

Seasonal and spatial variations in macrozooplankton quality as food for fish in a SW Atlantic Ocean gulf – the role of lipids and fatty acids

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Abstract

Macrozooplankton nutritional quality is essential information to understand the energy and matter fluxes in marine food webs and their value as prey for fish. Lipid-derived energy density (ED; kJ g^{-1}) and polyunsaturated fatty acids content (PUFA; $\mu\text{g mg}^{-1}$ total lipids) of *Euphausia* spp. and *Munida gregaria* were studied along a seasonal cycle (September 2016- November 2016-January 2017), and related with their size and the spatial environmental variability (satellite chlorophyll-a (chl-*a*) concentration and frontal structures) of the San Jorge Gulf (45° – 47°S , $65^{\circ}30'$ – $67^{\circ}30'$ W; Argentinean Continental Shelf, SW Atlantic Ocean). This gulf is a key nursery and feeding ground for many commercially and ecologically relevant fish species (e.g. *Merluccius hubbsi*). While ED was similar in both taxa, PUFA content was significantly higher in *Euphausia* spp. Quality indices showed seasonal and spatial variations, while the effect of size was non-significant. For both taxa, minimum ED values occurred in winter, while for *Euphausia* spp. the maximum was observed in summer and for *M. gregaria* in spring. *M. gregaria* ED tightly coupled with the seasonal chl-*a* cycle. PUFA content also varied seasonally, with an opposite trend. Spatially, higher ED and PUFA values occurred in locations with elevated chl-*a* concentrations. This was mostly manifested in *M. gregaria* indices and less evident in *Euphausia* spp. Results provide novel and baseline information of zooplankton, which can be applied in food web models to understand the trophic dynamics of many fish and top predators species in the Argentinean Shelf in the current global change context.

INTRODUCTION

Zooplankton constitutes a main compartment of marine food webs, playing a key role connecting the primary producers and the upper trophic levels (Suthers et al. 2019). They accumulate energy as organic substances, and their consumers, in turn, feed upon this energy (Lindeman 1942). In particular, zooplankton is a major food source for fish, and their access to adequate prey determines growth, survival and recruitment (Costalago et al. 2020). Hence, estimates of zooplankton quality constitute a central piece of information for generating accurate estimates of consumption, growth, the relative importance of prey items, and foraging behavior in the context of predator's trophic ecology.

Understanding how prey characteristics drive predators' foraging strategies and shape energy fluxes in the food web is one of the current challenges to improve our knowledge of ecosystem functioning (Dessier et al. 2018), and to predict consequences of challenges to predators, such as from climate change and increased fisheries (Schaafsma et al. 2018).

Prey quality is the degree to which the consumer's nutritional needs are fulfilled by the quantity and composition of the accessible food, which is known to vary depending on the season and trophic state of the ecosystem (Müller-Navarra 2008). It can be defined in terms of the energy and the essential nutrients delivered for vital functions and normal development of the individuals (Izquierdo et al. 2000). In this sense, lipids play a key role provided their higher energetic content (37 kJ g^{-1}) compared to proteins and carbohydrates (17 kJ g^{-1} each) (Müller-Navarra 2008). Zooplankton provides a rich and abundant source of lipids (Pinger et al. 2022), which can be converted to energy density units (ED; kJ g^{-1}), indicating the

caloric input as prey while being consumed by a predator (Clarke 1980). Prey ED is known to fluctuate spatially and temporally (Ruck et al. 2014; Chen et al. 2019). Representative energy densities for many functional groups and whole geographic regions are still unavailable, and only a few studies have examined the ED in temperate waters (Romero et al. 2006a; Ciancio et al. 2007; Varisco et al. 2020; Bruno et al. 2023).

In addition to meeting their energy demands, consumers need a balanced composition of essential nutrients in their diets to develop normally and achieve high growth rates (Hiltunen et al. 2022). Particularly, the fatty acid composition can cause a difference in the nutritional value of the species (Ahlgren et al. 1997; St. John et al. 2001). Fish require certain polyunsaturated fatty acids (PUFA) that are considered essential, including the omega-3 eicosapentaenoic (EPA, 20:5n3) and docosahexaenoic (DHA, 22:6n3) acids, and the omega-6 arachidonic acid (ARA, 20:4n6). Their deficiency in the diet of juvenile and adult fish leads to various morphological abnormalities, deterioration of vision and ability to search and catch prey, disturbance of behavioral responses (schooling and avoiding predators), and reduction in immunity and resistance to stress and diseases (Tocher 2003). In the long term, an inadequate PUFA supply along ontogeny can turn into a limiting factor in controlling fish populations (Litzow et al. 2006). In marine food webs, the main source of PUFA comes from primary producers since fish are unable to biosynthesize them *de novo* in adequate amounts to supply metabolic demands (Dalsgaard et al. 2003). In this sense, there is growing concern that climate change induced increases in water temperature may reduce the production of EPA and DHA at the base of the food web (Jónasdóttir 2019), resulting in lower availability for higher trophic level consumers such as zooplankton and, in turn, for fish (Hixson and Arts 2016; Colombo et al. 2020).

In the Argentinean Continental Shelf (ACS), the San Jorge Gulf (45°–47°S, 65°30'–67°30' W; SJG) is a semi-closed basin (maximum depth ~ 100 m) occupied by a mixture of Shelf Water (salinity 33.4 to 33.8) from the Cape Horn Current and Low-Salinity Coastal Water (salinity < 33.4; Bianchi et al. 2005) from the Magellan Plume. It exhibits strong seasonal and spatial fluctuations in the environmental features. Wind-driven upwelling mechanisms along the south and southwest coast (Tonini et al. 2006; Pisoni et al. 2020) have been described. Three highly productive frontal systems can be recognized: the North Patagonian Frontal System (NPFS; Sabatini and Martos 2002), the Southern Patagonian Frontal System (SPFS; Guerrero and Piola 1997), and the Outer front (Glembocki et al. 2015). While the NPFS and the Outer front mainly develop during austral spring and reach their maximum spread in summer, the SPFS has its maximum expression during the winter, reflecting the influence of the Magellan Plume. Associated with their dynamics, maximum phytoplankton concentrations occur from spring (diatom-dominated) until the end of the summer (dinoflagellate-dominated), with a secondary maximum in autumn and a minimum in winter (diatom-dominated) (Akselman 1996; Glembocki et al. 2015). The macrozooplankton community is mostly represented by early stages and adults of euphausiids (*Euphausia* spp.: *E. lucens*+ *E. vallentini*) and decapods (*Munida gregaria*) (Temperoni 2015 and references). Their abundance patterns and trophic regimes are greatly dependent on the seasonal stratification of the water column and the chlorophyll-*a* concentration that couples to the fronts (Cepeda et al. 2018 and references). Hence, a potential influence of the gulf's seasonal and spatial variability in productivity could be expected upon their energy stores.

Macrozooplankton in the SJG is the main food source of age-0 + individuals of Patagonian hake *Merluccius hubbsi* (Temperoni et al. 2018, 2020), one of the most important commercial resources in the ACS (Irusta 2016). This stage nurses within the gulf and is key for the recruitment of the species (Álvarez Colombo et al. 2011). A recent study has shown that their body condition varies spatially and seasonally, suggested to be driven by a bottom-up effect when consuming *Euphausia* spp. and *M. gregaria* (Temperoni et al. 2020). In addition, both macrozooplankters serve as prey of at least nine other commercially relevant fish species in the SJG. These include the pink cuskeel *Genypterus* spp. (Belleggia et al. 2023), the Argentine sea bass *Acanthistius brasilianus*, the long tail hake *Macruronus magellanicus*, and Rajidae skates (Sánchez and Prenski 1996).

Given the importance of macrozooplankton as prey in the diet of fish predators and their potential effect upon body condition, knowledge of their quality can be useful to better understand their feeding preferences and the population's success. However, for the ACS, this information remains unexplored. In this context, the main goal was to determine the prey quality of *Euphausia* spp. and *M. gregaria* in the San Jorge Gulf in terms of energy density and PUFA content, and to relate these results with the environmental variability along seasons and locations. We hypothesized a higher prey quality of *Euphausia* spp. and *M. gregaria* during spring, coupled with the main phytoplankton bloom in the region, particularly in sectors of the gulf influenced by frontal systems.

MATERIALS AND METHODS

Sampling

Zooplankton samples were collected during three research cruises carried out in the SJG in austral winter (September 2016), spring (November 2016), and summer (January 2017) (Fig. 1; Table 1). Winter and summer cruises were carried out onboard the R/V “Eduardo Holmberg”, while the spring cruise was performed onboard the R/V “ARA Puerto Deseado” (Pampa Azul program). Samples were obtained with Bongo (300 µm mesh) and Rectangular Midwater Trawl (500 µm) nets fitted with flowmeters (Hydrobios), by oblique tows from near the bottom to the surface. On board, euphausiids (*Euphausia* spp.) and the decapod *Munida gregaria* were removed from the samples and stored in liquid nitrogen at -70°C.

Table 1

Energy density (ED; kJ g^{-1}) and PUFA content ($\mu\text{g mg}^{-1}$ total lipids) (mean \pm standard deviation values) as indicators of zooplankton nutritional quality in the San Jorge Gulf during three consecutive seasons: winter 2016 (September), spring 2016 (November) and summer 2017 (January)

		<i>Euphausia</i> spp.	<i>Munida gregaria</i>
Winter	ED	0.8 ± 0.4	0.7 ± 0.3
	PUFA content	173.8 ± 99.1	113.5 ± 56.1
	Total length (mm)	16.9 ± 1.4	26.3 ± 3.0
	n	19	13
Spring	ED	1.2 ± 0.4	1.3 ± 0.4
	PUFA content	151.1 ± 71.4	111.7 ± 86.3
	Total length	16.4 ± 2.2	18.4 ± 10.0
	n	28	13
Summer	ED	1.3 ± 0.5	1.1 ± 0.5
	PUFA content	62.8 ± 21.5	29.5 ± 21.0
	Total length	15.6 ± 2.5	13.7 ± 2.9
	n	15	26

For each cruise, as a proxy of phytoplankton biomass, monthly averages of MODIS Aqua surface chlorophyll-*a* concentrations (chl-*a*; mg m^{-3}) with a spatial resolution of 2 km pixel^{-1} were obtained (NASA Goddard Space Flight Center, <http://oceancolor.gsfc.nasa.gov>). Coupled with these images, the position of the frontal systems was determined with the Simpson's stability index (ϕ , J m^{-3} ; Simpson 1981), from temperature and salinity data obtained from CTD castings that were processed with standard routines; a value of $\phi = 30 \text{ J m}^{-3}$ was considered as the limit separating homogeneous from stratified waters. Further details on sampling and processing of the oceanographic can be found in Temperoni et al. (2020).

Laboratory analyses

Total lipids were extracted from zooplankton (whole individuals) following Folch et al. (1957). A variable number of 5–10 individuals of each taxon (according to availability) were analyzed individually per sampling station. Before lipid extraction, total length (L, mm) and wet mass (g) of each individual were measured. For *Euphausia* spp., L was measured from the anterior margin of the eye to the tip of the telson; sub-mature males and females were defined as L between 10–11 mm, while larger individuals were considered mature *sensu* Bary (1956). For *M. gregaria*, L was determined from the tip of the rostrum

to the tip of the telson; sub-mature decapodites (= megalopa) were defined as $L \sim 10$ mm while larger individuals were considered juveniles *sensu* Roberts (1973).

The energy density (DE, kJ g^{-1}) of each taxon was determined from the total lipid content, its energetic equivalent (35.6 kJ g^{-1} ; Postel et al. 2000) and the individual wet mass (g). Fatty acids composition was determined by gas chromatography following transesterification to their methyl esters (FAME), where a rapid transmethylation method under alkali-catalyzed conditions was applied, based on ISO 12966-2 (International Organization for Standardization 2017) with minor modifications. Briefly, lipid sample was dissolved in isooctane (chromatographic quality) in a ratio of 1 mg ml^{-1} in a glass tube. Then, 0.5 ml of KOH methanolic solution (2 mol L^{-1}) reagent was added and the sample was stirred vigorously (1 min) with a vortex. Finally, NaCl ($40 \text{ g } 100 \text{ ml}^{-1}$) in the same amount as isooctane was added and mixed again for 1 min . The sample was allowed to stand for 5 min , and the upper (organic) fraction was separated, filtered (PTFE $0.2 \text{ }\mu\text{m}$ pore size) and transferred to a clean vial. FAME were determined with a Shimadzu GC-2010 (Shimadzu Corp., Kyoto, Japan), equipped with an auto-sampler (Shimadzu® AOC-20i) in split mode ($T^\circ = 250^\circ \text{ C}$; split rate = 5.0), a flame-ionization detector (250° C), a capillary column ($30 \text{ m} \times 0.32 \text{ mm}$; $0.25 \text{ }\mu\text{m}$ film thickness; Omegawax 320) and nitrogen as a carrier gas. A volume of $1 \text{ }\mu\text{l}$ of sample was injected and peaks were identified by comparison of their retention times with those of external reference standards (AccuStandard® FAMQ-005 + Supelco® PUFA N°1 Marine Source). PUFA content (= sum of EPA + ARA + DHA) was reported as $\mu\text{g mg}^{-1}$ total lipids, and the percentage contribution of the three fatty acids to the total amount was calculated.

Statistical analysis

Energy density and PUFA content values were compared among macrozooplankton items, sampling seasons and locations within each season through ANOVA or non-parametric Kruskal-Wallis tests, at a significance level of $P < 0.05$. The same procedure was applied to chlorophyll-*a* concentration data. Also, the relationship between both quality parameters and total length of the individuals was tested by simple regression. Statistical analyses were performed in STATISTICA 8.0 (StatSoft 2007).

RESULTS

A total of 114 determinations were performed on *Euphausia* spp. and *M. gregaria* individuals, ranging in size between $10.0\text{--}24.0 \text{ mm L}$ ($X \pm \text{SD} = 16.6 \pm 2.5 \text{ mm}$, $n = 62$) and $10.0\text{--}34.0 \text{ mm}$ ($X \pm \text{SD} = 18.2 \pm 7.6 \text{ mm}$, $n = 52$), respectively. Mean wet mass ranged between $0.02\text{--}0.08 \text{ g}$ ($X \pm \text{SD} = 0.03 \pm 0.01 \text{ g}$, $n = 62$) for the euphausiids and $0.01\text{--}2.4 \text{ g}$ ($X \pm \text{SD} = 0.3 \pm 0.4 \text{ g}$, $n = 52$) for the decapod. A general analysis without considering seasons and/or sampling locations showed no significant differences in the ED values between *Euphausia* spp. ($X \pm \text{SD} = 1.11 \pm 0.46 \text{ kJ g}^{-1}$, $n = 62$) and *M. gregaria* ($X \pm \text{SD} = 1.08 \pm 0.48 \text{ kJ g}^{-1}$, $n = 52$). On the contrary, PUFA content was significantly higher (ANOVA, $F(1, 112) = 20.59$, $P = 0.00001$) in the euphausiids ($X \pm \text{SD} = 136.68 \pm 84.43 \text{ }\mu\text{g mg}^{-1}$, $n = 62$) than in the decapod ($X \pm \text{SD} = 71.04 \pm 66.88 \text{ }\mu\text{g mg}^{-1}$, $n = 52$). When examining the link between the nutritional quality measures and the size of the individuals, *M. gregaria* ED was significantly and negatively related with L ($r = -0.36$, $R^2 = 0.13$, $P = 0.092$,

n = 49), although with a low coefficient. This tendency was not observed for the PUFA content, and no significant relationships with size were observed in *Euphausia* spp.

Seasonal variations in macrozooplankton quality

ED varied significantly among seasons (Table 1) for *Euphausia* spp. (ANOVA, $F(2, 59) = 8.07$, $P = 0.0008$) and *M. gregaria* (ANOVA, $F(2, 49) = 6.18$, $P = 0.004$) (Fig. 2a). For both species, the minimum values occurred in winter, while for the euphausiids the maximum was observed in summer and for the decapod in spring. The tendency observed in *M. gregaria* matched the seasonal mean values in chl-*a* concentration, which significantly increased (Kruskal-Wallis test, $H_2 = 6.38$, $P = 0.041$) in the gulf from winter ($\bar{X} \pm SD = 1.29 \pm 0.22 \text{ mg m}^{-3}$, $n = 9$) to spring ($\bar{X} \pm SD = 2.05 \pm 0.53$, $n = 6$), with intermediate values in summer ($\bar{X} \pm SD = 1.99 \pm 1.17$, $n = 7$). PUFA content also varied significantly among seasons (Fig. 2b). For *Euphausia* spp. (Kruskal-Wallis test, $H_2 = 24.14$, $P = 0.0000$), the maximum occurred in winter, with an intermediate value in spring and the minimum in summer. In the case of *M. gregaria*, similar values were recorded in winter and spring, with the minimum observed in summer (Kruskal-Wallis test, $H_2 = 26.80$, $P = 0.0000$). When examining the percentage contribution of each fatty acid to the total PUFA content (Fig. 3), seasonal differences were also observed, with a similar pattern in both species. While in winter and summer DHA largely prevailed over EPA (~ 75% vs. 25%, respectively), in spring the amount of EPA and DHA were fairly similar (~ 50% each). During this season, the EPA increase was more evident in *M. gregaria*. ARA contribution was very low in every season (~ 1–4%).

Spatial variations in macrozooplankton quality

In winter (Fig. 4, upper panels), *Euphausia* spp. ED values were higher in the north sector of the gulf (Fig. 4a), concurrent with the highest chl-*a* records observed close to shore (Fig. 4c); on the contrary, similar ED values among locations were recorded for *M. gregaria*. PUFA content of *Euphausia* spp. was fairly similar among sampling sites, with no marked spatial pattern (Fig. 4b), while higher values were observed for *M. gregaria* in the south end of the gulf.

During spring (Fig. 4, middle panels), oceanographic data (Fig supp. 1) indicated the onset of stratification ($\phi > 30 \text{ J m}^{-3}$) and the incipient formation of the frontal systems in the north (NPFS) and south (SPFS) ends of the gulf (Fig. 4c). ED values of euphausiids and *M. gregaria* (Fig. 4a) were higher in stations located in the central area of the gulf facing the mouth, while for the decapod higher values were also observed near shore towards the south. Accordingly, chl-*a* concentration was high in most areas of the gulf but especially in the southwest coastal and the southeastern areas, associated with the coastal upwelling and the Outer front, respectively (Fig. 4c). As observed in winter, PUFA values of euphausiids were similar among locations (Fig. 4b), while for *M. gregaria* higher values were observed near shore towards the south.

Lastly, in summer (Fig. 4, lower panels), water column stratification was the highest ($\phi > 40 \text{ J m}^{-3}$). *Euphausia* spp. ED values were maximum in a northern coastal station and near the south end of the

gulf, while for *M. gregaria* the highest records occurred towards the south and the mouth of the gulf (Fig. 4a). Chl-*a* values (Fig. 4c) followed a spatial distribution strongly linked to the bottom temperature field (Fig. supp. 1), being higher in the north and south ends where both frontal systems developed. For both species, PUFA values (Fig. 4b) were fairly similar among sampling sites.

DISCUSSION

This work provided more comprehensive information on the ED and PUFA content supplied by macrozooplankton to upper level zooplanktivorous consumers in the San Jorge Gulf, a nursery and feeding ground for many fish species of commercial and ecological interest. While many biochemical studies on zooplankton have been performed worldwide (Färber-Lorda et al. 2009; Barroeta et al. 2017; Jo et al. 2017; Chen et al. 2019), little work has been done on the South West Atlantic (Eder and Lewis 2005) and only few studies were available for the ACS (Romero et al. 2006a; Ciancio et al. 2007; Varisco et al. 2020; Bruno et al. 2023). It should be acknowledged that samples were collected in assessment and/or oceanographic cruises not specifically designed to evaluate zooplankton features. This represented a constraint concerning a comparable sampling design among seasons. In spite of this, results indicated that the nutritional quality of *Euphausia* spp. and *M. gregaria* were strongly modulated by season and location, correlating with changes in the broad scale environmental data.

Comparing our data with the literature was challenging due to the different plankton samplers, measuring methods, units in which results were expressed, and conversion factors used to calculate the energy content (Harmelin-Vivien et al. 2019). The most recent study in our region (Bruno et al. 2023) characterized the ED of plankton fractions (range 23–2000 μm) without distinguishing species. Romero et al. (2006a) determined the ED of *Munida subrugosa* during its reproductive cycle but in ash-free dry mass terms. At a species level, values of 2.5 J g^{-1} wet mass and 11.0 J g^{-1} dry mass were determined for *Euphausia lucens* and *M. gregaria* in Patagonian waters, respectively (Ciancio et al. 2007), while for the latter, ED values ranging from $3\text{--}4 \text{ kJ g}^{-1}$ were observed in the SJG (Varisco et al. 2020). Worldwide, scarce literature on ED was found for the genus *Munida*, but some studies are available on euphausiids. For *E. pacifica* in the Gulf of Alaska, a value of 3.9 kJ g^{-1} wet mass was obtained in individuals with sizes $> 15 \text{ mm}$ (Mazur et al. 2007), while for *E. superba* in the Southern Ocean, higher values were recorded ($16\text{--}25 \text{ kJ g}^{-1}$) although expressed in dry mass (Ruck et al. 2014). Most of these studies used a calorimetric bomb that provides the gross energetic content of the individuals. In this work, ED was derived from the quantification of total lipids, showing similar results to those reported for the region, despite the different methodological approach. This most likely occurs since lipids are the most common predictors of energetic density (Schaafsma et al. 2018). Regarding PUFA content, available qualitative data indicates their predominance in *Euphausia* spp. (Phillips et al. 2003; Quillfeldt et al. 2011) and *gregaria* (Varisco et al. 2020). Some quantitative studies for *E. superba* in the Scotia Sea (EPA: $10\text{--}100 \mu\text{g g}^{-1}$; DHA: $5\text{--}30 \mu\text{g g}^{-1}$; Ericson et al. 2018) and for *E. pacifica* in the Pacific Ocean ($300\text{--}1600 \mu\text{g g}^{-1}$; Yamada et al. 2017) reported concentrations in similar ranges as the ones obtained in this study.

Zooplankton size was found to influence the nutritional quality, particularly for *M. gregaria*. In the context of the optimal foraging theory and trophodynamic studies, evaluating this relationship is crucial, since predators usually consume specific prey size ranges that provide a higher nutritional content (Pyke 1984). In this study, the observed negative relationship between *M. gregaria* ED and size could be explained considering that the analysis included a wide size range from sub-mature individuals (~ 10 mm total length) to adults (> 20 mm) (Varisco 2013). Chen et al. (2019) found a decrease in zooplankton ED from medium (200–1000 µm) to large (> 1000 µm) size classes. The strictly herbivorous trophic regime of the smaller *M. gregaria* (Varisco and Vinuesa 2010) would provide high amounts of energy deriving from phytoplankton. On the contrary, in larger individuals, both the trophic regime (omnivorous and/or detritivorous) (Riquelme-Bugueño et al. 2020) as well as the potential investment in reproductive events (Varisco and Vinuesa 2015), might produce a decrease in the energy stores. Even though no relationship was observed between ED and PUFA content with size in *Euphausia* spp., a loss of up to 60% of lipids during spawning has been reported for *E. superba*, resulting in lower ED in mature and larger females (Clarke 1980; Färber-Lorda et al. 2009). In addition, larval krill has been shown to contain higher PUFA content than sub- and adult krill (Ju and Harvey 2004), which in species from temperate regions are known to be essential for embryonic development (Ju et al. 2009).

A seasonal trend in ED values for *Euphausia* spp. and *M. gregaria* was recorded, with minimum values in winter for both species, and maximums in spring and summer, respectively. *M. gregaria* energy reserves tightly coupled with the mean chl-*a* concentration cycle, which was the typical of temperate regions described for the gulf (Akselman 1996; Glembocki et al. 2015), thus confirming our initial hypothesis. However, for *Euphausia* spp., the temporal pattern was less evident. It has been suggested that fluctuations in ED at a species level can occur when lipid depots change in response to the environmental conditions (Spitz and Jouma'a 2013), with zooplankton of temperate regions showing an accumulation of their reserves during periods of high nutrient availability (Lee et al. 2006). In this sense, both species would be profiting from the higher phytoplankton biomass during the spring bloom in the SJG to build up their energy reserves, which translated into higher ED. Nevertheless, the allocation strategy might be different. In the study area, *M. gregaria* reproductive period starts in winter (August) (Varisco 2013), and during spring higher abundances of the herbivorous sub-mature individuals match the phytoplankton bloom. On the contrary, *Euphausia* spp. gonadal maturation occurs from winter (August) to spring (November), and the presence of juvenile stages in the plankton peaks during summer (January) (Ramírez 2016). This could explain the higher ED values during this season. In addition, it should be mentioned that although euphausiid species may be herbivorous or carnivorous, many are omnivorous at some point in their life history (Hagen et al. 2001). Hence, they can probably detach from the phytoplankton bloom, opposite to *M. gregaria*. In recent years, the presence of the pelagic morphotype *gregaria* has been increasing related to chl-*a*, favoring its persistence over the benthic morphotype *subrugosa* (Ravalli et al. 2013; Varisco 2013). A possible lag effect of lipids being metabolized and stored after the spring algal bloom should also be considered for both species, deserving further studies to better understand the seasonal strategies. Lastly, the decrease in ED values observed in winter could be

attributed to a low food intake period when chl-*a* concentrations in the SJG are the minimum (Glembocki et al. 2015), with both species probably using their lipid stores for maintenance during this season.

The seasonal trend in the PUFA content of both species followed an opposing pattern to the ED cycle. Zooplankton must either obtain specific PUFA such as DHA and EPA directly from their diet or synthesize them from C16 and C18n3 PUFA. However, the latter is usually negligible (Bell et al. 2007). The amount available in the diet can vary considerably in time depending on the stage and composition of phytoplankton blooms (Mayzaud et al. 1989). For instance, for krill species in the Southern Ocean, a strong seasonal cycle was observed in EPA and DHA quantities, building up lipid stores when food is abundant (Hagen et al. 2001). However, as mentioned, phytoplankton concentrations in the SJG are minimum in winter (diatom-dominated), with maximum values from spring (mixed contribution of diatoms and dinoflagellates) until the end of summer (dinoflagellate-dominated) (Akselman 1996; Glembocki et al. 2015). From our results, it can be suggested that both *M. gregaria* and *Euphausia* spp. might be preserving their PUFA content during the low productive period (winter), with a prioritized mobilization of saturated and monounsaturated fatty acids as an energy source. This was previously observed for *M. gregaria* in the Beagle channel (Ruiz-Ruiz et al. 2021) and for *Munida* spp. in the Galician Atlantic coast (García Soto et al. 2017). PUFA content can then be invested in eggs production before spawning and in the posterior development of larvae, as has been shown for krill species (Hellesey et al. 2020). In addition, not only phytoplankton abundance but also their fatty acids composition should be taken into account. Following the literature, dinoflagellates contain abundant DHA, whereas diatoms typically contain little if any, with EPA as the predominant PUFA (Sargent et al. 1995). In agreement, our results indicated that in winter and summer, DHA was the main contributor to the PUFA content of both species, while in spring a similar contribution of DHA and EPA was observed.

Spatially, a coupling between ED values and the chl-*a* field was recorded within each season, which was more evident in spring and summer. During spring, higher DE values were observed in the southwest area (mainly for *M. gregaria*) corresponding to the coastal upwelling (Pisoni et al. 2020), and near the mouth of the gulf concurrent with the Outer front (both species) (Glembocki et al. 2015). In summer, higher DE values for both species were mainly associated with the higher chl-*a* values derived from the development of the SPFS (Guerrero and Piola 1997), and particularly for *Euphausia* spp. in the coastal area towards the north, corresponding to the NPFS (Sabatini and Martos 2002). The elevated phytoplankton biomass in both frontal systems has been described from satellite and *in situ* data (Akselman 1996; Romero et al. 2006b; Carreto et al. 2007; Glembocki et al. 2015). Similarly, strong among-location trends in the content and composition of *E. superba* fatty acids were observed in the Scotia Sea (Ericson et al. 2018), with higher concentrations of lipids near frontal areas in the southwest Indian Ocean (Färber-Lorda et al. 2009). In winter, on the contrary, ED values for *M. gregaria* and *Euphausia* spp. were mostly homogeneous among locations, possibly as a response to low phytoplankton availability due to the lack of stratification. With respect to the PUFA content, high values of both species in spring were observed coupled to the coastal upwelling, while for euphausiids elevated records also occurred next to the NPFS and the Outer front. On the contrary, in summer and winter, PUFA values for both species showed no difference among locations.

Monitoring the total lipids and PUFA content of large crustacean zooplankton is a practice currently used by ecologists and fisheries scientists aiming to understand various ecosystem processes, such as the effect of climate change on trophic dynamics of commercially and ecologically important fish species (Pinger et al. 2022). Fish growth and survival are largely determined by the nutritional quality of their food, and the fish that grow quickly during early life stages are more likely to reproduce (Costalago et al. 2020). Results showed seasonal and spatial variations in the nutritional quality of *Euphausia* spp. and *M. gregaria* within the SJG, mostly coupled to the phytoplankton biomass, which can have potential implications in the energy transfer efficiency. In this sense, both species are key prey items in the diet of *M. hubbsi*, particularly during the age-0 + stage that determines recruitment (Temperoni et al. 2020). These authors found a seasonal cycle and spatial patterns in their nutritional condition that couple with the ones observed for the ED of their prey in this study, providing direct proof of the impact that the lipid dynamics of these prey can have upon a predator. However, not only the amount of available energy but also the PUFA contribution fluctuated in time, evidencing shifts from diatom-dominated to flagellate-dominated production in the gulf along seasons. The seasonal shift in primary producers within the gulf conferred a higher DHA:EPA ratio to zooplankton in winter and summer, indicating a better supply of these essential fatty acids for hake than in spring. These results highlight the importance of evaluating nutritional quality by considering the energy input from lipids but also their composition in terms of PUFA content, and set a baseline for a future monitoring of these variables along time. This is particularly relevant in light of the ongoing global climate change, which is already showing its influence upon the environmental features in the ACS; the analysis of time series of satellite chl-*a* and surface temperature anomalies in the reproductive area of *M. hubbsi* revealed increasing trends in both variables (Marrari et al. 2019), with potentially important implications for this and other species inhabiting the region.

Declarations

COMPLIANCE WITH ETHICAL STANDARDS

The authors have no conflict of interest to declare. All applicable national and institutional guidelines for sampling organisms have been followed and all necessary approvals have been obtained.

STATEMENTS AND DECLARATIONS

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

Brenda Temperoni conceived the investigation, performed laboratory and data analysis, acquired funding and wrote the manuscript. Rocío Isla Naveira and Yanina Turina performed the laboratory analysis. Agueda Elena Massa provided laboratory facilities and obtained funding. All authors contributed to the study, commented on previous versions, and read and approved the final manuscript.

Data Availability

The datasets generated during the current study are available from the corresponding author on reasonable request.

Ethics approval

No ethical clearance was required as the zooplankton tissue sample used in this study was taken from the dead animal collected from the research vessels.

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Figures

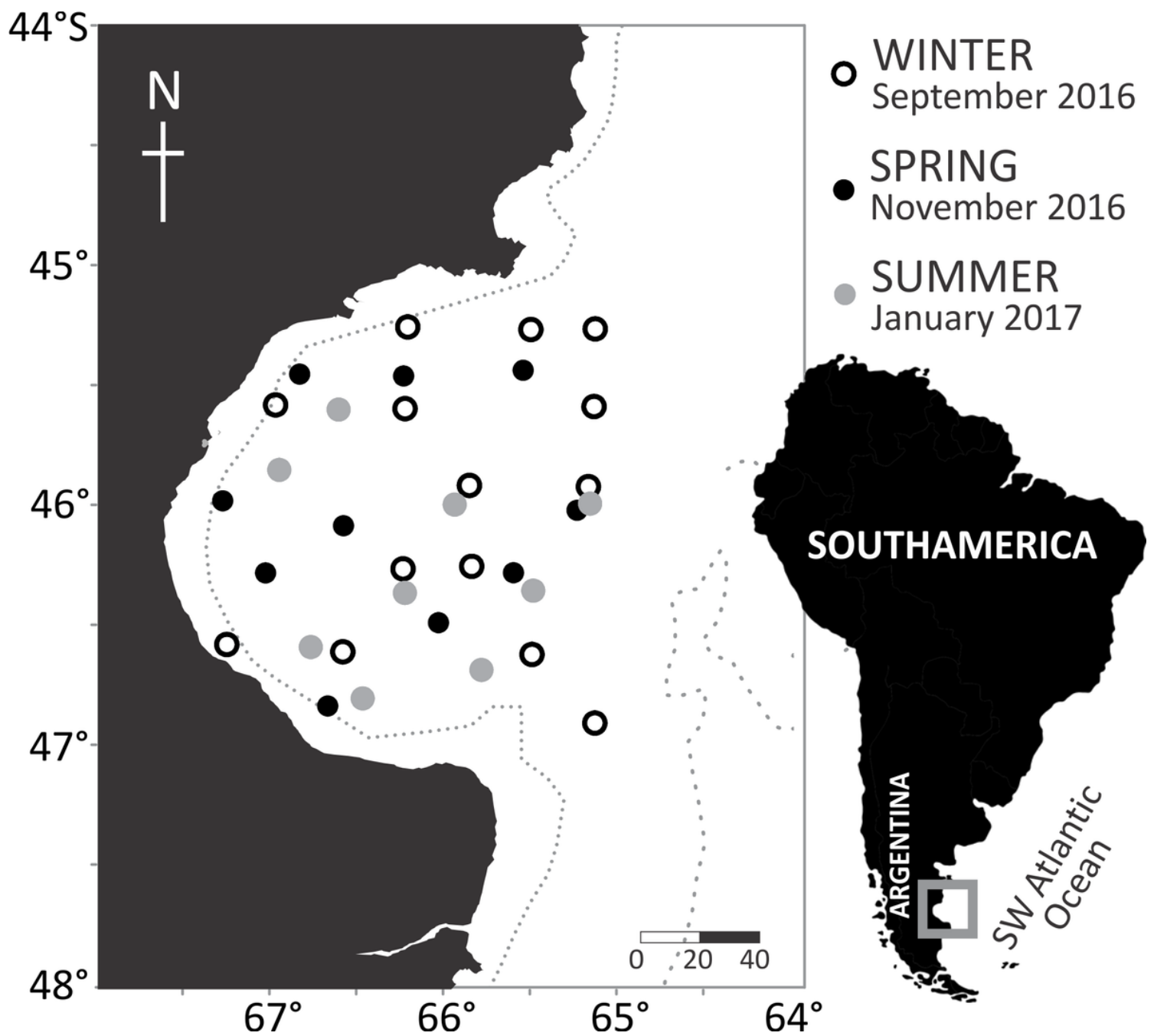


Figure 1

Sampling stations performed in the San Jorge Gulf during three consecutive seasons: winter (September 2016; white circles), spring (November 2016; black circles) and summer (January 2017; grey circles) to collect zooplankton

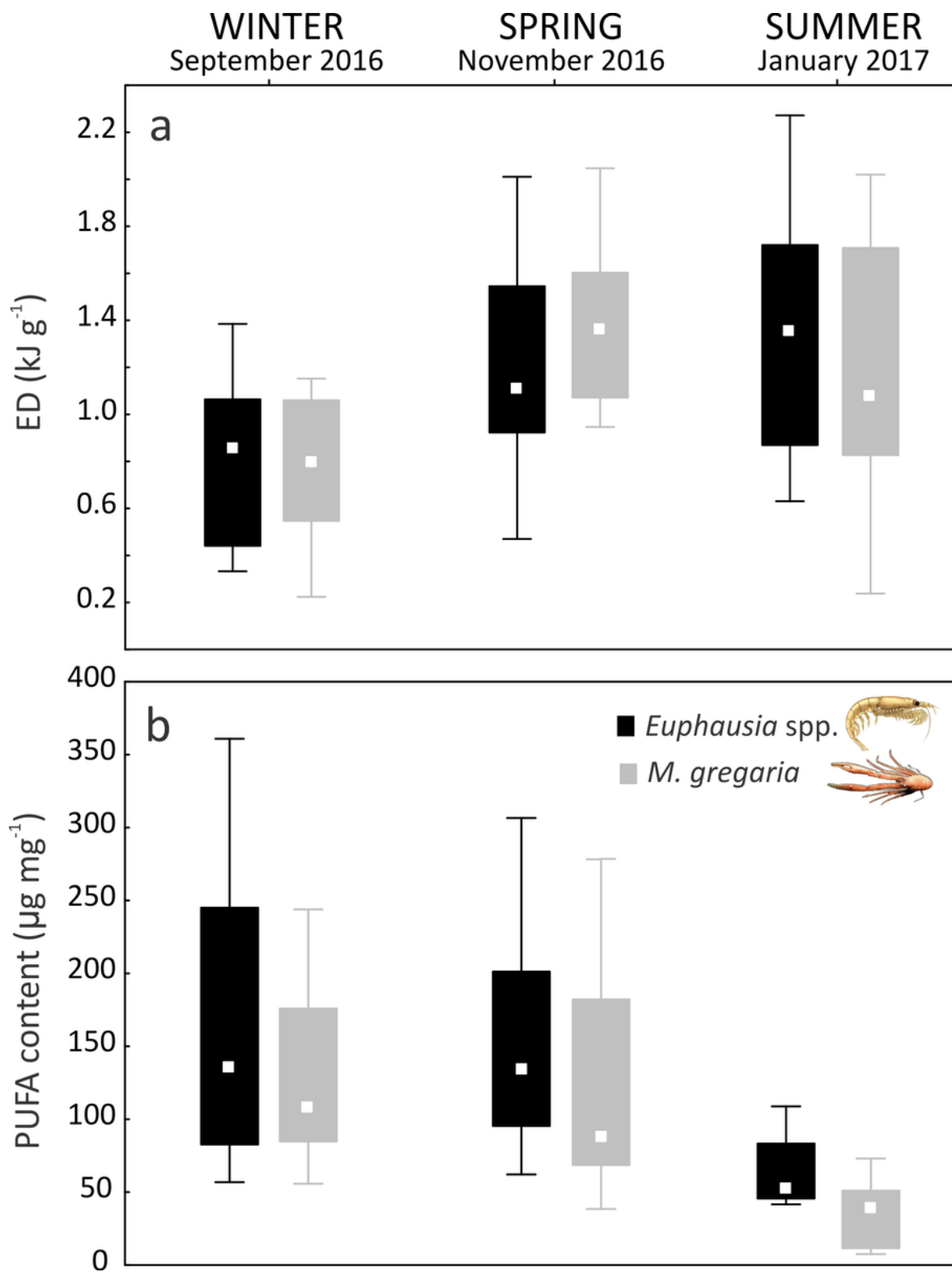


Figure 2

Seasonal variation in nutritional quality of *Euphausia* spp. (black boxes) and *Munida gregaria* (grey boxes) in the San Jorge Gulf. a) Energy density (kJ g^{-1}) and b) PUFA content ($\mu\text{g mg}^{-1}$ total lipids). The squares within the boxes indicate the medians, the boxes extend to the 25th and 75th percentiles, and the whiskers extend to the non-outlier range

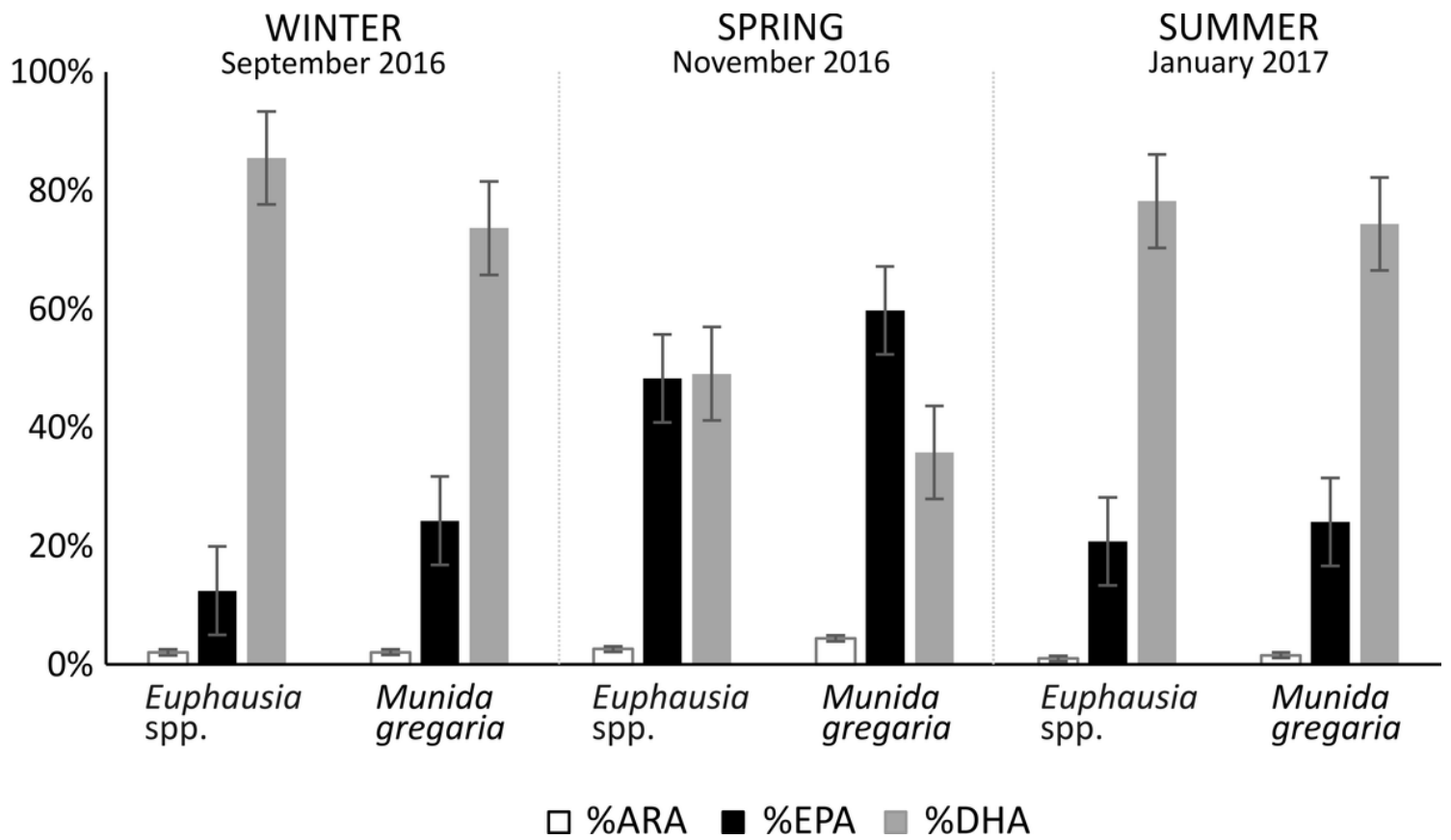


Figure 3

Seasonal percentage (%) contribution of ARA (white bars), EPA (black bars), and DHA (grey bars) to the total PUFA content of *Euphausia* spp. and *Munida gregaria* in the San Jorge Gulf. Lines in each bar indicate the standard error

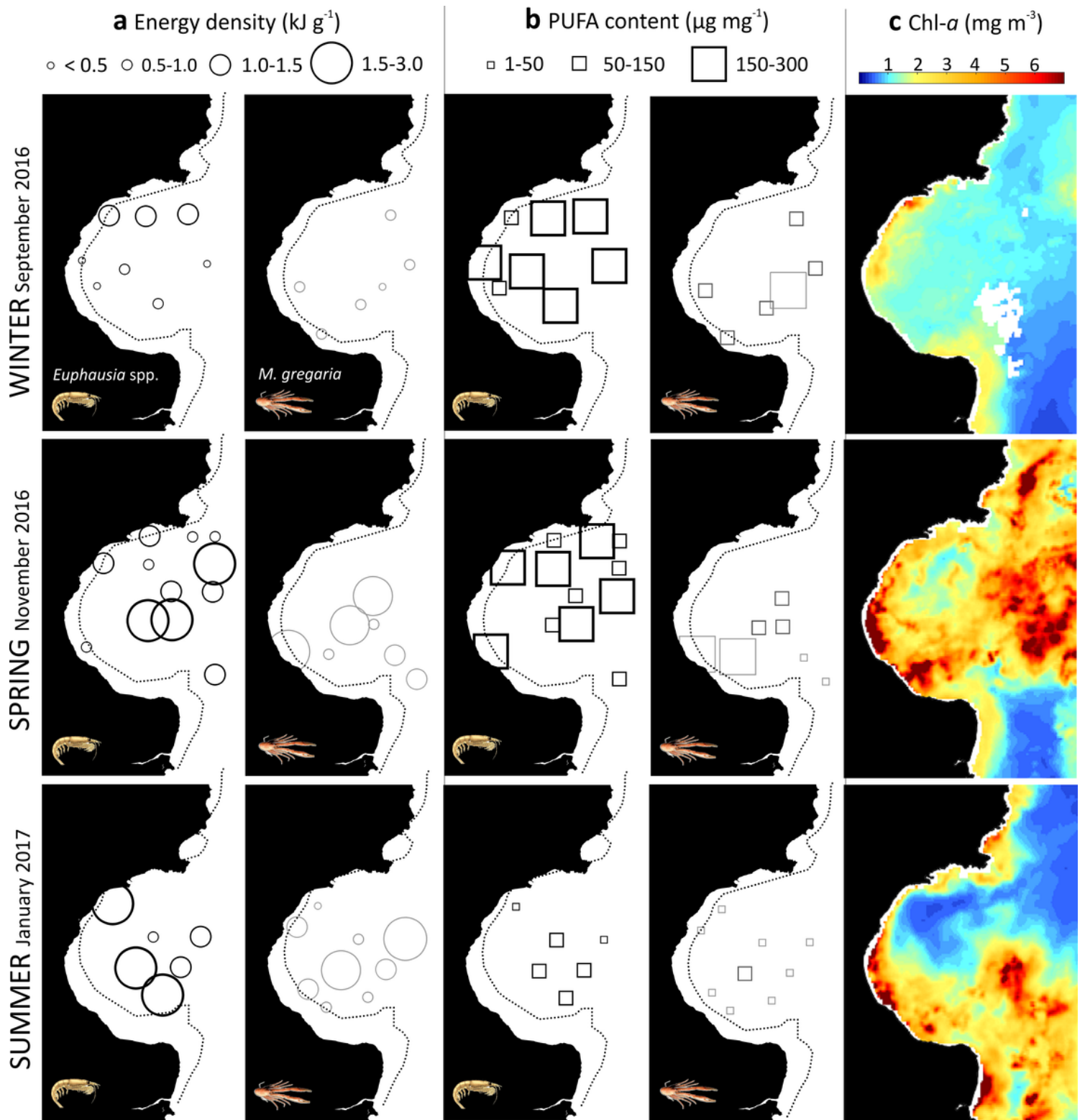


Figure 4

Spatial variation in nutritional quality of *Euphausia* spp. (black) and *Munida gregaria* (grey) in the San Jorge Gulf. (a) Energy density (kJ g^{-1} , circles), (b) PUFA content ($\mu\text{g mg}^{-1}$ total lipids, squares), and (c) satellite chlorophyll-*a* concentration (mg m^{-3}) (MODIS Aqua monthly average, spatial resolution of 2 km pixel^{-1}). Black lines in (c) indicate the average position (critical Simpson parameter $\phi = 30 \text{ J m}^{-3}$) of

the Northern (NPFS; full lines) and Southern (SPFS; dashed lines) Patagonian Frontal Systems, respectively

Supplementary Files

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