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ORIGINAL RESEARCH

Comparative diets of macrocrustacean species from the San Jorge Gulf, Argentina

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ABSTRACT. Macrocrustaceans have a central role in marine food webs given that they often dominate benthic communities and serve as link between basal levels and top predators. The aim of the present study was to describe the diet of six macrocrustacean species (*Eurypodius longirostris*, *Libidoclaea granaria*, *Lithodes santolla*, *Grimothea gregaria*, *Peltarion spinosulus* and *Pterygosquilla armata*) from San Jorge Gulf, Argentina. Stomach contents were analyzed in 331 individuals and the frequency of occurrence and relative abundance of the different prey items were estimated. Differences between the diets of the studied species were established by using an analysis of similarity (ANOSIM), and prey items responsible for dissimilarities were identified by a similarity percentage analysis (SIMPER). A high diet overlap was observed among most species, probably because crustaceans and particulate organic matter constituted very abundant prey items for the different species. The presence of sediment in the stomachs of *E. longirostris*, *G. gregaria* and *P. spinosulus* suggests that these species have a deposit feeding habit. The diet overlap may be the result of the generalist habit of species studied (except for *P. armata*). The deposit feeding strategy would be favoured by the high secondary productivity of the infaunal community of the San Jorge Gulf.

Key words: Feeding strategy, diet overlap, decapods, stomatopods, Patagonia.

Dieta comparada de especies de macrocrustáceos del Golfo San Jorge, Argentina

RESUMEN. Los macrocrustáceos desempeñan un papel central en las redes tróficas marinas, ya que a menudo dominan las comunidades bentónicas y actúan como un vínculo entre los niveles tróficos basales y los depredadores tope. El objetivo de este trabajo fue describir la dieta de seis macrocrustáceos (*Eurypodius longirostris*, *Libidoclaea granaria*, *Lithodes santolla*, *Grimothea gregaria*, *Peltarion spinosulus* y *Pterygosquilla armata*) del Golfo San Jorge, Argentina. Se analizaron los contenidos estomacales de 331 individuos, estimando la frecuencia de ocurrencia y abundancia relativa de los diferentes ítems presa. Las diferencias entre las dietas se evaluaron mediante un análisis de similitud (ANOSIM) y los ítems responsables de las disimilitudes fueron identificados mediante un análisis de porcentaje de similitud (SIMPER). Se observó un alto solapamiento dietario entre la mayoría de las especies, probablemente debido a que los crustáceos y la materia orgánica particulada constituyeron ítems presa muy abundantes para las diferentes especies. La presencia de sedimento en los estómagos de *E. longirostris*, *G. gregaria* y *P. spinosulus* sugiere que estas especies tienen un hábito de alimentación sedimentívoro. El solapamiento dietario podría ser resultado del hábito generalista (excepto *P. armata*). La estrategia de alimentación sedimentívora estaría favorecida por la alta productividad secundaria de la comunidad infaunal del Golfo San Jorge.

Palabras clave: Estrategia de alimentación, superposición de dieta, decápodos, estomatópodos, Patagonia.

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INTRODUCTION

Macrocrustaceans play a key role in marine food webs as they constitute a significant portion of the invertebrate biomass. Moreover, several macrocrustacean species are a link between basal levels of the food web and top predators. Macrocrustaceans are characterized by being consumers with a wide variety of feeding strategies which range from feeding on phytoplankton to active predation and can be either highly selective species or omnivorous-detritivorous species (Boudreau and Worm 2012; Štrus et al. 2019). In addition, several macrocrustacean species are considered as facultative scavengers (Kaiser and Moore 1999). Scavengers generate consequences in the structure and functioning of marine food webs, which are different from those of predators because they do not cause direct mortality or important demographic changes (Depestele et al. 2019). The role of scavengers is particularly important in ecosystems that sustain trawl fisheries, because they contribute an important number of dead organisms to the environment. In general, since the natural death rate of organisms is low, carrion is scarce. As a result, discarded products from fishing activities are an important food source for marine scavengers (Depestele et al. 2019).

Bottom trawl fisheries are also an important disturbance factor in marine ecosystems (Halpern et al. 2007). Among other ecological impacts, fisheries may lead to changes in the composition and structure of benthic communities and trophic webs (Hinz et al. 2017; Funes et al. 2022). Shifts in the feeding ecology of fishes (Belleggia et al. 2017; Funes et al. 2022) and birds in the San Jorge Gulf (SJG) and surrounding areas have been related to the intense fishing activity (González-Zevallos and Yorio 2011; Belleggia et al. 2017; Funes et al. 2022). Moreover, the dominance of macrocrustaceans in SJG would have been favored by large discards of the shrimp fishery (Roux and Piñero 2003; Varisco and Vinuesa 2007; Funes et al. 2022). According to Funes et al. (2022), fishing increases omnivory, raises the average trophic level and reduces the stability of food webs, ultimately leading to a new state where crustaceans become more abundant.

The San Jorge Gulf is one of the most productive fishing areas in the Argentine Sea. Demersal-benthic communities of the SJG have supported important fisheries, such as those of the Patagonian red shrimp (*Pleoticus muelleri*) and Argentine hake (*Merluccius hubbsi*). In 2018, shrimp fishing in the gulf was banned to protect shrimp stocks, particularly in areas critical for reproduction and recruitment, as outlined by Resolution 7/2018 of the Federal Fisheries Council (Consejo Federal Pesquero 2018). This management measure led to a significant reduction in fishing effort in the SJG and, consequently, a decrease in fishing discards.

Approximately, 27 species of decapod and stomatopod crustaceans have been recorded in the SJG (Vinuesa 2005). Both from a taxonomic and a functional approach, several species of macrocrustaceans appear as characteristic taxa of the different benthic assemblages of the SJG (Roux et al. 1995; Fernández 2006; Kaminsky et al. 2018). From the perspective of functional diversity, a significant portion of the SJG bottom is inhabited by a benthic community predominantly composed of species that depend on the recycling of organic matter. In contrast, other communities are associated with oceanographic fronts in the southern and northern areas of the gulf, exhibiting a direct reliance on primary production (Kaminsky et al. 2018). Previous studies have also shown that some macrocrustacean species in the SJG ecosystem, such as *Grimothea gregaria* or *P. muelleri*, play a key role in the recycling of organic matter and in the connection between basal and top trophic levels (Varisco and Vinuesa 2007; Kaminsky et al. 2018).

The knowledge about the trophic ecology of SJG macrocrustaceans species is quite dissimilar. Feeding habits of the squat lobster *G. gregaria* and the red shrimp *P. muelleri* have been widely studied (Roux et al. 1995; Varisco and Vinuesa

2007, 2010; Funes et al. 2018; Souto et al. 2024), whereas those of the stomatopod *Pterygosquilla armata* have been briefly analyzed by Marcinkevicius and Vinuesa (2003). Information on diets of crabs *Peltarion spinosulus* and *Eurypodius longirostris* has been previously described in individuals captured in coastal subtidal environments (Colombo 2021). In the SJG, the diet of *Lithodes santolla* was described for the period 1994-1995 (Balzi 1997). Given the generalist habits of several of these species, a high degree of overlap in their diets is expected. The aim of this paper was to describe the diet of six macrocrustacean species (*E. longirostris*, *Libidoclaea granaria*, *L. santolla*, *G. gregaria*, *P. spinosulus* and *P. armata*) belonging to the demersal-benthic system of the SJG and evaluate their diet overlap. We focused on these six species because they, along with *P. muelleri*, are the most abundant benthic macrocrustaceans in terms of biomass (Varisco, unpublished data) and are characteristic of different benthic assemblages in the study area (Kaminsky et al. 2018).

MATERIALS AND METHODS

Study area

The SJG is located between Dos Bahías Cape in the north and Tres Puntas Cape in the south. It is the largest semi-open basin in the Argentine Sea, covering an area of approximately 40,000 km² (Figure 1). The gulf resembles a basin with maximum depths of 110 m in the central area, gradually decreasing radially towards the coast and the mouth (Fernández 2006; Fernández et al. 2007). The bottoms of the SJG are characterized by the predominance of two distinct granulometric fractions: a coarse fraction, composed of gravel, sand, and rocks found in coastal areas and near the Dos Bahías and Tres Puntas capes, and a finer fraction of sand, silt, and clay, which predominates in the rest of the area. The grain size distribution reflects the hydrodynamic conditions resulting from sedi-

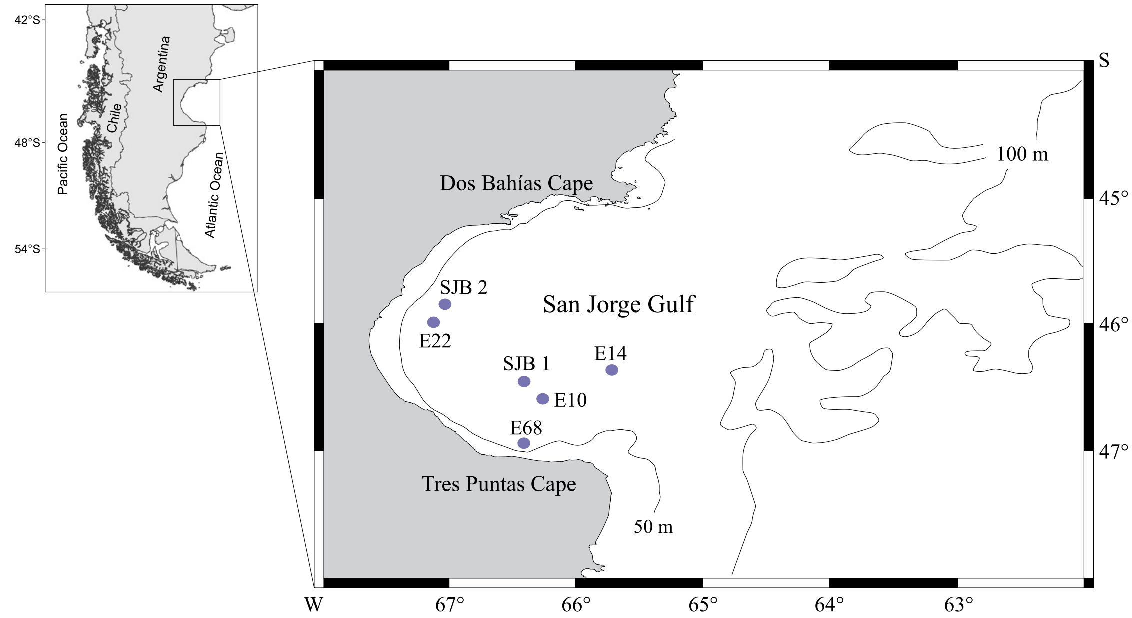

Figure 1. Positions of the fishing hauls in the San Jorge Gulf corresponding to the Pampa Azul-Golfo San Jorge survey in November 2017 (codes E10, E14, E22, E68), as well as those of the fishing hauls of the San Juan B fishing vessel (codes SJB1, SJB2) are shown.

ment transport and deposition processes. Coarser particles are generally associated with higher energy levels due to the influence of waves and currents leading to erosive environments. Conversely, finer particles are found in areas with lower hydrodynamic energy, where they settle, creating depositional environments (Fernández et al. 2003).

The SJG is influenced by low-salinity waters transported by the Patagonian Current, originating from the Strait of Magellan. This current consists of subantarctic waters from the Cape Horn Current, diluted by continental inputs. In the southern part of the gulf, this current splits into two branches: one enters the SJG from the south, while the other continues along the shelf (Matano and Palma 2018). Predominant westerly winds in the region create a permanent NNE circulation. Additionally, these strong winds transport large amounts of dust, providing nutrients for marine organisms and contributing to upwelling processes in coastal areas. When combined with the primarily silty nature of sediments from the Bajo Mazarredo area, this dynamic system creates a likely scenario for protracted sediment resuspension, enhancing turbidity and further influencing nutrient availability in the water column (Glembocki et al. 2015; Pisoni et al. 2020). Near-bottom waters vary between 9 °C and 13 °C in summer and from 6 °C to 9 °C in winter. Coastal salinity ranges from 33.13 to 33.55, decreasing toward the central part of the gulf with values below 33.30 (Fernández et al. 2005, 2007).

Primary production in the SJG follows a seasonal pattern typical of temperate-cold waters, with two characteristic peaks: a smaller one in autumn and a larger one in spring. The presence of oceanic fronts and upwelling zones enhances the productivity in the gulf. A significant tidal front forms near Tres Puntas Cape in spring, while geographical features on the northern coast of the gulf contribute to the formation of fronts due to topography (Glembocki et al. 2015).

The SJG comprises two management areas separated by 46° S: the provinces of Chubut and Santa Cruz. Jurisdictions of these provinces extend approximately 22 km beyond the gulf. To the east, the area falls under the jurisdiction of the national government.

Sampling

Samples were collected in November 2017 aboard the RV 'ARA Puerto Deseado' during the Pampa Azul-Golfo San Jorge cruise (Figure 1). Fishing hauls were performed using a bottom trawl net with a 6-m headrope, 7.2-m footrope and 50-mm mesh, with a 10-mm inner liner throughout the net and a 6-m top rope. Each fishing haul lasted 10 min of effective trawling at a speed of 2 to 3 kn. Macrocrustaceans *G. gregaria*, *L. santolla*, *L. granaria*, *P. armata*, *E. longirostris* and *P. spinosulus* were sorted from the rest of the catch and frozen on board (Figure 2). Additional sampling was conducted onboard the San Juan B fishing vessel, which operated in the Argentine hake fishery in January 2018.

Laboratory procedures

Once in the laboratory, the size of each individual was recorded using a digital caliper (± 0.01 mm). Carapace length (CL) of decapods species was measured from the posterior edge of the ocular orbit to the posterior mid-dorsal edge of the carapace. Decapods were sexed based on the morphology of their abdomen or presence/morphology of their pleopods. *Grimothea gregaria* has two morphotypes: *subrugosa* (benthic) and *gregaria* (pelagic). Differentiation was based on rostrum length, eyestalk length and width, and eye shape, following Tapella and Lovrich (2006). According to Meyer et al. (2013), *E. latreillii* and *E. longirostris* are very similar to each other but can be distinguished by the absence or presence of the postorbital spine. Total length (TL) of *P. armata* was measured along the dorsal midline, from the anterior margin of the rostral plate to an imaginary line located between the apices of the submedian teeth of the telson, which is a commonly body mea-

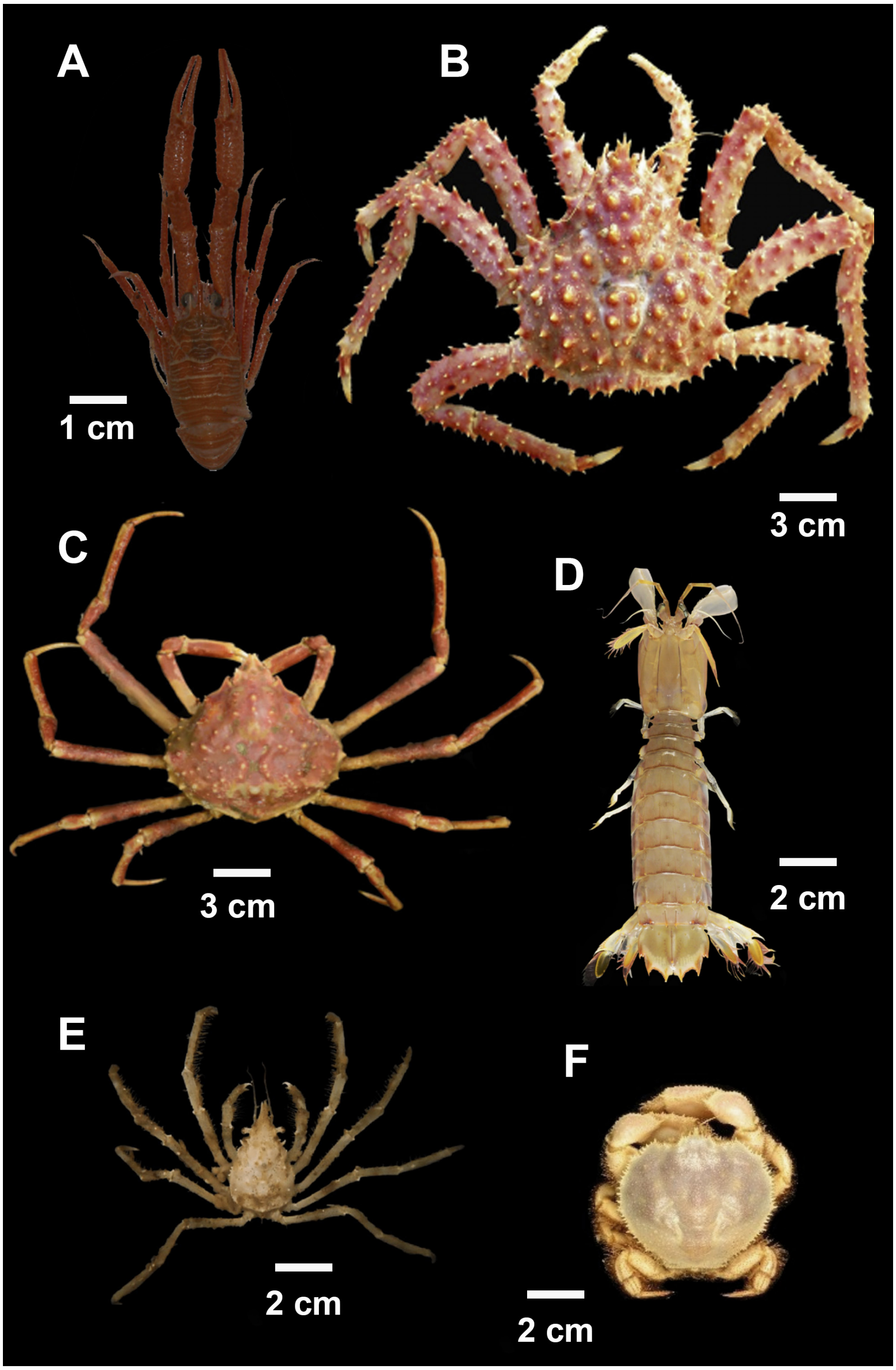

Figure 2. Macrocrustacean species analysed. *Grimothea gregaria* (A), *Lithodes santolla* (B), *Libidoclaea granaria* (C), *Pterygosquilla armata* (D), *Eurypodius longirostris* (E) and *Peltarion spinosulus* (F). Images C and D courtesy of Cecilia Ravalli. Used with permission.

surement for Stomatopoda species. Stomatopods were sexed by direct observation of the copulatory organs. Males possess a pair of copulatory tubular structures (penises) located at the base of the eighth, or last, pair of thoracic legs, whereas females lack these structures and instead have gonopores placed submedially on the sixth thoracic somite (Moreira Reyes 2019).

Stomachs were subsequently dissected and preserved in a 5% formaldehyde-seawater solution. A repletion index (RI) was assigned using the following scale: 0 (empty, 0%), 1 (semi-empty, 0-25%), 2 (moderate, 25-50%), 3 (semi-full, 50-75%), and 4 (full, 75-100%). Stomach contents were carefully separated and initially observed under a stereoscopic microscope at 20x magnification. In some cases, contents were observed under an optical microscope to improve their identification. The presence of sediment was recorded but not included in statistical analyses. Prey items were photographed and quantified using a 160-point grid (modified from Varisco and Vinuesa 2007). Prey items were identified to the lowest possible taxonomic level.

The frequency of occurrence (FO) was calculated for each food item. Only specimens with $RI \neq 0$ were considered. The FO was computed as $(N_i/N_t) \times 100$, where N_i is the number of stomachs containing item *i*, and N_t is the total number of stomachs for a given species. The relative abundance (RA) of the diet components identified were estimated as $(ia / \sum i) \times 100$, where ia is the number of times a given item coincides with points on the grid, and the summation is the total number of coincidences. The RA highlights the importance of each food item in the diet of animals.

Statistical analyses

Cumulative trophic diversity curves were created to test whether the number of stomachs analysed were sufficient to properly describe the diet of each species. The Brillouin index (Hz) was calculated, and curves were constructed by randomizing the order in which the stomachs were added. Curves were considered asymptotic if the two previous values fell within the range of Hz ± 0.05. The sample size was considered adequate if 70% of curves were asymptotic (Koen Alonso et al. 2002; Cordone et al. 2022). This analysis was conducted using R software (version 4.4.3) (R Core Team 2025).

To evaluate differences in the diet composition among macrocrustaceans species, a matrix of similarities was calculated for RA data by using the Bray-Curtis similarity index. To determine possible differences an analysis of similarity (ANOSIM) was performed. This analysis is based on rank similarities between samples in the similarity matrix and produces a test statistic (R). The value of this statistic is based on the similarity within and between the defined groups, ranging from -1 to 1. An $R > 0$ indicates greater similarity within groups than between them; an $R \cong 0$ suggests no differences in similarity within and between groups; and an $R < 0$ indicates greater similarity between groups than within groups (Clarke and Warwick 2001). The ANOSIM technique used a Bonferroni correction for paired comparisons, which includes dividing the significance level α by the number of comparisons. This correction ensures that the probability of finding a false positive among all comparisons is $\leq \alpha$. Moreover, a similarity percentage analysis (SIMPER) was performed to quantify the contribution of different dietary components to the differences observed between species. These analyses were conducted using the PRIMER-e software (version 6) (PRIMER-e 2009).

Diet overlap

The Morisita-Horn index modified by Auriolles-Gamboa and Camacho-Ríos (2007) was used to evaluate the overlap in macrocrustaceans diets by major taxa (class/phylum) as follows:

WW

$$C_H = 2 \sum_i^n pij \cdot pik \,/\, \sum_i^n pij^2 + pik^2$$

where p_{ij} represents the relative abundance of prey *i* in predator *j*, and p_{ik} represents the relative abundance of prey *i* in predator *k*, with *n* being the total number of prey items. The index value ranges from 0 to 1; values below 0.29 indicate low dietary overlap, values from 0.30 to 0.65 indicate moderate overlap, and values above 0.65 are associated with high overlap (Langton 1982).

RESULTS

A total of 331 stomachs of the six studied species (*E. longirostris*, *L. granaria*, *L. santolla*, *G. gregaria*, *P. spinosulus*, and *P. armata*) were dissected (Table 1). Overall, most of the analysed stomachs were empty (RI = 0, 40.2%), or semi-empty (RI = 1, 27.9%), while individuals with moderate or full repletion (RI = 2, 3, or 4) represented 31.9% (Figure 3). The number of empty stomachs was highest in *P. spinosulus* (81.93%) and lowest in *L. granaria* (9.1%). The number of stomachs analysed was considered sufficient to provide a good description of the diet, as the trophic diversity curves were asymptotic for most species. However, *L. santolla* (59%) was close to the reference value (Figure 4). Stomach contents of the species were characterized by a high degree of digestion, making it difficult to identify prey items at lower taxonomic levels (Figure 5). This degraded content was generally referred to as particulate organic matter (POM) and consisted of amorphous aggregates of decomposing organic matter complexed with microorganisms. This implied that decomposing organic matter was chemically or physically bound to, associated with, or interacting with sediments or microorganisms such as cyanobacteria, foraminiferans, diatoms, and others. Unidentifiable semi-digested remains were grouped in the category of 'unidentified organic remains' (UOR) following the nomenclature of Vinuesa et al. (2013). Nematodes were also identified in some contents characterized by high sediment concentration, although they were not identified to the species level. In *E. longirostris*, *G. gregaria*, and *P. spinosulus*, numerous stomachs contained significant amounts of sediment. Decapod crustaceans such as *P. spinosulus*, *P. muelleri* and *G. gregaria* were the main prey in the diet of the studied species (Tables 2 and 3), which were identified from shell remains or characteristic segments of each species. No algae were found in the stomach contents of any of the species identified. The POM was an important dietary item for the squat lobster *G. gregaria*, the crab *P. spinosulus* and the spider crab *L. granaria* (Table 2). Most abundant items in the diet of the spider crab *E. longirostris* were polychaetes and decapod crustaceans. Decapods, fish, and sea urchins were the main component in the south-

Table 1. Morphometric measurements of macrocrustacean species analysed. Size was measured as carapace length (CL) for decapod crustaceans, while total length (TL) was measured for stomatopods (*Pterygosquilla armata*). The table also includes the number of males (M) and females (F), the number of individuals with a stomach repletion index (RI) ≠ 0, and the total number of individuals analysed for each species (n).

Species	Size (mm)	M	F	IR ≠ 0	n
Eurypodius longirostris	32.80-89.23	27	18	28	45
Libidoclaea granaria	53.12-107.80	19	3	20	22
Lithodes santolla	78.20-110.70	14	11	18	25
Grimothea gregaria	10.90-29.60	73	38	83	111
Peltarion spinosulus	21.00-60.29	40	43	15	83
Pterygosquilla armata	41.42-127.57	21	24	26	45

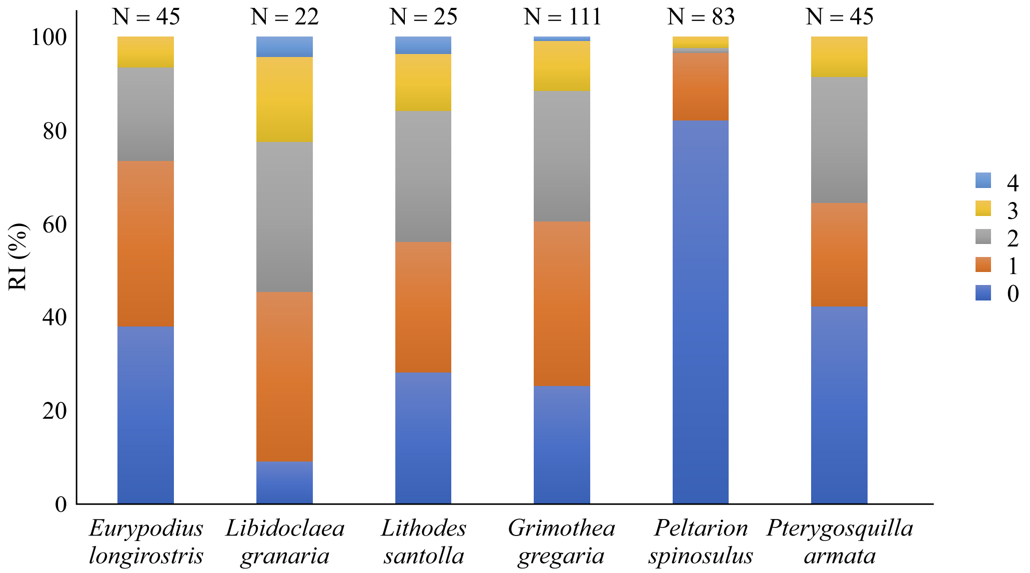

Figure 3. Repletion index (RI) for the species studied. The number of specimens for each species is shown above each bar. Scale: 0 (empty, 0%), 1 (semi-empty, 0-25%), 2 (moderate, 25-50%), 3 (semi-full, 50-75%), and 4 (full, 75-100%).

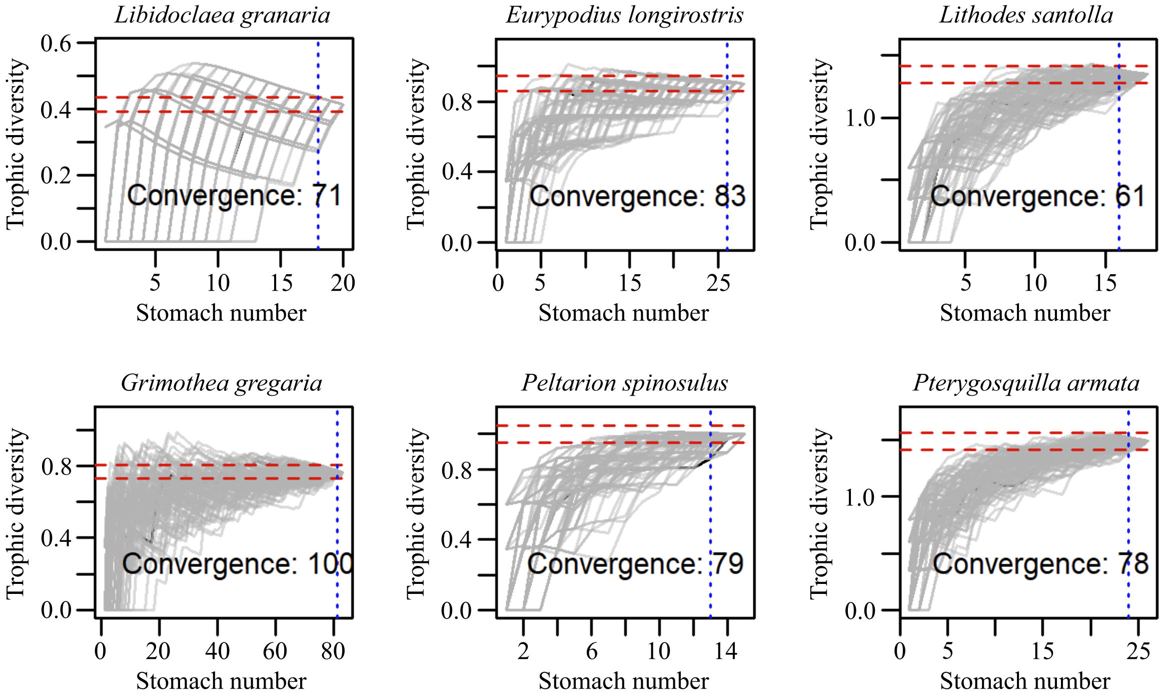

Figure 4. Cumulative trophic diversity curves for each analysed species: *Eurypodius longirostris*, *Libidoclaea granaria*, *Lithodes santolla*, *Grimothea gregaria*, *Peltarion spinosulus*, and *Pterygosquilla armata*. Reference lines for the Brillouin index (Hz) are shown in red indicating the range (Hz ± 0.05) where curves are considered asymptotic, while the convergence point is represented in blue. Additionally, the figure displays the percentage of curves that reach asymptotic behaviour.

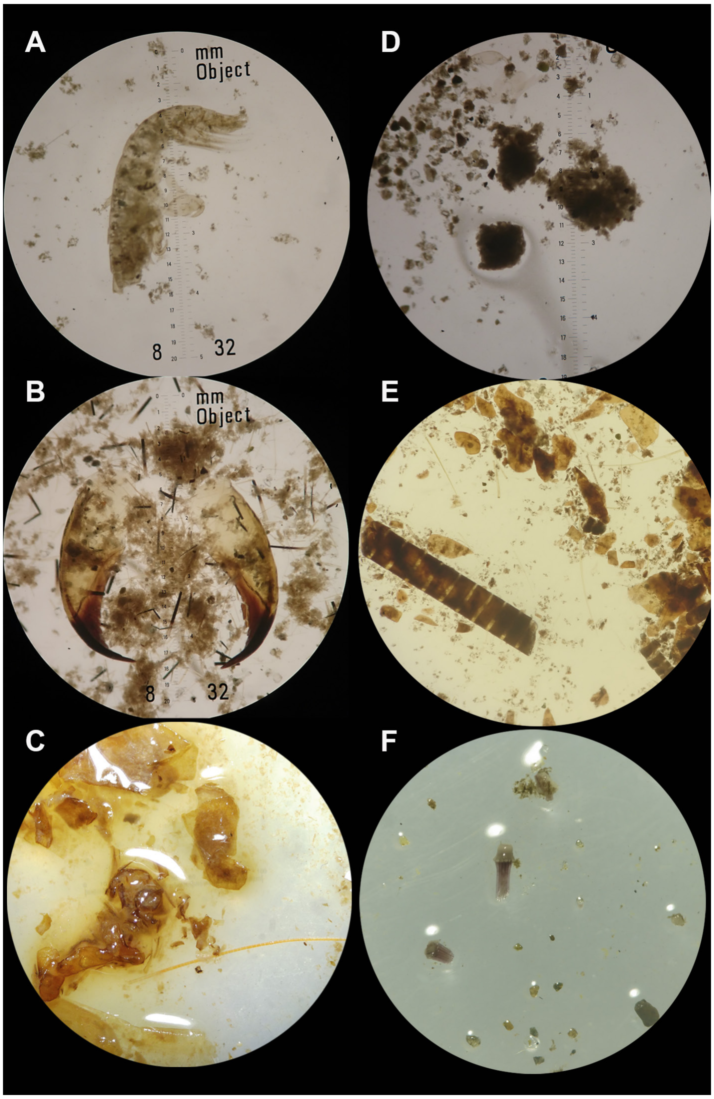

Figure 5. Prey items identified in stomachs of some species of interest. Amphipod (A), polychaete remains (jaw and setae) (B); crustacean remains (carapace and antennae) (C), particulate organic matter (POM) (D), crustacean remains (E), and urchin remains (spine) (F).

ern king crab *L. santolla*, and decapods and UOR were the most abundant items in the stomatopod *P. armata*. Standard deviations of RA values were generally higher than the means. This was related to the frequent observation of stomachs within the same species that either lacked a certain item (0%) or contained it exclusively (100%), contributing to the high dispersion (Table 2).

Significant differences were found in the diets of some species studied when considering the relative abundances of each prey item (ANOSIM, $R = 0.192$, $p < 0.001$) (Table 3). However, all species exhibited some degree of dietary overlap with respect to the other analysed species (Table 4). Moreover, paired comparisons showed that most species share the same diet, at least when

Table 2. Frequency of occurrence (FO) and relative abundance (RA) of main prey items, both expressed as percentages for the studied species. UOR: unidentified organic remains.

	Eurypodius longirostris		*Libidoclaea granaria*		*Lithodes santolla*		*Grimothea gregaria*		*Peltarion spinosulus*		*Pterygosquilla armata*	
Items	FO	RA	FO	RA	FO	RA	FO	RA	FO	RA	FO	RA
Decapoda	60.71	36.43 (± 36.74)	85	81.85 (± 37.96)	66.67	59 (± 46.82)	83.49	74.50 (± 38.69)	33.33	32.58 (± 48.80)	73.08	54.11 (± 40.23)
POM	7.14	3.57 (± 13.11)	20	18.15 (± 37.96)	0	0	22.01	9.43 (± 21.31)	26.67	12.1 (± 28.42)	15.38	7.35 (± 16.90)
Polychaeta	67.86	51.43 (± 42.66)	0	0	11.11	3.89 (± 12.43)	13.33	2.86 (± 14.36)	53.33	29 (± 44.55)	11.54	8.46 (± 27.23)
Echinoidea	7.14	1.43 (± 5.24)	0	0	22.22	14.89 (± 33.28)	0	0	6.67	5.26 (± 25.82)	0	0
Other Crustacea	0	0	0	0	0	0	0	0	20	7.93 (± 25.69)	19.23	11.15 (± 26.43)
Bivalvia	0	0	0	0	5.55	1.66 (± 7.07)	0	0	0	0	11.54	7.69 (± 23.20)
Osteichthyes	0	0	0	0	16.67	15 (± 35.02)	0	0	0	0	3.85	0.23 (± 1.18)
UOR	0	0	0	0	16.67	15 (± 35.02)	3.67	3.51 (± 16.79)	0	0	15.38	10.15 (± 24.64)
Nematoda	0	0	0	0	0	0	0	0	0	0	3.85	0.27 (± 1.37)
Bryozoa	0	0	0	0	0	0	0	0	0	0	0	0
Cnidaria	0	0	0	0	0	0	0	0	0	0	3.85	0.58 (± 2.94)

Table 3. Analysis of similarity (ANOSIM) to determine similarities between species studied. Comparisons showing significant differences (p < 0,0033) are indicated with an asterisk.

	E. longirostris	*L. granaria*	*L. santolla*	*G. gregaria*	*P. spinosulus*
Eurypodius longirostris					
Libidoclaea granaria	0.001*				
Lithodes santolla	0.002*	0.005			
Grimothea gregaria	0.001*	0.817	0.017		
Peltarion spinosulus	0.037	0.007	0.027	0.006	
Pterygosquilla armata	0.001*	0.233	0.175	0.010	0.037

Table 4. Morisita-Horn index assessing diet overlap by major taxa (class/phylum) for each of the studied species.

	E. longirostris	*L. granaria*	*L. santolla*	*G. gregaria*	*P. spinosulus*
Eurypodius longirostris					
Libidoclaea granaria	0.553				
Lithodes santolla	0.581	0.862			
Grimothea gregaria	0.600	0.988	0.907		
Peltarion spinosulus	0.891	0.630	0.670	0.673	
Pterygosquilla armata	0.664	0.880	0.904	0.925	0.798

considering large taxonomic groups, except for *E. longirostris*, which, in comparison with most of the other crabs, has a lower consumption of decapod crustaceans and a higher consumption of polychaetes. The species showed a moderate to high degree of overlap. Even the stomatopod *P. armata*, which exhibits active predation habits, showed a high overlap with the other species. As previously mentioned, decapod crustaceans are the main prey item for most species and contribute the most to the dietary similarity across species considering the relative abundance of principal prey items in each species. Coincidentally, the abundance of decapods and polychaetes accounts for the dietary dissimilarities among the analysed species (Table 5).

DISCUSSION

Macrocrustaceans exhibit a wide range of feeding strategies, from phytoplankton consumers to active hunters, including species that are highly selective as well as omnivorous-detritivorous species (Kaiser and Moore 1999). Several macrocrustaceans species are dominant in the benthic community of the SJG (Kaminsky et al. 2018; Funes et al. 2022). Information on the diets of these species is scarce, and in some cases, it comes from shallow environments (Colombo 2021), where the food supply differs from that of soft bottom environments of the SJG. This study provides the first data on the feeding habits of one of these species in the soft bottoms of the SJG.

The presence of individuals with empty stomachs is common among decapod crustaceans and could be related to the molt, feeding habits, reproductive behaviour or intra/interspecies competition. The stomach wall of crustaceans is of ectodermal origin, meaning that it is replaced during each molting event, limiting the possibility of ingesting food in the days before and after molting (Schultz and Shirley 1997; Kim et al. 2007). Although the molt stage was not formally assessed in this work, soft-carapace crabs were not identified in our samplings. Therefore, the molt is unlikely to account for the high number of specimens with empty or semi-empty stomachs. Given that some decapods species can endure long periods of fasting without significant decreases in body mass or meat yield, the proportion of specimens with low RI could be related to the feeding habits of these species, e.g. up to two months in *L. santolla* under laboratory conditions (Sacristán et al. 2019). This ability may be advantageous for scavenging species in areas where the supply of organic matter is sporadic. The length of the intestinal transit may also have an impact on the observed IR. While lobsters have longer intestinal transit durations (up to 150 h), some euphausiids and crabs have shorter times (McGaw and Curtis 2013). The stomach of the blue crab *Callinectes sapidus*, for example, is empty between 8 and 10 h after feeding (McGaw and

Table 5. Similarity percentage analysis (SIMPER) to quantify the contribution of prey items to dietary differences among the studied species. *Eurypodius longirostris* (Eul), *Libidoclaea granaria* (Lig), *Lithodes santolla* (Lis), *Grimothea gregaria* (Grg), and *Pterygosquilla armata* (Pta). Ab_{sp1}: abundance of the prey item in species 1. Ab_{sp2}: abundance of the prey item in species 2. CD: contribution to the difference expressed as a percentage. CCD: contribution to the cumulative difference expressed as a percentage.

Comparison	Item	Ab_{sp1}	Ab_{sp2}	CD (%)	CCD (%)
Eul versus Lig	Decapoda	36.43	81.85	44.72	44.72
	Polychaeta	51.43	0.00	38.55	83.27
Eul versus Lis	Decapoda	36.43	59.00	33.16	33.16
	Polychaeta	51.43	3.89	32.62	65.78
Eul versus Grg	Decapoda	36.43	74.57	44.78	44.78
	Polychaeta	51.43	2.86	42.02	86.80
Eul versus Pta	Polychaeta	51.43	8.46	36.61	36.61
	Decapoda	36.43	54.12	32.85	69.46

Reiber 2000). Despite the lack of local information on gut transit time, this short time is probably more similar to that reported in crabs than that observed in lobsters. Fast gut transit (or starvation) could contribute to explaining the high proportion of empty stomachs observed in the species analysed. Sample preservation is another factor that could help explain the low IR. Freezing does not prevent some prey from continuing to be digested, since some digestive enzymes remain active even when animals are frozen, which could have affected the preservation of tissues, especially soft tissues (Meijer et al. 1977; McGaw and Curtis 2013).

The presence of sediment and organic matter in stomach contents was frequent and revealed a deposit-feeding habit on the surface sediments. Specifically, sediment was found in the stomachs of *E. longirostris*, *G. gregaria*, and *P. spinosulus*, and organic matter was found in *G. gregaria* and *P. spinosulus* with high frequency of occurrence. Surface deposit-feeding habits in the squat lobster *G. gregaria* (Varisco and Vinuesa 2007) and the crab *P. spinosulus* (Colombo 2021) have been previously reported. Regarding the amount of organic matter in sediments from SJG, Massé-Beaulne (2017) highlighted the significant flow of carbon from the photic zone to the seafloor of the SJG, largely driven by faecal pellets of the pelagic morphotype of *G. gregaria*, contributing to the organic matter content of superficial sediments. Furthermore, previous studies have recorded high levels of benthic secondary production in the SJG, which can be attributed to the high diversity of benthic infauna supported by soft-bottom areas (Suby 2021). The significant vertical flux of carbon and the high benthic secondary production driven by infaunal organisms may help to explain the deposit-feeding habits observed in some of the species here studied.

Decapod crustaceans and polychaetes showed a higher relative abundance and frequency of occurrence in the diets analysed. The importance of decapods in the diet of the studied species may be linked to their high abundance in the benthic-demersal community of the SJG. The shrimp *P. muelleri* and the squat lobster *G. gregaria* are dominant taxa in benthic assemblages in the SJG (Varisco et al. 2018). Funes et al. (2022) noted that these species are the most connected nodes of the food web in the north of the SJG. Meanwhile, polychaetes of families Spionidae, Paraonidae, Eunicidae, and Maldanidae dominate the infaunal fraction and contribute substantially to the infaunal secondary production in the SJG (Suby 2021). Given that softer parts of prey items, such as the muscle, are cleared faster, but harder parts take longer to digest and may have a longer gut transit time, the RA of these taxa could be overestimated (McGaw and Curtis 2013).

The analysis of gut contents of this six macrocrustacean species reveals omnivorous feeding habits and no evidence of dietary specialisation. The high degree of dietary overlap between other species may be related to the generalist feeding habits exhibited by these species and the shared resources in soft-bottom habitats of the SJG. As previously highlighted, the low taxonomic resolution of analyses may have influenced on the diet overlap by hiding differences that may have been identified at a finer taxonomic level. Notwithstanding, preliminary results from indirect analyses using stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) also support the high degree of overlap in the trophic roles of these species (Galván et al. 2020). Since dietary overlap was observed at sites where these species coexisted, it may serve as a potential indicator of competition. However, assessing food competition using gut contents or isotope analysis is difficult, and alternative methodologies are necessary.

As previously stated, no evidence of dietary specialization was found, with the probable exception of the spider crab *E. longirostris*. Crab diets can differ among habitats in response to differences in prey availability (Campbell et al. 2021). In the subtidal environment, *E. longirostris* inhabits kelp forests of *Macrocystis pyrifera*. A high contribution of polychaetes to the diet of *E. longirostris* has been recorded by Colombo (2021) in subtidal rocky shore crabs. Despite habitat differences with soft bottoms in locations where the samples were taken, the species appears to have specialised in the consumption of polychaetes. On the other hand, the diet of *P. spinosulus* differs among habitats, with a more diverse diet including algae in coastal areas (Colombo 2021). However, the presence of sediments and POM in both sites suggests deposit-feeding habits.

The southern king crab *L. santolla* shows a generalist feeding habit. Over 40 species were identified in the stomach contents of this crab in the Beagle Channel, with gastropods dominating in terms of frequency of occurrence (Comoglio and Amin 1996). Balzi (1997) reported that diet in the SJG is primarily composed of four main prey items, with a fish (presumably *M. hubbsi*) and the squat lobster *G. gregaria* being the most important. To explain the high abundance of very mobile prey such as fish, Balzi (1997) suggested that the diet composition is heavily influenced by fishing discards. Our samples were collected before the red shrimp fishery closure in the SJG. The low trophic diversity seems to be in line with suggestions of this author. Given the shrimp fishery closure in the SJG and the resulting decrease in discards, potential shifts in dietary composition should be examined in greater detail in future studies in order to assess implications of new fishery scenario in the SJG.

Feeding habits of the squat lobster *G. gregaria* have been thoroughly investigated in several regions of the Argentine Sea, since it is an important species in the benthic-demersal ecosystem of the SJG and the continental shelf (Romero et al. 2004; Varisco and Vinuesa 2007; Funes et al. 2018). In the Beagle Channel, *subrugosa* morphotype shows two different and simultaneous feeding habits: as a predator and also as a deposit feeder (Romero et al. 2004). Previous studies in the SJG showed that the primary energy source of *G. gregaria* (*subrugosa* morphotype) comes from feeding on surface organic matter deposits and carrion (Varisco and Vinuesa 2007; Funes et al. 2018). These studies suggest that both particulate and decomposing organic matter are abundant in the region due to the past fishing activity in the SJG, where tons of trawling discards were released each year. Like *L. santolla*, the squat lobster is a suitable model species for evaluating how factors such as the current lower fishing intensity affect its dietary composition.

Competition for food in stomatopods may have favoured the evolution of a highly specialized diet, accompanied by a distinct morphology allowing access to prey with few predators. *Pterygosquilla armata* is known for having a morphotype based on slower-moving appendages, which enables it to feed on soft-bodied prey, such as fish and small crustaceans (deVries 2017). Results of this study are consistent with those reported by Marcinkevicius and Vinuesa (2003), who examined the trophic role of *P. armata*. These authors found that the diet of this species is primarily composed of cephalopods, decapod crustaceans, and small fish, with crustaceans being the most abundant prey. Despite its seemingly different feeding habits, *P. armata* shows dietary overlap with decapod species analysed in this study. This may be related to the high prevalence of crustaceans in its diet, since they represent nearly half of its prey in terms of relative abundance.

In marine ecosystems, several decapod species play a role in matter recycling by feeding on carrion or partially decomposed organic matter (Catchpole et al. 2006; Bellido et al. 2011). Additionally, the ability to consume carrion, whether as decomposing organic matter resulting from the natural feeding processes of species or as fishing discard, appears advantageous in a scenario of intense fishing effort. In such cases, scavenging organisms benefit from a diet subsidized by discarded biomass that settles on the seafloor (Ramsay et al. 1997; Catchpole et al. 2006). In this regard, Funes et al. (2022) suggested that the intense fishing activity occurring in the SJG until a few years ago caused changes in trophic networks favouring the proliferation of generalist species, particularly *G. gregaria*. Although the relation between the diet and fishery discards was not analysed in this study, as mentioned above this relation has been suggested for *G. gregaria* and *L. santolla* and is expectable that other macrocrustacean species with overlapping diet will also feed on fishing discard. Since the trawling activity in the SJG is currently constrained to the hake fishery, feed support from fishing discards is reduced and is expected to fit in the diet of macrocrustacean species.

The SJG is one of the most productive areas of the Argentine Sea providing numerous services to society, such as fisheries, oil transport, biodiversity conservation and tourism, among others. However, this contrasts with the limited knowledge about the ecosystem functioning and the processes and driving factors behind this productivity. Knowledge on the trophic relationships within the ecosystem is essential to promote the sustainability of the gulf services and ecosystem-based management (Dans et al. 2020). In this context, the present work provides information about the diets of various macrocrustacean species in the SJG. Understanding interspecific interactions may allow for a deeper comprehension of ecosystem functioning, population or community dynamics, energy transfer between trophic levels, and how these relationships can influence the long-term persistence of organisms.

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Conflict of interest

The authors of the manuscript declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Statement of the welfare of animals

All applicable international, national, and/or institutional guidelines for the proper care and use of animals were followed.

Author contributions

Matias L. Vallejos: formal analysis; investigation; data curation; writing-original draft; writing-review and editing; visualization. Martin A. Varisco: conceptualizationv methodology; formal analysis; resources; data curation; writing-review and editing; visualization; supervision; funding acquisition.

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