turbulence in this area.

497

498 **5.1 Diel vertical migration patterns**

499 Consistent evidence from multiple echo-sounder surveys, ADCP moorings and semi-
500 continuous *in-situ* zooplankton measurements supported the existence of major circadian
501 displacements of macrozooplankton during night hours between mid-depth (20-120 m) and
502 subsurface waters in our study area. Similar DVM patterns have been found in Reloncaví
503 Fjord (41.5° S), from 300 and 600 kHz ADCP data, by Valle-Levinson et al., (2014) and by
504 Días-Astudillo et al., (2017) using a 75 kHz acoustic device. Given its larger resolution, the
505 later work was able to confirm that the DVM affected the whole water column of the fjord
506 (~200 m). These studies found the presence of euphausiids, decapods, mesopelagic shrimps,
507 copepods and other groups in the Reloncaví Fjord in July and November, 2006 (Valle-
508 Levinson et al., (2014), as well as in July 2013 (Días-Astudillo et al., 2017).

509 DVM patterns of zooplankton are expected to be associated with visible light
510 intensity, in particular, diel changes in visible light in the photic zone (from surface to ~100
511 m). This is so the zooplankton can avoid predators during daytime hours and have safe-
512 feeding conditions at night. However, small irradiance levels, around 10^{-7} times surface levels,
513 can be still detected at 600 m or deeper in some areas (Haren and Compton, 2013; Sato et al.,
514 2013 and 2016), requiring zooplankton DVM to reach depths below 500 m (Haren and
515 Compton, 2013). Moreover, DVM patterns of zooplankton have been observed in Arctic fjords
516 (e.g., the Kongsfjordena and Rijpfjorden fjords) even during the polar night, suggesting the
517 influence of solar and/or lunar light (Berge et al., 2009). Since Puyuhuapi Fjord is not deeper
518 than 300 m, enough light should be able to reach the bottom layer and stimulate zooplankton
519 DVM across the whole water column. However, our results show that DVM did not go below

520 the hypoxic boundary layer (~100 m; Fig. 5), providing indirect support to the idea that
521 hypoxia may limit DVM in low-ventilated Patagonian fjords and elsewhere (Ekau et al.,
522 2010).

523

524 **5.2 Zooplankton avoidance of hypoxic waters**

525 In Puyuhuapi Fjord, hypoxic conditions have been reported below ~100 m depth, all year
526 round (Schneider et al., 2014; Silva and Vargas 2014), with sporadic deep ventilation events
527 that increase the DO concentration from 1.4 to 2.8 mL L⁻¹ (Pérez-Santos, 2017). These
528 pervasive hypoxic conditions seem related to ventilation conditions, however, they are not
529 common in all Patagonian Fjords. For instance, seasonal hydrographic data from Reloncaví
530 Fjord showed well ventilated conditions along the fjord, with deep DO values between 3-3.5
531 mL L⁻¹ (Castillo et al., 2016).

532 In the current study, acoustic measurements and zooplankton sampling were carried
533 out in hypoxic conditions, revealing that most zooplankton remained above the hypoxic
534 boundary layer (Fig. 5 and Fig. 9). Thus, lower DO values in Puyuhuapi Fjord act as a barrier
535 to DVM and zooplankton distribution throughout the year. Similar findings were reported in
536 Oslofjord, Norway, where hypoxic conditions dominated the water column beneath ~60 m
537 depth, and no fish or krill were observed below this depth (Røstad and Kaartvedt, 2013).
538 Moreover, similar findings have been previously reported in other Chilean waters for a
539 number of copepod species and life-stages (Castro et al. 1993, Escribano et al. 2009), as well
540 as for most gelatinous zooplankton groups (Pages et al. 2001; Giesecke and Gonzalez 2005;
541 Escribano et al. 2009).

542 In Puyuhuapi Fjord, higher S_v values occurred at DO concentrations ranging from 2 to
543 5 mL L⁻¹ and in Jacaf Channel with DO concentrations between 3 to 6 mL L⁻¹. This indicates
544 that DO values of 3.5 mL L⁻¹ and 4.5 mL L⁻¹ represent appropriate conditions for most
545 zooplankton species in Puyuhuapi Fjord and Jacaf Channel (Fig. 9), respectively, which are
546 similar to values indicated by Ekau et al., (2010) for zooplankton. Results also showed that
547 zooplankton prefer oceanic water with salinity values >31 g/kg, and temperature between 8
548 and 10° C (Fig. 9). Nonetheless, it must be considered that these preference values were
549 estimated from observational data, and therefore limited sampling, rather than from controlled
550 experiments.

551 In our study, hypoxic conditions regulated the depth limit of zooplankton DVM. This
552 implied that hypoxic boundary layers are an important environmental factor promoting the

553 generation of a dense zooplankton scattering layers in Puyuhuapi Fjord. The overlap between
554 the fish and zooplankton abundances at nearly the same layers suggests also that the prey-
555 predator relationships might be enhanced under this condition, as evidenced in the
556 zooplankton and fish echograms (Fig. 5). In the context of climate change, hypoxic conditions
557 are continually increasing around the world, both in coastal waters and open oceans (Breitburg
558 et al., 2018), therefore leading to spatial habitat reductions and prey-predator relationship
559 enhancement, which in turn, might cause changes in zooplankton groups' distributions and
560 abundance, particularly those that do not tolerate low DO concentrations.

561 The fact that some backscatter was detected in hypoxic water in our study indicates
562 that hypoxia does not affect all zooplankton species equally and that some of them can inhabit
563 this deeper layer. Hypoxia tolerant species residing below and within minimum DO layers
564 have been reported, in fact, further north along the Chilean coast during the upwelling season,
565 leading to support hypotheses on predation evasion and horizontal transport aimed to explain
566 such behavior (Castro et al., 2007). Within this context *Euphausia pacifica* has been reported
567 to exhibit the highest abundance of zooplanktonic species present in hypoxic waters in Hood
568 Canal, Washington (Sato et al., 2016). Other euphausiids have also been reported to be
569 present in other hypoxic systems in Chile (Escribano et al, 2009; Gonzalez et al., 2016). Being
570 *Euphasia vallentini* a dominant euphausiid, known to carry out extensive vertical migrations
571 in Patagonian fjords, we speculate it might be one of the species occurring in the less
572 oxygenated waters of our study. Unfortunately, due to sampling gear restrictions, we were
573 unable to sample the hypoxic layer, nor to identify firmly the species occurring at this depth.
574 Therefore, future research will be necessary to understand the relationship of the deep, yet
575 scarce, zooplankton with hypoxic waters in Puyuhuapi Fjord.

576

577 **5.3 Turbulent mixing at the fjord sill**

578 Patagonian fjords and channels cover an area of $\sim 240,000 \text{ km}^2$ and feature a complex marine
579 topography, including submarine sills and channel constrictions (Pantoja et al., 2014; Inall
580 and Gillibrand, 2010). Bernoulli aspiration, internal hydraulic jumps and intense tidal mixing
581 are all processes that can be found near a fjord sill (Farmer and Freeland, 1983; Klymark and
582 Gregg, 2003; Inall and Gillibrand, 2010; Whitney et al., 2014). Our data showed elevated
583 values of dissipation rate of turbulent kinetic energy in the Jacaf Channel ($\varepsilon = 10^{-5} \text{ W kg}^{-1}$ and
584 $K_p = 10^{-3} \text{ m}^2 \text{ s}^{-1}$) near the sill in the subsurface layer (0-60 m). These values are similar to those
585 observed at the sill of Knight Inlet in Canada (Klymark and Gregg, 2003). Lower dissipation

586 rate of turbulent kinetic energy were found in Puyuhuapi Fjord (Fig.10). The elevated vertical
587 mixing (high K_p) in Jacaf Channel is probably due to the barotropic tide interacting with the
588 submarine sill (Schneider et al., 2014; Fig. 10, Fig.11 and Table 2). This was also observed in
589 Martinez Channel (Pérez-Santos et al., 2014), Central Patagonia, where semidiurnal internal
590 tides were found to dominate the estuarine dynamics (Ross et al., 2014). This region is highly
591 influenced by the Baker river, whose discharge enhances stratification, introduces suspended
592 solids that subsequently limit productivity in the water column (González et al., 2010; Daneri
593 et al., 2012; González et al., 2013).

594 The evident aggregation of zooplankton and fish found near Jacaf sill (within ~1 km)
595 matches the area exhibiting the highest dissipation rate of turbulent kinetic energy ($\sim 10^{-5}$ W
596 kg^{-1} ; Fig.11). Thin (2-5 m) and thick (10-50 m) shear layers measured directly with the VMP-
597 250 microstructure profiler contribute to vertical mixing that enhance the exchange between
598 the subsurface rich nutrient layer and the photic layer, leading to increased phytoplankton
599 productivity (Montero et al., 2017a; Montero et al., 2017b), as shown in the conceptual model
600 of figure 12. Thus, the acoustic and turbulence measurements collected near the Jacaf sill
601 promote the importance of a sill modulating vertical mixing and also, influencing the vertical
602 distribution of oxygen, zooplankton and fish on both sides of the sill.

603 The effect that sills have on zooplankton distribution has been studied in a variety of
604 systems, including fjords (McQuillen 2005, Ianson et al., 2011), using both field sampling
605 (stratified zooplankton sampling, echo-sounding, or *in situ* imaging) and biophysical
606 modeling (Ianson et al., 2011). The interaction of horizontal flows with a steep sloping
607 surface usually results in a vertical component of the flow inducing turbulence that can be
608 sensed by zooplankton. Multiple hypotheses have been formulated to explain zooplankton
609 concentration around sills aside from increased productivity. Depending on the species
610 swimming capabilities, areas of increased turbulence may favor zooplankton feeding
611 aggregations by increasing the likelihood of encounters between the zooplankton and their
612 prey (Rothchild and Osborn, 1988). If a rotational flow develops above the sill (eg. Taylor
613 columns), both zooplankton and their food may also concentrate around the sill, thus
614 increasing plankton retention. Turbulence generated around the sill enhances ventilation of
615 the water column and reduces the extent of hypoxic layers, which allows zooplankton to
616 migrate and accumulate at deeper depths.

617 A summary of the processes that can contribute to zooplankton vertical distribution
618 and aggregation in Puyuhuapi Fjord and Jacaf Channel are presented in a conceptual model

619 (Fig. 12). In Puyuhuapi Fjord, a shallow oxycline around 100 m depth separates a high
620 nutrient and high production layer (Daneri et al., 2012; Montero et al., 2017a; Montero et al.,
621 2017b) from a hypoxic layer below, which limits species distribution and lacks high
622 aggregations of zooplankton. Above the hypoxic waters, turbulent mixing favors contact
623 between zooplankton predators and their prey (Visser et al., 2009). In Jacaf Channel, the
624 hypoxic layer occurs deeper in the water column than in Puyuhuapi Fjord, which stretches
625 the vertical distribution of zooplankton to a deeper range. Turbulent mixing also increases
626 primary and secondary production, through enhanced nutrient availability and favors
627 encounters of zooplankton with potential prey, increasing growth and survival rates.

628

629 **5.4 Other findings and considerations**

630 Results showed similar groups of macrozooplankton (>5 mm) in Puyuhuapi Fjord and
631 Jacaf Channel: euphausiids, chaetognaths, medusae and siphonophores during summer
632 (January 2014) and winter (winter 2014). However, euphausiids were not observed in fall
633 2013, which was an unexpected result which deserves further confirmation and analysis. In
634 contrast, fall 2013 sampling presented the highest acoustic abundances within the time series
635 (Fig. 3). The elevated accumulation of zooplankton species around the sill may impose a
636 significant modification in the amount and quality of carbon exported to deeper waters in
637 particular zones of the fjords. Future studies on carbon flux quantification in fjords should
638 incorporate sill regions to test this hypothesis, in order to improve ocean pumping
639 assessments in the context of climate change and variability.

640

641 **6 Conclusions**

- 642 • A hypoxic layer ($DO < 2 \text{ mL L}^{-1}$ and $< 30\%$ oxygen saturation) was observed below
643 ~100 m depth along Puyuhuapi Fjord whereas in Jacaf Channel it was deeper. This is
644 because the water column in Jacaf Channel was more ventilated due to enhanced
645 vertical mixing caused by tidal flow interacting with the shallow sill.
- 646 • Diel vertical migration (DVM) of zooplankton was detected in Puyuhuapi Fjord and
647 Jacaf Channel using ADCP backscatter signal and scientific echo-sounders. In
648 Puyuhuapi Fjord most of the larger migrating zooplankton species stopped DVM
649 above the hypoxic boundary layer, therefore implying that they can not tolerate
650 hypoxic conditions. As the hypoxic layer was located deeper in the water column in

651 Jacaf Channel, due to the enhanced turbulent mixing at the sill, the zooplankton DVM
652 patterns penetrated deeper in the water column.

- 653 • The most prevalent zooplankton groups detected with *in-situ* zooplankton net
654 sampling were siphonophores, chaetognaths, euphausiids, medusae and copepods. A
655 correlation was demonstrated between oceanographic variables and the relative
656 abundance of zooplankton (DO, $R^2=0.6$, salinity, $R^2=0.3$ and temperature, $R^2=0.35$).
657 This highlighted the preference of zooplankton for well oxygenated water (3-6 mL L⁻¹,
658 60-80 % saturation) and temperatures of 8-10°C, conditions characteristic of
659 oceanic waters (MSAAW and SAAW).
- 660 • Scientific echo-sounder records showed high aggregation of zooplankton and fishes
661 around the Jacaf sill, where high dissipation rates of turbulent kinetic energy ($\epsilon \sim 10^{-5}$
662 W kg⁻¹) and vertical diapycnal eddy diffusivity ($K_\rho \sim 10^{-3}$ m² s⁻¹) were recorded.
663 Turbulence therefore contributes to vertical mixing in Jacaf Channel, which promotes
664 the interchange of nutrients, zooplankton feeding and prey-predator relationships, and
665 organic carbon cycling.

666

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678

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904

905 **Figure captions**

906 Figure 1. Study area in relation to South America and the Pacific Ocean is the small panel in
907 the top right. The main figure enlarges the study area (Puyuhuapi Fjord and Jacaf Channel)
908 and indicates the instruments used for data collection, fixed point station positions, and the sill
909 location near the head of Jacaf Channel. The contours indicate the depth of the fjords.

910 Figure 2. Hydrographic measurements from Puyuhuapi Fjord. (a) Map of the study area
911 showing the transect (red lines) conducted on June 16, 2016 where black dots indicate
912 locations where profiles were taken, (b) Conservative temperature, (c) absolute salinity, (d)
913 dissolved oxygen and (e) oxygen saturation. For (b) to (e) the black vertical lines denote
914 along-channel profile locations.

915 Figure 3. (a) Volume backscattering strength (S_v) calculated from the ADCP-1 backscatter
916 signal in Puyuhuapi Fjord, deployed at 50 m depth from the 8th to the 26th of May, 2013. (b)
917 Zoom of the S_v data and the times of *in-situ* zooplankton sampling (black dots) carried out
918 during May 25-26, 2013. (c) Vertical abundance of main zooplankton groups (>5 mm length)
919 from the *in-situ* sampling at 18 h on May 25th and (d) 11 h on May 26th.

920 Figure 4. (a) Volume backscattering strength (S_v) calculated from the ADCP-2 backscatter
921 signal in Puyuhuapi Fjord from the 22nd to the 24th of January, 2014. The *in-situ* zooplankton
922 sampling (in 3 h intervals) are represented by black dots at the surface. (b) Depth integrated
923 abundance of zooplankton from the surface to 100 m depth varying throughout time, where
924 the top panel is zooplankton > 5 mm in length (excluding copepods) and the bottom panel is
925 the abundance of copepods. (c) vertical abundance of the principal zooplanktons groups on
926 January 23rd at 2 h (night time) and (d) same as (c) but on January 23rd at 14 h (daytime).

927 Figure 5. Along-fjord transects using a scientific echo-sounder SIMRAD with 38 kHz
928 frequency during the Summertime field campaign (January 2014). Distribution indicated by
929 colors representing S_v . (a) Day transect of echo-sounder measurements (S_v) throughout depth
930 (y-axis) from the mouth (0 km) to the head (80 km) of Puyuhuapi Fjord on January 22, 2014.
931 (b) Average profiles derived from the Nautical Area Scattering Coefficient (NASC) from the
932 daytime transect with standard deviation bars, (c) Same as (a), but for fishes. (d) to (f) are the
933 same as (a) to (c) but for the night time starting at 21:57 January 24th through early in the
934 morning of January 25, 2014. The ADCP-2 mooring location is marked with a black dot in (a)
935 and (d). (g) Dissolved oxygen profiles obtained every three hours from January 23rd to 24th,
936 2014. The location of the hypoxic boundary layer is depicted by the white contour line of 2
937 mL L⁻¹.

938 Figure 6. (a) Scientific echo-sounder transects along Puyuhuapi Fjord (0-18 km) and Jacaf
939 Channel (18-35 km) on August 17, 2014 using the combination of 38 and 120 kHz frequency.
940 (a) Fluid like and (b) blue noise echogram for zooplankton and (c) the fish echogram.
941 Distribution indicated by colors representing S_v values. The black arrow in (a) represents the
942 entrance to Jacaf Channel.

943 Figure 7. Acoustic transect over Jacaf sill using the combination of 38 and 120 kHz frequency
944 on August 18, 2014. (a) Fluid-like echogram, (b) blue noise echogram for zooplankton and (c)
945 the fish echogram. Distribution indicated by colors representing S_v values.

946 Figure 8. (a) Depth integrated abundance of zooplankton groups from surface to 150 m depth
947 for various sampling hours (b) euphausiids contined in depth strata (mean and standard
948 deviation) during daytime (red) and night (black) hours, (c) and (d) same as (b) but for
949 chaetognaths and copepods. (e) The vertical abundance of the main zooplankton groups found
950 during the Wintertime survey during a night hour (23 h) and (f) a day hour (17 h).

951 Figure 9. Relationships between the relative abundance of zooplankton (expressed in S_v
952 values) using 38 kHz frequency echo-sounder measurements (y-axis) and temperature in (a)
953 Puyuhuapi Fjord and (b) Jacaf Channel; salinity in (c) Puyuhuapi Fjord and (d) Jacaf
954 Channel; dissolved oxygen in (e) Puyuhuapi Fjord and (f) Jacaf Channel; oxygen saturation in
955 (g) from Puyuhuapi Fjord and (h) Jacaf Channel. The black lines denote the quadratic fit
956 curves, contour colors indicate depth.

957 Figure 10. Profiles of water temperature (blue line), vertical shear (red line) and dissipation
958 rate of turbulent kinetic energy (black line with green dots) obtained with the VMP-250
959 microprofiler at the depth of the Jacaf sill (~140 m depth) in (a) Jacaf Channel on 21
960 November 2013 (c) Puyuhuapi Fjord on 22 November 2013 and (e) in Puyuhuapi Fjord on 23
961 January 2014. (b, d, f) Representative spectrum of velocity shear ($\partial u/\partial z$) for shear probe 1
962 (blue line) and 2 (red line) in wavenumber space in Jacaf Channel on 21 November 2013,
963 Puyuhuapi Fjord on 22 November 2013 and Puyuhuapi Fjord on 23 January 2014,
964 respectively. The black line denotes the dimensional Nasmyth spectrum and the red and blue
965 triangles the cut-off of maximum wavenumber (k_{max}) for each shear probe. The shear
966 spectrums were carried out in the same layer (135-145 m) for all turbulence profilers.

967 Figure 11. (a) Microstructure profile locations along Jacaf Channel and sill using VMP-250
968 in November 2013. (b) The color bar showed the dissipation rate of turbulent kinetic energy
969 (ϵ) and the blue lines depict the velocity shear at each station location along Jacaf Channel (as
970 shown in (a). The horizontal scale (-2 to 2 s^{-1}) applied to profiles at stations 160, 162 and 163.

971 Station 164 is located at the confluence of Jacaf Channel and Puyuhuapi Fjord (10.5 km) (c)
972 The diapycnal eddy diffusivity profiles (K_p), obtained at each station shown in (a).
973 Figure 12. Conceptual model to show the oceanographic processes that contribute to the
974 distribution and aggregation of zooplankton in (a) Puyuhuapi Fjord and (b) Jacaf Channel.

975

976 **Table captions**

977 Table 1. Data set collected during oceanographic campaigns in Puyuhuapi Fjord and Jacaf
978 Channel.

979 Table 2. Harmonic analysis implemented to water level time series in Puyuhuapi Fjord and
980 Jacaf Channel.

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