Seasonal and diel variations in the vertical distribution, composition, abundance and biomass of zooplankton in a deep Chilean Patagonian fjord

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Abstract

Comau Fjord is a stratified fjord in the northern part of Chilean Patagonia. In spite of aragonite-undersaturated waters causing an energetic burden to coral calcification, this deep body of water harbors dense populations of cold-water corals (CWC). While the paradox has been attributed to a rich supply of zooplankton, quantitative data to support this hypothesis are so far lacking. In this study, we investigated the seasonal and diel changes of the zooplankton community over the entire water column. We used a Nansen net (100 µm mesh) to take stratified vertical hauls between the surface and the bottom (0-50-100-200-300-400-450 m). Samples were scanned with a ZooScan, and abundance, biovolume and biomass were determined for 41 taxa identified on the web-based platform EcoTaxa 2.0. Zooplankton biomass was the highest in summer (209 g dry mass m^{-2}) and the lowest in winter (61 g dry mass m^{-2}). Abundance, however, peaked in spring, suggesting a close correspondence between reproduction and the phytoplankton spring bloom (Chl *a* max. 50.86 mg m^{-3}, 3 m depth). Overall, copepods were the most important group of the total zooplankton community, both in abundance (64-81%) and biovolume (20-70%) followed by mysids and chaetognaths (in terms of biovolume and biomass), and nauplii and Appendicularia (in terms of abundance). Throughout the year, diel changes in the vertical distribution of biomass were found with a daytime maximum in the 100-200 m depth layer and a nighttime maximum in surface waters (0-50 m), associated with the diel vertical migration of the calanoid copepod genus *Metridia*. In addition, our study provides a good background knowledge for the understanding of the ecological connection between zooplankton and CWC. Based on our zooplankton data, we calculated that a zooplankton supply rate of 790 prey $polyp^{-1}$ day^{-1} would be necessary to sustain a viable population of CWC in Comau Fjord. Therefore, the high abundance of CWC in the aragonite-undersaturated waters of Comau Fjord may be due to the high food availability provided by the zooplankton biomass.

Keywords. zooplankton, seasonality, diel vertical migration, cold-water corals, ZooScan, EcoTaxa, Comau Fjord, Chilean Patagonia.

Introduction

Coastal marine ecosystems are among the most productive on earth (Mann & Lazier, 1991). They provide substantial economic and ecological services, such as high biological production, nutrient cycling or shoreline stability and erosion control (Escribano et al., 2003; Liu et al., 2010; Pan et al., 2013; Barbier, 2017). The Chilean Fjord Region extends over large and complex hydrographic and geomorphologic conditions, particularly rich in productivity and biodiversity (Försterra et al., 2017; Häussermann et al., in press), but also endangered by human exploitation, which has been increasing significantly – e.g. salmon aquaculture – over the last two decades (Iriarte et al., 2010; Buschmann et al., 2021; Navedo and Vargas-Chacoff, 2021).

The hydrography of the fjords and channels of Patagonia can be considered a transitional estuarine-marine system where a surface layer of silicate-rich terrestrial freshwater meets nitrate- and phosphate-rich marine waters. These fjords receive freshwater from rivers, surface runoff and groundwater flow due to the high rainfall and glacier melting (Pantoja, Iriarte & Daneri, 2011). The upper brackish layer within the top 10 m water depth is usually poor in nitrate and phosphate but rich in silicate and organic matter from terrestrial inputs (Sánchez, González & Iriarte, 2011). Below the halocline, a water mass with higher salinity (>31), named Modified Subantarctic Water (MSAAW), flowing landward from the adjacent oceanic area provides the fjords with macronutrients (nitrate and phosphate). Both water masses, surface-freshwater and MSAAW, generate a two-layer structure in the water column with sharp vertical and more gradual horizontal salinity gradients (Sievers and Silva, 2008; Pérez-Santos et al., 2014; Meerhoff et al., 2019). The vernal stratification creates a barrier which may hinder the exchange of nutrients within the water column and alter the functioning of the pelagic food web and productivity patterns (Silva et al., 1997; González et al., 2011). During austral spring, the Comau Fjord receives an intense riverine input of fresh water, rich in silicic acid used by bloom-generating diatoms and, thus, leading to high primary production (González et al., 2010). In austral summer, the high concentration of phytoplankton promotes an increase in the abundance and biomass of zooplankton as secondary producers (Antezana, 1999; González et al., 2010). In fjord systems, seasonal patterns are modulated by other oceanographic processes, such as estuarine circulation (Palma & Silva, 2004), tidal regimes and lateral advection (Castro et al., 2011) or water column stratification (Sánchez, González & Iriarte, 2011) influencing the zooplankton biomass and community structure on shorter time scales.

Zooplankton plays an essential role in the functioning of marine ecosystems and in the oceanic carbon cycle. It includes a wide variety of organisms and displays extreme variability in terms of community composition and vertical, seasonal and geographical distribution (Palma & Kaiser, 1993). Many taxa are known to perform diel vertical migrations (DVM), most likely to evade predators (Stich and Lampert, 1981; Iwasa, 1982). According to the predator-evasion hypothesis, migrating zooplankton resides in deep waters during daytime hours where the probability of being perceived by visually orientated predators is lower than if they remained in more illuminated shallow waters, and at night, in the refuge of darkness, they migrate upwards to feed. However, DVM is not performed by all organisms in a zooplankton community or even not by all individuals of one species. For example, while late copepodites and adults of the copepod genus

Metridia migrate, a large fraction of the young developmental stages remains in surface waters, saving the energy of performing the DVM, suggesting a lower probability of being perceived and consumed by visual predators (Hays, 1995). Both, migrating and resident species are important elements of the biological carbon pump via the production of sinking fecal pellets that transport carbon from the surface to the seafloor (Urrère and Knauer, 1981; Fowler and Knauer, 1986; Emerson and Roff, 1987). Zooplankton also provides a trophic link between primary production and higher consumers such as fish, birds and mammals, but also invertebrate predators, such as corals (Nemoto, 1970; Gili et al., 2006; Höfer et al., 2018).

Cold-water corals (CWC) depend on zooplankton as their principal food source to maintain their physiological processes, such as respiratory metabolism and growth (Carlier et al., 2009; Mayr et al. 2011, Naumann et al. 2011). Therefore, their diet is susceptible on the zooplankton seasonal, diel and vertical distribution. In Comau Fjord, azooxanthellate scleractinian CWC are wide-spread despite aragonite-undersaturated waters (Häussermann and Försterra, 2007; Fillinger and Richter, 2013; Jantzen et al., 2013). In aragonite-undersaturated waters, the dissolution of exposed parts of the skeleton, enhanced bioerosion, and reduced CWC growth and survival have been observed (McCulloch et al., 2012; Maier et al., 2016). The calcification of the CWC skeleton is energetically costly, and thus food requirements in these adverse environments are higher compared to aragonite-saturated waters. According to Fillinger & Richter (2013a), in Comau fjord, the CWC *Desmophyllum dianthus* thrive but coral densities decrease below 280 m despite available substrate, suggesting that a shortage of zooplankton could be limiting coral growth. However, up to now little is known about the zooplankton of Comau Fjord in the northern Patagonian region and its role in sustaining the rich CWC communities living in the fjord. Most studies were carried out in the central-southern part of Patagonia (from Penas Gulf to Cape Horn, S 46.50° – S 55.55°), while studies performed in the northern area (from Puerto Montt to San Rafael Lagoon, S 41.20° – S 46.40°) mainly focused on selected microzooplankton taxa in the upper water column, on bulk measurements of zooplankton biomass, or on the carbon flow through the pelagic food web (e.g., Palma, 2008 and references therein; Villenas et al., 2009; González et al., 2010; González et al., 2011; Palma et al., 2011; Sánchez et al., 2011). Other studies addressed the physical oceanographic processes and their effect on zooplankton distribution (e.g., Marín and Delgado, 2009; Castro et al., 2011) and, more recently, investigated zooplankton migration patterns by acoustic backscatter and vertical velocity profiles (Valle-Levinson et al., 2014; Díaz-Astudillo et al., 2017; Pérez-Santos et al., 2017). The information on zooplankton diversity and migration patterns is, however, still very fragmentary and the linkage between the abundance of CWC and zooplankton supply in Comau Fjord remains unknown.

Commenté [A1]: Any reference? Not sure whether this assertion is based on literature data or is an hypothesis?

Commenté [A2]: To me it is not exactly what these authors reported. Fillinger & Richter 2013a "only speculate that the lower oxygen concentration, combined with a lower pH, may entail higher metabolic expenditures for the corals" and further speculate that "The likely reduced water exchange may in addition limit the supply of food to D. dianthus", consisting of zooplankton…
So your assertion is a bit of a shortcut.

In this study, we aim to (i) describe the diel, vertical, and seasonal distribution of mesozooplankton groups of Comau Fjord, with a focus on the dominating taxa, particularly those that migrate and are more likely to aggregate; and (ii) investigate if the zooplankton densities retained in the fjord are sufficient to sustain the population of CWC. Samples were collected day and night with net hauls through the whole water column in spring, summer, autumn and winter. They were processed with a high-resolution image analysis system (ZooScan, Gorsky et al. 2010). The zooplankton taxa were identified using EcoTaxa 2.0 (Picheral, Colin & Irisson, 2017), allowing to assess the influence of the seasonal environmental changes on the zooplankton dynamics, and the natural food available to CWC.

Materials & Methods

Field work was carried out in Comau Fjord, Northern Patagonia, Chile (Fig. 1). Zooplankton was sampled four times at a fixed station (24°14.95S, 72°28.83W) in central Comau Fjord: in austral spring (28th September 2016), summer (17th January 2017), autumn (7th May 2017), and winter (29th July 2017), during both~~,~~ day and night. Samples were collected with a 70 cm-diameter Nansen closing net (mesh size: 100 µm) equipped with a non-filtering cod end. Vertical hauls were carried out at 0.45 m s^{-1} to sample the depth strata 0-50-100-200-300-400-450 m. Immediately after the collection, the samples were sieved through a 50 µm mesh and preserved in 4% borax-buffered formaldehyde for laboratory analyses. After every zooplankton haul, a CTD multi-probe (SBE 19plusV2 Profiler - with RS 232 Interface, Sea-Bird Electronics Inc.) was deployed from the surface to the bottom, measuring conductivity, temperature, oxygen, pH and Chl *a*-fluorescence (Fig. 2).

Commenté [A3]: Should be 42 not 24? (Fig. 1)

Commenté [A4]: Could you give the hours of sampling?

Sample analysis and image processing

Commenté [A5]: This is the only subsection in the Mat & Met. So either remove or add a first one such as “sampling”, the second being analysis and image processing.

In the laboratory, zooplankton samples were washed with fresh water and prepared for analysis with a ZooScan digital imaging system (Grosjean et al., 2004, Gorsky et al., 2010). ZooScan (CNRS patent, www.hydroptic.com) provides a quick and reliable method for the analysis of preserved plankton samples, storing digitized images for later examination, reprocessing and dissemination. Concentrated samples were subsampled with a Folsom plankton splitter to avoid cluttering the images with more than approximately 1000-1500 individuals. Up to six binary splitting steps were carried out (corresponding to a minimum 1/64th fraction of the original sample). Routinely, the two final splits were scanned with ZooScan yielding images of 2400-dpi resolution (14200×22700 pixels). The hinged base of the ZooScan allowed the recovery of the complete undamaged subsample, which was later stored in 70% ethanol for archiving. Most

Commenté [A6]: Not sure about the term…

overlapping individuals on the scanning surface were manually separated to ensure an even distribution before scanning. Image analysis was performed with the software ZooProcess (Gorsky et al., 2010), a plug-in for the image processing and analysis software ImageJ (Schneider, Rasband & Eliceiri, 2012). The processing involved (1) the automatic subtraction of background noise, (2) the automatic thresholding and detection of objects, and (3) the automated storage of detected objects in separate images (“vignettes”). ZooScan detection limit was set at the standard of 300 µm. Detected zooplankton organisms ranged from 0.3 to 59 mm. Automatic processing was successful in 75-80% of the cases. Despite the manual separation, some individuals overlapped, resulting in vignettes with two or more objects. These objects were manually separated using the “separation with mask” tool of the ZooProcess software. Separated vignettes were stored, while the original vignette containing multiple objects was eliminated from the database to avoid duplicate counts. In some cases, the separation of individuals was not possible as cutting the vignette would mean losing information about the taxonomy of the organisms (i.e. cutting overlapping urosomes from two different copepods or small copepods embedded in cnidarians). Overall, the contribution of vignettes with multiple objects was always < 10% of the total amount of vignettes.

Commenté [A7]: Probably not easy with 100 µm mesh size. See following sentence: ZooScan detection limit was set at the standard of 300 µm. What does this mean ? Measurement of all objects then removing small ones?

Commenté [A8]: Not clear.

Commenté [A9]: What does this mean?

Commenté [A10]: Does this mean that some individuals smaller than 300 µm could be included here?

Commenté [A11]: Do you mean all or only those that could not be separated?

Vignettes were subjected to the semi-automated taxonomic classification in EcoTaxa 2.0 (Picheral, Colin & Irisson, 2017). This web-based machine learning application uses training sets of expert-identified taxa and random forest classification to automatically identify and sort the objects. Although EcoTaxa contains more than 160 million objects on its server, no ZooScan training set was available for Patagonian waters. Therefore, manual identification of individuals on a subset of the images was first necessary to train an initial model, which was later used by the system to predict the taxonomic classification of the scanned organisms. After the initial prediction, the automatic classification had an accuracy rate of 44%. We therefore manually validated the classifications of the initial learning set by sorting more objects into the given categories. This produced the final learning set for the classification of the entire image data set. At the end, all classified objects were validated by an expert to assure a correct taxonomic classification. The organisms were classified to the lowest possible taxonomic level; for most copepods this was the genus level. However, small calanoid copepods (<1.5 mm) were not distinguishable on genus level and were comprised as one category: “Calanoids (<1.5 mm)” including five groups (copepodites (all calanoid taxa, <1mm), *Clausocalanus*, *Microcalanus*, *Neocalanus* and *Paracalanus*). The category Cnidaria was constituted by organisms from the class Hydrozoa (mostly medusa and Siphonophorae). Another category contained all images that were out of focus (“bad focus”) and likely comprised individuals from all copepod taxa. From the total of 83,516 vignettes, 23,227 could not be assigned to zooplankton taxa, but were labelled as

Commenté [A12]: Which means? The manually annotated vignettes were only identified with 44% success? At what taxonomic level? The success probably depends on this.

Commenté [A13]: What is not clear here is whether your training set was the global one + Patagonian one, or only the Patagonian one.

Commenté [A14]: How many?

“detritus”, “fiber”, “leg” “bubble” and “other” and were not considered in our analyses. ZooProcess provides information about the length and width of each object, allowing the calculation of its volume as a proxy for its biomass (Gorsky et al., 2010). The program automatically fits an ellipse around the object, from which the major and minor axis and volume (V) is computed:

$$V\ (mm^3) = \frac{4}{3} \times \pi \times \frac{major\ axis\ (mm)}{2} \times \left(\frac{minor\ axis\ (mm)}{2}\right)^2$$

Biovolume (BV) was then calculated as the sum of the volumes of all objects (ΣV) divided by the fraction of the sample (e.g., F=1/64) and by the volume filtered by the Nansen net (V_N):

Commenté [A15]: No flowmeter? Not possible for strata?

$$BV\ (mm^3/m^3) = \frac{\left[\frac{\sum V\ (mm^3)}{F}\right]}{V_N\ (m^3)}$$

V_N was calculated as:

$$V_N\ (m^3) = \left[\pi\ \times \left[\frac{net\ diameter\ (m)}{2}\right]^2\right] \times\ depth\ interval\ (m) \times\ filtration\ efficiency$$

where filtration efficiency was estimated as the theoretical 100% efficiency (value = 1).

For the estimation of biomass, a regression between the dry mass of a specimen and its body area [DM (µg) = ($a\ A^b$)] was used (Hernández-León and Montero, 2006; Lehette and Hernández-León, 2009), where A is the area (mm^2) of each individual. The conversion of ZooScan-based biovolume into dry mass required different conversion factors depending on the organism, as for instance, gelatinous zooplankton with high water content may not be compared to crustaceans or echinoderms (Table 1). Such coefficients have been successfully published in previous studies for mid-latitude shelf areas (Marcolin, Gaeta & Lopes, 2015) or Chilean upwelling region (Tutasi & Escribano, 2020).

Commenté [A16]: Not clear what you did… You did not convert volume into dry mass, because you use area, given by the ZooScan. No?

The biomass (B) of each taxon was then calculated as the sum of the individual dry masses of the respective taxon (ΣDM) divided by the fraction of the sample (e.g., F=1/64) and by the volume filtered by the Nansen net (V_N):

$$B\ (mg\ dry\ mass/m^3) = \frac{\left[\frac{\sum DM (mg)}{F}\right]}{V_N (m^3)}$$

Biovolume and biomass were calculated to obtain the sum of the values of all individuals for a given taxon. In multiple vignettes, the automatic calculation of biovolume and biomass was not possible because of overlapping specimens from different taxa. Then, the organisms were counted manually and biovolume and biomass were estimated by multiplying the mean volume or DM of the given taxon from all automatic calculations by the extra number of multiple vignettes. Groups with large size variability (e.g., chaetognaths, cnidarians or Euchaetidae) were divided into two categories (big and small) in order to get a better biovolume/biomass assessment.

Commenté [A17]: Please detail: what ranges?

The integrated values of abundance, biovolume and biomass (Fig. 3), were calculated down to 400 m water depth, taking out the last 50 m from summer and winter, to make it comparable to the spring and autumn seasons, where samples were collected down to that specific depth.

Commenté [A18]: Please do not indicate here as it is a result.

Results

The physicochemical parameters measured in the water column of Comau Fjord showed stronger seasonal variability in surface waters (0-50 m) than in the deep (50-450 m) (Fig. 2). The temperature profile indicated summer stratification, followed by surface cooling, breakdown of the thermocline in autumn, and reverse temperature gradients in winter and spring. Accordingly, the surface temperature values were the lowest in winter and spring (8.6-11 °C), and the highest in summer (16.7 °C), getting cooler again in autumn (12 °C). In deeper waters, temperatures were more stable with an average value of 11.4 ± 0.2 °C (mean average ± sd; Fig. 2A). Salinity was between 10-30 in the upper 20 m and 32.9 ± 0.4 below 20 m (Fig 2B). The pH ranged between 8.5 and 7.7 in the upper 50 m and was 7.9 ± 0.1 in deeper waters in all seasons, except for autumn, where we interpret the sudden drop of pH values as an instrument malfunction (Fig. 2C). Oxygen concentration showed the largest variations in the upper 50 m during the spring season (137.2-410.5 µmol kg^{-1}), while below 100 m depth it was on average 180 ± 9.3 µmol kg^{-1} (Fig. 2D). The chlorophyll *a* (Chl *a*) concentration peaked in early spring (50.86 mg Chl *a* m^{-3} at 3 m depth), followed by a decrease towards the end of the summer and low values through autumn and mid-winter (2.5-5 mg Chl *a* m^{-3} at 5-10 m depth) (Fig. 2E). Below 25 m, the concentration of Chl *a* was < 1.8 ± 0.5 mg m^{-3} throughout the year (Fig. 2E).

Commenté [A19]: Please give the depth of the thermocline

Commenté [A20]: What difference do you place in the two terms?

Commenté [A21]: Is it a common unit? Not µmol L-1?

The zooplankton community exhibited large seasonal and diel differences. Abundance, integrated over the upper 400 m of the water column (individuals m^{-2}) showed the highest values in spring and the lowest during autumn (Fig. 3A). Interestingly, the ~~seasonal~~ integrated biovolume (cm^{3} m^{-2}) and biomass (g dry mass m^{-2}) showed a different pattern with the highest values in summer and the lowest in autumn and winter (Fig. 3B, C). Diel differences in integrated abundances generally showed higher values during the day than at night, except for autumn (Fig. 3A). Diel differences in integrated biovolume and biomass were surprisingly large, with generally higher values during

Commenté [A22]: Maybe you can add “for both day and night”.

Commenté [A23]: Unnecessary in the results. Why is it interesting?

the night, except for spring (Fig. 3B, C), indicating that during daytime, particularly in spring, zooplankton was more numerous but smaller in size.

Zooplankton vertical distribution also showed pronounced seasonal and diel changes. Zooplankton abundance exhibited the highest values in the 0-50 m layer during day and night at all seasons, with the exception of autumn during day time. In autumn, the day-time peak was absent with overall low values throughout the water column (Fig. 4A). During day and night time, the lowest abundances were found in >300 m depth in spring and summer, and in 50-100 m depth in autumn. In winter, the abundance was the lowest in 200-300 m in day time, and below 200 m in night time (Fig. 4A). During the day, the highest values of biovolume ~~(cm^3 m^{-3})~~ and biomass ~~(g dry mass m^{-3})~~ were observed in 0-50 m and 100-200 m water depth in spring and summer, and in 100-300 m in autumn. In winter, day time biovolume and biomass were similarly low over the entire water column (Fig. 4B, C). At night, the highest biovolume and biomass values were found at the surface 0-50 m in all seasons, indicating that the different zooplankton taxa that reside in the 100-200 m water depth performed upward vertical migration. The lowest biovolume and biomass values were found in >300 m depth in spring and summer, in 50-100 and 200-300 m depth in autumn and in >50 m depth in winter (Fig. 4B, C).

Commenté [A24]: Overall I think this paragraph is too long and detailed, as everything is in the Fig. 4. Could you try shorten it, keeping only the key results?

Commenté [A25]: Units are useless here.

Commenté [A26]: This is an interpretation and should not be in the results section but in the discussion. At this stage in the paper, it is a bit a very short interpretation that would be discussed, so I suggest to remove and keep for the discussion. Further, at this stage you did not look at the taxonomic composition, so it seems difficult to talk about the "different zooplankton taxa"…

The taxonomic~~al analysis~~composition showed strong differences between the biovolume and abundance of zooplankton groups (Fig. 5, 6A; biovolume—not biomass—was used to better represent the gelatinous taxa). Copepoda were the most important group, constituting ~~seasonally~~ 20-70% of the total biovolume, and 64-81% of the total abundance. Within the copepod community, individuals smaller than 1.5 mm included (a) copepodites and adults of small calanoid genera, such as *Clausocalanus*, *Microcalanus*, *Neocalanus* and *Paracalanus*; (b) cyclopoids~~ copepods~~ of the genera *Oithona* and *Oncaea*; (c) harpacticoids~~ copepods~~; and (d) crustacean nauplii (mostly from copepods). Small copepods accounted for 58-86% of the total copepod community. Overall, 14 out of 41 taxa contributed 45-98% of the total biovolume and 45-86% of the total zooplankton abundance (Fig. 5). The other 27 taxa were constituted by other copepod~~s~~ taxa (Acartiidae, Aetideidae, Calanoida (non-identifiable), Candaciidae, Centropagidae, Copepoda (non-identifiable), Eucalanidae, Heterorhabdidae, Lucicutiidae, Oncaeidae, Pontellidae, Rhincalanidae), Actinopterygii (eggs and larvae), Appendicularia, Ascidiacea (larvae), Brachiopoda (larvae), Bryozoa (larvae), Cirripedia, Cladocera, Decapoda (zoea), Echinodermata (larvae), eggs, Isopoda, Nemertea (pilidium), Platyhelminthes (larvae), Polychaeta (larvae) and non-identifiable organisms.

Commenté [A27]: I find this sentence poorly said. If the sense is the same, I suggest: "Looking at the taxonomic composition, the relative contribution of the taxa greatly differed between biovolume and abundance.

Commenté [A28]: Those < 1.5 mm? If yes, it should be clearly stated, for example "these small copepods"

Commenté [A29]: Abundance? If yes clearly state it

Commenté [A30]: It is really not clear if the small copepod above are part of these 14.

Commenté [A31]: At several places you mention the Euchaetidae, but they are not included here. Why? From Fig. 5 they should be in the 14…

The most important groups differed regarding biovolume and abundance. For biovolume, Mysida (1-21%) constituted a ~~strong~~ large part of the zooplankton community, followed by Chaetognatha

Commenté [A32]: This is exactly what you already stated line 266-267. It seems to me that you talk about the 14 taxa most important. True?

(3-15%) and Cnidaria (2-23%). Metanauplii and calyptosis stages of Euphausiacea were found mostly in spring and summer accounting for 0-7% of the total biovolume and when one adult specimen was found during winter in 0-50 m water depth at night, the total biovolume of this taxon increased to 65%. Regarding the abundance~~number of specimens~~, crustacean nauplii (2-9% with its maximum in spring and minimum in autumn) and Appendicularia (0.4-6%) were the second and third most abundant groups after Copepoda, respectively. The fourth most abundant group differed among seasons: Echinodermata larvae (5% in spring), Mollusca larvae (2-5% in summer, 3-9% in autumn), Ostracoda (4-5% in autumn) and Bryozoa larvae (2-10% in winter). ~~In~~ Across all samples and seasons, taxa that represented more than 5% of total biovolume were Cnidaria (13%), *Calanus* (12.9%), Mysida (12.7%), *Metridia* (12.6%), Chaetognatha (9.6%) and Euchaetidae (8.7%). The most abundant groups with more than 5% of the total abundance were Harpacticoida (14.0%), Cyclopoida (9.1%) and *Metridia* (8.4%) (Fig. 5, 6A).

Commenté [A33]: Better to use the terms as they appear in the other parts.

~~Seasonally, t~~The integrated abundance of the most dominant taxa followed the phytoplankton cycle for small and large copepods and chaetognaths, with high values in spring to generally low values in autumn and winter (Table 2). Highest abundances of crustacean nauplii and cnidarians were found in early spring with a minimum in autumn and raising up again in late-winter. Mysida presented a stable abundance over the seasons with a minimum in summer. These groups presented clearly different vertical distributions (Fig. 6). *Metridia*, a large and important copepod with regard to both biovolume and abundance, resided generally above 200 m, exhibiting a peak between 100-200 m during the day and a bimodal distribution (peaks at 0-50 m and 100-200 m) during the night (Fig. 6B). The largest individuals (0.62 ± 0.3 mm^3; average size ± sd) were found in the intermediate waters during the day, but in spring, a significant proportion of the *Metridia* population was also found during the day in shallow waters where smaller individuals (0.14 ± 0.08 mm^3) were identified. The copepod *Calanus* was found mainly in intermediate waters (100-300 m) during day~~-~~time where the largest individuals (1.37 ± 0.5 mm^3) resided, whereas at night part of the population migrated upwards and the other part remained at depth. Small specimen of *Calanus* (0.30 ± 0.003 mm^3) were found in shallow waters also during daytime in spring. At night, only in spring and winter, individuals were present in shallow waters (<50 m depth). Despite the low number of *Calanus* specimens found at shallow waters, they contributed considerably to the biovolume in these layers (Fig. 6C). The Euchaetidae showed higher abundance and biovolume in the deeper part of the water column during day time, ascending to shallower waters at night (Fig. 6I). Small copepods of the taxa Harpacticoida and Cyclopoida were very abundant, but, as expected, they only represented a small fraction of the total biovolume. Harpacticoida were mainly abundant below 50 m during both day and night time, and their abundance increased with depth (Fig. 6D). Cyclopoida were mainly present in the upper 200

Commenté [A34]: I suggest you rephrase this sentence: you only have 4 points, you did not test any correlation… You have high abundance in spring which corresponds to high chl-a concentrations. This is the result. The term value is here too vague: I guess it is the abundance but could be also “phytoplankton”. So I suggest writing abundance if it is abundance.

Commenté [A35]: What does it mean? Too vague. I guess you mean with high biovol and high abundance. If yes you have to use these words.

Commenté [A36]: Not so clear based on fig. 6C…

m during day and night in all seasons (Fig. 6H). Cnidarians were overall not very abundant, but constituted an important fraction of the biovolume, especially in 200-300 m depth during day in all seasons, and 50-100 m depth during day time in summer and autumn. At night, they were mainly present in deeper layers 200-450 m (Fig. 6E). Mysida were mainly present in >100 m depth during the day, while a small fraction was found at night between 0 and 50 m in spring and between 50 and 100 m in autumn and winter (Fig. 6F). Chaetognatha were present mainly in intermediate layers between 100-300 m during day and night in all seasons (Fig. 6G).

Discussion

Physicochemical properties and mesozooplankton seasonal dynamics

The present study provides the first detailed data on the zooplankton community composition, distribution and dynamics in the northern Chilean Patagonia. There are only few zooplankton records with a high taxonomic resolution in Patagonian Chilean waters. Most of such studies were conducted in the central and southern parts. Only recently, zooplankton in the northern fjords is receiving more interest, particularly *Calanus* and *Euphausia* (e.g. Marín and Delgado, 2009; Sánchez et al., 2011; Valle-Levinson et al., 2014; Díaz-Astudillo et al., 2017). Palma (2008) described zooplankton distribution and abundance in the north, central and south of Chilean Patagonia, however, with a gap regarding zooplankton diversity in the northern fjords.

The Comau Fjord is connected to the Pacific Ocean by the Chacao Channel and Ancud Gulf. It possesses a two-layer system in water masses causing an estuarine circulation, characterized by a strong pycnocline, in which salinity increases from 10 to 32 over a depth of 15 m (Fig. 2B). The physicochemical observations in our study are consistent with earlier descriptions from Comau Fjord, subjected to strong terrestrial inputs, where surface waters (0-50 m) present higher variability than the deeper and quasi-homogeneous layer (Fig. 2). Clear differences were observed in temperature, pH, oxygen and Chl *a* in relation to the season, likely caused by the strong seasonal variability in solar radiation (maximum between spring and summer), precipitation and river discharge (maximum in late autumn and winter) (González et al., 2010).

In Comau Fjord, a thermal inversion of the surface layer (0-50 m) in winter is visible (Fig. 2), probably due to heat loss in the surface layer caused by winds and the discharge of cold freshwater from rivers and glaciers (Silva, Calvete & Sievers, 1997). Later in the year, the thermal density stratification stabilizes the water column, triggering a phytoplankton bloom in austral spring (Iriarte et al., 2007) with a strong peak in chlorophyll *a* (Fig. 2E). As shown by previous studies in the area (Palma and Silva, 2004; Vargas et al., 2008; González et al., 2010), this peak in chlorophyll *a* was most likely due to blooming chain-forming diatoms. The high phytoplankton biomass is expected to be grazed predominantly by copepods, increasing their biomass and establishing the classical diatom-to-zooplankton food web (Palma and Silva, 2004; Vargas et al., 2008; González et al., 2010). Accordingly, we found the highest zooplankton abundance during the most productive season, the austral spring. At this time, crustacean nauplii and young stages of calanoid copepods, which are indicative of intense zooplankton reproduction, accounted for a large proportion of the zooplankton community. During summer, biovolume and biomass reached their maxima (Fig. 3), indicating the growth of the zooplankton organisms. Subsequently, in autumn and winter, zooplankton abundance, biovolume and biomass decreased. At this time, primary production should be low, as reflected by low Chl *a* values (Fig. 2E), and likely zooplankton growth was food limited (Escribano et al., 2007). In winter, it is known that the plankton in the fjord shifts towards a microbial loop based community grazed by heterotrophic nanoflagellates, which become the main mesozooplankton prey (Vargas et al., 2008; González et al., 2010) but do not support a high secondary production.

Pronounced seasonality of environmental variables often results in high biological production and are associated to seasonal changes in the holoplankton community (Mauchline, 1998; Balbotín and Bustos, 2005; Aracena et al., 2011), and meroplankton abundance (Ladah et al., 2005; Landaeta & Castro, 2006). The northern part of the fjord region, the area between Puerto Montt and Guafo Mouth, represents the most productive area of Chilean Patagonia in terms of primary production and zooplankton biomass (Palma, 2008). In contrast, the phytoplankton production in the southern area is low due to the influence of glaciers, resulting in cold, fresh and turbid waters (Palma and Rosales, 1997; Palma and Silva, 2004; Iriarte et al., 2007; Palma, 2008), and consequently low zooplankton survival and growth (Giesecke et al., 2019). Previous studies described ranges for zooplankton biomass, expressed as the plankton wet volume, of 65 to more than 1386 ml zooplankton 1000 m^{-3} outside Comau Fjord, in the Inner Sea of Chiloé (Palma, 2008). This is in line with the present results (250-1500 ml zooplankton 1000 m^{-3}), showing an especially high biovolume during the summer season in Comau Fjord. Palma and Rosales (1997) also found the highest values of zooplankton biomass in the northern part (interior of Reloncaví Fjord and Ancud Gulf) with values that ranged between 56-1626 ml zooplankton 1000 m^{-3}, but a low zooplankton biomass in the inner of Comau Fjord. The observed variations may potentially be due to (a) temporal differences with a much lower Chl *a* concentration in their year of study for the same season (Ramírez, 1995); and/or (b) methodological and analytical differences, e.g. different sampling gears and proxies for biomass estimation (i.e. measurement of zooplankton wet volume vs. image analysis in this study).

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In fjord systems, oceanographic processes such as estuarine circulation, tidal mixing or water column stratification may influence the composition and abundance of zooplankton communities (Palma & Silva, 2004; Sánchez, González & Iriarte, 2011). Overall, copepods were the main contributors to the total biomass and biovolume of the zooplankton community, especially during summer (69-78%). This is in agreement with previous studies showing that in Chilean fjords, planktonic crustaceans, such as copepods and euphausiids, have the highest abundances and biomasses, followed by chaetognaths and gelatinous plankton (Defren-Janson et al., 1999; Palma and Silva, 2004). Copepods are the most abundant and diverse components of marine zooplankton worldwide (Mauchline, 1998), and the abundance of small copepods (<1.5 mm) generally surpasses the abundance of larger ones (Fransz, 1988; Gallienne and Robins, 1998; Gallienne et al., 2001). Similarly, small copepods accounted for 58-86% of the total copepod community in the present study. Small copepods are an important link between primary producers and epipelagic consumers, and it is thus important to quantify their contribution to the zooplankton community (Turner, 2004). Another important contributor to the zooplankton communities in Chilean fjords is the ~~most abundant and common~~ euphausiid *Euphausia vallentini*. This species mainly occurs in MSAAW, from the ocean to the interior waters of the fjords, where they are often found in dense swarms performing strong vertical migrations (Palma and Silva, 2004; Hamame and Antezana, 2010) . The present study revealed young stages of euphausiids during spring and summer but only one adult specimen in winter, indicating that euphausiids are present in Comau fjord, but have not been caught quantitatively in our samples. This is likely related to the small volume filtered by our net and the patchy distribution of *E. vallentini*, as well as the ability of these micronekton organisms to avoid small nets (Brinton, 1962).

Zooplankton diel vertical migration and population dynamics

Diel Vertical Migration (DVM) is usually associated with differences in light intensity within the photic zone, taking place periodically in 24 h cycles (Brierley, 2014). During day~~-~~time, zooplankton organisms migrate to deeper, darker waters to avoid visual predators, such as fishes, while they come to the surface for feeding at night (Hays, Webb & Frears, 1998). In Comau Fjord, we ~~see~~ saw patterns of DVM related to the size of the zooplankton. Here, a large proportion of zooplankton organisms that inhabit the intermediate waters (100-300 m) during day time ascended to shallow waters at night. But small organisms (individuals <1.5 mm), composed mainly of cyclopoids and harpacticoids, did not perform~~ed~~ a clear DVM. The two copepod groups, however, differed with regard to their vertical distribution. The highest abundances of cyclopoid copepods were found in the upper 100 m, whereas harpacticoids were found between 200-400 m (Fig. 6D). Their population dynamics followed the phytoplankton seasonal cycle, with the highest abundance in spring, while diminishing in summer to minima abundances in autumn and winter (Table 2).

Large individuals from several calanoid copepod taxa (*Metridia*, *Calanus*, Euchaetidae), mysids, chaetognaths and cnidarians did perform DVM over 300 m. This agrees with the findings by Hays (1995) that DVM is pronounced in large and pigmented species due to their susceptibility of being perceived by visually orientated predators. Similarly, studies in northern Patagonia have shown that conspicuous zooplankton organisms tend to avoid well illuminated waters (Villenas, Soto & Palma, 2009). According to Hays et al. (2001), large individuals of *Metridia* usually reside in deep waters, but a fraction of these ascends to shallow waters at night, whereas smaller individuals stay at the surface continuously. In Comau Fjord, *Metridia* showed the highest values of biovolume and abundance at intermediate depths (100-200 m) during daytime, but in the surface layers at night (Fig. 6B), which suggested the migration of the largest individuals towards the surface. In spring, a significant proportion of the *Metridia* population was found in shallow waters during the day. This was probably due to the smaller size of the individuals and the higher amount of food available here. Following the same pattern as *Metridia*, larger individuals of *Calanus* were found in deeper waters during day-time, whereas small specimens were found in shallow waters also during daytime in spring, where they likely escaped visual predators due to their small size. It is possible that the size differences between day and night might be a consequence of the presence of different species or life stages. Euchaetidae also performed DVM where most of the organisms lived continuously in the deepest waters (200-450 m) during the day, but a small proportion of the population migrated to the surface during night (Fig. 6I). These three copepod groups presented higher abundances in spring. In upwelling areas, where seasonal changes of environmental conditions are also pronounced, the highest abundances of *Calanus chilensis* were observed in spring and low abundances through autumn and winter (Hidalgo & Escribano, 2007).Therefore, the high abundance of their populations during these seasons is in association to the maximum concentration in phytoplankton, which decreased over time with minima during fall and winter.

Mysids were mainly detected in deep waters (>200 m water depth) accounting for up to 70% of the total zooplankton biovolume. Despite their high variability in their geographic distribution, mysids are typically hyperbenthic and able to feed on a wide range of food sources (Mauchline, 1980), from organic detritus on the seafloor during day (where they reside), and zooplankton, especially cyclopoids and harpacticoids, during the night when they migrate upwards. However, in Comau Fjord they were rarely found in the surface layer. According to Sánchez et al. (2011), the distribution of mesozooplankton in the upper 30 m is strongly influenced by the salinity stratification, which may act as a barrier for the DVM of some oceanic larger zooplankton organisms. Thus, the variability in surface temperature, salinity, pH, and oxygen could have acted as a barrier to the mysids' upward migration in Comau Fjord. Besides their important contribution to the total zooplankton biovolume in deep waters, mysids are often overlooked because of sampling limitations (Mauchline, 1980). Like euphausiids, mysids can form dense swarms, making them a potential food resource for a wide range of organisms, from predatory fishes to benthic CWC, but despite their importance in the marine food web, poor attention has been given to their presence in Chilean Patagonia. To our knowledge, there are only two studies describing mysids in this area: Guglielmo and Ianora (1997) found that the most abundant species for the Strait of Magellan is the deep-dwelling *Boreomysis rostrata*; Díaz-Astudillo et al. (2017) found higher abundances of mysids during night and inside the fjord for the Reloncaví Fjord and Ancud Gulf. Thus, this study constitutes the first record of mysids in Comau Fjord.

Chaetognaths were distributed throughout the water column with the highest biovolumes between 100-300 m, during both day and night (Fig. 6G). This is in accordance with the distribution found by Guglielmo and Ianora (1995) for the Strait of Magellan. Cnidarian~~´s~~ highest biovolumes were found in 50-100 m and in deeper layers (<200 m) during day and night, respectively. South of Comau Fjord, between Boca del Guafo and Pulluche Channel, the vertical distribution of cnidarians (i.e. Hydromedusae and Siphonophorae) showed that most of the specimens were distributed in the upper 100 m water depth and in deeper waters only in Moraleda and Darwin channels (Palma, Apablaza & Soto, 2007). Considering that copepods compose the principal source of food for cnidarians and chaetognaths (Palma & Kaiser, 1993), a higher abundance of carnivorous zooplankton was observed in spring, probably as a result of the increasing copepod abundance in Comau Fjord during this time. Therefore, the overall decline in copepod abundance from spring to winter may be explained by the decrease in phytoplankton concentration and the increase of the predation pressure imposed by carnivorous zooplankton.

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In the 50-100 m water layer a minimum in zooplankton abundance and biomass was found in all seasons (Fig. 4). This "zooplankton gap" could be related to a high concentration of predators in this water depth. In the northern fjords, the high biomasses and abundances of gelatinous organisms are correlated to a decrease in chitinous biomass of other organisms (Palma and Silva, 2004; Villenas et al., 2009; this study). It is known that chaetognaths and cnidarians can grow at high rates, form dense aggregations and seasonally dominate the zooplankton biomass (Casanova, 1999; Brodeur et al., 2002). Large densities of chaetognaths and gelatinous organisms, such as medusae and siphonophores, could decimate a zooplankton population as they are characterized by being voracious consumers of copepods and larvae from other organisms (Lie et al., 1983; Palma and Rosales, 1997). For instance, large aggregations of the siphonophore *Muggiaea atlantica*, common in the area (Palma & Rosales, 1997; Palma & Silva, 2004; Villenas, Soto &

Palma, 2009), lead to a decrease in fish stocks, due to competition over the same mesozooplankton prey (Purcell, 1985). In our study, we found a disproportionately large biovolume of carnivorous organisms (68-82% of the total zooplankton biovolume) in this water layer, particularly in summer and autumn, although it was not evident for spring and winter (Fig. 7). This may be due to the fact that euphausiids were not quantitively sampled and they may peak in this layer. According to Försterra and Häussermann (2012), euphausiids may reside around 150 m during daytime and migrate upwards close to the pycnocline at night. Because euphausiids are a potential food for many organisms, they could attract many predators, such as anchovies or blue whales, into the 50-100 m water depth which may reduce the mesozooplankton community. Therefore, this suggest that carnivorous zooplankton may have depleted zooplankton in this twilight zone and predation may play a role in structuring the vertical distribution of species in Comau Fjord.

In the present study, zooplankton abundance, biovolume and biomass, integrated over the entire water column, differed between day and night. It is difficult to reconcile this with a resident zooplankton community, where diel vertical migrations change the vertical distribution but not the water-column-integrated values. These differences were probably due to the high patchiness the zooplankton exhibited during day and night, especially by larger zooplankton individuals, and those able to form swarms (i.e. mysids and euphausiids). Biological processes, such as diel vertical migration, predator avoidance, location of food patches and mating are mechanisms by which the underlying zooplankton behavior present high spatial heterogeneity (Folt & Burns, 1999). Therefore, in Comau Fjord, those biological drivers are considered to be the main factors governing the distribution of zooplankton.

Ecological connection with cold-water corals

Mesozooplankton plays an important role in the food web as a food source for many pelagic and benthic organisms (González et al., 2013), including cold-water corals (CWC) (Gili et al., 2006; Carlier et al., 2009; Mayr et al., 2011). In Comau Fjord, CWC thrive despite the naturally acidified waters, in which the pH ranges from 8.4 to 7.4, representing aragonite over- to aragonite undersaturated waters (Häussermann and Försterra, 2007; Försterra et al., 2017). The occurrence of dense CWC banks colonizing the steep walls of the fjord is a long-standing enigma (Häussermann and Försterra, 2007; Fillinger and Richter, 2013a), as coral calcification is a challenge in aragonite-undersaturated waters (Orr et al., 2005; Guinotte et al., 2006). According to a laboratory study by Martínez-Dios et al. (2020), a high ingestion rate of the CWC *Desmophyllum dianthus* showed a positive impact on their calcification rates, regardless of the seawater pH.

Due to the difficulty of studying CWC *in situ*, little is known about their natural diet and their feeding capacity. Only recently, a study confirmed that *D. dianthus* preyed on medium and large sized calanoid copepods and euphausiids (Höfer et al., 2018). Based on our recent DVM data, shallow-dwelling CWC in Comau Fjord might feed on small copepods (e.g. cyclopoid and calanoid) and/or nauplii (Tsounis et al., 2010) during the day, and on larger organisms during night hours when zooplankton migrates upwards. Deeper-dwelling corals, by contrast, may mainly encounter larger prey, such as mysids or large calanoid copepods (Calanidae, Euchaetidae). Large seasonal variability affected the abundance and biomass of the zooplankton in Comau Fjord. Therefore, CWC must be adapted to differences in food availability, i.e. high zooplankton abundances during spring and summer and low concentrations during autumn and winter. In summer, CWC in Comau Fjord display high growth rates (Jantzen et al., 2013b) which may be associated with the high zooplankton availability. In winter, when zooplankton biomass is low, CWC may slow down their metabolism to cope with the low concentration of food available (Naumann et al., 2011).

Höfer et al. (2018) observed in laboratory experiments that *D. dianthus* showed no feeding saturation, when prey was up to five times more abundant than in nature. They suggested that CWC are able to exploit dense swarms of zooplankton which may aggregate near boundaries (Mauchline, 1980; Genin et al., 2005). *D. dianthus* is found in high densities, attached to the hard substratum of the steep walls from Comau Fjord, which can be found from 8 m water depth (directly below the pycnocline) down to the seafloor (~480 m) (Cairns, Häussermann & Försterra, 2005; Fillinger & Richter, 2013a). The highest abundances were, however, found above 270 m, where *D. dianthus* forms coral banks (Fillinger & Richter, 2013b). In these depths, as the present study shows, also the zooplankton biomass was the highest. If we assume a freestream flow of 5 cm s^{-1} and a current of 2.5 cm s^{-1} in the coral canopy near the wall, with a dense tentacle crown of 7 cm in diameter for a given coral individual capturing zooplankton in a volume of 250 ml at 0.5 efficiency (every second individual retained), we found that below 300 m water depth, CWC would have an annual mean capture of less than 790 preys per polyp a day. In shallow waters, CWC would have a supply rate of 5809-10754 preys per polyp a day between day and night. This could explain, why despite the availability of hard substrate, *D. dianthus* is not found in high numbers below 270 m (Fillinger & Richter, 2013a). We then conclude that 790 prey $polyp^{-1}$ day^{-1} could be the zooplankton flux necessary to sustain a viable coral population, beyond which a surplus of occasional krill swarms would be needed. Therefore, the high abundance of CWC in the aragonite-undersaturated waters of the Comau Fjord might be due to the high food availability provided by the zooplankton biomass (Cairns et al., 2005; González et al., 2010; this study).

Conclusions

The seasonal changes of zooplankton over the entire water column showed that abundance peaked in spring, likely due to a phytoplankton bloom during this time. In summer, biovolume and biomass ~~was~~ were the highest and decreased thereafter over time, reaching the lowest values in late autumn and mid-winter. Probably, the low concentration of Chl-*a* during the cold seasons could not support secondary production. The vertical distribution of zooplankton biovolume and biomass differed between day and night, with a daytime maximum in the 100-200 m water depth and a nighttime maximum in surface waters (0-50 m) associated with the diel vertical migration of the calanoid copepod *Metridia*. Overall, copepods were the dominant group of the total zooplankton community with an important contribution of the small organisms (individuals < 1.5 mm), followed by mysids, chaetognaths and cnidarians (biovolume and biomass), and nauplii and Appendicularia (abundance).

In Comau Fjord, cold-water corals (CWC) thrive despite its naturally acidified waters. To maintain their metabolic functions, CWC need to ingest a high amount of zooplankton. This study provides a description of the natural food spectrum for CWC where shallow corals may feed on small copepods or nauplii during day and larger organisms during night, while deeper-dwelling corals may mainly feed on mysids, euphausiids or larger calanoid copepods. CWC need to be adapted to the seasonal zooplankton variability with higher zooplankton abundances and biomass in spring and summer, and lower concentrations in autumn and winter. The high amount of zooplankton in Comau Fjord provides sufficient nourishment to maintain a viable coral population despite the aragonite under-saturated waters. Nevertheless, future studies are necessary to understand how CWC cope with small and large zooplankton preys and how much of the carbon and nitrogen ingested are directed to which metabolic pathways. Therefore, the Comau Fjord constitutes a natural laboratory where we can understand the bentho-pelagic coupling between zooplankton and CWC under low pH, in an area where anthropogenic activities are gaining importance jeopardizing the natural conditions for the marine biota.

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Tables:

Table 1: Regression equations between individual dry mass and body area to estimate biomass for different taxonomic groups given by Lehette and Hernández-León (2009)

Table 2: Integrated abundances (ind m^{-2}) of the most important zooplankton taxa over the entire water column sampled on four dates throughout a year.

Figures:

Fig. 1: Study site. (A) Overview of Chilean Patagonia. Red square denotes area in panel B. (B) Inner Sea of Chiloé where Comau Fjord (red dot) is located**.** (C) Comau Fjord with the bathymetry and location of the station where zooplankton samples were taken (red dot). Adapted from Fillinger & Richter (2013a).

Fig. 2: Vertical profiles of physico-chemical parameters in the Comau Fjord**.** ~~Physico-chemical parameters for~~ (A) temperature, (B) salinity, (C) pH, (D) oxygen and (E) Chlorophyll-*a* ~~of Comau Fjord~~. Note the break at 100 m with the different scales above and below.

Fig. 3: Zooplankton seasonal and diel distribution. Seasonal distribution of integrated (A) abundance, (B) biovolume and (C) biomass of the zooplankton community during day and night.

Fig 4: Zooplankton vertical distribution. Seasonal, diel and vertical distribution of (A) abundance, (B) biovolume and (C) biomass of the zooplankton community during day and night.

Fig 5: Taxonomic composition. ~~Percentage of taxonomic composition of~~Relative (A) biovolume and (B) abundance of major zooplankton groups. Taxa comprising less than 3% of the total zooplankton community (27 taxa) were pooled together as “other”.

Fig 6: Seasonal, diel and vertical distribution of the most important taxa. Vertical, diel and seasonal distribution of the most important taxa representing their biovolume and abundance (%) in relation to the rest of the zooplankton community. In (A) is presented the total sum of biovolume and abundance in all samples. Vertical distributions of (B) Metridinidae, (C) Calanidae, (D) Harpacticoida, (E) Cnidaria, (F) Mysida, (G) Chaetognatha, (H) Cyclopoida and (I) Euchaetidae is represented. The group “small calanoids (<1.5 mm)”, although higher than 5% both in biovolume and abundance, is not represented here as it is composed of a mix of taxa with different functions.

Fig 7: Copepods versus carnivorous zooplankton. Percentages of copepods versus carnivorous zooplankton for (A) total biovolume and (B) total abundance.

Table 1 Regression equations between individual dry mass and body area to estimate biomass for different taxonomic groups given by Lehette and Hernández-León (2009)

Commenté [A40]: Inadequate caption: the table does not give the regression equation, but the coefficients of this equation. You can give the general equation here also. Please explain what the "Area" column means: is it the range over which the coefficients are applicable (i.e. range from Lehette) or the range of areas you observed for each category in your own data?

Organism	*a*	*b*	*Area (mm^2)*
Actinopterygii (eggs and larvae)	43.38	1.54	0.079 – 1.198
Appendicularia	43.38	1.54	0.056 – 6.071
Ascidiacea (larvae)	43.38	1.54	0.072 – 1.652
Amphipoda	43.38	1.54	0.103 – 59.854
Brachiopoda (larvae)	43.38	1.54	0.193 – 0.366
Bivalvia	43.38	1.54	0.071 – 2.040
Bryozoa (larvae)	43.38	1.54	0.067 – 0.240
Chaetognatha	23.45	1.19	0.068 – 15.935
Cirripedia	43.38	1.54	0.071 – 0.286
Cladocera	43.38	1.54	0.072 – 0.455
Cnidaria	4.03	1.24	0.051 – 95.743
Copepoda	43.97	1.52	0.068 – 9.177
Crustacea (nauplii)	43.38	1.54	0.070 – 0.878
Decapoda (zoea)	43.38	1.54	0.072 – 6.733
Echinodermata	43.38	1.54	0.070 – 0.757
Euphausiacea	43.38	1.54	0.145 – 461.813
Eggs	43.38	1.54	0.070 – 1.952
Gastropoda	43.38	1.54	0.071 – 2.266
Isopoda	43.38	1.54	0.073 – 0.930
Mysidacea	43.38	1.54	0.126 – 43.504
Nemertea (pilidium)	43.38	1.54	0.082 – 0.777
Ostracoda	43.38	1.54	0.066 – 1.270
Platyhelminthes (larvae)	43.38	1.54	0.075 – 0.162
Polychaeta (larvae)	43.38	1.54	0.068 – 7.535

Commenté [A41]: Larvae, I guess

Commenté [A42]: Is it a mix between nauplii of copepods and those of cirripeds?

Commenté [A43]: I suggest you choose between the name of a larva, here pilidium, or the more general term "larvae". For example, for Bryozoa you can have cyphonautes

Table 2 Integrated abundances (ind m^{-2}) of the most important zooplankton taxa over the entire water column sampled on four dates throughout a year.

		SPRING		SUMMER		AUTUMN		WINTER	
		Day	Night	Day	Night	Day	Night	Day	Night
Cyclopoida		47,894	28,198	5,974	6,501	2,227	4,342	3,209	3,477
	Total	76,093		12,475		6,569		6,686	
Harpacticoida		48,632	47,978	9,664	12,421	9,929	7,486	6,514	4,345
	Total	96,610		22,084		17,415		10,859	
Nauplii		20,600	18,129	1,481	2,583	431	2,094	2,463	1,616
	Total	38,730		4,064		2,526		4,080	
Metridia		27,772	9,287	25,691	8,105	12,696	18,262	4,438	1,684
	Total	37,059		33,795		30,958		6,122	
Calanus		11,288	7,447	5,898	2,827	3,622	3,087	1,977	889
	Total	18,735		8,726		6,709		2,866	
Euchaetidae		1,840	4,259	1,731	1,110	790	873	1,060	733
	Total	6,091		2,840		1,663		1,793	
Cnidaria		4,895	2,546	1,520	3,713	702	2,432	4,636	2,848
	Total	7,442		5,233		3,134		7,484	
Chaetognatha		3,108	1,216	2,528	1,187	884	1,390	1,000	598
	Total	4,324		3,716		2,235		1,598	
Mysida		239	171	62	164	151	411	239	166
	Total	411		226		561		405	

Commenté [A44]: I think you cannot sum day and night abundances, because it artificially increases the abundance: the organisms present at nighttime are not added to those of the daytime, they replace them. So I suggest using a mean, not a sum.