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

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Abstract

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

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

1 Introduction

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

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

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

In Patagonian fjords, a comprehensive description of zooplankton distribution patterns has been provided by Palma (2008), considering a total of 220 *in-situ* plankton samples, from a number of depth strata between the surface and ~200 m. Main zooplankton groups included siphonophores, chaetognaths, cladocerans, copepods and euphausiids. Although a positive north to south gradient in the abundance of major zooplankton species was found, potential relationships between the vertical distributions and environmental variables were not deeply assessed. Later on, Landaeta et al., (2013) studied the vertical distribution of microzooplankton and fish larvae in Steffen fjord (47.4° S) at four depth strata (200-50 m, 50-25 m, 25-10 m and 10-0 m depth) during November 2008. Copepod nauplii and copepodites of *Acartia tonsa* together with *Maurolicus parvipinnis* fish larvae were observed around the pycnocline region, suggesting that the vertical structure of the water column might play a role in larval fish distribution. More recently, studies on zoo- and ichthyo-plankton vertical distributions in Reloncaví Fjord revealed that DVM timing might be modified by the tidal regime which is particularly strong in this area (Castro et al., 2014). However, none of these studies provided explicit assessments of the relationships between vertical distribution of zooplankton and turbulence or water column properties.

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

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

The present study aims to evaluate the effects of water column properties, such as dissolved oxygen and turbulent mixing, on the horizontal and vertical distributions of dominant zooplankton groups along a Patagonian Fjord system. To achieve this goal ADCP and scientific echo-sounder data are combined with biological observations from *in-situ* stratified zooplankton samples and water column measurements from microstructure profilers and conductivity-temperature-depth-oxygen (CTDO) profilers. The remainder of this article will include a detailed description of the study area in section 2 followed by an explanation of the data collected and the data analysis methodology in section 3. The results will be presented in section 4 with a discussion, focusing on differences between two Patagonian fjords, presented in section 5. The main conclusions of the study will be presented in section 6.

2 Study Area

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

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

3 Data and methodology

3.1 Water column properties

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

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

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

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

Using the values of ε, the diapycnal eddy diffusivity (K_ρ) was calculated. The most used formulation was proposed by Osborn (1980),

$$K_\rho = \Gamma\frac{\varepsilon}{N^2}, \tag{2}$$

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

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

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

3.2 Acoustic data

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

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

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

3.2.1 Echo-sounder data analysis

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

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

Volume backscattering strength (S_v, dB re 1 m^{-1}) values were integrated using a grid of 20 m (depth) by 50 m (distance), and re-scaled into the customary index "nautical area scattering coefficient" (NASC, in units of m^2 n mi^2). Since NASC lies on the linear domain, it can be considered proportional to and suitable for indexing zooplankton abundance (Ballón et al., 2011).

3.2.2 Acoustic data analysis from ADCPs

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

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

where, C is a sonar-configuration scaling factor (-148.2 dB for the Workhorse Sentinel), T_x is the temperature at the transducer (°C), L_{DBW} is $\log_{10}$(transmit-pulse length, L=8.13 m), P_{DBW} is $\log_{10}$(output power, 15.5 W), α is the absorption coefficient (dB m^{-1}), K_c is a beam-specific sensitivity coefficient (supplied by the manufacturer as 0.45), E is the recorded AGC (automatic gain control), and E_r is the minimum AGC recorded (40 dB for ADCP-1 and 41 dB for ADCP-2). The beam-average of the AGC for the 4 transducers was used to obtain optimal results following the procedure in Brierley et al. (2006). Finally, R is the slant range to the sample bin (m), which uses the vertical depth as a correction (Lee et al., (2004)). Therefore, R is expressed as,

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

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

3.3 Zooplankton sampling

In situ mesozooplankton samples were collected with a WP2 net (60 cm diameter mouth opening, 300 µm mesh, flow meter mounted in the net frame) towed vertically from 50 m to the surface in May 2013, and with a Tucker trawl (1 m^2 mouth opening, 300 µm mesh with flow meter) used to obtain stratified oblique tows in January 2014 and August 2014 (Table 1). All samples were preserved in a 5% formaldehyde solution. Zooplankton abundances were standardized to individuals per m^3 of filtered seawater. WP2 vertical tows consisted of 5 depth intervals from surface to 50 m, every 10 m (0-10, 10-20, 20-30, 30-40, 40-50 m).

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

3.4 Tidal harmonic analysis

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

4. Results

4.1 Hydrographic features

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

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

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

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

4.3 Acoustic data from scientific echo-sounder

4.3.1 Summertime surveys

Summer daytime S_v values along the Puyuhuapi Fjord averaged -89.1 ±7 dB re 1 m^{-1} and ranged between -110 and -77.3 dB re 1 m^{-1}, from the mouth to the head of the fjord (Fig. 5a). Most of the backscatter was concentrated in the first 100 m of the water column, matching ADCP results (Fig. 3 and 4). At the ADCP-2 mooring location (black dot in Fig. 5a), higher backscatter signals were found between 50-100 m depth, showing good agreement between echo-sounder and ADCP-2 data (Fig. 3, 4 and 5). Average NASC profiles for zooplankton showed higher values between 50-100 m (above the hypoxic layer) both during day and night (Fig. 5b and e). Although some NASC values were observed within the hypoxic layer (below ~120 m depth), all dense aggregations were observed above it (Fig. 5g). Daytime S_v signals attributed to fishes were typically detected at ~50 m depth, being much higher (<-60 dB re 1 m^{-1}; Fig. 5c) than S_v signals attributed to zooplankton.

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

4.3.2 Wintertime Surveys

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

Continuous acoustic sampling repeated over the Jacaf Channel sill confirmed the presence of intense backscatter signals (Fig. 6 and 7), and the presence of two backscattering layers: one denser layer between 100-150 m and a second, less dense layer from 200 to 250 m (Fig. 7a). The *in-situ* zooplankton sampling at the fixed station located in Jacaf Channel detected DVM patterns (Fig. 8). The depth integrated abundance of zooplankton >5 mm showed increased values during night time hours (23 h and 22 h in Fig 8a, in particular for euphausiids). Further, theelevated abundance of zooplankton groups (euphausiids and chaetognaths) were found in the 100-150 m layer particularly at day time (Fig. 8b-f), which matched well with acoustic data for the fluid-like group (Fig. 7a).

A correlation was found between the *in-situ* zooplankton sampling (species >5mm) and the 38 kHz S_v values from Jacaf Channel. In particular, a positive correlation was again 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 S_v vs. copepods (species >1 mm).

4.4 Relationships between acoustic records and water column properties

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

4.5 Tidal regime

The harmonic analysis carried out with the sea level time series obtained in Puyuhuapi Fjord and Jacaf Channel, denoted the dominance (in terms of amplitude) of the semi-diurnal constituents (M_2 and S_2; Table 2). Diurnal constituents (O_1 and K_1) were also important, specifically at the Jacaf ADCP-3 station located close to the Jacaf sill region (Table 2 and Fig 1). The contribution of diurnal constituents added the mixed character to the tidal regimen in the study area. The spectral analysis implemented at all sea level stations showed maximum energy in the semi-diurnal band (Table 2), with the highest spectral energy (57.29 m^2 cph^{-1}) at Jacaf sill (Jacaf ADCP-3 station), which could be due to the extreme convergence of the channel at this location accelerating the tidal flows.

4.6 Mixing process

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

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

5 Discussion

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

5.1 Diel vertical migration patterns

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

DVM patterns of zooplankton are expected to be associated with visible light intensity, in particular, diel changes in visible light in the photic zone (from surface to ~100 m). This is so the zooplankton can avoid predators during daytime hours and have safe-feeding conditions at night. However, small irradiance levels, around 10^{-7} times surface levels, can be still detected at 600 m or deeper in some areas (Haren and Compton, 2013; Sato et al., 2013 and 2016), requiring zooplankton DVM to reach depths below 500 m (Haren and Compton, 2013). Moreover, DVM patterns of zooplankton have been observed in Artic fjords (e.g., the Kongsfjordena and Rijpfjorden fjords) even during the polar night, suggesting the influence of solar and/or lunar light (Berge et al., 2009). Since Puyuhuapi Fjord is not deeper than 300 m, enough light should be able to reach the bottom layer and stimulate zooplankton DVM across the whole water column. However, our results show that DVM did not go below the hypoxic boundary layer (~100 m; Fig. 5), providing indirect support to the idea that hypoxia may limit DVM in low-ventilated Patagonian fjords and elsewhere (Ekau et al., 2010).

5.2 Zooplankton avoidance of hypoxic waters

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

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

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

In our study, hypoxic conditions regulated the depth limit of zooplankton DVM. This implied that hypoxic boundary layers are an important environmental factor promoting the generation of a dense zooplankton scattering layers in Puyuhuapi Fjord. The overlap between the fish and zooplankton abundances at nearly the same layers suggests also that the prey-predator relationships might be enhanced under this condition, as evidenced in the zooplankton and fish echograms (Fig. 5). In the context of climate change, hypoxic conditions are continually increasing around the word, both in coastal waters and open oceans (Breitburg et al., 2018), therefore leading to spatial habitat reductions and prey-predator relationship enhancement, which in turn, might cause changes in zooplankton groups' distributions and abundance, particularly those that do not tolerate low DO concentrations.

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

5.3 Turbulent mixing at the fjord sill

Patagonian fjords and channels cover an area of ~240,000 km^2 and feature a complex marine topography, including submarine sills and channel constrictions (Pantoja et al., 2014; Inall and Gillibrand, 2010). Bernoulli aspiration, internal hydraulic jumps and intense tidal mixing are all processes that can be found near a fjord sill (Farmer and Freeland, 1983; Klymark and Gregg, 2003; Inall and Gillibrand, 2010; Whitney et al., 2014). Our data showed elevated values of dissipation rate of turbulent kinetic energy in the Jacaf Channel (ε =10^{-5} W kg^{-1} and K_ρ =10^{-3} m^2 s^{-1}) near the sill in the subsurface layer (0-60 m). These values are similar to those observed at the sill of Knight Inlet in Canada (Klymark and Gregg, 2003). Lower dissipation rate of turbulent kinetic energy were found in Puyuhuapi Fjord (Fig.10). The elevated vertical mixing (high K_ρ) in Jacaf Channel is probably due to the barotropic tide interacting with the submarine sill (Schneider et al., 2014; Fig. 10, Fig.11 and Table 2). This was also observed in Martinez Channel (Pérez-Santos et al., 2014), Central Patagonia, where semidiurnal internal tides were found to dominate the estuarine dynamics (Ross et al., 2014). This region is highly influenced by the Baker river, whose discharge enhances stratification, introduces suspended solids that subsequently limit productivity in the water column (González et al., 2010; Daneri et al., 2012; González et al., 2013).

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

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

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

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

5.4 Other findings and considerations

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

6 Conclusions

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

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

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

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Figure captions

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

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

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

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

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

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

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

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

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

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

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

Station 164 is located at the confluence of Jacaf Channel and Puyuhuapi Fjord (10.5 km) (c) The diapycnal eddy diffusivity profiles (K_p), obtained at each station shown in (a).

Figure 12. Conceptual model to show the oceanographic processes that contribute to the distribution and aggregation of zooplankton in (a) Puyuhuapi Fjord and (b) Jacaf Channel.

Table captions

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

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