Composition, Spatial Distribution, and Trophic Structure of the

ZOOPLANKTON COMMUNITY

in San Jorge Gulf, Southwestern Atlantic Ocean

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The zooplankton of San Jorge Gulf adrift in the southwestern Atlantic Ocean. *Photo credit: Eloísa M. Giménez*

ABSTRACT. The goal of this study was to understand the zooplankton community composition and food web structure in San Jorge Gulf (45°–47°S, 65°30'W), a highly productive marine ecosystem in southern Argentina. A spatial grid of 14 stations was sampled in 2014. The sampled zooplankton community was composed of 30 taxa, with copepods accounting for 83% of the total abundance. Community composition was strongly related to surface temperature and water column stratification. Two distinct zooplankton assemblages were present. The zones designated North and Center were dominated by *Ctenocalanus vanus*; copepodite stages of *C. vanus*, *Clausocalanus brevipes*, and *Paracalanus parvus*; appendicularians; and *Oithona helgolandica*. The South zone was dominated by *P. parvus*, copepodites, *Acartia tonsa*, and *Drepanopus forcipatus*. The plankton food webs were increasingly enriched in carbon and nitrogen stable isotopes from the North to the South. Depleted δ¹³C signatures in the North may be explained by terrigenous inputs derived from strong westerly winds. The zooplankton taxa displayed a wide feeding range in the North, whereas the narrow trophic space of the South food web suggested similar feeding strategies among the taxa. Appendicularians were positioned at the base of the food webs, copepods were in the middle, and chaetognaths occupied high trophic positions.

INTRODUCTION

Zooplankton occupy a key position in pelagic food webs. They play a major role in the productivity and functioning of marine ecosystems by transferring energy from primary producers to upper trophic levels (Legendre and Rassoulzadegan, 1995). Environmental features usually control zooplankton community composition, structure, and distribution. Water mass properties were found to influence not only zooplankton distribution patterns but also the trophic structure of the entire plankton community (Kiørboe, 1993). Chlorophyll *a* (chl *a*) concentrations are closely linked to herbivorous or omnivorous zooplankton that occupy different trophic levels (TLs) within a community according to different feeding modes (Thompson et al., 2013). Zooplankton abundances and distributions may also control higher TLs such as fish larvae and juveniles (Temperoni and Viñas, 2013). Hence, knowledge of the trophic structure in marine food webs is essential because it provides a way to understand energy and matter flows in the ecosystem. Trophic relationships may influence the persistence and the dynamics of zooplankton populations through resource availability and predation pressure (De Ruiter et al., 2005).

San Jorge Gulf (SJG) is located on the Argentine continental shelf. Because it includes highly diverse and productive coastal and marine environments, there is great interest in conservation of this region (Yorio, 2009). Spawning and breeding grounds as well as important commercial fisheries make the gulf important economically. A more complete understanding of the zooplankton community and its trophic structure is crucial for improving estimates of food availability for many commercially exploited species, which depend wholly or partly on zooplankton as a food source (Góngora et al., 2012). Previously, zooplankton community composition and distribution patterns were mostly studied in the North and South zones as well as on the outer shelf of the SJG (Pérez Seijas et al., 1987; Viñas et al., 1992; Temperoni et al., 2014). However, no previous research had covered the entire gulf.

The aim of the study was to describe zooplankton community composition and distribution across the entire SJG in relation to environmental variables during austral summer and to characterize the zooplankton food web structure. We hypothesized that environmental differences in three SJG zones, defined according to oceanographic features previously reported, would give rise to significant variability in zooplankton composition and trophic structure at the bases of the pelagic food webs.

MATERIALS AND METHODS
Study Area

The SJG is located between 45°S and 47°S, and from 65°30'W to the coastline. In situ sampling data (Cucchi Colleoni and Carreto, 2001; Louge et al., 2004), satellite images (Glembocki et al., 2015), and numerical simulations (Palma and Matano, 2012) show that surface and bottom temperatures and salinity increase from south to north in the gulf. In contrast, chl *a* concentrations are higher in the south and east. Based on this information, we defined three zones prior to the analyses: North, Center, and South (Figure 1a). Further information on the characteristics of the study area is presented in the online supplementary materials.

Sample Collection: Environmental Variables and Zooplankton Sampling, Identification, and Quantification

Within the framework of the MARES Project (MArine ecosystem health of the San Jorge Gulf: Present status and RESilience capacity), a research cruise aboard R/V *Coriolis II* took place in February 2014. Fourteen stations were sampled, covering most of the gulf (Table S1). All stations were sampled for environmental variables and zooplankton distribution patterns, while samples from 10 selected stations were used for stable isotope analyses (Figure 1b).

Physico-chemical data (temperature, stratification, chl *a*) in the water column were obtained at all stations, and
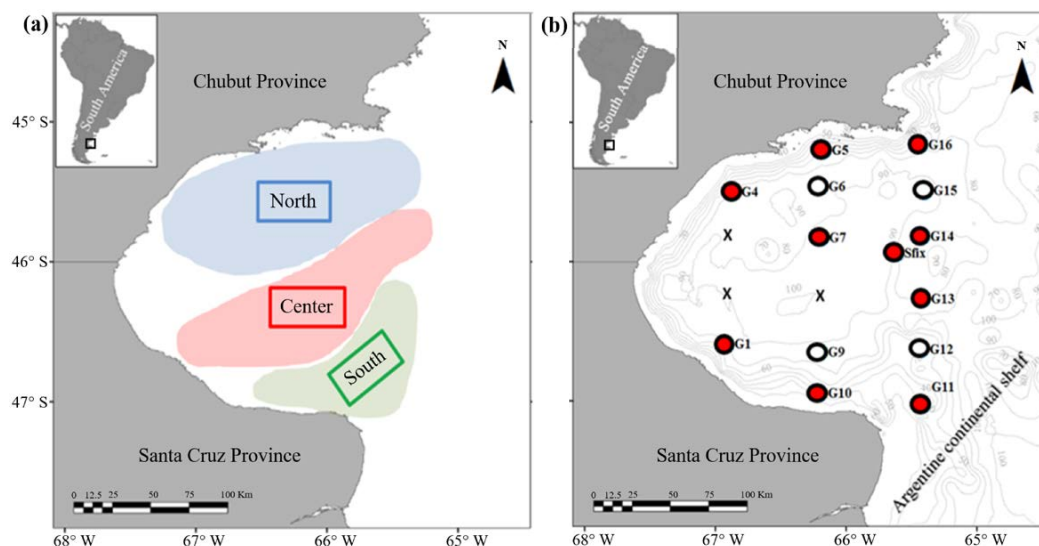
FIGURE 1. San Jorge Gulf (SJG). (a) Three hydrographic zones, North, Center, and South, defined according to Cucchi Colleoni and Carreto (2001), Louge et al. (2004), Palma and Matano (2012), and Glembocki et al. (2015). (b) Zooplankton stations sampled in February 2014 from R/V *Coriolis II*. Black circles represent stations where environmental variables and zooplankton were collected. Red dots indicate stations where stable isotope analyses were performed. X indicates stations without samples. Bathymetry was adapted from Chart H-365 from the National Hydrographic Survey (Servicio de Hidrografía Naval) of Argentina.

particulate organic matter (POM) above and below the pycnocline was analyzed. Vertical zooplankton tows throughout the entire water column were carried out with a Jacknet. In the laboratory, organisms were identified to the lowest taxonomic level possible. Depth-integrated abundances (ind m^{-2}) and biomass (mg m^{-2}) were calculated for each taxon. The detailed methodologies used for both sampling and laboratory analyses of environmental variables and zooplankton, as well as the statistical approaches, are presented in the supplementary materials.

Stable Isotope Analyses: Sample Processing and Trophic Level Estimation

Zooplankton and surface and bottom POM samples were analyzed to obtain isotopic ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N). δ^{15}N is used to determine the trophic position of taxa because each consumer is enriched in N relative to its diet (Minagawa and Wada, 1984). In contrast, δ^{13}C changes little from the resource to the consumer (~1‰), so it can be used to determine the carbon source for a consumer (Peterson and Fry, 1987). The stable isotope spaces covered by the zooplankton community were visualized by isotope biplots (δ^{13}C vs. δ^{15}N) for each of the three SJG zones. In addition, TLs were determined for all zooplankton taxa in each zone. The detailed methodologies used for sampling, sample processing, laboratory analyses, and TL calculations are presented in the supplementary materials.

RESULTS
Environmental Variables and Zooplankton Community

SJG surface temperature in summer ranged from 12.51°C to 15.62°C, while bottom temperature ranged from 14.16°C at the shallowest station to 8.41°C at the deepest one. Integrated chl *a* varied between 29.92 mg m^{-2} and 79.56 mg m^{-2} (Table S1). Salinity varied little among stations, ranging from 33.03 psu to 33.46 psu. Environmental conditions differed among regions (ANOSIM, global R = 0.281; p <0.05). The South was different from the Center (R = 0.583; p = 0.029) and the North (R = 0.421; p = 0.019). However, the North and Center zones were similar (R = 0.091; p = 0.238). The first two axes of a principal component analysis explain to 90.7% the spatial heterogeneity in environmental conditions (Figure 2; PC1 = 65.8%, PC2 = 24.9%). Bottom temperature and stratification were mostly related to PC1, and surface temperature and chl *a* were related to PC2 (Table S2). North stations exhibited a stratified water column with an intense pycnocline, while the South water column was homogeneous. Intermediate stratification patterns were found in the Center zone (Figure 3).

Thirty zooplankton taxa were identified over the study area, with total abundance per station ranging from 55,356 ind m^{-2} to 425,469 ind m^{-2}. Copepods represented 83% of total zooplankton abundance, followed by appendicularians (*Oikopleura* spp. accounted for 10% of the total). The copepod assemblage was dominated by medium-sized adult copepods *Ctenocalanus vanus* (36%), followed by copepodites stages (29%) of Clausocalanidae (*C. vanus, Drepanopus forcipatus* and *Clausocalanus brevipes*) and *Paracalanus parvus*. Adults of *P. parvus*, the ubiquitous *Acartia tonsa*, and the small-sized cyclopoid *Oithona helgolandica* (= *O. similis*; Cepeda et al., 2016) contributed 8%, 5%, and 3% to the total zooplankton community, respectively. Large-sized individuals of the

family Calanidae (adults of *Calanoides carinatus* and *Calanus australis* and their copepodites) were the least abundant, representing less than 1% of zooplankton composition. Means and ranges of abundance and biomass were very variable among the three SJG zones (Table S3).

Zooplankton community composition displayed high variability among the three zones (Figure 4; ANOSIM global R = 0.569, p = 0.02). In accordance with environmental patterns, the zooplankton assemblage in the South differed from that in the North (R = 0.730, p = 0.005) and the Center (R = 0.833, p = 0.029), which were similar (R = 0.282, p = 0.057). Five taxa accounted for the difference between the zooplankton assemblages in the North/Center and the South: higher abundances of *C. vanus*, copepodite stages of *C. vanus*, *C. brevipes*, and *P. parvus* (copepodites hereafter), and appendicularians were found in the North/Center, whereas higher abundances of *P. parvus* and *A. tonsa* occurred in the South (SIMPER, Table S4). The spatial structure of the zooplankton community was best correlated with surface temperature and stratification (BIOENV procedure: Spearman's coefficient R = 0.479, p <0.05).

Zooplankton Food Web Structure

The planktonic food web structure was described with stable isotope trophic markers. Stable carbon isotope signatures (δ^{13}C) of both surface and bottom POM values showed enrichment from the North to the South zone (Figure 5a,c), while the opposite was observed for stable nitrogen isotopes (δ^{15}N) of surface and bottom POM, which were increasingly depleted from the North to the South (Figure 5b,d).

Zooplankton carbon signatures showed a wide range throughout the SJG, from −30.6‰ in *O. helgolandica* to −18.0‰ in mysids. Nitrogen signatures ranged from 10.7‰ in *Oikopleura* spp. to 15.2‰ in predatory chaetognath *Sagitta* spp. (Figure 6, Table S5). Similar to POM stable isotope signatures, the zooplankton food webs showed enrichment in δ^{13}C from the North to South zone, including enrichment of total copepod δ^{13}C. However, the carbon signatures of *Oikopleura* spp. were similar in the North and the Central zones. The small-sized copepod *P. parvus* and copepodites of *A. tonsa* and *O. helgolandica* were significantly enriched in δ^{13}C in the South compared to the two other zones. Copepods were depleted in δ^{13}C compared to euphausiids. Euphausiids, composed of larvae and juveniles of *Euphausia* spp., and adults of *E. lucens*, *E. vallentini*, and *Nematoscelis megalops* showed similar δ^{13}C signatures in all zones. *Sagitta* spp. chaetognaths showed a wide range in δ^{13}C mean values among the three zones (−26.2 to −19.1; Figure 6).
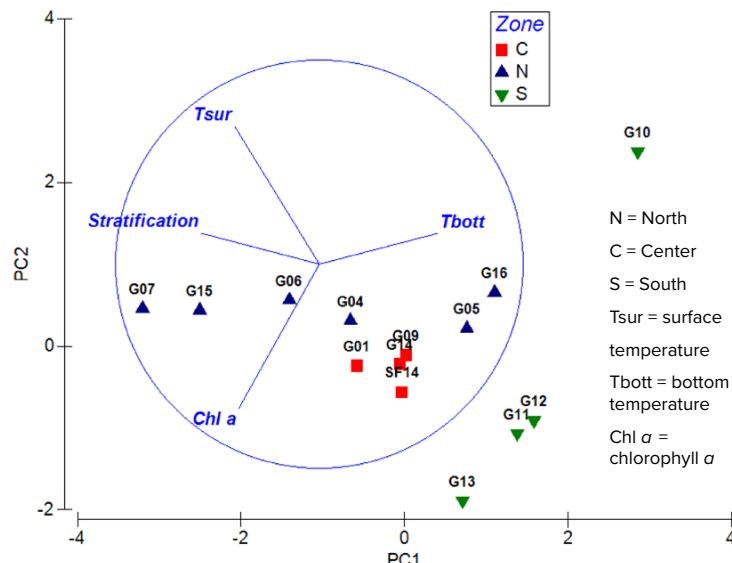

FIGURE 2. Principal component analysis (PCA) showing the ordination space of environmental variables (surface and bottom temperature, chlorophyll *a* integrated over the water column, and stratification) with the first two axes (PC1 and PC2).

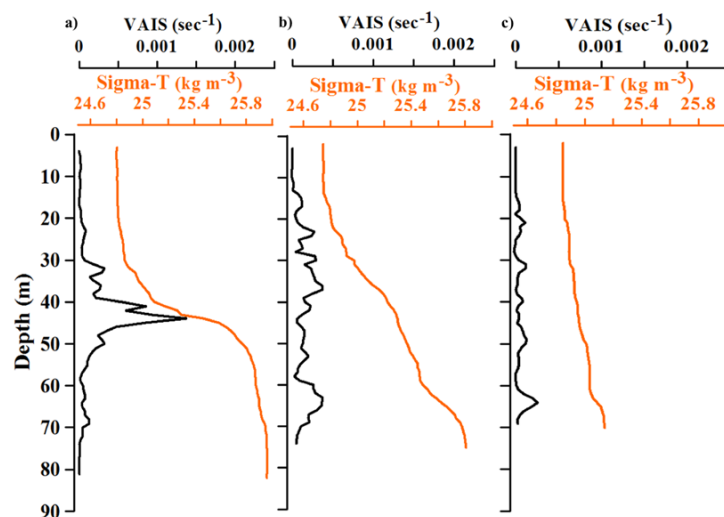**FIGURE 3.** Density (Sigma-T, kg m^{-3}) and Brunt-Väisälä frequency (VAIS; sec^{-1}) profiles representative of stations located in the (a) North (G06), (b) Center (G09), and (c) South (G11) zones of the SJG in February 2014.
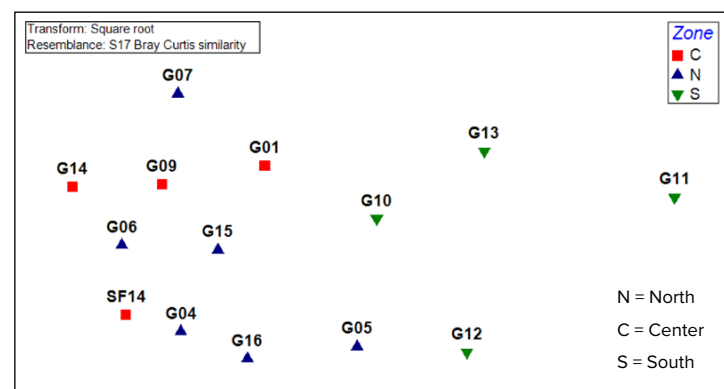

FIGURE 4. Non-metric multidimensional scaling (nMDS) showing zooplankton assemblages at 14 SJG stations divided into three geographic zones, North (N), Center (C), and South (S).
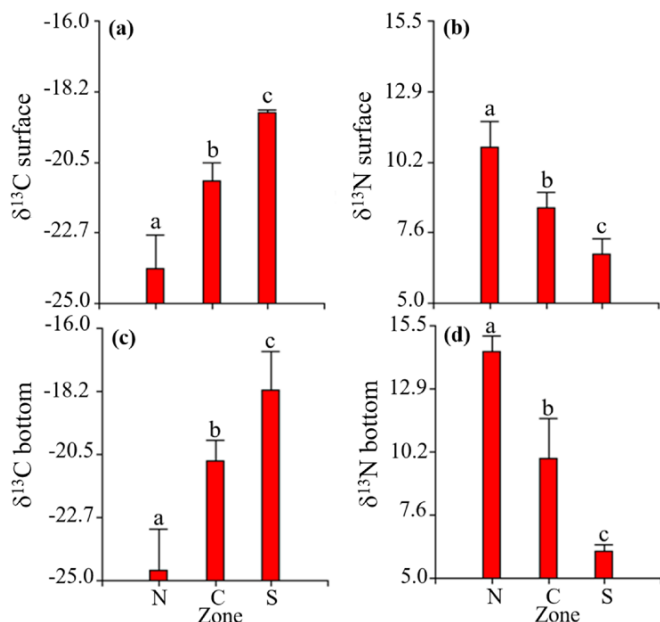
FIGURE 5. Surface and bottom $\delta^{13}C$ (a,c) and $\delta^{15}N$ values (b,d) of particulate organic matter for North (N), Center (C), and South (S) zones of the SJG. Different letters indicate significant differences in $\delta^{13}C$ and $\delta^{15}N$ among zones. Bars show standard errors.

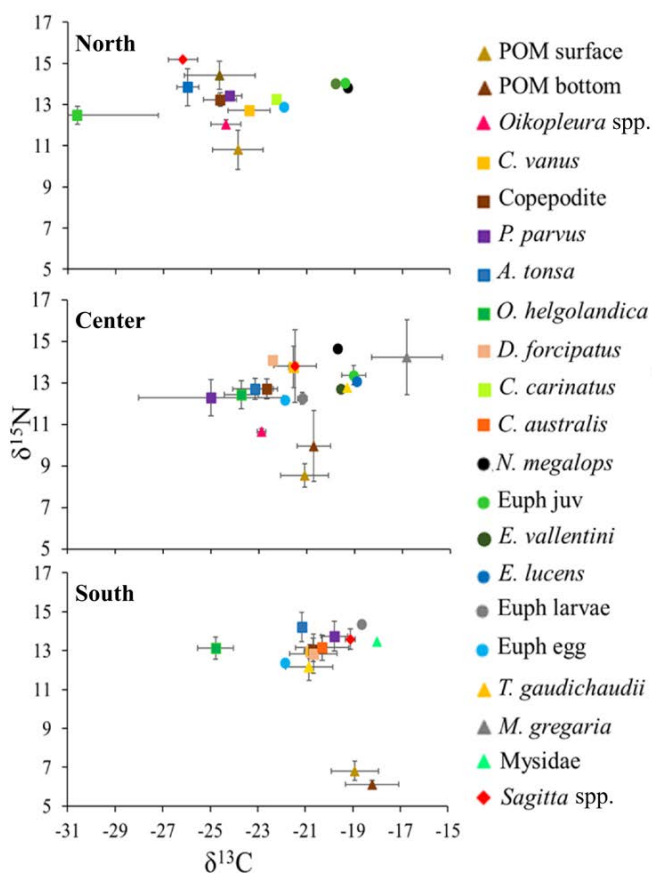**FIGURE 6.** Biplots of stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of the main zooplankton community components in the North, Center, and South zones of the SJG. Bars indicate standard errors. The $\delta^{13}C$ values on the x-axis reflect potential carbon sources, while the $\delta^{15}N$ values in the y-axis show the taxa trophic position. POM = particulate organic matter. Copepodite = development stages of *Ctenocalanus vanus*, *Clausocalanus brevipes*, *Paracalanus parvus*, and *Drepanopus forcipatus*. Euph = euphausiids.

Trophic levels of the copepod community increased significantly from the North to the South zone in the SJG (ANOVA: F = 65.06, df = 2, p <0.0001; Figure 7a). However, mean TLs of the copepod taxa within each zone were similar. Mean TL of euphausiids was significantly lower in the North compared to the Center (Figure 7b). *Sagitta* spp. TL increased from the North to the South, and they occupied the highest trophic position in the North and the Center, but in the South this position was replaced by the copepod *A. tonsa*. The appendicularian *Oikopleura* spp. occupied the lowest TL when present (Figure 7c).

DISCUSSION

Zooplankton Composition and Its Relationships with Environmental Conditions

Two distinct hydrographic zones were identified in the SJG during summer, the North/Central and the South. Mean values of surface temperature were lower in the southern area and increased toward the North, consistent with previous observations (Akselman, 1996; Louge et al., 2004). Colder temperatures in the South can be explained by the influence of the Magellan Plume, a tongue of relative cold, low-salinity water consisting mostly of discharge from Magellan Strait (53°S). It extends along the Patagonian shelf up to 42°S, from the surface to the bottom of the water column, and it detaches off the coast at the southern SJG (Palma and Matano, 2012; Glembocki et al., 2015). The plume is vertically homogeneous, consistent with the lack of stratification found in our southern study area. Stratification increased from the South to the North, except in some northern coastal stations. These mixed waters could result from the interaction between coastal topography, wind stress, and tidal energy (Tonini et al., 2006). Glembocki et al. (2015) described the northern SJG thermal front, which develops in spring and is strongest during summer. Integrated chl *a* distribution patterns in the SJG were similar to those described in Cucchi Colleoni and Carreto (2001), showing higher values in the southeast and central-east, and in some northern stations.

As is common for secondary producers in many pelagic environments, copepods formed the largest component of the SJG zooplankton community, followed by appendicularians. High appendicularian growth rates may compensate for their low biomass (Hopcroft and Roff, 1998). Two distinctive, spatially segregated zooplankton assemblages were revealed: one in the North/Center and the other in the South, coinciding with the occurrence of the two distinct water masses mentioned above. While *C. vanus*, *O. helgolandica*, and appendicularians defined the North/Center assemblage, the small

and medium-sized copepods *P. parvus*, *A. tonsa*, and *D. forcipatus* were characteristic of the South assemblage. These groups are also the most conspicuous components of zooplankton communities in Argentine continental shelf waters and specifically in the SJG (Sabatini et al., 2004; Spinelli et al., 2012; Temperoni et al., 2014). Viñas et al. (1992) reported pre-adult euphausiids (i.e., furcilia larvae and juveniles) as the secondmost abundant group in the SJG in summer, with highest abundances in the Center-South region. In our study, euphausiid peak abundances were characterized respectively by larvae and juvenile abundances in the North and the Center. However, macrozooplankton were likely undersampled due to the vertical towing of the zooplankton net. Most previous studies lacked either spatial or taxonomic resolution, as they compared density patterns of copepod groups and not species (Pérez Seijas et al., 1987).

Surface temperature and stratification explained a fairly high percentage (48%) of the variation in zooplankton composition. The association between stratification and elevated copepod abundances on the Argentine continental shelf was previously documented (Marrari et al., 2004; Temperoni et al., 2014), often associated with the occurrence of highly productive frontal areas (Acha et al., 2004). When light and nutrients are available, the upper layer of any stratified water column permits the growth and retention of phytoplankton that support zooplankton (Alemany et al., 2014). In the present study, chl *a* was used as a proxy for phytoplankton biomass. No direct relationship between chl *a* and zooplankton abundance and distribution was found. Glembocki et al. (2015) reported the chl *a* field for February and found high values associated with an outer SJG front near the stations where we found the highest zooplankton abundances and biomass (G14 and SF14), which might explain our results. Alternatively, evidence of zooplankton retention zones created by physical processes have been described in

other environments (Mackas et al., 2005), and the high zooplankton abundance and biomass we found could reflect passive accumulation. High-resolution modeling results describing SJG circulation patterns revealed a clockwise gyre in the North and a counterclockwise gyre in the South (Tonini et al., 2006) that would potentially support retention in the central region. Furthermore, wind stress contributes to lateral and horizontal exchange of water, affecting drift trajectories of organisms (Molinero et al., 2008). These explanations remain hypothetical regarding SJG zooplankton distribution and aggregation patterns, as the sampling design of the present study did not allow adequate resolution of these mesoscale features.

Zooplankton Food Web Structure

Stable carbon isotopes in bottom and surface POM (bPOM and sPOM, respectively) showed enrichment from the North to the South, suggesting distinct carbon sources in the three zones. POM dominantly derived from terrestrial plant

and soil material has a strongly negative $\delta^{13}C$ signal (Fry and Sherr, 1989; Martineau et al., 2004). The land mass to the north of the SJG contains mollisols, dark soils with high organic matter content (Coronato et al., 2008; Durán et al., 2011). Mollisols composed of material carried by the region's strong westerly winds might contribute terrestrial organic matter to the North zone of the SJG. Such terrestrial organic matter was likely causing depletion of the stable carbon isotopes in POM. Furthermore, the North was the most enriched in nitrogen stable isotopes compared to the Center and South zones. This might be due to high decomposition rates of organic matter and detritus that are enriched in $\delta^{15}N$ during the process (Thornton and McManus, 1994).

The presence of seabird colonies along the northern SJG coast (Yorio, 2009) and subsequent inputs of guano into the gulf might also influence the isotopic ratios (Hawke and Clark, 2010). Alternatively, the positioning of POM in the trophic
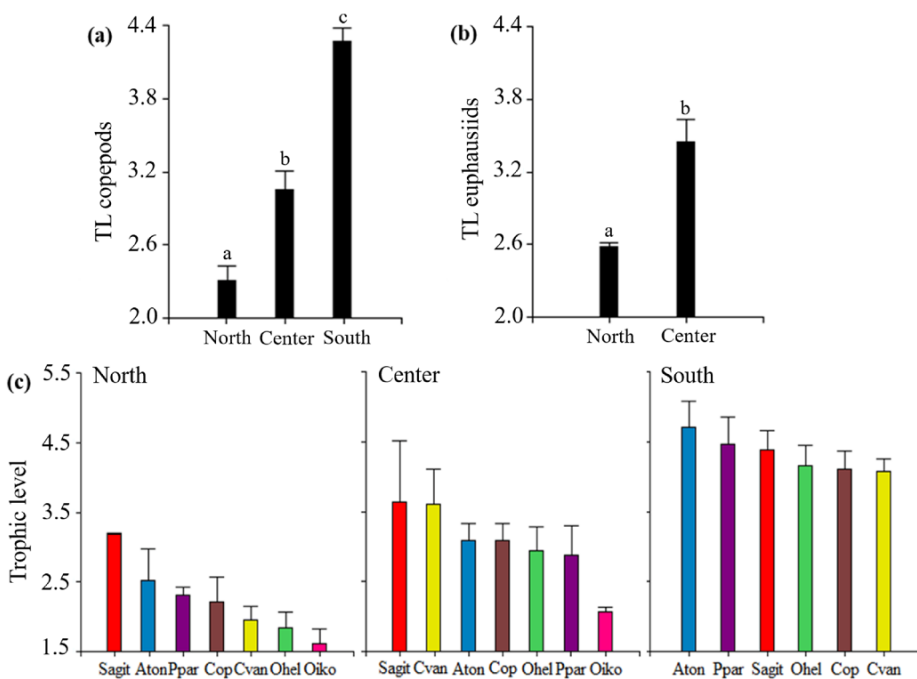

FIGURE 7. Mean trophic levels (TLs) of SJG (a) copepods and (b) euphausiids. Different letters indicate significant differences in mean TLs among zones. Bars represent standard errors. (c) Mean trophic levels of copepods, chaetognaths, and appendicularians for the North, Center, and South. Sagit = *Sagitta* spp. Aton = *Acartia tonsa*. Ppar = *Paracalanus parvus*. Cop = Copepodites of *Ctenocalanus vanus*, *Clausocalanus brevipes*, *Drepanopus forcipatus*, and *Paracalanus parvus*. Cvan = *Ctenocalanus vanus*. Ohel = *Oithona helgolandica*. Oiko = *Oikopleura* spp. Different letters indicate significant differences among zones (Tuckey post-hoc tests, p <0.05).

space throughout the SJG could be due to the differential contribution of algae to the bulk POM (Gearing et al., 1984), with increasing phytoplankton contributions from North to South as found in the present study. In contrast, detritus and terrestrial components seemed to be higher in the North, as suggested by depleted $\delta^{13}C$ and enriched $\delta^{15}N$, and

> The results of this investigation demonstrate the strong link between physical features and the spatial heterogeneity and trophic complexity of this key group of organisms.

also potentially related to high abundance of discarded appendicularian mucus houses in that zone. These constitute a substratum for the aggregation of small particles and are used as feeding and resting sites for microorganisms. They also contribute to the formation of "marine snow" (Alldredge and Silver, 1988), which sinks and could have influenced bPOM isotopic signatures. This hypothesis is supported by Video Plankton Recorder images obtained and analyzed during the cruise, which show the presence of abundant marine snow. In contrast, diatoms and dinoflagellates dominated the micro-autotroph community in the South, whereas diatoms were mostly absent in the Center and North (Latorre et al., 2018, in this issue). These differences in algal distribution between the three zones might also be responsible for the differences found in POM stable isotope signatures that showed general enrichment in $\delta^{13}C$ and depletion in $\delta^{15}N$ when diatoms were present. These results reinforce the idea that diatoms were likely an important food source in the South zone at the time of this study.

The wide range of $\delta^{13}C$ values found

throughout the zooplankton community in the three SJG zones might reflect different carbon sources. Relatively enriched $\delta^{13}C$ signatures close to −18.1‰ for zooplankton might indicate the use of carbon originating from diatoms (Fry and Wainright, 1991). In the present study, euphausiids and mysids with signatures of approximately −19‰ $\delta^{13}C$ were the closest to algal signatures. However, their high $\delta^{15}N$ signatures do not suggest a strictly algal diet. The copepod community showed more depleted $\delta^{13}C$ signatures, suggesting a more omnivorous feeding behavior, which is also supported by the TL >2 found in the Center and South zones. This remains uncertain because we lack isotopic information about a possible link between the algae and the zooplankton (i.e., the microzooplankton). Zooplankton feed not only on phytoplankton but also on heterotrophic protists that link the microbial loop (Azam et al., 1983) with the classic pelagic food web (Turner, 2004). Zooplankton $\delta^{13}C$ for the different taxa identified in the SJG are similar to the values documented in previous investigations for Southern Ocean invertebrates (Rau et al., 1991). Copepods were depleted in $\delta^{13}C$ compared to euphausiids within the three SJG zones, suggesting that the two groups employ different food sources. In the present study stable isotope signatures did not indicate that medium-sized planktonic copepods played a major role as herbivores, as was found by Turner and Granéli (1992); all signatures suggested

an omnivorous feeding mode in the three zones. This supports the increasing evidence that some species (e.g., *A. tonsa*, *O. helgolandica*, and *P. parvus*) are important components of the microbial loop while feeding as predators upon heterotrophic flagellates and ciliates, which in turn are bacterivorous and phytoplanktivorous. *A. tonsa*, which exhibited intermediate $\delta^{13}C$ values, has been considered omnivorous, feeding on diatoms, dinoflagellates, and other autotroph and heterotroph protists, as well as on eggs and larval stages of co-specifics and other copepods (Turner, 1984, and references therein). However, it might show a carnivorous feeding behavior in the SJG, considering its high TL in all the three zones.

The narrow trophic space occupied by copepods in the South zone implies that there is considerable dietary overlap among them, whereas in the North zone their signatures differed considerably, suggesting a certain degree of diet differentiation. Trophic niche differentiation through selective feeding might be a strategy for minimizing competition among species of the same taxonomic group (Turner, 1991). Other copepods appear to feed both as carnivores upon metazoans or as detritivores upon organic aggregates and detritus, as suggested for cyclopoids of the genus *Oithona*, which were reported as detritivores (Lampitt and Gamble, 1982), showing all types of feeding strategies (González and Smetacek, 1994). The depleted $\delta^{13}C$ values we found in the three zones for *O. helgolandica*, and for *P. parvus* in the Center zone, suggest that they might be feeding as detritivores. Euphausiid enrichment in $\delta^{13}C$ in the SJG suggests an herbivore feeding behavior, because euphausiids show a signature similar to that reported for phytoplankton in temperate seas (Fry and Sherr, 1989). Krill is morphologically adapted to phytoplankton consumption, as shown by several gut content studies (Hamame and Antezana, 2010).

Our $\delta^{15}N$ values are much more enriched in $\delta^{15}N$ compared to those reported for the Southern Ocean (Jia

et al., 2016). A narrow range in zooplankton community δ^{15}N values was found for the North, Center, and South zones of 3.2‰, 4‰, and 2.1‰, respectively. This might be interpreted as a reflection of dietary differences within zones as well as differential feeding strategies among species. These results also depend strongly on how many community species have been analyzed. *Oikopleura* spp. presented the most depleted δ^{15}N values in the North and Center zones, close to POM values and consistent with their filter feeding habit. Appendicularians feed on phytoplankton and are capable of efficiently utilizing pico- and nanoplankton and even colloidal material (Capitanio and Esnal, 1998). They showed the lowest mean TL of all zooplankton taxa and are considered to be an energetic food source for higher TLs (Spinelli et al., 2012). In contrast, chaetognaths were the most enriched in δ^{15}N, especially in the North. They presented the highest TL in the North and the Center, suggesting a carnivorous diet, confirming their documented role as predators that play an important part in regulating copepod populations by removing a significant fraction of their standing stock (Giesecke and González, 2004). However, the role of chaetognaths as dominant and exclusive predators should be revisited. Grigor et al. (2015) reported the presence of green detritus in *Parasagitta elegans* guts and high levels of a dinoflagellate fatty acid trophic marker, which may suggest omnivory or detritivory. These feeding behaviors might explain the unexpected depleted δ^{15}N values and lower TL of chaetognaths found in the South compared to the other zones.

Euphausia spp. juveniles and adults occupying the same trophic space in our study in the North and Center contrasts with the results obtained by Rau et al. (1991), who found that δ^{15}N increased with the sizes of individuals. The mean TL of euphausiids was higher in the Center than in the North, which might indicate an omnivorous feeding behavior within this zone, alternative to the herbivory

proposed above. Omnivory was previously observed in *Euphausia* spp. feeding carnivorously on a wide range of prey (e.g., nauplii, copepods, and their own furcilia) and on phytoplankton (Price et al., 1988). The highest TL values for the entire zooplankton community were found in the South. This is due to depleted δ^{15}N values of bulk POM measured there, as discussed above. Thus, the TL estimates should be considered as relative values during summer rather than as absolute values and need to be interpreted with great caution, because the POM values taken as baselines were significantly different in each zone. The present study represents the first work done on the trophic structure of SJG zooplankton using stable isotope techniques.

CONCLUSIONS

The results of this research reveal two clearly distinctive, spatially segregated zooplankton assemblages, one in the North/Center and the other in the South. Distribution of the two assemblages is consistent with the concept that there are two zones with distinct water column stratification characteristics. This confirms the strong association between physical properties of the water column and zooplankton assemblages previously documented for the Argentine continental shelf. Species composition also differed between these assemblages. However, isotopic δ^{13}C values ranged widely throughout the SJG, with a general enrichment from the North to the South, suggesting different carbon sources among zones and among taxa. Variations in TL calculated from δ^{15}N provided evidence of different zooplankton feeding behaviors. The results of this investigation demonstrate the strong link between physical features and the spatial heterogeneity and trophic complexity of this key group of organisms. These characteristics may in turn control the structure and function of the whole pelagic trophic food web. Consequently, a deep understanding of these interactions is

essential for the adequate management of ecosystem services, including fisheries, in this highly productive area. ⟳

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