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Vertically distinct sources modulate stable isotope signatures and distribution of Mesozooplankton in central Patagonia: The Golfo de Penas - Baker Channel connection and analogies with the Beagle Channel

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ABSTRACT

Using hydrographic and zooplankton sampling along with stable isotope analyses, we determined the influence of freshwater input and of oceanic water ingress at the Golfo de Penas to the Baker Channel (47°S), central Patagonia, on the zooplankton community during mid-spring. Our results show that different taxonomic and functional groups occurred within the mesozooplankton community along an offshore-inshore-oriented transect. Some groups occurred mostly offshore (i.e. euphausiids, fish larvae, stomatopods, amphipods), while others occurred in higher abundance inshore (i.e. medusae, chaetognaths, siphonophores, ostracods). Early life stages of ecologically key species, such as *Euphausia vallentini* and pelagic stages of *Munida gregaria*, occurred mostly at the Golfo de Penas. Higher trophic positions estimated from $\delta^{15}N$ occurred in mesozooplankton groups inshore (Baker Channel) and lower at the Golfo de Penas, coinciding with the decrease in C:N ratio in zooplankton and with an increase in chlorophyll-a values in the seawater seawards. The $\delta^{13}C$ distribution in the zooplankton groups along the offshore-inshore transect showed a positive gradient from the inshore most stations towards the Baker Channel mouth, suggesting a negative relationship with freshwater carrying terrestrial organic carbon and a positive relationship with seawater. However, from the channel mouth seawards, a decrease in $\delta^{13}C$ in most zooplankton groups occurred. Within the Baker Channel, low $\delta^{13}C$ values occurred in particulate organic matter (POM) at the surface layer, higher values at intermediate depths, and low values at the deepest zones. This uneven distribution of $\delta^{13}C$ values in POM and zooplankton, along with the presence of different water masses at different depths suggest an along-basin transport of organic carbon of different sources at different layers: of terrestrial origin at surface, marine origin at mid depth, and from degraded organic matter from offshore entering at higher depths. Thus, a complex scenario of lateral transport of water of different characteristics modulates the presence of zooplankton in different locations and their food sources along the area. These findings resemble others observed in further south in the Beagle Channel (57°S) also in spring but the relative contribution of different carbon sources may differ between Patagonian systems.

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1. Introduction

The connection of zooplankton between the continental shelf and fjords has not been studied intensively along Pacific Patagonia. Holoplanktonic species showing a circumpolar sub-Antarctic distribution (e.g. *Euphausia vallentini*) have been reported in inshore areas in the northern and southern Patagonia and well as in offshore waters (Hamame and Antezana, 2010). Recent studies have also documented eggs and larvae of some mesopelagic and demersal fish species occurring at the continental shelf break and inshore simultaneously (*Maurolicus parvipinnis*, Molina-Valdivia et al., 2021, *Macruronus magellanicus*, Veroes et al., 2022), or in offshore and inshore zones in consecutive seasons (offshore in winter; inshore in spring; *Merlucius australis*, Flores et al., 2019, 2020), suggesting the movement of adults to reproduce and use different nursery areas. Whether this capability of utilizing different habitats is a common feature shared by many zooplankton and ichthyoplankton taxonomic groups in Patagonia remains unknown.

The ingress of offshore organisms into the fjords and channels has been proposed to be triggered by seasonal changes in food webs. Along the inshore areas of the Chilean Patagonia, the pelagic food web is fueled by the classical diatom-based primary production in spring and summer, in contrast with the microbial-based trophic web that dominates during winter (González et al., 2010, 2011, 2013). In this region, the production of autochthonous organic matter by phytoplankton combined with allochthonous organic materials derived from terrestrial or anthropogenic origin, provides a heterogeneous pool of organic substrate available as food for microorganisms, pelagic and benthic consumers (González et al., 2019; Montero et al., 2021, 2022). Some key mesozooplankton components that may use this pool of organic matter and which drive the pelagic carbon flux at intermediate levels of the pelagic trophic web have been identified (e.g., *Euphausia vallentini* and pelagic juvenile *Munida* (=*Grimothea) gregaria;* Hamame and Antezana, 2010; Diez et al., 2012; González et al., 2016; Riccialdelli et al., 2017; Castro et al., 2021) but their seasonal variations in abundance and distribution along inshore and offshore areas of Patagonia have received less attention.

In the central Chilean Patagonia, the Baker Channel (47°S) is connected westwards to the Golfo de Penas while eastwards (inshore) it receives a large amount of freshwater from the most important rivers in Patagonia (Pascua and Baker rivers) and from runoff (Aiken, 2012; Moffat et al., 2018). Freshwater input in Patagonian fjords and channels tend to stabilize the water column and increase silicate concentrations, thus promoting diatoms growth and better feeding conditions for the zooplankton community (Goebel et al., 2005; Montero et al., 2017). However, the Baker Channel is characterized by a low surface phytoplankton biomass (dominated mainly by picoplankton) but in the river plume areas, terrestrial carbon could represent a significant food substrate for copepods (Vargas et al., 2011). Changes in meroplankton larval abundance in the Baker Channel system have been associated with seasonal variations in the freshwater outflow from the Baker River, with higher barnacle larvae abundance in spring (low river flux season) and bivalve larval dominance of meroplankton communities in summer, when the maximum river outflow occurs (Meerhoff et al., 2014). The key role of freshwater outflow driving advective processes has also been proposed, as the net transport of meroplankton has been determined at the surface moving layer towards the channel mouth (Meerhoff et al., 2015).

The zooplankton and ichthyoplankton distribution along fjords and channels are often associated with food availability (Hamame and Antezana, 2010; Contreras et al., 2014; Landaeta et al., 2012, 2015, 2019). However, feeding studies are not very common in Patagonia (e.g. gut content analyses) because they are very laborious, require detailed knowledge of microplankton taxonomy to identify the diet (sometimes partially digested) or use on-board experimentation which often is not applicable for multiple groups simultaneously, particularly in high latitudes due to rough weather conditions. The use of stable isotope analysis to study trophic webs represents a methodological advantage because it can be utilized for multiple taxonomic groups simultaneously and provide information that may be connected to environmental conditions that affect the spatial and temporal distribution of food sources. Stable isotopes are incorporated into the diet and heavier isotopes accumulate in the tissues of organisms. Carbon (^{13}C:^{12}C, δ^{13}C) and nitrogen (^{15}N:^{14}N, δ^{15}N) stable isotopes are widely utilized in trophic web studies (Bode and Alvarez-Ossorio, 2004; Riccialdelli et al., 2017; Presta et al., 2023a). Because the accumulation of ^{15}N in the tissues of consumers is relatively constant between trophic levels, the trophic position of an organism may be estimated by comparing its δ^{15}N isotope value with that at the base of the trophic web (Post, 2002). Similarly, because primary producers on land (such as C3 plants) fractionate C isotopes differently than primary producers in marine environments (such as diatoms and macroalgae), the proportion of terrestrial (transported by rivers, runoff, etc.) vs. marine organic carbon at any given trophic level may be estimated if the δ^{13}C values from the sources in an area are known (Vander Zanden and Rasmussen, 1999, 2001; Bode et al., 2006).

Along the northern and central Chilean Patagonia, δ^{13}C and δ^{15}N values were utilized recently to connect ichthyoplankton or zooplankton near surface distributions and their food and some oceanographic processes occurring between the inner and outer zones of the Sea of Chiloé (Bernal et al., 2020), at inner stations in the Baker Channel (Vargas et al., 2011) or during environmental disturbance (Glacial Lake Outburst Flows, GLOFs) in the Baker Channel (Meerhoff et al., 2019). These studies showed that the isotopic composition of some zooplankton groups at the shallower layers could be associated with terrestrial organic carbon entering the inner zone of the fjords and channels where the ingress of fresh water is high. However, the influence of seawater entering at deeper layers from offshore to the inner zones, on the zooplankton community has not been assessed in fjords and channels of Patagonia.

This study aims to determine how the oceanic water ingress at the Golfo de Penas and the freshwater input to the Baker Channel, affect the zooplankton community structure and feeding during mid-spring in the channel. The overall hypothesis of the paper proposes that the zooplankton distribution and food sources (as determined by stable isotopes) are modulated by lateral transport along the gulf and channel. The methodological approach consisted of determining the oceanographic conditions and collecting mesozooplankton at different depths along a transect from the Golfo de Penas to the Baker channel head, measuring the isotope composition in the zooplankton groups and in key species (*E. vallentini* and *M. gregaria* pelagic stages) to evaluate the origin of carbon supply (terrigenous vs. marine, based on their δ^{13}C values) in their diet, and to assess their trophic position (based on their δ^{15}N values) in the food web. Aiming to explore whether these distributional processes are recurrent along Patagonian fjords and channels, this study also compares our Baker Channel results with those in the Beagle Channel (57°S) reported in this issue (Presta et al., 2023a, 2023b; Bruno et al., 2023b) in which a detailed description was made of zooplankton distribution, pelagic food webs and energy budgets along the eastern side of the channel, an area where the fresh – salt water gradient along the channel is also a main hydrodynamics feature.

2. Methods

2.1. Study area

The Baker Channel system (48°S, 74°W; Fig. 1) is located in the central Chilean Patagonia between the two largest ice fields in South America, the Northern and Southern Patagonian Ice Fields. Along with glaciers, rivers, runoff, and groundwater, they supply fresh water to the Baker Basin system, increasing the water column stability and driving a positive estuarine circulation. Underneath the surface freshwater-influenced layer, an intermediate layer of warmer but saltier water ingresses the channel from the Golfo de Penas situated adjacent, seawards

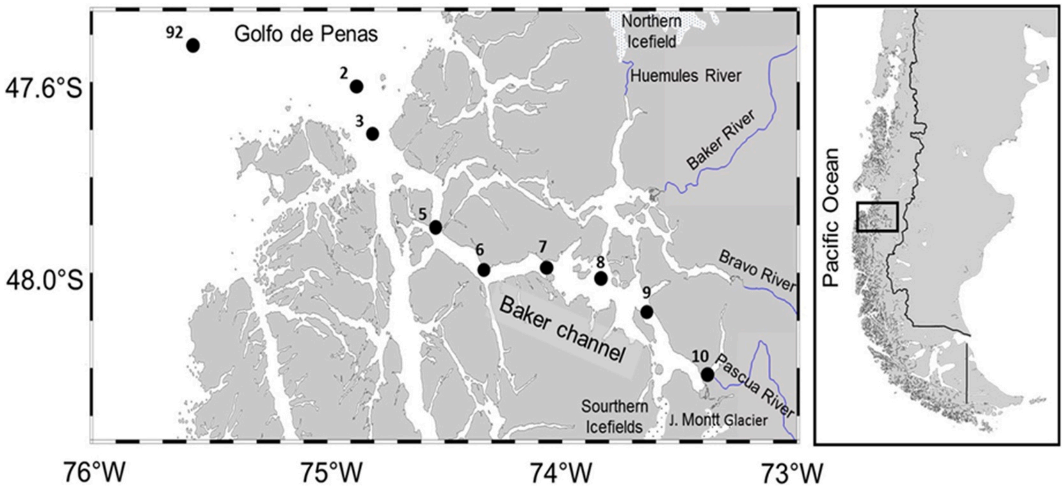

Fig. 1. Area studied showing the oceanographic stations sampled in the Golfo de Penas (92, 2, 3) and baker Channel (5, 6, 7, 8, 9 and 10).

to the Baker Channel mouth (Aiken, 2012; Moffat et al., 2018). Three water masses were identified offshore adjacent to the northern Patagonian zone: Sub-Antarctic Water (SAAW, 33–33.8 psu) up to 150 m in depth, remnants of Equatorial Subsurface Water (ESSW, 33.8–34.9 psu) between 150 and 300 m in depth, and Antarctic Intermediate Water (AAIW, 34 psu and 3 °C) below 300 m depth (Sievers and Silva, 2008). Out of them SAAW and ESSW have been identified in channels and fjords. The water resulting from SAAW and fresh water (FW) mixing is denominated estuarine water (EW, <33 psu) and it has been subdivided based on the salinity values as: Modified Subantarctic Water (MSAAW; 31 and 33 psu), Estuarine Saline Water (ESW, 21–31 psu), Estuarine-Brackish Water (EBW,11–21 psu) and Estuarine-Fresh Water (EFW, 2–11 psu) (Sievers and Silva, 2008). The ingress of freshwater around the head of the channel and intruding nutrients occur along with large amounts of glacial sediment that augments turbidity and modifies light penetration. These processes affect primary production and zooplankton behavior, as detected when glacial lake outbursts (GLOFs) have occurred, a process becoming more recurrent during the last decades in the entire Patagonia (Dussaillant et al., 2009; Ross et al., 2020).

2.2. Field work

From October 27 to November 15, 2017, a research cruise (CIMAR Fiordos-23) was carried out on board the RV Cabo de Hornos to Central Chilean Patagonia (47°S – 53°S). Three oceanographic stations at the Golfo de Penas (47°S, offshore) and five stations in the Baker Channel (inshore) were sampled along a transect from the continental shelf break (station 92, offshore) to the Pascua River mouth (station 10, inshore) at the head of the fjord (Fig. 1).

Hydrographic profiles were obtained at all oceanographic stations utilizing a 24-bottles (2 L) rosette equipped with a Seabird 25 CTD from the surface to approximately 10 m from the bottom. At each station, seawater samples from four depths (1 m (except station 92), 5, 10, and 50 m) were filtered (Whatman GF/F) for chlorophyll-a determination and then stored at −20 °C until the analysis. The chlorophyll-a concentration (mg/m^3) was subsequently determined fluorometrically (Turner Designs Model 10-AU Fluorometer) using the method described by Parsons et al. (1984). In addition, seawater samples were collected from all inshore stations (Baker Channel) at seven depths (0, 5, 10, 25, 50, 100, and 500 m) and filtered (GFF 0.7 um pore precombusted filters) for δ^{13}C analysis in particulate organic matter (POM). All samples were stored onboard at −20 °C and transferred to −80 °C in the laboratory.

Mesozooplankton samples were collected at all oceanographic stations by means of oblique tows using a mouth-opening Tucker trawl (300 μm mesh, equipped with a GO flowmeter) at three depth strata: 0–50, 50–100, and 100–300 m. Zooplankton sampling in both zones (offshore and inshore stations) included stations sampled during the day (stations 2, 3, 7, and 10) and at night (stations 92, 5, 6, and 9), depending on the cruise track. Once on board, the samples were split, and one fraction was preserved in 5% formalin for zooplankton identification and quantification. The other was drained and then frozen at −20 °C for later isotope (δ^{13}C, δ^{15}N) analyses. Additional zooplankton samples (0–50 m depth) were collected at a single station inshore (station 8) twice during the day and night to increase the number of organisms for isotopic analyses.

2.3. Laboratory work

In the laboratory, all the formalin-preserved zooplankton samples were identified to the major groups level and counted. Some samples were also identified at the species level (fish larvae) or developmental stage (squat lobster *M. gregaria*: Zoeae I—V, megalopa; euphausiid *E. vallentini*: calyptopis, furcilia, adults). All groups' abundances along the 0–300 m water column were expressed as ind/m^2. For visual purposes, in profiles showing the vertical distribution of zooplankton groups, abundance per stratum is expressed as individuals per m^3.

We intended to obtain individuals from all stations and depths for isotope analyses and total carbon and nitrogen determinations from the frozen zooplankton samples. However, the number of organisms (weight) requested for isotope analyses was not always accomplished at all stations or depths, particularly at the inshore stations where we obtained enough individuals from seven groups (along with some of the developmental stages of *M. gregaria* and *E. vallentini*). The number of individuals in each zooplankton group used for isotope analyses was estimated from the weight per sample, as described in the Stable Isotope Facility web page at the University of California at Davis (http://stableisotopefacility.ucdavis.edu/). The ^{13}C and ^{15}N isotopes in the samples were determined using an Elementar Vario EL Cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced with an Isoprime VisION IRMS (Elementar UK Ltd., Cheadle, UK) isotope ratio mass spectrometer, or a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The final delta values were expressed relative to the international standards Vienna Pee Dee Belemnite and Air for carbon and nitrogen, respectively.

2.4. Hydrographic data

The hydrographic data obtained at the different stations were utilized to construct maps with the horizontal distribution of sea surface salinity, sea surface temperature, and diagramming vertical sections of all hydrographic variables along the inshore-offshore sampled transect (ODV, V.5.3.0). T-S plots and mixing triangles were diagrammed in MATLAB R2015a (*pwma* y *theta_sdiag* functions) to identify the presence of the different water masses described for the zone at the Golfo de Penas and in the Baker Channel. The hydrographic characteristics reported by Silva et al. (1998), Sievers et al. (2002), Sievers and Silva (2008), and Silva et al. (2009) were used as references to classify these water masses.

2.5. Stable isotopes

A correction for δ^{13}C due to the lipid content in the mesozooplankton groups was performed following Kiljunen et al. (2006).

$$L = \left(93/\left(1+\left(0.246\times(C:N)\text{–}0.775\right)^{-1}\right)\right) \tag{1}$$

$$\delta^{13}C' = \delta^{13}C + D\times\left(I+\left(3.90/(1+287/L)\right)\right) \tag{2}$$

where L is the proportional lipid content of the sample, δ^{13}C' is the lipid-normalized value, C: N are the proportions of carbon and nitrogen, δ^{13}C is the measured value, D is the isotopic difference between the protein and lipid (7.02), and I is a constant (assigned a value of 0.048).

The relative importance of terrestrial particulate organic carbon (POC) in the diet of all zooplankton groups was estimated by applying a two-source mixing model (Bianchi, 2007):

$$\%POC_{terrestrial} = \left(\delta^{13}C_{sample}-\delta^{13}C_{marine}\right)/\left(\delta^{13}C_{terrestrial}-\delta^{13}C_{marine}\right) \tag{3}$$

where $\delta^{13}C_{\ sample}$ is the mean isotopic composition of each zooplankton group, $\delta^{13}C_{marine}$ is the marine end-member, and $\delta^{13}C_{terrestrial}$ is the terrestrial end-member. We utilized δ^{13}C values reported by Riccialdelli et al. (2017) for the Beagle channel and Patagonia, from C3 plants as terrestrial end-members ($\delta^{13}C_{terrestrial} = -27.5‰$, similar to that utilized by Vargas et al. (2011) in this same Patagonian region ($\delta^{13}C = -27.4‰$), and macroalgae values (mean from Chlorophyta, Rhodophyta, Phaeophyta) as marine end members ($\delta^{13}C_{imarne} = -13.9‰$), also reported by Riccialdelli et al. (2017).

The trophic positions of the different groups were estimated based on isotopic ^{15}N enrichment following the method described by Vander Zanden et al. (1997):

$$\text{Trophic Position (TP)} = \lambda + \left(\delta^{15}N_{organism}-\delta^{15}N_{base}\right)/3.4 \tag{4}$$

where $\delta^{15}N_{organism}$ is the isotopic value measured, 3.4 is the average $\delta^{15}N$ enrichment per trophic level (Post, 2002), and $\delta^{15}N_{\ base}$ is the δ^{15}N value from organisms that show an herbivorous feeding mode. In this study, we used a $\delta^{15}N_{\ base}$ value of 5.001 which was the lowest δ^{15}N value obtained from 45 samples of small-sized copepods (< 1 mm), collected in our zooplankton samples along the transect, most of which correspond to *Paracalanus parvus*. Assuming they were herbivorous (Jeyaraj and Santhanam, 2013), we utilized a λ (Trophic level of the base) reference value of 2 in the food web.

To estimate the isotopic niche widths, we used the SIBER package (Stable isotope Bayesian Ellipses) in R v3.6.1 (Jackson et al., 2011). The program first estimates the standard ellipse area (SEA) that describes the data in a δ^{13}C–δ^{15}N space for each group. Subsequently, it performs an arithmetic correction for a small number ($n < 30$) of samples (SEA corrected, SEAC). After that, the Bayesian estimate of the standard ellipse areas (SEAB) of all zooplankton groups was calculated.

2.6. Statistical analyses

Statistical tests included those assessing whether the zooplankton abundance of each taxon differed between the Baker Channel and Golfo de Penas areas and at sampled depths. A two-way PERMANOVA, utilizing sites (inshore/offshore) and depths (three depths) as factors, was employed to test these differences and determine the interaction between factors. The tests were run in R version 3.5.1 with the PERMANOVA function (version 1.0; Anderson, 2005, 2008). Tests were conducted for 20 mesozooplankton-ichthyoplankton groups. $p < 0.05$ was considered significantly different.

Kruskal–Wallis's non-parametric tests were utilized to look for differences in stable isotope values between zooplankton collected during the day and night. We used the same tests to explore differences in isotope values between locations (Baker Channel vs. Golfo de Penas) in the groups present in both areas, in which we counted with enough number of replicates for the different isotopes to run the tests. To determine whether the data showed a normal distribution we utilized a Kolmogorov-Smirnov test with the Lilliefors correction. All analyses were carried out in R (v. 3.3) using the library nortest and function Lillie. test.

Testing for potential changes associated with diel vertical migration (interaction terms) was not possible due to the low (and uneven) number of stations and isotope replicates of most groups at different depths in each zone.

To assess whether the isotope values in zooplankton groups present in the Golfo de Penas and Baker Channel could be associated with the hydrographic characteristics present in each area, principal component analyses (PCA) were carried out utilizing the zooplankton isotope values at different strata and the values of hydrographic variables (temperature, salinity, dissolved oxygen) corresponding to the mean depth of the zooplankton sampled strata at each station.

3. Results

3.1. Hydrographic characteristics

Marked gradients in hydrographic characteristics occurred from the head of the Baker Channel to offshore stations on the continental shelf. Surface (2 m) salinity and temperature values increased from 3.25 psu and 8.8 °C at the head of the Baker basin to 33.52 psu and 10.2 °C offshore at station 92 (Fig. 2 a–b).

Vertically, the effect of the freshwater ingress at the head of the basin (cold and low-salinity layer; EW) was noticeable down to 40–50 m all along the channel up to the Baker Channel–Golfo de Penas connection (Station 3), where it was interrupted but continued further offshore at

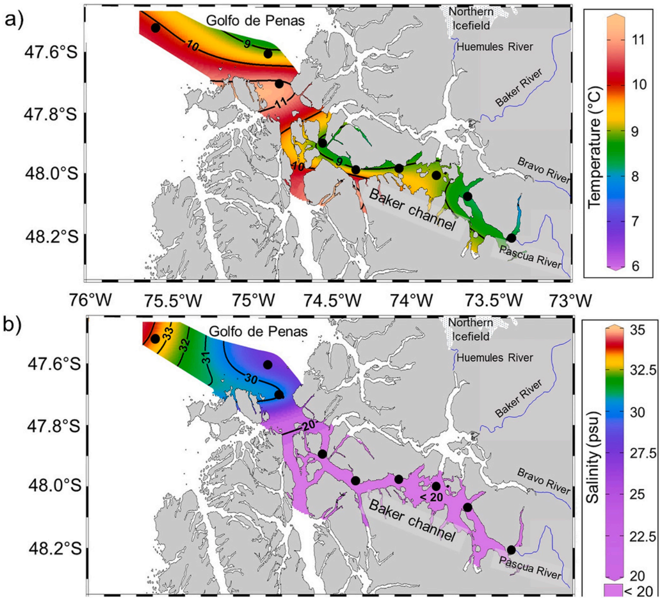

Fig. 2. Surface (1 m depth) a) Temperature (°C) and b) Salinity (psu) along the Baker Channel- Golfo de Penas transect. Isohalines and color codes below 20 psu (see text) are not shown for visual purposes.

the Golfo de Penas (Fig. 3). At the inshore stations, a large salinity and temperature difference occurred between depths of 5 and 10 m. The difference decreased along the channel (insert of Fig. 3 a, b). The vertical structure of temperature along the sampled transect showed that at least three layers of seawater were present at different depths. At the surface, low-temperature water resulting from the ingress of cold freshwater from the Pascua River and glaciers (Jorge Montt) occurred in the inshore area and flowed seawards along the basin (EW). At station 3, warmer and saltier seawater from offshore encountered the outgoing surface low-salinity water and sank below it, forming a second layer that extended along the entire Baker Channel at mid-depths (centered at 40–80 m but extending down to 120-150 m; SAAW). This layer connected with salty and warmer water located at offshore station 92. Cold and salty water occurred at the deepest zones along the channel basin (150–1000 m, stations 8–9) and extended from the external seaward stations (station 92) to the inshore-deep zone. At the offshore station at the shelf break, salty and even colder water than the minimum values observed at the same depth inshore occurred from ~200 m down to the maximum sampled depth offshore (> 1000 m). An inspection of the T–S diagrams indicated that a mixture of the same three water masses found at station 92 at the Golfo de Penas (SAAW, ESSW, and AAIW) were also present in the Baker Channel. The water located deeper at station 8 in the Baker Channel had the same temperature and salinity values as those found in water located at 200–300 m in the Golfo de Penas, coinciding with the description in the vertical sections (Fig. 4) and with previous reports in both zones (Silva and Neshyba, 1979/1980).

The dissolved oxygen concentration also varied along the sampled transect (Fig. 3). High values of dissolved oxygen occurred in a narrow depth range (< 10 m) at the surface of the inshore stations, with a depth range that broadens along the Baker Channel and extends seawards to

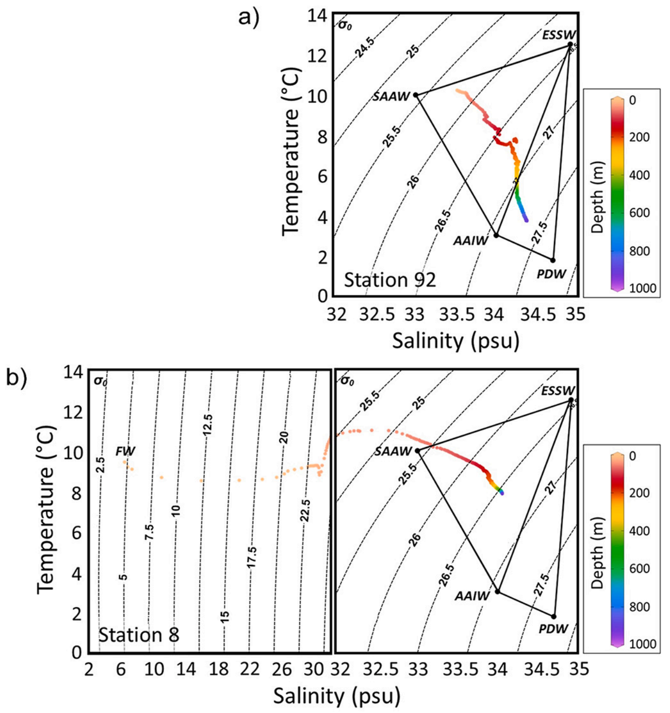

Fig. 4. T-S diagram showing three water masses identified a) offshore (Station 92) and b) inshore (Station 8) at different depths.

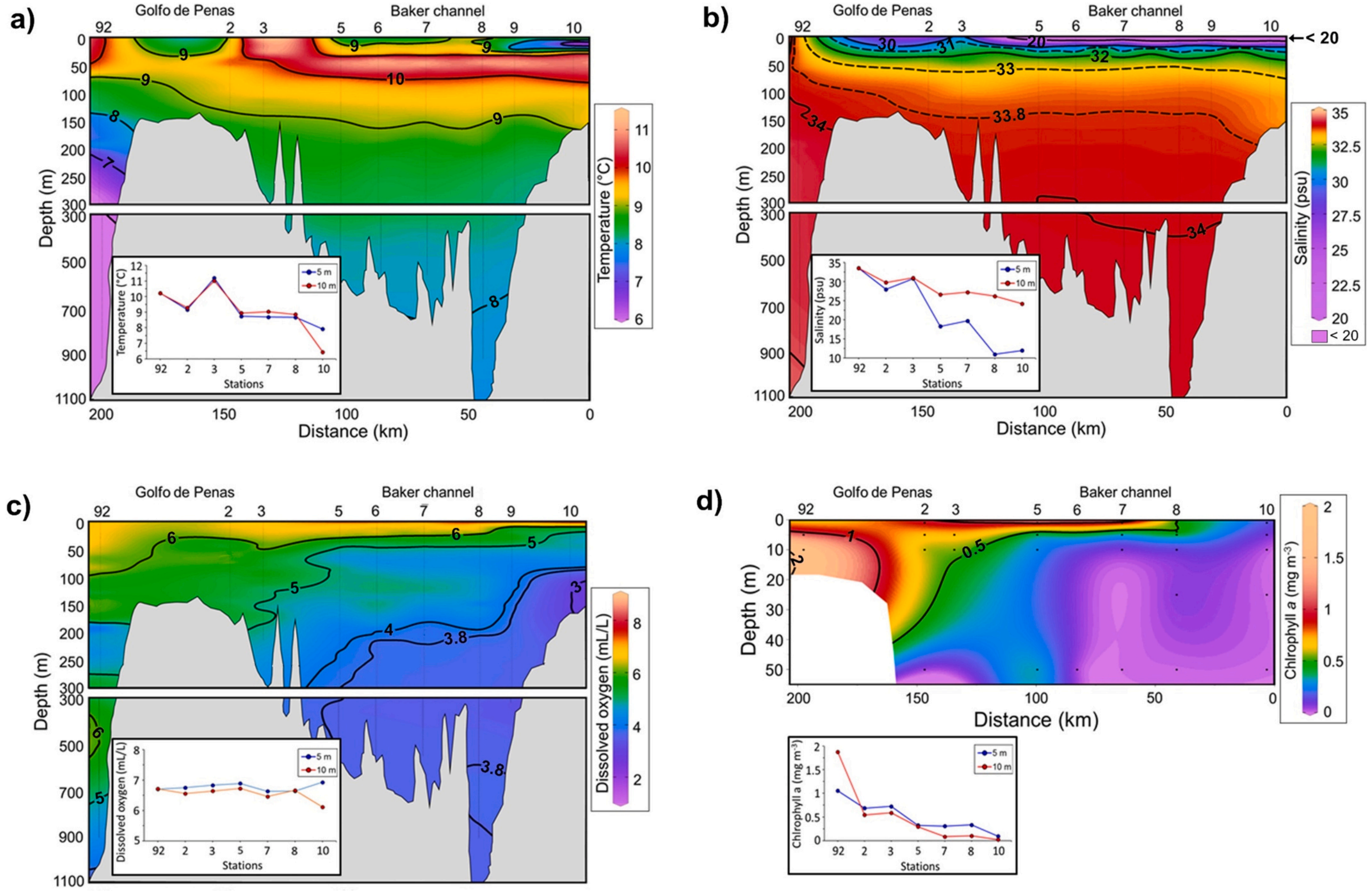

Fig. 3. Vertical sections of a) temperature (°C), b) salinity (psu), c) dissolved oxygen (mL O_2/ L) and d) chlorophyll *a* concentration (mg/m^3). Isohalines and color codes below 20 psu (see text) are not shown for visual purposes. Inserts in the sections are values at 10 and 15 m depth along the transect.

the Golfo de Penas. Below this layer of high dissolved oxygen concentrations, oxygen values below 4 mL/L were observed all along the Baker Channel. At the offshore station (92), most of the water column was well oxygenated with values >5 mL O_2/L down to 700 m deep, except at a mid-water layer between 200 and 250 m and again below 900 m, where values decreased.

Chlorophyll-a concentrations also changed from the Baker Channel to the Golfo de Penas (Fig. 3). Along most of the Baker Channel, chlorophyll-a values at 5 m depth were slightly lower than those at 10 m depth and increased steadily seawards. However, offshore at station 92, chlorophyll-a values at 10 m increased more than at 5 m depth reaching values approximately one order of magnitude higher (from 0.2 to 2.0 mg Chl-a/m^3) concerning 10 m inshore concentrations (Fig. 1 e, insert). Considering all values, chlorophyll-a values differed between the Golfo de Penas and the Baker Channel (K—W, $X^2 = 4.36$, $p = 0,037$), being higher in the Golfo de Penas (mean 0.72 ± 0.58 mg/m^3) than in the Baker Channel (mean 0.27 ± 0.34 mg/m^3).

The particulate organic matter (POM) along the Baker Channel showed low δ^{13}C values (−26.52‰ to −27.57‰) in surface water (0–50) and at higher depths (−26.21‰ to −27.88‰ at 300–550 m) (Fig. 5). The highest δ^{13}C values (−22.76‰ and − 25.20‰) in POM all along the Baker Channel were observed at the high-salinity intermediate layer (100 m) at stations 8 and 5.

3.2. Zooplankton distribution

Fifteen mesozooplankton groups were found along the sampled transect: three were gelatinous (siphonophores, medusae, chaetognaths), eight were chitinous (copepods, ostracods, euphausiids, zoea, *Sergestes arcticus*, amphipods, stomatopods, *Munida gregaria*), two were ichthyoplankton (eggs and larval fish), and two were mollusks (paralarvae) and polychaetes (Table 1). Most euphausiids were *Euphausia vallentini*, the dominant euphausiid in Patagonia. Within this group, we classified them into three developmental stages: calyptopis, furcilia, and adults. Five zoeae and the megalopa stage were classified as the galatheid *Munida gregaria*. Ichthyoplankton included total fish eggs (not identified to the species level) and larvae (five species: *Maurolicus parvipinnis, Sebastes oculatus, Pinguipes chilensis, Lampanyctodes hectoris*, and *Macruronus magellanicus*).

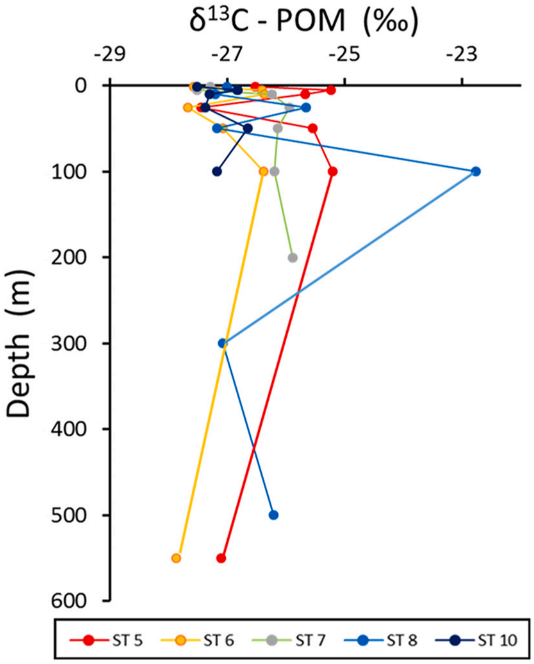

Fig. 5. Carbon δ^{13}C values in particulate organic matter (POM) along the water column at stations located in the Baker Channel.

The most abundant zooplankton groups (> 500 ind/m^3) were copepods, euphausiids, and ostracods, which were present at almost all stations (7–8) along the transect. Gelatinous groups were intermediate in abundance (50–500 ind/m^3) and were present at all stations. Other groups that occurred at all stations were chaetognaths, zoeae, and polychaetes, while the first two occurred in moderate abundance and the latter was present in low numbers (< 50 ind/m^3). Fish eggs and larvae occurred at very low abundances (< 5 ind/m^3). Larvae identified at the species level were present in only a few stations (2–5 stations).

The horizontal distribution of the zooplankton groups differed along the transect (Fig. 6). Euphausiids, fish larvae, zoea stages (*M. gregaria*), stomatopods, amphipods, and *S. arcticus* were more abundant offshore at Golfo de Penas. Other groups, such as gelatinous groups (medusae, chaetognaths, and siphonophores) and ostracods, occurred mostly at the inshore stations close to the inner area of the Baker Channel. Fish eggs and polychaete larvae occurred at similar abundances at most stations along the transect. Copepods, with high numbers along the transect, were more abundant at the inshore station (Table 2).

The vertical distribution of the different mesozooplankton groups also varied between the Golfo de Penas (offshore) and Baker Channel (inshore). While groups present in higher abundance at the offshore stations tended to occur at all sampled depths, often showing high numbers in the shallow sampled stratum (0–50 m) (Fig. 7), mesozooplankton groups occurring inshore at higher abundance were also present along the sampled water column, but in higher abundance at the intermediate sampled stratum of higher salinity (50–100 m). The statistical results shown by the zone × depth interaction term in the PERMANOVA analyses indicated significant differences mostly for larval stages of the groups in which these stages were considered (zoeae in *M. gregaria*, calyptopis, and furcilia in euphausiids, and fish larvae) (Table 2).

3.3. Stable isotope (δ^{13}C, δ^{15}N) and C:N ratio variation in mesozooplankton groups

Stable isotope values were obtained from nine mesozooplankton groups in the Golfo de Penas and six groups in the Baker Channel (Table 3). At the Golfo de Penas, seven were crustaceans (copepods, euphausiids (three developmental stages), ostracods, *M. gregaria* (five developmental stages), amphipods, stomatopods, and *S. arcticus*), one was gelatinous (chaetognaths), and one was a mollusk (paralarvae). In the Baker Channel, all the groups were crustaceans and were present at the Golfo de Penas also.

There was a general trend of increasing δ^{13}C values in zooplankton groups from the inshore to the outer stations along the Baker Channel and then from stations 3–4, a slight decrease again towards the outer stations at the Golfo de Penas. This trend occurred in the mesozooplankton groups, independent of whether they were more abundant at the inner or outer stations (Fig. 8). A decrease in δ^{15}N values occurred in mesozooplankton groups from the inner parts of the Baker Channel towards the outer stations at the Golfo de Penas. The C:N ratios in zooplankton followed an increasing pattern from the inner stations to most offshore stations along the sampled transect (Fig. 8).

Considering all groups and both zones, the overall range of mean δ^{13}C values in the groups was narrow (−18.2‰ to −15.2‰; zoea IV *M. gregaria* at Baker Channel and megalopa *M. gregaria* at Golfo de Penas, respectively). At the Baker Channel, the mean δ^{13}C values in mesozooplankton groups ranged from −18.2‰ to −15.6‰. At the Golfo de Penas, they ranged between −18.1‰ and − 15.2‰. The groups that were present in both zones (copepods, euphausiids, ostracods, zoea IV of *M. gregaria*, and *S. arcticus*) tended to show slightly lower mean δ^{13}C values at the Baker Channel than at the Golfo de Penas, except for amphipods that showed the opposite trend (Table 3).

The mean δ^{15}N values in all mesozooplankton groups in both zones ranged from 6.8‰ (ostracods, offshore) to 14.1‰ (*S. arcticus*, inshore).

Table 1
Mean abundance (±standard deviation) of zooplankton groups and number of stations with presence of those groups at the sampled along the entire Baker Channel – Golfo de Penas transect and at each of these two zones. Total number of stations where zooplankton was quantified along the transect are 8 (3 offshore and 5 inshore).

	TOTAL		GOLFO DE PENAS		BAKER CHANNEL	
	Stations	Abundance	Stations	Abundance	Stations	Abundance
	n	Ind/m^3	n	Ind/m^3	n	Ind/m^3
Copepods	8	4495.6 ± 5249.1	3	2750.4 ± 1773.2	5	5542.7 ± 6556.7
Euphausiids						
Euphausia vallentini (all stages)	7	1445.8 ± 3489.6	3	3667 ± 5542.8	4	112.7 ± 160.2
Calyptopis	7	431.6 ± 964.0	3	1089.2 ± 1486.9	4	37.1 ± 42.9
Furcilia	7	336.6 ± 628.4	3	776.9 ± 942.7	4	72.5 ± 118.8
Adults	3	675.4 ± 1908.4	1	1799.5 ± 3116.8	2	0.9 ± 1.8
Ostracods	8	536.8 ± 886.6	3	57.7 ± 70.5	5	824.2 ± 1047.7
Chaetognaths	8	434.3 ± 584.2	3	70.4 ± 43.5	5	652.6 ± 661.3
Siphonophores	8	109.0 ± 156.3	3	42.2 ± 32.3	5	149.1 ± 192.0
Zoea all taxa	8	104.5 ± 104.0	3	200.4 ± 118.9	5	46.9 ± 28.2
Decapods, Galatheidae						
Munida gregaria (all stages)	4	53.0 ± 94.9	2	137.8 ± 119.4	2	2.2 ± 3.2
Zoea I	3	1.4 ± 2.5	2	3.2 ± 3.6	1	0.4 ± 0.9
Zoea II	3	3.2 ± 7.0	2	8.4 ± 10.3	1	0.1 ± 0.2
Zoea III	4	7.5 ± 13.7	2	19.3 ± 18.0	2	0.4 ± 0.6
Zoea IV	4	25.2 ± 46.1	2	65.8 ± 58.7	2	0.8 ± 1.7
Zoea V	4	15.3 ± 28.2	2	39.9 ± 36.4	2	0.6 ± 1.0
Megalopa	2	0.4 ± 1.0	2	1.1 ± 1.5	0	0
Medusae	8	67.5 ± 126.4	3	20.5 ± 8.4	5	95.8 ± 158.9
Amphipods	7	16.3 ± 14.4	3	23.6 ± 12.4	4	12.0 ± 14.9
Polychaeths	8	15.1 ± 14.8	3	13.1 ± 7.3	5	16.3 ± 18.7
Stomatopods	2	0.2 ± 0.4	2	0.5 ± 0.5	0	0
Cephalopods						
Paralarvae	2	0.1 ± 0.2	2	0.2 ± 0.3	0	0
Decapods, Sergestidae						
Sergestes arcticus	3	0.4 ± 0.8	1	0.8 ± 1.4	2	0.1 ± 0.3
Fish eggs	7	26.1 ± 28.9	3	34.0 ± 39.5	4	21.4 ± 24.7
Fish larvae (total)	6	11.3 ± 24.8	3	27.7 ± 38.6	3	1.4 ± 1.8
Maurolicus parvipinnis	2	1.6 ± 4.5	2	4.3 ± 7.3	0	0
Pinguipes chilensis	5	1.4 ± 2.2	3	3.3 ± 2.8	2	0.3 ± 0.6
Macruronus magellanicus	3	0.2 ± 0.3	3	0.5 ± 0.4	0	0
Lampanyctodes hectoris	3	3.9 ± 10.2	3	10.3 ± 16.2	0	0
Sebastes oculatus	2	0.4 ± 0.9	2	1.0 ± 1.4	0	0
Not identified larvae	6	3.8 ± 7.2	3	8.4 ± 11.3	3	1.1 ± 1.3

Comparing the δ^{15}N values of the groups present in both zones, the mean δ^{15}N values tended to be higher in zooplankton in the Baker Channel (Table 3) than in the Golfo de Penas. The stable isotope values (δ^{13}C, δ^{15}N) of the individuals collected of the four groups that were present at the Golfo de Penas and Baker Channel did not show differences between day and night (Kruskal-Wallis, $P > 0.05$), except for amphipods (Kruskal–Wallis's, $p = 0.049$).

The mean C:N ratios varied between 4.7 ± 1.0 and 11.8 ± 2.8 in zooplankton from the Golfo de Penas and between 0.2 ± 3.3 and 5.9 ± 1.7 at the Baker Channel. The groups that were present in both zones tended to have higher mean C:N ratios in the Golfo de Penas (Table 3).

Principal component analyses (PCA) combining isotope data and hydrographic characteristics were possible for the four groups that were present in the Golfo de Penas and Baker Channel (Fig. 9). The three first principal components explained >83% of the total variability in the four zooplankton groups (Appendix, Table 1). In amphipods, the first and second principal components explained 34.2% and 30.2% of the total variability, respectively. In copepods, the first and second principal components explained 34.7% and 26.4% of the total variability. In ostracods, the first and second principal components explained 36.4% and 31.6% and in *E. vallentini*, they explained 36.1% and 30.5% of the total variability, respectively. Dissolved oxygen exhibited the highest (positive) correlation coefficients with the first principal components in amphipods (0.93), copepods (0.89), and *E. vallentini* (0.90), and the second highest correlation with the second principal component in ostracods (0.86) (Appendix, Table 2). Salinity was highly correlated with the first and second principal components in copepods (0.82), ostracods (−0.82), and *E. vallentini* (0.86). δ^{15}N also showed high correlation values with the first or second principal components in copepods (0.93) and ostracods (−0.81).

3.4. Trophic positions, terrigenous organic carbon, and isotopic niche widths, in mesozooplankton groups

Trophic position estimated for the mesozooplankton groups varied from 2.5 (ostracods) to 4.3 (mollusk paralarvae) at the Golfo de Penas, and between 3.3 (zoea IV *M. gregaria*) and 4.7 (*Sergestes arcticus*) at the Baker Channel (Table 4). Except for zoea IV *M. gregaria*, all mesozooplankton groups tended to have higher trophic positions in the Baker Channel (Table 4).

The proportion of terrigenous-derived organic carbon in the mesozooplankton groups varied from 10% (megalopa *M. gregaria*) to 31% (Chaetognaths) at the Golfo de Penas (Table 4). A similar range of terrigenous carbon was observed in the mesozooplankton groups analyzed at the Baker Channel (from 12% to 31%). However, when the same mesozooplankton groups were compared inshore and offshore, those present in the Baker Channel showed higher proportions of terrigenous organic carbon than those from the Golfo de Penas (except amphipods).

The isotopic niche widths were estimated for only four groups that were present in sufficient numbers at the Golfo de Penas and Baker Channel. The δ^{13}C–δ^{15}N plots showed that these groups had different isotopic mean values depending on their zone of collection (Fig. 10a), and these values were determinants of the separation of the different group ellipse plots (Fig. 10b) and the area of the estimated isotope ellipse (Fig. 10c). Copepods showed the largest ellipse areas in both zones. However, the areas occupied by the other three groups did not follow the same order between zones (i.e., while ostracods showed the narrowest

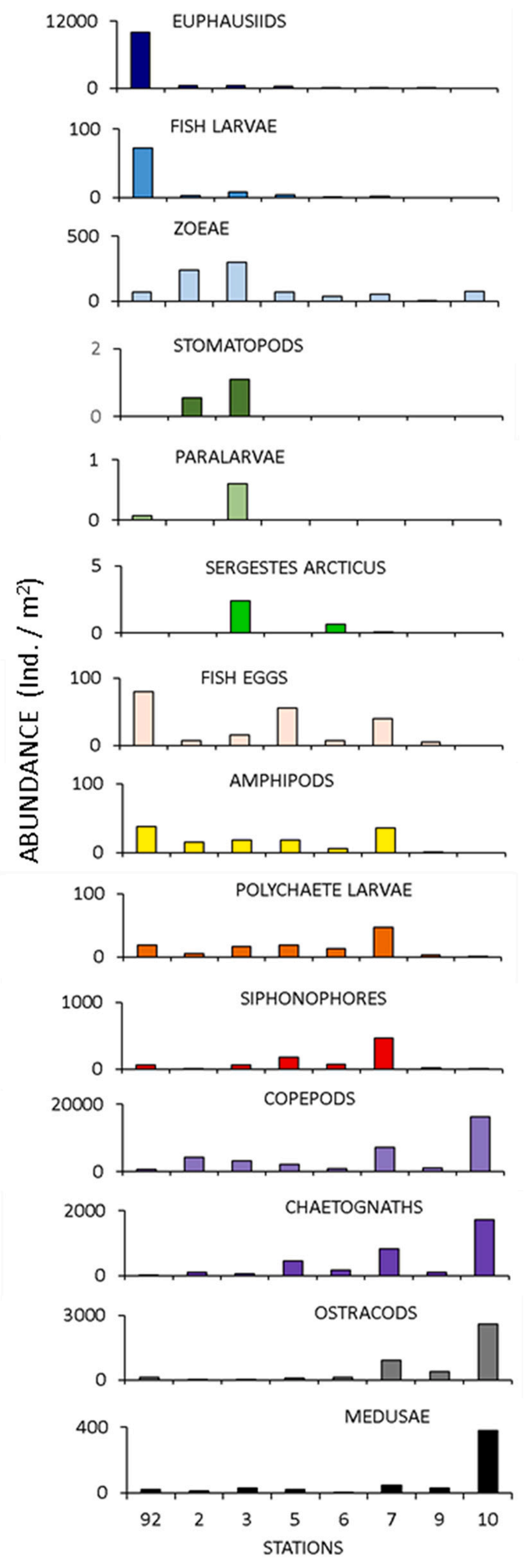

Fig. 6. Abundance (ind./m^3) of mesozooplankton groups (0-150 m depth) along the Golfo de Penas- Baker Channel transect.

ellipse area at the Baker Channel, euphausiids presented the narrowest ellipse area at Golfo de Penas). The ellipse area of zooplankton groups showed no trend in terms of ellipse areas being consistently larger (or smaller) in one or the other zone (ellipse areas were larger inshore for some groups and smaller for others) (Table 4, Fig. 10c).

3.5. *Euphausia vallentini*

The developmental stages of *E. vallentini* were more abundant in the Golfo de Penas than in the Baker Channel (Fig. 11a). Adults were the most abundant stage, followed by the calyptopis and furcilia. The three stages occurred in all strata sampled (Fig. 11b). Calyptopis and furcilia showed differences in vertical distribution between the Baker Channel and Golfo de Penas (PERMANOVA, site × depth, $P < 0.05$; Table 2).

The mean δ^{13}C values were similar between the calyptopis and furcilia and decreased at the adult stage in both zones (Tables 3 and 4, Fig. 11c). An increasing trend of δ^{15}N values occurred from the youngest to the oldest stages in both zones. The C:N values, instead, showed an opposite trend, decreasing from the youngest to the adult stage in both zones.

The trophic position and proportion of terrigenous organic carbon increased from the calyptopis to furcilia and the adult stage in both zones (Tables 3 and 4). In the two older stages, the mean trophic position and terrigenous carbon were higher in the Baker Channel than in the Golfo de Penas. As depicted by the elliptical areas (Tables 3 and 4), while the isotopic niche width was larger in adult *E. vallentini* inshore (4.7) than offshore (2.0), the opposite occurred for the furcilia stage (1.6 vs. 3.1) (Figs. 11d, e).

3.6. *Munida gregaria*

All developmental stages of *M. gregaria* were more abundant in the Golfo de Penas than in the Baker Channel (Fig. 12a). Zoea IV was the most abundant stage of all. The vertical distribution of all stages included all sampled strata along the water column. The oldest stages, zoea V and megalopa, tended to occur at a higher abundance in the deepest layer (Fig. 12b). From zoea III to the megalopa stage, differences in vertical distribution were detected between those in the Baker Channel and Golfo de Penas (PERMANOVA, site × depth, $P < 0.05$; Table 2).

The δ^{13}C values showed a decrease from zoea I to zoea V, followed by an increase during the megalopa stage (Fig. 12c). The δ^{15}N values followed a different trend: they increased steadily from zoea I to megalopa. Zoea IV was the only stage at which isotopes were measured in both areas. This stage presented lower δ^{13}C values at the Baker Channel than at the Golfo de Penas, in contrast to the δ^{15}N values that were higher at the Baker Channel than at the Golfo de Penas. The C:N ratios were similar among *M. gregaria* zoeae (means per station 7.1 ± 0.7 to 7.3 ± 0.6) but higher than megalopae (6.1 ± 1.8) of this species. Zoea IV had a lower C:N ratio in the Baker Channel (5.3 ± 0.9) than in the Golfo de Penas (7.1 ± 0.7).

At the Golfo de Penas the trophic position of *M. gregaria* megalopae (overall mean: 3.5 ± 0.3) were higher than those of zoeae of this species (zoeae trophic position means: 3.0 ± 3.1±) (Table 4). While the proportion of organic carbon of terrestrial precedence in zoea stage tissues varied from 18% to 21%, the proportion in megalopa reached only 10% (Table 4). Zoea IV, the only *M. gregaria* developmental stage in both zones, presented higher terrigenous organic carbon content in individuals from the Baker Channel (31%) than from the Golfo de Penas (20%). The ellipse areas (isotopic niche width) were estimated only for Golfo de Penas individuals. These were similar for all zoea stages but different for megalopa, which showed a larger area (Figs. 12d, e).

4. Discussion

The overall results revealed, for the first time in central Patagonia, that the zooplankton groups differed along the offshore-inshore transect and that δ^{15}N values and trophic position of the different groups also varied, a spatial trend concordant with the C:N ratios of the zooplankton groups along the transect. The inshore-offshore δ^{13}C in zooplankton groups changed also along the Baker Channel and Golfo de Penas transect. Similarly, δ^{13}C in POM changed horizontally and vertically,

Table 2

Results of a two-way PERMANOVA testing for differences in zooplankton abundance (imd./3) between the Baker Channel and the Golfo de Penas, among sampled depths and the interaction between these two factors. In bold*, significant values (<0.05).

	Groups	Factor	df	F	p	Groups	Factor	df	F	p
Mesozooplankton	Copepods	Site	1	7.52	**0.050**	Stomatopods	Site	1	9.18	**0.015***
		Depth	2	1.64	0.129		Depth	2	2.44	**0.033***
		Site/depth	2	1.14	0.804		Site/depth	2	3.56	**0.036***
	Euphausiids	Site	1	1.77	**0.041**	Paralarvae	Site	1	5.36	**0.026***
		Depth	2	0.95	0.217		Depth	2	2.11	**0.047***
		Site/depth	2	0.22	0.132		Site/depth	2	10.11	0.066
	Chaetognaths	Site	1	2.72	**0.012**	Zoea I	Site	1	4.00	**0.043***
		Depth	2	0.69	0.421		Depth	2	1.08	0.234
		Site/depth	2	1.73	0.295		Site/depth	2	0.10	0.264
	Siphonophores	Site	1	3.07	**0.049**	Zoea II	Site	1	7.24	**0.018***
		Depth	2	0.18	0.784		Depth	2	0.55	0.447
		Site/depth	2	0.97	0.899		Site/depth	2	0.47	0.123
	Zoea all taxa (total)	Site	1	1.39	0.117	Zoea III	Site	1	7.92	**0.009***
		Depth	2	0.44	0.743		Depth	2	0.88	0.344
		Site/depth	2	1.09	0.619		Site/depth	2	5.30	**0.030***
	Ostracods	Site	1	1.91	**0.043**	Zoea IV	Site	1	8.40	**0.019***
		Depth	2	0.79	0.336		Depth	2	0.11	0.749
		Site/depth	2	0.62	0.464		Site/depth	2	2.26	**0.023***
	Amphipods	Site	1	4.39	**0.020**	Zoea V	Site	1	8.35	**0.008***
		Depth	2	0.83	0.312		Depth	2	0.84	0.322
		Site/depth	2	0.59	**0.026**		Site/depth	2	5.63	**0.026***
	Hydrozoa	Site	1	0.31	0.592	Megalopa	Site	1	7.79	**0.009***
		Depth	2	0.49	0.834		Depth	2	1.03	0.245
		Site/depth	2	2.02	0.450		Site/depth	2	6.68	**0.028***
	Polychaets	Site	1	0.02	0.905	Furcilia	Site	1	9.68	**0.004***
		Depth	2	0.57	0.515		Depth	2	0.68	0.464
		Site/depth	2	2.51	0.491		Site/depth	2	5.76	**0.035***
	S. arcticus	Site	1	3.82	**0.049**	Caliptopys	Site	1	10.34	**0.003***
		Depth	2	0.54	0.518		Depth	2	0.94	0.295
		Site/depth	2	0.17	0.092		Site/depth	2	6.99	**0.022***
Ichthyoplankton	*M. parvipinnis*	Site	1	4.54	**0.025**	*L. hectoris*	Site	1	10.27	**0.004***
		Depth	2	2.42	**0.028**		Depth	2	1.03	0.278
		Site/depth	2	11.04	0.069		Site/depth	2	6.27	**0.013***
	P. chilensis	Site	1	7.79	**0.010**	*S. oculatus*	Site	1	3.19	0.086
		Depth	2	1.05	0.251		Depth	2	0.75	0.398
		Site/depth	2	1.06	0.148		Site/depth	2	1.09	0.285
	M. magellanicus	Site	1	8.79	**0.006**	–	–	–	–	–
		Depth	2	4.39	**0.006**	–	–	–	–	–
		Site/depth	2	6.83	**0.040**	–	–	–	–	–

which coincided with water of different characteristics and sources. Altogether, these results suggest that an along-basin transport of organic carbon from different origins occurs at different depths (terrestrial origin at surface, marine origin at mid depth, and apparently from degraded organic matter from offshore at higher depths), influencing the δ^{13}C availability in the offshore and inshore zones, and subsequently affecting the zooplankton isotopic composition.

Strong salinity and temperature gradients were observed along the Baker Channel-Golfo de Penas transect and vertically along the water column, respectively. The hydrographic sections revealed the ingress of cold freshwater from the Pascua River and adjacent glaciers at the head of the channel from where it moves seawards at the sea surface, which has been documented in estuaries and fjords in this area (Valle-Levinson et al., 2007; Sievers and Silva, 2008). At the seaward zone of the transect, salty but warmer and more oxygenated water subsided and entered the Baker Channel, moving horizontally towards the inner part of the channel below the surface freshwater plume. Deeper along the Baker Channel, colder, salty, and less oxygenated water (probably residual ESSW cold water carrying degraded organic matter) is present below warm and salty water. The seawater characteristics of this deeper layer extend from the Golfo de Penas, where it was observed along the upper half of the water column (100–200 m). This complex hydrographic scenario, which includes layers with different hydrographic characteristics moving in different directions, has been described for the Golfo de Penas-Baker Channel. The intrusion of warm water from the Golfo de Penas and its advection below the freshwater surface layer have been reported during different seasons (Aiken, 2012; Moffat et al., 2018). This subsurface temperature maximum is part of the intermediary circulation and is a common feature in Chilean Patagonian fjords (Pickard, 1971; Silva and Calvete, 2002; Valle-Levinson et al., 2007; Aiken, 2012). The ecological role of the subsurface warm water intrusion in Patagonian fjords and channels, along with the occurrence of hydrodynamic fluctuations associated with the sub-Antarctic annual mode, have been identified in recent years, including the intrusion of nutrient-rich water from the continental shelf, vertical water column mixing at the head of the channel bringing nutrients to the surface illuminated layer and enhancing primary production, and potentially, the ingress of zooplanktonic organisms to the inner part of the channel (Meerhoff et al., 2015; Moffat et al., 2018).

The zooplankton groups were distributed differently along the inshore-offshore transect. At the inner zone of the Baker Channel, some of the most abundant zooplankton groups were medium-sized crustaceans (1–2.5 mm in length; copepods, ostracods) and gelatinous organisms (medusae, chaetognaths, siphonophores). At the Golfo de Penas, they were large-sized crustaceans (2–8 mm in length; euphausiids, stomatopods, *S. arcticus*, and zoea) and ichthyoplankton. Differences in zooplankton distribution along inshore-offshore transects have been detected in northern Patagonia before. Reported medusae and siphonophores distributions along a Boca del Guafo – Reloncaví Fjord transect (Palma et al., 2011), for instance, coincided with our results on higher abundances of these groups at inner zones of the Baker Channel where a more stratified water column and higher copepod abundance occurred. Moreover, further south, in the Beagle Channel (Tierra de Fuego) Presta et al. (2023a) found differences in taxonomic composition

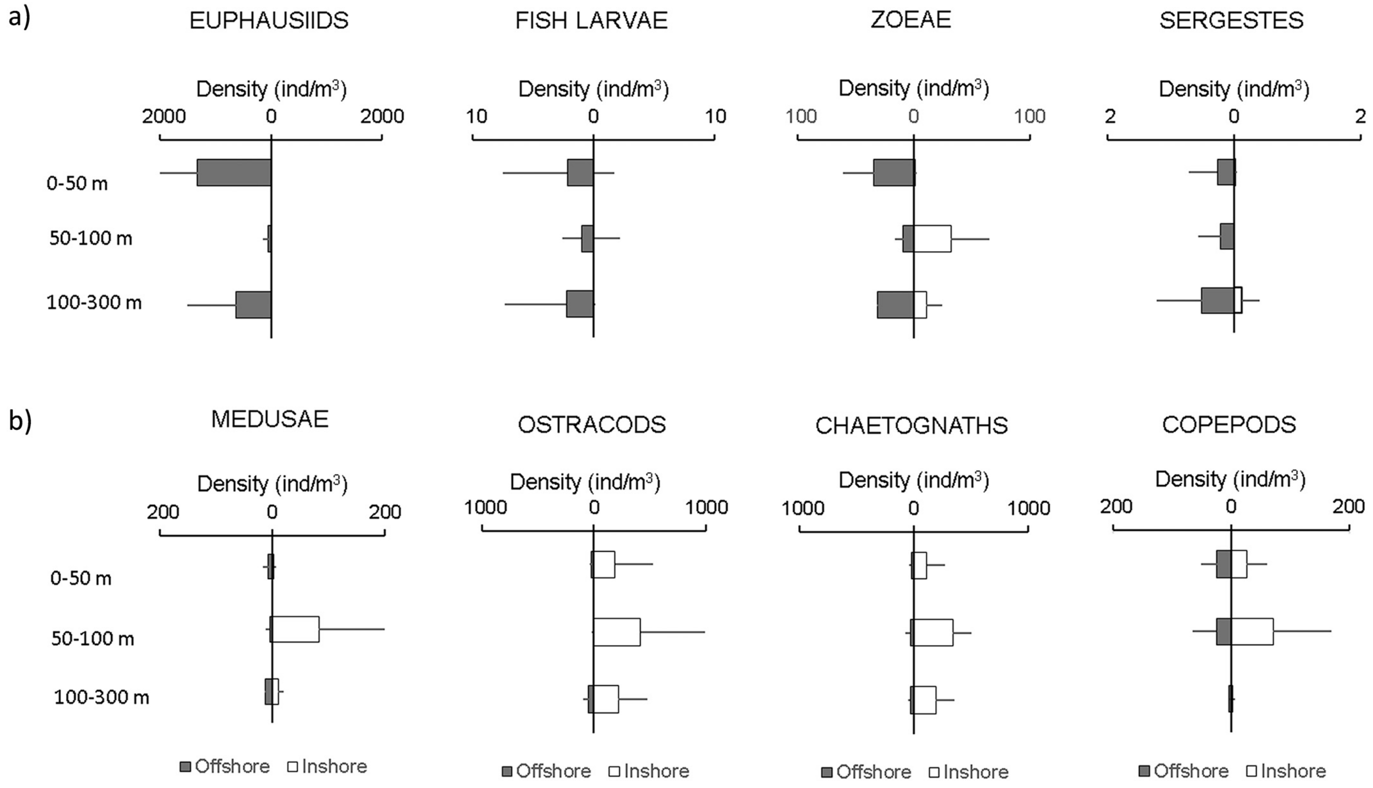

Fig. 7. Vertical distribution of zooplankton groups located in higher abundance at the a) offshore most stations in the Golfo de Penas and b) inshore most stations in the Baker Channel. Values are mean abundance and standard deviations per sampled stratum.

Table 3
Number of samples analyzed for stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and C:N ratios in zooplankton from the Baker Channel and Golfo de Penas. Values correspond to mean and standard deviations per zone.

	GOLFO DE PENAS				BAKER CHANNEL			
	Samples	$\delta^{13}C$	$\delta^{15}N$	C:N	Samples	$\delta^{13}C$	$\delta^{15}N$	C:N
	n	‰	‰		n	‰	‰	
Copepods	33	−16.88 ± 1.4	8.8 ± 2.0	11.0 ± 4.4	63	−18.1 ± 1.0	13.4 ± 2.2	5.4 ± 0.8
Euphausia vallentini								
Caliptopys	4	−17.1 ± 0.3	7.6 ± 0.3	7.5 ± 0.6	0	–	–	–
Furcila	19	−17.0 ± 0.6	8.6 ± 0.8	7.0 ± 1.1	5	−17.3 ± 0.5	9.9 ± 1.7	5.9 ± 1.7
Adults	28	−17.9 ± 1.3	9.5 ± 1.5	4.7 ± 1.0	24	−18.1 ± 0.9	11.8 ± 0.6	4.1 ± 0.5
Ostracods	10	−17.2 ± 0.9	6.8 ± 0.5	8.8 ± 0.9	17	−17.8 ± 1.3	13.6 ± 1.0	5.7 ± 0.5
Chaetognaths	4	−18.1 ± 1.2	8.8 ± 0.4	11.8 ± 2.8	0	–	–	–
Siphonophores	1	−18.4	5.3	3.3	0	–	–	–
Munida gregaria								
Zoea II	5	−16.4 ± 0.5	8.4 ± 0.8	7.3 ± 0.3	0	–	–	–
Zoea III	10	−16.6 ± 0.5	8.5 ± 0.4	7.3 ± 0.6	0	–	–	–
Zoea IV	12	−16.6 ± 0.3	8.6 ± 0.6	7.1 ± 0.7	2	−18.2 ± 0.5	9.6 ± 1.0	5.3 ± 0.9
Zoea V	9	−16.8 ± 0.4	8.6 ± 0.5	7.3 ± 0.5	0	–	–	–
Megalopa	9	−15.2 ± 1.1	10.0 ± 0.9	6.1 ± 1.8	0	–	–	–
Amphipods	19	−17.2 ± 1.0	9.2 ± 1.5	9.9 ± 5.3	17	−15.6 ± 1.3	11.7 ± 1.4	0.2 ± 3.3
Stomatopods	5	−16.8 ± 0.5	9.9 ± 1.2	6.6 ± 0.4	0	–	–	–
Paralarvae	2	−17.1 ± 0.7	12.8 ± 1.0	6.7 ± 0.7	0	–	–	–
Sergestes arcticus	8	−17.2 ± 0.8	8.9 ± 0.9	6.3 ± 0.3	2	−17.8 ± 0.7	14.1 ± 4.4	4.2 ± 1.0

and abundances of the mesozooplankton community between an inshore to offshore gradient of this channel also associated to environmental conditions.

The trophic positions we estimated were different between zones: while at the Baker Channel (inshore) their trophic position varied between 3.3 and 4.7 (suggesting their feeding was as first or second order carnivores), at the Golfo de Penas their position varied between 2.5 and 4.3 suggesting they were feeding at lower trophic levels offshore that might include phytoplankton, omnivores or first order carnivores (Post, 2002). Higher C:N ratios were determined in zooplankton located offshore, at the Golfo de Penas, compared with those inshore, at the Baker Channel. Thus, assuming that the high C:N values in zooplankton tissues indicate a high carbon content in the diet (or lower consumption of highly nitrogenated compounds), the C:N ratios of the different zooplankton groups conform to the general expectations based on their trophic positions and the inshore-offshore distribution of their food sources (i.e. lower trophic position in offshore zooplankton where higher phytoplankton biomass was determined).

The vertical distribution of the different zooplankton groups within the Baker Channel and Golfo de Penas varied in association with the

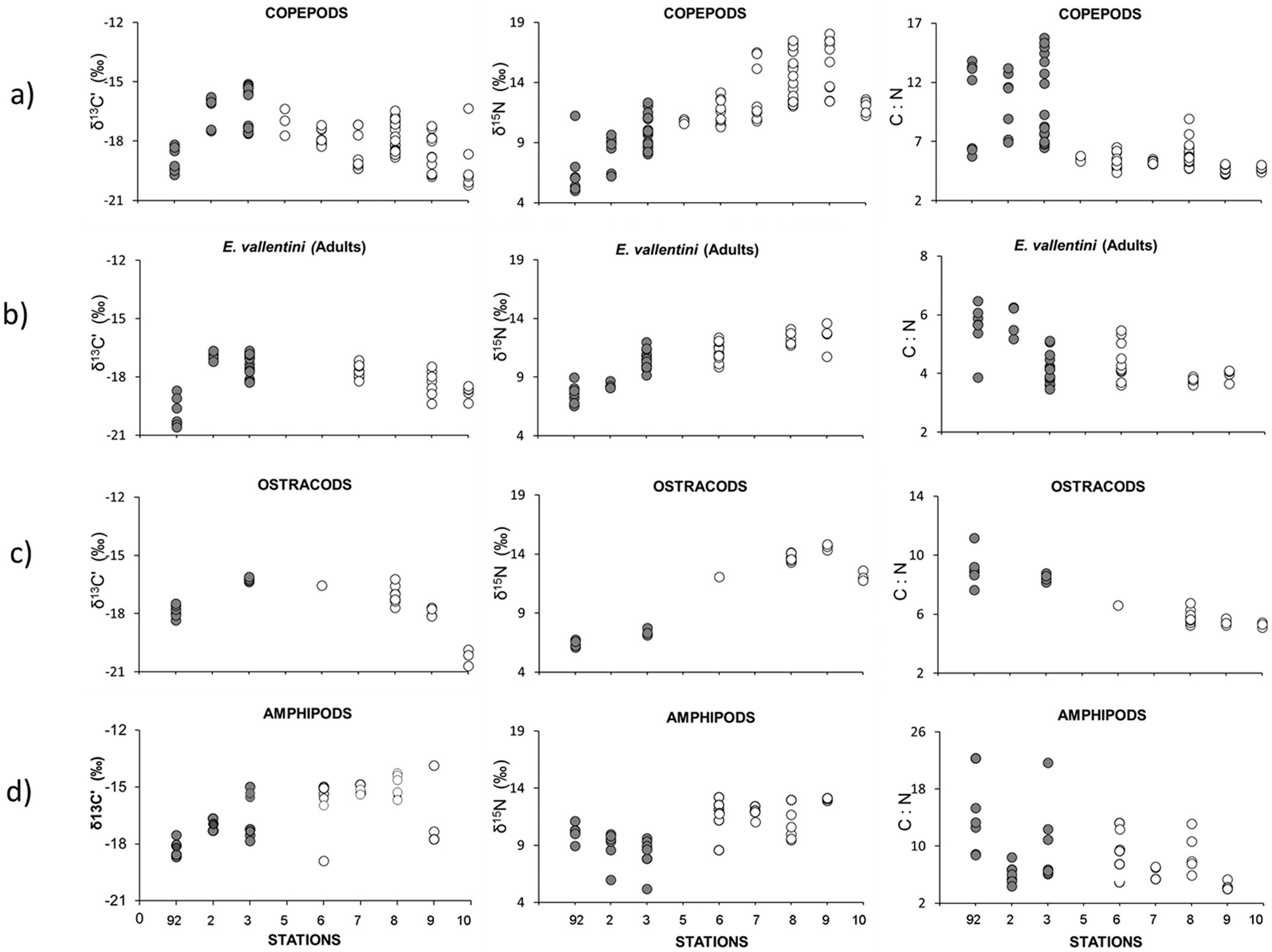

Fig. 8. Stable isotope ($\delta^{13}C$, $\delta^{15}N$) values and C:N rations in a) copepods, b) euphausiids (adult *E. vallentini*), c) ostracods and d) amphipods along the Golfo de Penas – Baker Channel transect. Dark circles: Golfo de Penas stations; open circles: Baker Channel stations. Values are from all zooplankton sampled strata in each station.

hydrographic characteristics. In the Baker Channel, most zooplankton groups tended to occur in higher abundance at intermediate depth (50–100 m) coincident with the presence of warm and salty water that entered the channel from the offshore area (Aiken, 2012). At that depth, water contained POM with high $\delta^{13}C$ values indicated organic carbon of marine origin, as opposed to lower $\delta^{13}C$ values at shallower depths indicating organic content of terrestrial origin (Vargas et al., 2011; Lafón et al., 2014). Similarly, but in a horizontal variation, Presta et al. (2023a) found the highest abundances in mesozooplankton at outer sectors of the Beagle Channel were saltier and warmer waters occurred in concomitant with high $\delta^{13}C$ values. The opposite was found at the inner sector of the Beagle Channel. In Golfo de Penas, the vertical distribution of the mesozooplankton groups was broader at the offshore station where the water column was less stratified and where the phytoplankton concentrations were high at most sampled depths. The different vertical distributions per zone were statistically detected for some groups, but more clearly for those in which their early life stages were studied. The reasons for this difference between older and earlier stages are not clear and may probably be the result of the more limited mobility of the former compared with older stages that can vertically migrate over longer distances or to ontogenetic differences in tolerance to contrasting hydrographic conditions at different depths (Castro et al., 1993, 2011; Valle-Levinson et al., 2014). In this study, we sampled stations at night and during the day inshore and offshore. However, due to the uneven and low number of stations in both zones, we could not test for diel vertical migrations that may have contributed to the larger variability in the mean abundance of older individuals per strata that precluded the detection of statistical differences in their vertical distribution per zone.

4.1. *E. vallentini and M. gregaria early life stages, distribution, ontogenetic changes in feeding*

Euphausia vallentini and *M. gregaria* pelagic stages have been reported as key species in pelagic trophic webs in Patagonia. The three developmental stages of *E. vallentini* studied here occurred in both sampled zones. However, their abundance was one to three orders of magnitude (depending on the stage) higher in the Golfo de Penas, particularly at the offshore station (St. 92), than in the Baker Channel. *Euphausia vallentini* is a pelagic species of the southern hemisphere located in sub-Antarctic areas and is reported to be abundant in oceanic waters of the Indic and Pacific Oceans, and in fjords and channels in Patagonia (Hamame and Antezana, 2010). Although this species is the dominant and most frequent euphausiid species in Patagonia, information on potential differences in the abundance of its life stages latitudinally or inshore versus offshore remains limited. Literature on the distribution of adult stages suggests two areas of higher abundance: the inner Sea of Chiloe (northern Patagonia) and the Magellanic zone (southern Patagonia), which coincide with the presence of baleen whales that feed on this euphausiid species (Buchan et al., 2021; Castro et al., 2022). Within

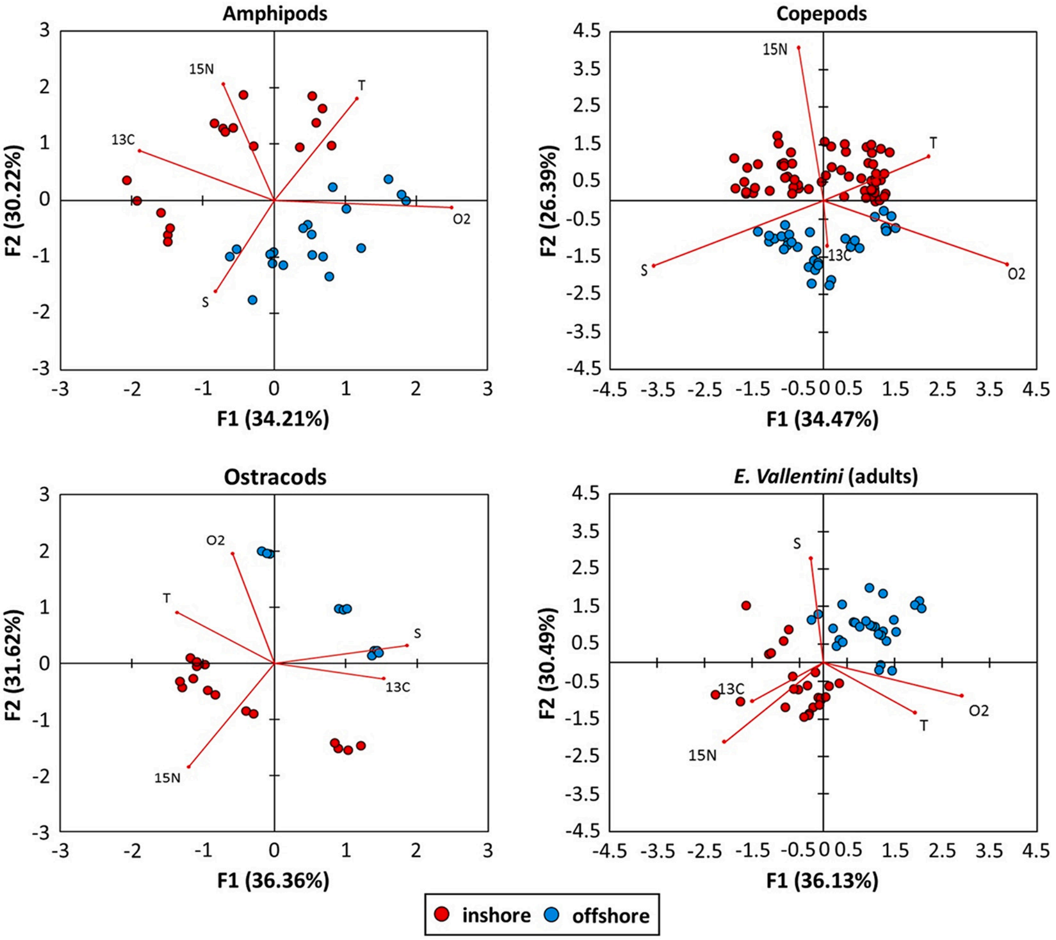

Fig. 9. Principal component analysis (PCA) in four zooplankton groups (amphipods, copepods, ostracods and *E. vallentini* (adults)), located at the Golfo de Penas (●) and Baker Channel (●) stations, in which isotopes (δ^{13}C, δ^{15}N) and hydrographic variables (T: temperature (°C); S: Salinity; O2: dissolved oxygen (mL/L)) were included.

Table 4

Proportion of terrigenous carbon (%) in body tissues, trophic position and isotopic niche width (corrected Stable Isotope Bayesian Ellipse Areas, SEAc) of the different mesozooplankton groups at the Baker Channel and Golfo de Penas stations. The number of samples analyzed per mesozooplankton group at each zone are the same as for isotopes in Table 2. Groups without isotope niche width estimated are because of number of replicates for the SEAc analyses were not enough.

	GOLFO DE PENAS			BAKER CHANNEL		
	Terrigenous Carbon	Trophic position	Isotopic niche width	Terrigenous Carbon	Trophic position	Isotopic niche width
Copepods	0.22 ± 0.11	3.1 ± 0.6	6.58	0.31 ± 0.07	4.5 ± 0.7	9.33
Euphausia vallentini						
Calyptopis	0.24 ± 0.02	2.8 ± 0.1	–	–	–	–
Furcila	0.23 ± 0.05	3.1 ± 0.2	–	0.25 ± 0.04	3.4 ± 0.5	–
Adults	0.29 ± 0.10	3.3 ± 0.4	1.96	0.31 ± 0.07	4.0 ± 0.2	4.69
Ostracods	0.24 ± 0.06	2.5 ± 0.2	3.50	0.29 ± 0.02	4.5 ± 0.3	0.62
Chaetognaths	0.31 ± 0.08	3.1 ± 0.1	–	–	–	–
Siphonophores	0.33	2.1	–	–	–	–
Munida gregaria						
Zoea II	0.18 ± 0.04	3.0 ± 0.2	0.90	–	–	–
Zoea III	0.20 ± 0.04	3.0 ± 0.1	0.70	–	–	–
Zoea IV	0.20 ± 0.02	3.6 ± 0.2	0.50	0.31 ± 0.04	3.3 ± 0.3	–
Zoea V	0.21 ± 0.03	3.1 ± 0.2	0.70	–	–	–
Megalopa	0.1 ± 0.08	3.5 ± 0.3	2.85	–	–	–
Amphipods	0.24 ± 0.08	3.2 ± 0.4	5.62	0.12 ± 0.09	4.0 ± 0.4	3.68
Stomatopods	0.21 ± 0.04	3.4 ± 0.4	–	–	–	–
Paralarvae	0.24 ± 0.05	4.3 ± 0.3	–	–	–	–
Sergestes arcticus	0.24 ± 0.06	3.1 ± 0.3	–	0.29 ± 0.05	4.7 ± 1.3	–

these zones, the locations where they have been reported in higher abundance correspond to high phytoplankton abundance and scarce glacial silt. In our study area, the Baker Channel is surrounded by glaciers lying between the two glacial fields (northern and southern ice fields) that drain and transport abundant amounts of silt that enter the inner part of the channel, inducing high seawater turbidity and

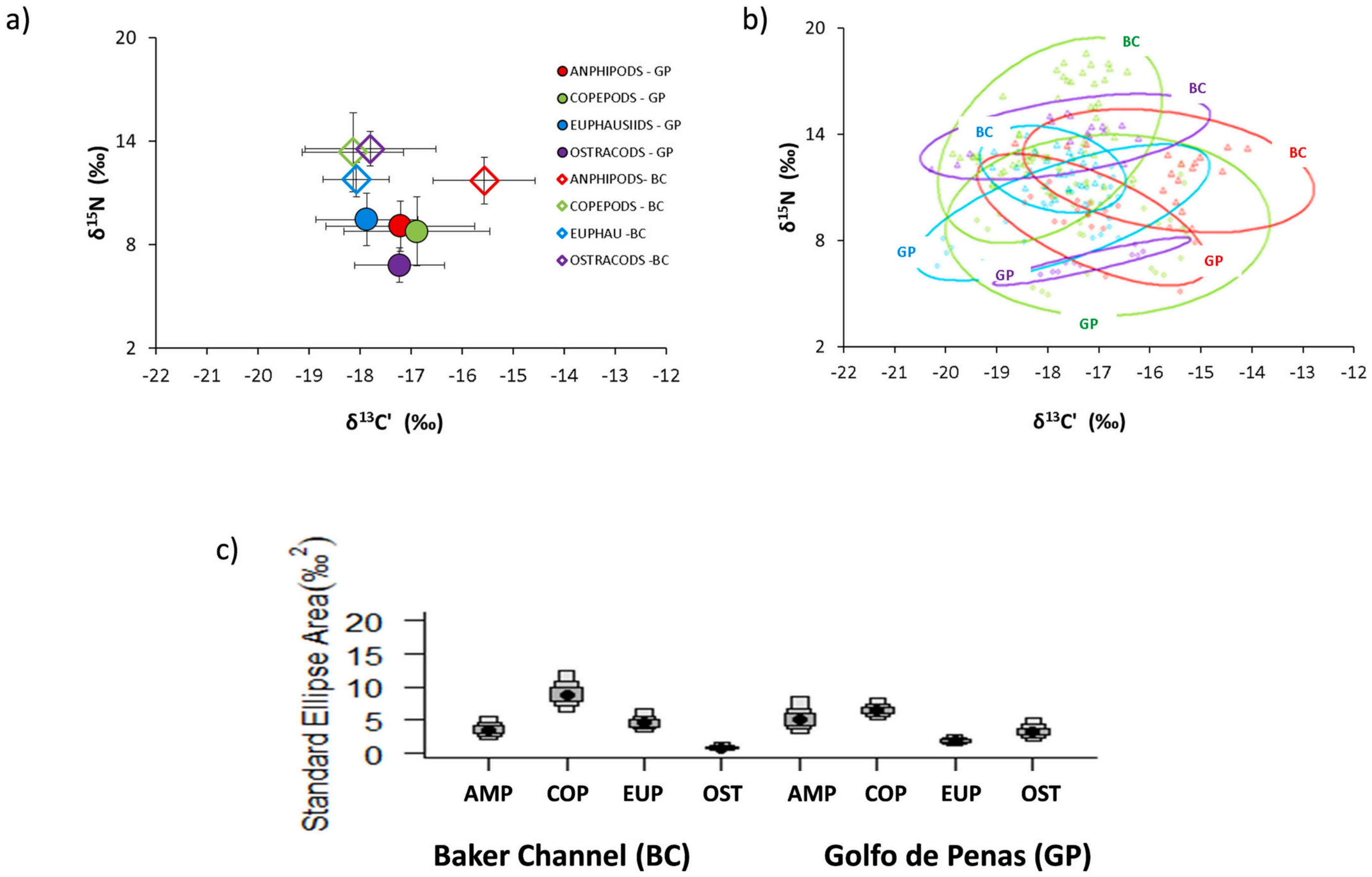

Fig. 10. a) Stable isotope ($\delta^{13}C$, $\delta^{15}N$) plots, b) Siber Ellipse corrected Areas and c) standard ellipse areas (isotope niche width) estimated for the four zooplankton groups (*E. vallentini* (adults), amphipods, copepods, and ostracods) located at the Golfo de Penas and Baker Channel. The boxplots show 50, 75 and 95% intervals. Black dots are modes per group.

precluding high phytoplankton production (Marín et al., 2013; Aracena et al., 2011; Meerhoff et al., 2019). The higher chlorophyll-a and *E. vallentini* abundance in all stages offshore and not inshore probably respond to these combined environmental factors.

The differences in the vertical distribution of both early *E. vallentini* life stages (calyptopis and furcilia) compared with that of the adult stages coincided with differences in isotope values and C:N ratios between the young and adult stages, suggesting an ontogenetic change as the organisms develop. The trophic positions and proportion of terrigenous carbon in their tissues also indicate an increase at more advanced stages in the Baker Channel and the Golfo de Penas. Limited information exists on the vertical distribution and diet of the different stages of development in *E. vallentini*. While in other euphausiid species (*Euphausia lucens*) calyptopis, and furcilia were classified mainly as herbivores, juveniles, and adults were reported to ingest large amounts of copepods or other crustaceans (Stuart and Pillar, 1990). *E. vallentini* adults have been reported as phytoplankton feeders also (Mauchline, 1980). However, in the Magellan Strait, they may shift from a more herbivorous to a more omnivorous diet, depending on their proximity to the bottom, from where they may even feed on polychaetes (Hamame and Antezana, 2010). This change in feeding behavior has been observed in other euphausiid species in which herbivorous feeding in areas of higher phytoplankton abundance changed to a carnivore feeding mode in adult stages when food became scarce (Stuart and Pillar, 1990). In this study, an increase in $\delta^{15}N$ values and trophic position was observed in adult *E. vallentini* from the Golfo de Penas to the inner areas of the Baker Channel, coinciding with the decrease in phytoplankton concentrations in the water column and coincident with the decrease in C:N ratios in *E. vallentini* tissues. High $\delta^{15}N$ values (14.5‰) have also been observed in other channels further south in Patagonia, particularly in winter when the phytoplankton biomass is very low (Castro et al., 2021). Accordingly, our study's overall results suggest that ontogenetic changes in feeding occur in *E. vallentini* and that spatial differences occur along inshore-offshore environmental gradients, such as from the Baker Channel and the Golfo de Penas.

All zoea (I to V) and megalopa stages of *M. gregaria* were present in the study area. Among these stages, zoea IV was the most abundant, consistent with the duration of the stages from the main winter reproductive season in the area (León et al., 2008). All young stages occurred along the transect but were more abundant at the Golfo de Penas near the Baker Channel mouth (Station 3). In this area, zoea stages have been previously reported in very high abundances in spring (Meerhoff et al., 2013), coincident with the lower seasonal river discharges, with decreased amount of sediment load to the channel (Aracena et al., 2011) and with the increased biomass of phytoplankton in the area (Montero et al., 2011; Meerhoff et al., 2013). During summer, pelagic *M. gregaria* juveniles have been collected at the head of the channel, a stage known to feed on both detritus and microplankton. In these individuals, $\delta^{15}N$ values in their tissues varied between 10 and 12‰ and $\delta^{13}C$ values ranged from −19‰ to −12‰ (Meerhoff et al., 2019). These $\delta^{13}C$ values were lower, and the $\delta^{15}N$ values were higher than those we observed in zoea IV ($\delta^{13}C = -18.2 \pm 0.5$‰ and $\delta^{15}N = 9.6 \pm 1.0$‰) at the Baker Channel. Notably, we determined changes in isotopic content among the stages (increase in $\delta^{13}C$ and $\delta^{15}N$ values from zoea stages to megalopa). We also observed changes in the vertical distribution among developmental stages, from a wide distribution of early zoea (ZI–ZIV) to a deeper distribution (100–150 m) in zoea V and megalopa stage. Thus, the results suggest that an ontogenetic change in feeding occurs from

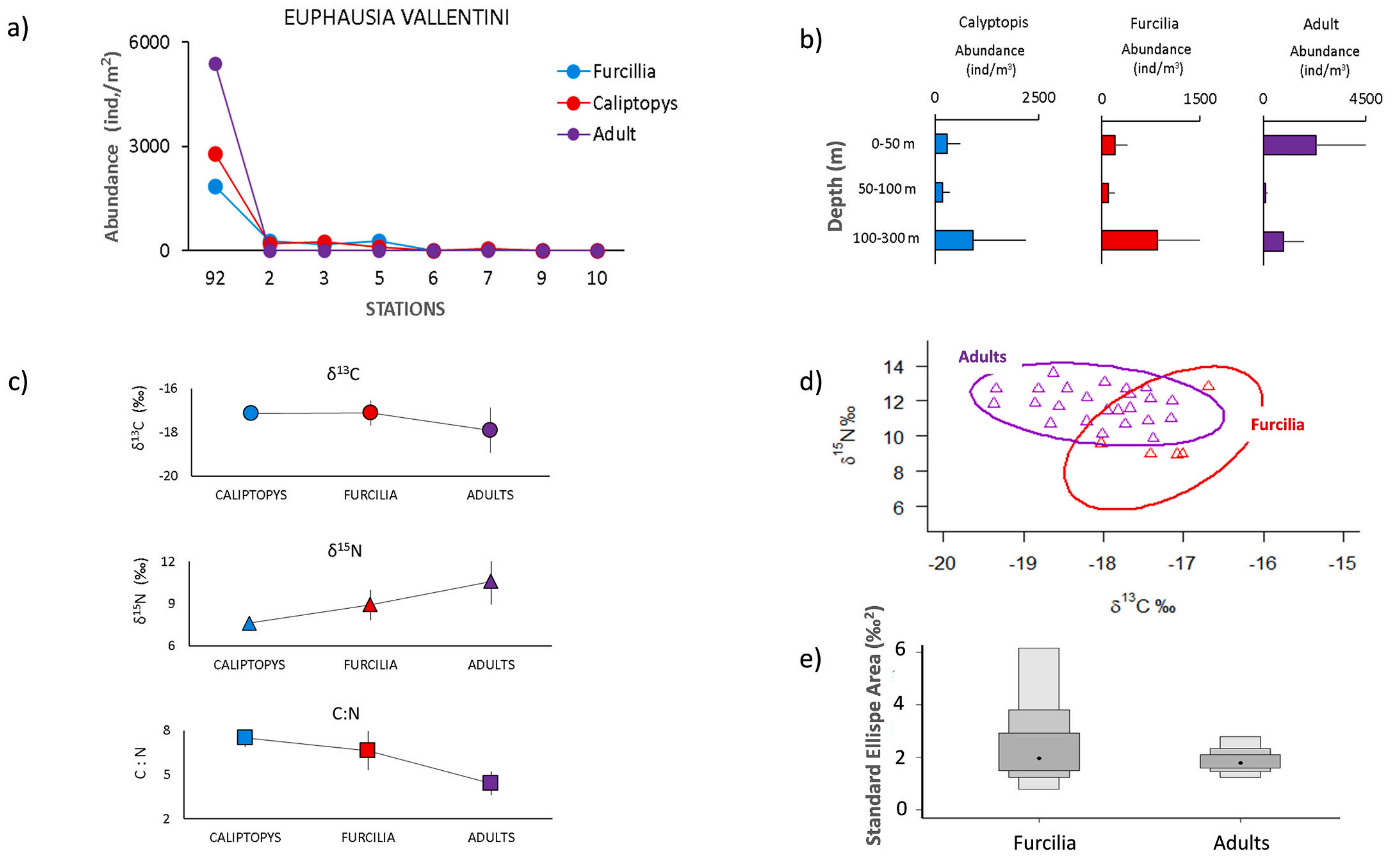

Fig. 11. a) Abundance of the *E. vallentini* stages (calyptopis, furcilia and adults) along the Baker Channel - Golfo de Penas transect, b) profiles (and standard deviations) of their mean vertical distribution, c) mean (and standard deviations) stable isotope values, d) Siber Ellipses and e) standard ellipse areas (stable isotope niche widths). The boxplots show 50, 75 and 95% intervals. Black dots are modes per group. Due to low number of replicates, ellipses were nor diagramed for calyptopis.

early zoea to megalopa and juvenile *M. gregaria*, coinciding with variations in vertical and horizontal distributions along the Baker Channel-Golfo de Penas system. These ontogenetic changes are consistent with the hypothesis on connectivity that proposes an ingress of *M. gregaria* individuals as they develop towards the inner section of the channels and fjords in northern Patagonia (León et al., 2008).

4.2. Zooplankton offshore-inshore connections in the Baker Channel and in the Beagle Channel

The Beagle Channel in southern Patagonia (57°S) is geomorphologically different from the Baker Channel-Golfo de Penas system (47°S) as the former connects to the Pacific Ocean at its western end and to the Atlantic Ocean to the east, which deeply modifies its hydrography and dynamics (Giesecke et al., 2021). Both systems receive a large amount of organic matter from terrigenous origin that end up at the seawater and it is subsequently incorporated into the pelagic food web reaching zooplankton (Vargas et al., 2011; Meerhoff et al., 2019; Riccialdelli et al., 2017, 2020; Bruno et al., 2023a). However, the proportion of organic matter of different origin (terrestrial, marine) and the processes that ingress particulate organic carbon to the pelagic environment and the pelagic food web seem to vary between systems. While in the Baker system the main particulate organic sources include autochthonous organic matter, terrestrial organic matter (Vargas et al., 2011; Meerhoff et al., 2019) plus an underdeterminded amount of degraded matter entering the channel in Equatorial Subsurface Water (ESSW) at depth (this study), in the Beagle Channel the main sources are also autochthonous and terrestrial (Riccialdelli et al., 2017; Presta et al., 2023a; Rodríguez-Flóres et al., 2023) but also include resuspended organic matter from sediments from the eastward shallow areas through Mackinlay passage (Bruno et al., 2023a; Presta et al., 2023a). Both systems show, as results of glacial ice melting and rainfall, a strong salinity gradient at the sea surface, a subsurface ingress of ASSW and topographic constrictions that restricts inshore-offshore connectivity which, along with different organic matter sources, creates different environments at the basins located at each side if the constrictions. Interestingly, in both systems the highest zooplankton abundances are located at the seaward side of the constrictions (Presta et al., 2023a).

The Beagle Channel show different community structures at each side of the Mackinlay passage, different energetic density in the different plankton size fractions (Bruno et al., 2023b) but a similar food web functioning at each side of the sill, at least during the spring season when phytoplankton abundance is higher (bottom-up; Presta et al., 2023a). Our study at the Baker system in spring also shows differences in zooplankton composition between the Golfo de Penas (seawards) and the Baker Channel (inshore; e.g. higher trophic level predators, lower C:N in zooplankton, contrasting δ^{13}C and δ^{15}N in most zooplankton groups) which suggests differences in the food web structure and potentially, in carbon fluxes as well, the latter an hypothesis to be tested in future studies. The distribution of some of the key species shared by the Baker and Beagle channels (e.g. *Munida gregaria*) also show similarities in terms abundance as late zoea stages were located at the seaward located stations (Presta et al., 2023b) but not in terms of the youngest stages (in the Baker Channel they were practically absent inshore, in contrast with the Beagle Channel where they occurred inshore and offshore). The presence of young zoea stages in late summer and early fall out of the peak hatch seasons (Presta et al., 2023b) has also been observed in the Baker Channel (Henríquez, 2018). The distribution

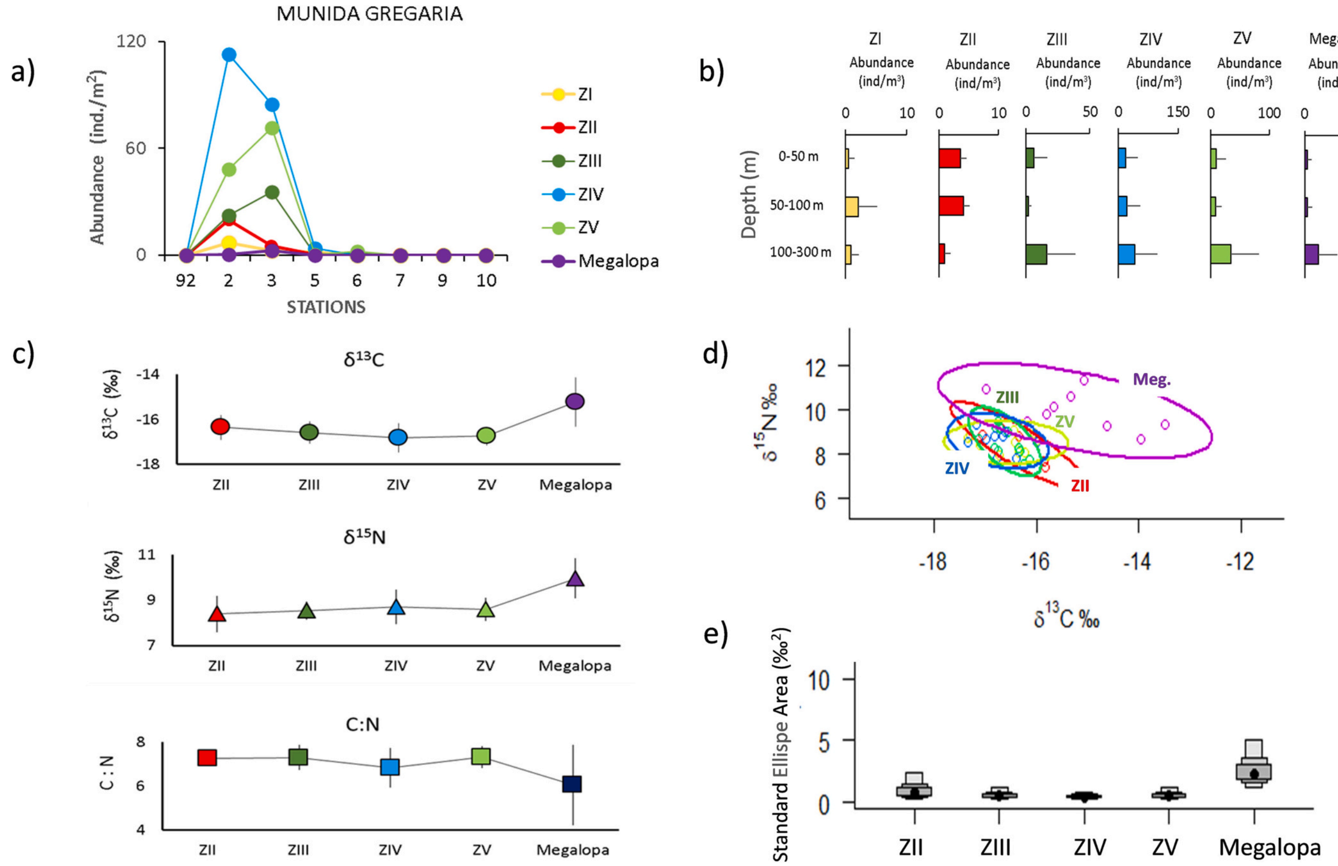

Fig. 12. a) Abundance of the *Munida gregaria* early life stages (zoea I-V and Megalopa) along the Baker Channel - Golfo de Penas transect, b) profiles (and standard deviations) of their mean vertical distribution, c) mean (and standard deviations) stable isotope values, d) Siber Ellipses and e) standard ellipse areas (stable isotope niche widths). The boxplots show 50, 75 and 95% intervals. Black dots are modes per group. Due to low number of replicates, ellipses were nor diagramed for Zoea I.

of the adult stages, though, remains still to be determined at the Baker Channel-Golfo de Penas system.

In this study, we determined that the distribution of zooplankton groups and of their potential food sources in the Baker Channel and Beagle Channel and in adjacent semi-enclosed areas over the continental shelf are affected by the intrusion and output of different types of water. The isotope values observed in zooplankton at both channel and in their adjacent shallow seaward zones highlight the role of physical processes connecting inshore and offshore environments (Garzón-Cardona et al., 2016). Similarly, the influx of freshwater into both systems increases during summer when the glacial ice melts and decreases in late autumn and winter when rain changes to nival precipitation (Aiken, 2012; Moffat et al., 2018; Rodríguez-Flóres et al., 2023). How larger-scale atmospheric and global changes will affect the inshore-offshore connection and the overall Patagonian fjords communities remains unclear. Thus far, increases in glacial melting have already occurred in both areas, processes such as glacial lake outbursts (GLOFs) have increased in frequency during the last decades in the Baker Channel area and globally, and some of their effects on the zooplankton community have begun to be observed along Patagonia (Kattelmann, 2003; Breien et al., 2008; Casassa et al., 2010; Margold et al., 2011; Marín et al., 2013; Cook et al., 2016; Meerhoff et al., 2019; Ross et al., 2020).

5. Conclusions

Recent research in northern and central Patagonia revealed that organic matter from terrestrial origin carried by fresh water enters the marine environment affecting the isotopic composition of zooplankton in surface waters. However, the influence of seawater entering fjords and channels at deeper layers from offshore on the zooplankton community inshore had not been assessed. Our results at the Golfo de Penas - Baker Channel connection reveal that attributes of the zooplankton community (functional groups, δ^{15}N and δ^{13}C values, trophic positions, and their C:N ratios) change in concordance with the phytoplankton biomass in the field and with the different organic carbon sources (terrestrial, oceanic) at different depths along the Golfo de Penas-Baker Channel system. Altogether, the results suggest an along-basin transport of organic matter of different sources at different depths. Thus, a complex scenario of lateral transport of water of different characteristics modulates the presence of zooplankton and its food along these inshore-offshore oriented systems, a feature apparently shared by other channels and fjords that connect to semi-closed coastal zones along Patagonia, such as the Beagle Channel at higher latitudes.

Credits

All co-authors contributed to the writing of the original draft, review and editing. LRC conducted the investigation and conceptualization. SS-M, PB, HG, MG, IM and BD contributed to the data curation and formal analyses. LRC, GD, PM and BD contributed with resources and funding.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Appendix

Table 1
Principal component analyses. Proper Values (PV), explained variability (%, VE), total and cumulative variability of components (%, CV).

	Amphipods			Copepods			Ostracods			*E. vallentini*		
Factor	PV	EV (%)	CV (%)	VP	VE (%)	AC (%)	VP	VE (%)	AC (%)	VP	VE (%)	AC (%)
1	**1.71**	**34.21**	**34.21**	**1.73**	**34.74**	**34.74**	**1.82**	**36.36**	**36.36**	**1.81**	**36.13**	**30.13**
2	**1.51**	**30.22**	**64.43**	**1.32**	**26.39**	**60.86**	**1.58**	**31.62**	**67.98**	**1.53**	**30.49**	**66.62**
3	**1.14**	**22.78**	**87.22**	**1.11**	**22.16**	**83.01**	**0.90**	**18.09**	**86.07**	**0.96**	**19.19**	**85.81**
4	0.47	9.38	96.59	0.74	14.80	97.82	0.64	12.72	98.78	0.59	11.93	97.73
5	0.17	3.41	100	0.11	2.18	100	0.06	1.22	100	0.11	2.27	100

Table 2
Principal component analyses. Correlations matrix of original variables (T: temperature (°C); S: Salinity; O2: Dissolved oxygen (mL/L)), with the principal components. Significant correlations in bold.

	Amphipods			Copepods			Ostracods			*E. vallentini*		
Variable	F1	F2	F3	F1	F2	F3	F1	F2	F3	F1	F2	F3
^{13}C	**−0.70**	0.33	−0.53	0.02	−0.28	**0.87**	**0.67**	−0.12	−0.49	−0.46	−0.32	**0.73**
^{15}N	−0.27	**0.77**	0.42	−0.12	**0.93**	0.20	−0.53	**−0.81**	−0.07	−0.64	**−0.66**	−0.13
T	0.43	**0.67**	0.38	**0.51**	0.27	0.50	**−0.60**	0.40	0.44	**0.60**	−0.41	0.50
S	−0.31	−0.60	**0.69**	**−0.82**	−0.40	0.25	**0.82**	0.14	0.54	−0.08	**0.86**	0.40
O_2	**0.93**	−0.05	−0.24	**0.89**	−0.39	−0.05	−0.26	**0.86**	−0.43	**0.90**	−0.28	−0.02

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