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Trophic Niche Dynamics and Diet Partitioning of King Crab *Lithodes santolla* in Chile's Sub-Antarctic Water

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Abstract: The southern king crab *Lithodes santolla* is one of the most economically important fishery species in the southern waters of the Atlantic and Pacific Oceans. A combination of stomach content and stable isotope analyses was used to reveal the potential dietary characteristics, isotopic niche, overlap among maturity stages and sexes, and trophic relationships of an *L. santolla* population in the Nassau Bay, Cape Horn region. Stable isotope analyses indicated that *L. santolla* assimilated energy from a basal carbon source, the giant kelp *Macrocystis pyrifera*, forming the trophic baseline of the benthic food web. Moreover, the trophic position of *L. santolla* varied among late juveniles and adults, suggesting that the southern king crab does undergo an ontogenetic diet shift. *L. santolla* exhibited intraspecific isotopic niche variation, reflecting niche differentiation which allows the species to partition resources. The trophic relationships of *L. santolla* with the associated fauna suggested some potential interactions for food resources/habitat use when they are limited. This study is the first attempt to characterize the trophic dynamics of the southern king crab in the Cape Horn area and, by generating more data, contributes to the conservation of the king crab population and the long-term management of local fisheries that rely on this resource.

Keywords: Crustacea; trophic ecology; *Macrocystis pyrifera*; isotopic niche; stable isotopes; stomach content; fisheries; omnivory

1. Introduction

Large stocks of the southern king crab *Lithodes santolla* (Molina, 1782) (Decapoda, Lithodidae) are distributed along coastal waters and fjords in the sub-Antarctic Magellan and Cape Horn region, at the southern tip of South America. Currently, the species has very high economic value, depending on small-scale local artisanal fisheries that have, however, generated dynamic histories of overfishing and governmental management. It is considered a high-status seafood source and a gastronomic footprint for tourism [1]. The modern history of its exploitation shows a peak towards the beginning of the 21st century. Previously, in the 1950s, it was only subject to local consumption and rapidly started to acquire significant status within regional gastronomy during the following decade. Then, since the late 1970s, it has had a consistent exploitation and high valuation as an export product for elite consumption (Mateo Martinic, 2022, personal communcation).

For more than 40 years, many biological studies aiming to improve *L. santolla* fisheries' knowledge have been made [2–7], there is limited knowledge about the species' trophic ecology relationship to the habitat that the species uses [8,9]. It is important to note that trophic ecology information is crucial for the design and planning of ecosystem-based management strategies of the Chilean benthic fishery [10]. In addition, a holistic approach to studying trophic relationships in terms of prey availability and predator–prey interactions among species in a particular area is critical to understanding their ability to co-exist [11,12].

Between 2010 and 2016, annual landings of southern king crab in Chilean fisheries ranged from 3022 to 5193 t, while in 2019, landings were less than 3000 t per year, the lowest figure recorded so far [13]. This suggests a decline in king crab natural abundances, which could be primarily attributed to overfishing [1]. Hence, major consequences for trophic dynamics and food web structure can be expected, as previous studies have described that *L. santolla* constitutes a significant part of the benthic invertebrate biomass [14]. *L. santolla* are commonly assumed to be generalist feeders, able to exploit a broad range of resources [4], predating preferentially on gastropod mollusks, crustaceans, bryozoans, and algae [15]. *L. santolla* occupies a key role in the trophic ecology in fjord waters because of its role as both predator and scavenger in coastal benthic ecosystems depending on the availability of food [14,16]. However, information about the feeding preferences of king crabs is still limited, and its trophic level has not been thoroughly assessed to date. Additionally, the complex life cycle of *L. santolla* [17] may cause changes in its diet according to the environment and prey availability, especially during ontogeny. Larvae recruit in shallow waters in complex substrates [18], and juveniles grow up associated with kelp forest [19], but then adults perform a seasonal bathymetric migration [19,20]. Vinuesa [21] and Vinuesa et al. [17] reported different diets for king crab juveniles from shallow rocky areas and adults inhabiting deeper shelf waters in the San Jorge Gulf, Argentina. Under laboratory conditions, *L. santolla* diet can also exhibit intra-specific predation, which occurs intensely during molting periods of early developmental stages when king crabs have soft exoskeletons and, consequently, are more exposed to cannibalism [9]. Cannibalism has been recorded in the wild as well [19].

In general, no studies have assessed how different strategies in feeding behavior, ontogenetic changes in habitats, sex, and partitioning of food resources relate to the trophic niche of *L. santolla.* However, it has been suggested that this species shares resources in the same habitat due to similar food requirements within a wide generalist diet [14]. Since sharing resources can lead to intra-specific competition [22], it is important to assess the extent of trophic niche overlap in resource utilization [23,24] to improve *L. santolla* fisheries management. In addition, studies of other crabs in other environments have demonstrated how ontogeny influences diet composition shifts because as the crab size increases, it allows them to capture larger prey [25,26] and improve predator-avoidance behavior [27].

The utilization of stable isotopes δ^{13}C and δ^{15}N in ecological studies has proven useful to trace trophic relationships [28], quantify the isotopic niche as a proxy for trophic niche [29,30], estimate niche overlap, and determinate niche region [31]. Some relevant research employing the isotopes technique has contributed to, for example, elucidating the dietary niche differences of the snow crab *Chionoecetes opilio* in complex environments [32] or to predicting the impacts of the invasive species red king crab *Paralithodes camtschaticus* on the native biota of a subarctic fjord by determining its trophic role in the food web [26]. These and other studies demonstrate the possibilities offered by stable isotope analysis of δ^{13}C and δ^{15}N to investigate the population's niche widths [24,29].

In the area where the present study was conducted, the high density and biomass of giant kelp *Macrocystis pyrifera* (Laminariales, Phaeophyceae), which offer nursery areas, abundant food, and protection [33], as well as the presence of various economically important species, provide an ideal scenario to examine *L. santolla*'s trophic interactions. Indeed, the microhabitat proportioned by *M. pyrifera* for juveniles and/or adults of *L. santolla* may shape different foraging strategies linked to podding behavior, which is still

not understood [8]. At present, there are no studies that establish the niche differentiation of *L. santolla* and the relationships among co-existing species.

The main objective of this study was to analyze the stomach content and isotopic composition of *L. santolla* to establish its diet, trophic niche width, position, and overlap, while also to determine the niche width of the community comprised together with the associated fauna within the benthic food web. This information may help understand the habitat and resource use of *L. santolla* as well as the energy pathways that determine the trophic structure of the system.

2. Materials and Methods

2.1. Study Site

The study was conducted in Nassau Bay (55°41′67″ S; 67°66′67″ W), located south of Navarino Island and north of Cape Horn Archipelago, Chile (Figure 1). The bay is about 100 km wide, with a shallow water environment less than 70 m depth. The water column presents a homogeneous vertical structure with a mean temperature of 6.5 °C, mean oxygen content of 6.5 mL L^{-1}, and salinity of 32.5 [34]. The weather is characterized by a temperate-cold climate with a minimum temperature of 5 °C and a maximum of 10 °C [35].
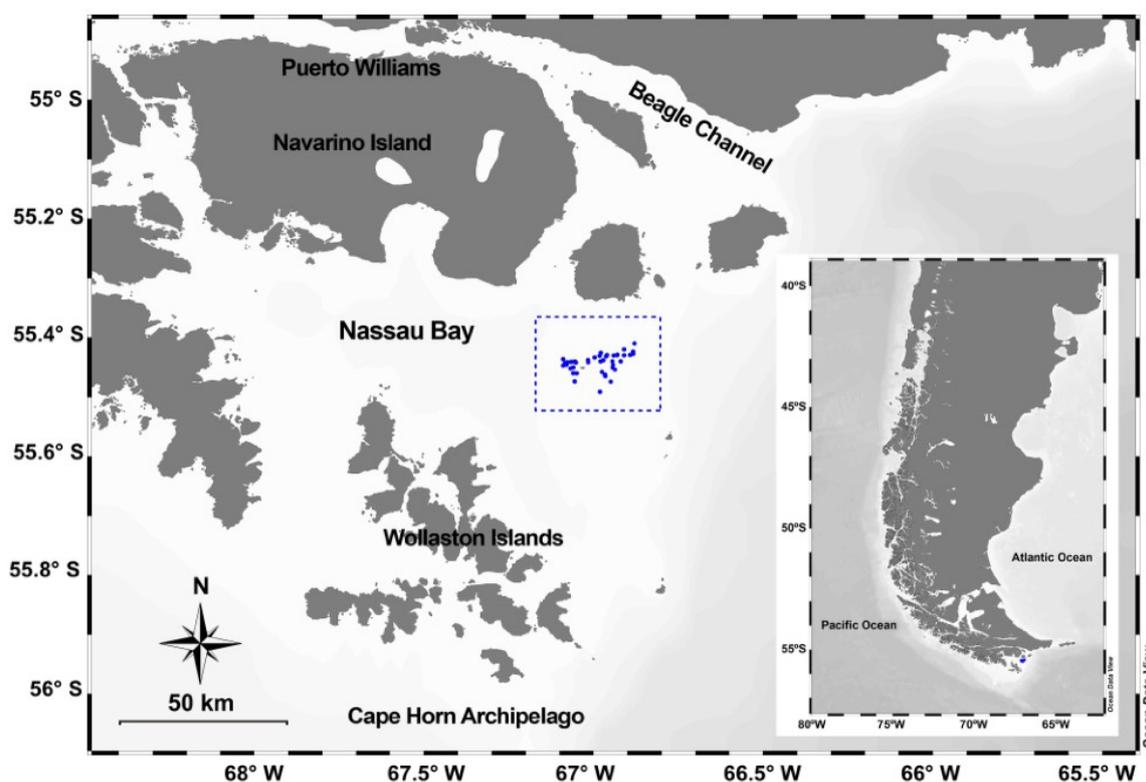

Figure 1. Map showing the sampling locations where southern king crab *Lithodes santolla*, their primary food sources, and associated fauna organisms were collected in Nassau Bay, Cape Horn.

The surrounding area hosts marine fauna that supports numerous fisheries, not only king crab (*L. santolla*) but also Patagonian toothfish (*Dissostichus eleginoides*), southern blue whiting (*Micromesistius australis*), southern hake (*Merluccius australis*), golden conger eel (*Genypterus blacodes*), and false southern king crab (*Paralomis granulosa*), among other species [33,36]. This marine ecosystem is particularly abundant in large forests of the giant kelp *Macrocystis pyrifera* and the southern bull kelp *Durvillaea antarctica*, which sustain a high diversity of invertebrates such as polychaetes, crustaceans, echinoderms, and sponges [37], and cold-water coral species can also be found [38].

2.2. Sampling

Samples were caught between September and November 2017 at 35 stations by personnel of the Instituto de Fomento Pesquero (IFOP) during artisanal small-scale fishing operations. King crabs and associated fauna were caught by randomly distributed crab traps positioned 24 to 35 m deep. Potential food sources such as macroalgae and surface bottom sediment samples were collected by SCUBA diving. On board, crabs were sexed according to their external morphology, following guidelines by Stevens and Jewett [39] and Lovrich and Vinuesa [40]. Individual wet weight (g), length (mm), and width (mm) of the carapace were recorded (see Supplementary Material Table S1 for further details). The maturity stage of king crabs was classified as follows: those with a cephalothorax length of >80 mm were considered adults, while those with a cephalothorax length of <80 mm were considered late juveniles [5,41,42] (Table 1). Stomachs were collected and kept in a 10% formaldehyde–seawater solution. For stable isotopes, muscular tissue of vertebrates and invertebrates, whole flora, and sediment samples were preserved in 1.5 mL cryovials in a liquid nitrogen tank and transported to the Laboratorio de Ecología Funcional, Instituto de la Patagonia, Universidad de Magallanes, for further processing.

Table 1. Size and weight ranges of *Lithodes santolla* by maturity stage and sex. Sample size and sampling method of southern king crab collected in Nassau Bay, Cape Horn.

	N	Length (CL mm)	Width (mm)	Weight (gr)	Sampling Method
Lithodes santolla Adult Males	46	88–163	90–175	600–3200	Crab traps
Lithodes santolla Adult Females	45	90–140	94–145	500–2000	Crab traps
Lithodes santolla Juvenile Males	30	54–79	54–84	95–354	Crab traps
Lithodes santolla Juvenile Females	28	56–80	58–85	100–355	Crab traps
Lithodes santolla All	149	54–163	54–175	95–3200	Crab traps

2.3. Stomach Content Analysis (SCA)

Once in the laboratory, each stomach sample was dissected, and the Stomach Fullness Index SFIi was assigned, where the estimated overall fullness value ranged from 0 (empty) to 16 (stuffed) with intermediate values of 1 (traces of food), 2 (little food), 4 (some food), 8 (half-filled), and 12 (almost filled). Prior to the analysis, empty stomachs were excluded. The available contents were transferred to a petri dish for identification and recording of food items to the lowest taxonomic level under a binocular stereoscope at 20x magnification. When needed, items were placed on a slide and observed under a binocular microscope at 100x magnification. The unidentified material was grouped under a miscellaneous item group. Prey items were stored in 95% denatured ethanol. Quantitative estimates of diet composition were made by using an online computation spreadsheet [43], following the Point Method of Hynes [44], modified by Brun [45], Fratt and Dearborn [46], and Dearborn et al. [47], where the percentage mean volumetric contributions of food items were obtained for each individual.

2.4. Stable Isotope Analysis (SIA)

Eighty-eight king crabs, nine decapods, sixteen algae, four fish, twenty-one invertebrates, and four sediment samples were analyzed. Biota was sorted to the lowest possible taxonomic resolution following adequate literature [48–50]. Where taxonomic doubt existed, extra specimens were preserved in a formaldehyde–seawater solution for later verification by experts (see Acknowledgments section).

Samples were lyophilized for isotope analysis for 24 h at $-60\,°C$ or oven-dried at $60\,°C$ for 48 h. After drying, samples were ground into a fine powder using an Agatha mortar and pestle. SIA, including the determination of carbon and nitrogen concentrations was carried out in the Laboratory of Biogeochemistry and Applied Stable Isotopes (LABASI) at the Pontificia Universidad Católica de Valparaíso, Chile using an isotope ratio mass spectrometer (IRMS) Thermo Delta Advantage coupled to an Elemental Flash EA2000

analyzer. Some samples were acidified to remove $CaCO_3$ in accordance with Fry [51] and Jacob et al. [52]. Stable isotope ratios were expressed in the delta notion $\delta^{13}C$ and $\delta^{15}N$ as the deviation from the conventional standard Pee Dee Belemnite (PDB) for carbon and air N_2 for nitrogen in per mill (‰). After obtaining the isotope results, we did not perform lipid extraction of muscle tissue for the $\delta^{13}C$ values of king crab since their mean muscle C:N was <3.2, which shows nonlipid-rich tissues for decapod crustaceans [53]. However, we applied the lipid correction factor for fish $\delta^{13}C$ values in the associated fauna following Kiljunen et al. [54].

2.5. Data Analysis

Prior to statistical analysis, the arcsine transformation of percentage data (volumetric contribution of the *L. santolla* diet obtained by SCA) was performed. Then, normality and homogeneity of variance of all data were checked using the Shapiro–Wilk and Levene's tests, respectively. To compare king crab diets in both maturity stage and sexes, a factorial PERMANOVA was performed on the matrix of volumetric contribution per item for each southern king crab using the Bray–Curtis similarity matrix. In addition, a similarity percentage analysis (SIMPER) was conducted to determine which food item made the greatest contribution to dissimilarities in the diet between maturity stages and sexes. All analyses were performed in PRIMER v7 [55].

To account for differences among sex (males and females) and maturity stage (juveniles and adults), the values of $\delta^{13}C$ and $\delta^{15}N$ of the southern king crab were tested, through the PERMANOVA routine. When significant differences between groups were found, pairwise tests were performed (adult males, adult females, juvenile males, juvenile females as covariates).

In the absence of data normality, a non-parametric Kruskal–Wallis *H* test was performed to compare the $\delta^{13}C$ and $\delta^{15}N$ values of basal sources. In all cases, a significance level of 0.05 was assumed which was used to test the significance of the null hypothesis. All statistical analyses were carried out in the PAST version 4.08 software [56].

Bayesian isotopic mixing models were performed by using the SIMMR package from R software, version 4.0.2 [57], first to create a biplot of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values from individual southern king crabs grouped by sex and maturity stages and the potential food sources and second, to estimate the proportional contribution of macroalgae and sediment as basal carbon sources to the southern king crab population across sex and maturity stage. The SIMMR package uses the Markov Chain Monte Carlo algorithm to estimate parameters from observed data and user-specified prior distributions [58]. This approach allows the user to incorporate uncertainty in trophic enrichment factors, sources, and mixtures [58]. The trophic enrichment factor (TEF) used for computing the mixing model was 2.3‰ (SE = 0.28) for $\delta^{15}N$ and 0.4‰ (SE = 0.17) for $\delta^{13}C$ for aquatic consumers [59].

The relative trophic positions (TPs) of *L. santolla* and associated fauna were estimated using the following equation according to Post [60]:

$$\text{Trophic Position}_{\text{consumer}} = 1 + [(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}})/(\text{TEF } \delta^{15}N)],$$

where $\delta^{15}N_{\text{consumer}}$ is the $\delta^{15}N$ value for an individual consumer, $\delta^{15}N_{\text{baseline}}$ represents the food-web baseline value of the macroalgae *Macrocystis pyrifera* in our study (trophic level 1) and TEF $\delta^{15}N$ is the mean trophic enrichment factor of 2.3‰ for aquatic consumers [59].

To investigate ontogenetic shifts in the diet of *L. santolla*, linear regression models were fitted using log-transformed variables, such as carapace length (mm), as proxy of body size, body mass (g), and trophic position versus $\delta^{13}C$ and $\delta^{15}N$.

To determine the size of isotopic niches of *L. santolla*, their variability across sex and maturity stage and overlap, carbon and nitrogen stable isotope data of adult males/females and late juvenile males/females were used to calculate the standard ellipse area (SEA) and corrected for small sample size (SEAc) with the Stable Isotope Bayesian Ellipses (SIBER) package in R [61]. The SEAc was set to contain 40% of isotopic observations of each

group [62], along with the traditional standard convex hull which represents the isotopic total area (TA) occupied by individuals [30].

Additionally, to quantify differences in isotopic niche use among sex and maturity stages of *L. santolla*, the probability of a group appearing within the niche region (space) of another group was estimated by using the R package nicheROVER [32] with 95% credible intervals based on 10,000 iterations.

To explore preliminary community niche width, we ran the SIBER package in R [61] on the complete dataset which includes δ^{13}C and δ^{15}N values of all king crab and the relationship with associated fauna species with at least three samples. The degree of interspecific trophic overlap was calculated as the overlap index of the model SIBER, where a value greater than 1 indicates high overlap, and below 0.30 indicates low overlap [61].

3. Results

3.1. Stomach Content

In total, 149 stomach contents of *L. santolla* were dissected. Of these, 63.1% were found with traces of food, and 12.1% were empty. In lower percentages, 6.7% of the stomachs were found with little food, 5.4% with some food, 4.7% showed almost filled stomachs, 4.7% stuffed stomachs and, finally, only 3.4% showed half-filled stomachs. Of the total, only adults presented stuffed stomachs (7.7%) and the highest number of both traces of food (56%) and empty stomachs (13.2%). Meanwhile, no full stomachs were found in late juveniles, a high number of stomachs showed traces of food (74.1%) and the proportion of empty stomachs (10.3%) was lower (see Supplementary Material Table S1).

The diet composition of *L. santolla* comprised 16 major prey items. Of these, crustaceans and bivalves were found to be of higher importance (18.9% and 14%, respectively), followed by hydrozoans (13.2%), algae (12.3%), and fish (11.1%) and in less quantity, detritus (1.2%), cephalopods (0.8%), gastropods (0.7%), sediment (0.7%), and others (0.2%). Crustacean items included mostly body parts of the carapace/exoskeleton of king crabs, the algae items were fragments dominated by the brown algae *Macrocystis pyrifera,* and the fish items included body parts such as flesh, spines, scales, and otoliths of *Merluccius australis.* Among groups, in adult males, the highest contributors of prey items were crustaceans (31.9%), algae (23.8%), hydrozoans (11.3%), and fish (9%). In adult female crabs, it was hydrozoans (20.1%), fish (15.3%), bryozoans (14%), crustaceans (12.6%), and bivalves (12.6%). Late juvenile male crabs consumed greater amounts of crustaceans and bivalves (19.7% and 17.1%, respectively), followed by plastic (11.5%) and echinoderms (10.6%). In late juvenile females, the most important items were bivalves and porifera (24.3% and 14.9%, respectively), followed by hydrozoans (10.8%) and crustaceans (10.6%) (Table 2).

The standardized volumetric contribution (%) of prey to individual diet showed differences among maturity stage and sex (Supplementary Material Table S2). Indeed, the PERMANOVA showed differences between adults and juveniles (Pseudo-*F* = 3.62; *p* = 0.001) and between males and females (Pseudo-*F* = 2.19; *p* = 0.014) (Table 3). The SIMPER analysis showed an 83% dissimilarity in stomach contents between adults and juveniles, where crustaceans, hydrozoans, bivalves, and algae were the prey that contributed most to these differences (19.8%, 14.1%, 11.3%, and 11%, respectively) (Table 4). Among sex groups, the SIMPER analysis showed an 81.2% dissimilarity between males and females, where crustaceans, hydrozoans, algae, and bivalves were the prey that contributed most to the differences between them (14.5%, 13.6%, 12.4%, and 11%, respectively) (Table 5). We identified dominant fragments of brown algae *Macrocystis pyrifera* and, in very little proportion, unidentified calcareous red algae and some green filamentous algae.

Table 2. Mean volumetric contribution (%) of food items in the diet of *Lithodes santolla* among sex and maturity stage, Nassau Bay, Cape Horn.

Prey Groups	Adult Males	SD	Adult Females	SD	Juvenile Males	SD	Juvenile Females	SD	All	SD
Algae	23.8	37.01	9	13.4	7.7	14.4	6.3	12.2	12.3	23.4
Hydrozoa	11.3	27.3	20.1	25.6	6.7	12.6	10.8	15.8	13.2	22.8
Bryozoa	5	17.2	14	27.5	1.2	4	3.1	9.1	6.8	19.2
Porifera	-	-	-	-	3.4	14.8	14.9	32	3.6	16.5
Foraminifera	0.5	1.8	2.5		2.6	4.7	6	9.1	2.7	5.3
Polychaeta	1.9	5.1	2.5	5.8	4.8	14.1	0.7	3.7	2.4	7.8
Echinodermata	3.1	16.7	3.8	10.2	10.6	23.2	1.4	4.1	4.5	15.1
Crustacea	31.9	40.2	12.6	22.4	19.7	23.2	10.6	18	18.9	28.9
Bivalvia	5.9	20.1	12.6	20.9	17.1	17.6	24.3	33	14	23.7
Gastropoda	0.5	2.3	0.4	1.6	0.7	3.7	1.2	4.3	0.7	2.9
Cephalopoda	3	11	-	-	-	-	-	-	0.8	5.9
Fish	10.9	23.6	15.3	27.0	6.5	20.8	9.1	19.9	11.1	24
Plastic	2.1	3	6.5	16.8	11.5	23	9.6	15.5	6.9	16
Sediment	-	-	0	0	3.6	12.6	0	0	0.7	5.7
Detritus	-	-	0.1	1	3.8	19.6	1.9	6.1	1.2	9.1
Other	-	-	0.6	3	-	-	-	-	0.2	1.7
Number of stomachs with food	36		43		26		26		131	

Table 3. Factorial PERMANOVA to test differences between maturity stage and sexes in diet contribution from 16 prey items.

Source of Variation	df	Sums of Square	Pseudo-*F*	*F* (Perm)	Perm
Maturity (M)	1	12458	3.6216	**0.001**	999
Sex (S)	1	7526.5	2.1879	**0.014**	999
M × S	1	5184.5	1.5071	0.111	999
Res	127	3440.1			
Total	130				

Bold figures indicate significant results ($p < 0.05$).

Table 4. Contribution of principal food items (%) to dissimilarity in stomach contents between adults and juveniles of *Lithodes santolla* from Cabo de Hornos. Av.Abund = average abundance of prey item, Av.Diss = average dissimilarity, Diss/SD = average contribution divided by the standard deviation, Contrib% = Contribution to the dissimilarities, Cum% = Cumulative contribution to the dissimilarities. All items representing >10%.

ITEMS	Av.Abund Adults	AvAbund Juveniles	AvDiss	Diss/SD	Contrib%	Cum%
Crustaceans	6.17	1.57	12	1.81	19.84	19.84
Hydrozoans	1.76	4.07	8.49	1.31	14.05	33.89
Bivalvia	2.69	4.64	6.85	1.29	11.34	45.23
Algae	3.61	2.55	6.65	1.18	10.99	56.22
Average Dissimilarity 83.0						

Table 5. Contribution of principal food items (%) to dissimilarity in stomach contents between males and females of *Lithodes santolla* from Cabo de Hornos. Av.Abund = average abundance of prey item, Av.Diss = average dissimilarity, Diss/SD = average contribution divided by the standard deviation, Contrib% = Contribution to the dissimilarities, Cum% = Cumulative contribution to the dissimilarities. All items representing >10%.

ITEMS	AvAbund Male	AvAbund Female	AvDiss	Diss/SD	Contrib%	Cum%
Crustaceans	18.37	12.64	11.92	0.83	14.5	14.5
Hydrozoans	10.31	16.84	11.14	0.77	13.55	28.04
Algae	14.09	10.45	10.15	0.75	12.35	40.39
Bivalvia	11.39	13.05	9.03	0.75	10.99	51.38
Fish	8.69	9.43	8.22	0.59	10	61.38
Average Dissimilarity 81.2						

3.2. King Crab Stable Isotope Composition and Potential Basal Carbon Sources

The results are shown in Table 6, including a full list of taxa, their classification, stable isotope values, and relevant trophic traits. Overall, $\delta^{13}C$ values in *L. santolla* tissues ranged from $-16.9‰$ to $-13.2‰$ (mean -14.9), while $\delta^{15}N$ values ranged from $10.5‰$ to $12.6‰$ (mean 11.6) within the population. In addition, the $\delta^{13}C$–$\delta^{15}N$ biplot revealed segregation among maturity stages and sexes (Figure 2).

Table 6. Summary statistics of the isotopic composition of $\delta^{13}C$ and $\delta^{15}N$ values (range, mean, and standard deviation), sample size, trophic position, diet, feeding mode and sample type of *Lithodes santolla*, associated fauna, primary producers, and sediment collected in Nassau Bay, Cape Horn.

Phyla/Taxon	N	$\delta^{15}N$ Range	Mean $\delta^{15}N$	SD	$\delta^{13}C$ Range	Mean $\delta^{13}C$	SD	TP	Diet	Feeding Mode	Sample Type
Arthropoda											
Crustacea											
Lithodes santolla Adults	60	10.5–12.6	11.6	0.4	−16.9– −13.3	−14.7	0.8	3.3	Om	Pr	MT
Lithodes santolla Juveniles	28	10.9–12.6	11.4	0.3	−16.4– −14.3	−15.3	0.5	3.3	Om	Pr	MT
Lithodes santolla Males	44	11.2–12.6	11.7	0.4	−16.9– −13.3	−15.1	0.8	3.4	Om	Pr	MT
Lithodes santolla Females	44	10.5–12.2	11.4	0.3	−16.4– −13.7	−14.8	0.7	3.2	Om	Pr	MT
Lithodes santolla All	88	10.5–12.6	11.6	0.4	−16.9– −13.3	−14.9	0.8	3.3	Om	Pr	MT
Paralomis granulosa	3	10.4–11.5	11	0.6	−14.7– −14.6	−14.7	0.1	3.1	Om	Pr	MT
Propagurus gaudichaudi	3	12.3–12.7	12.5	0.2	−16.3– −15.1	−15.8	0.6	3.7	Om	Sc, DF	MT
Eurypodius sp.	3	11.7–12.8	12.3	0.5	−15.8– −14.6	−15.2	0.6	3.6	Om	Sc, DF	MT
Austromegabalanus psittacus	1	8.7			−19.1			2.1	Om	SF	ST, a
Mollusca											
Cephalopoda											
Enteroctopus megalocyathus	6	13.4–14.2	13.7	0.4	−16.6– −15.7	−16.1	0.4	4.2	Ca	Pr	MT
Gastropoda											
Adelomelon ancilla	4	12.7–13.3	13	0.3	−15.5– −15.2	−15.4	0.1	3.9	Ca	Pr	MT, a
Echinodermata											
Asteroidea											
Cosmasterias lurida	6	11.4–12.4	12	0.5	−16.8– −14.1	−15.9	1	3.5	Ca	Pr	TF, a
Chordata											
Ascidiacea											
Ascidia indet.	1	9.1			−20.3			2.2	Om	SF	ST, a
Actinopterygii											
Zoarcidae											
Crossostomus chilensis	4	10.4–12.3	11.7	0.9	−15.4– −14.7	−15	0.3	3.4	Ca	Pr	MT, b
Porifera											
Mycale sp.	1	8.9			−19			2.1	Om	SF	ST, a
Haliclona sp.	2	8.2–9.1	8.6	0.6	−19.8– −18	−18.9	1.3	2	Om	SF	ST, a
Primary producers											
Rhodophyta											
Gigartina skottsbergii	3	6.5–6.7	6.6	0.1	−23.2– −22.4	−22.8	0.4		Aut		a
Gracilaria chilensis	5	4.3–6.6	5.8	1	−30.5– −28.9	−29.5	0.6		Aut		a
Porphyra columbina	2	6.7–8.1	7.4	0.9	−21.9– −19.9	−20.9	1.4		Aut		a
Chlorophyta											
Ulva lactuca	3	6.4–7	6.7	0.3	−23.7– −23.1	−23.4	0.3		Aut		a
Ochrophyta											
Macrocystis pyrifera	3	6.1–6.5	6.3	0.2	−15.6– −15.6	−15.6	0.00		Aut		a
Sediment	4	4.9–6.4	5.6	0.7	−18.6– −18	−18.3	0.3				a

N = sample size; TP = Trophic position; SD = Standard deviation; a = acidified treatment; b = mathematical correction of lipids; Om = Omnivorous; Ca = Carnivorous; Aut = Autotroph; Pr = Predator; Sc = Scavenger; DF = Deposit feeder; SF = Suspension feeder; MT = Muscle tissue; TF = Tube feet; ST = Soft tissue.
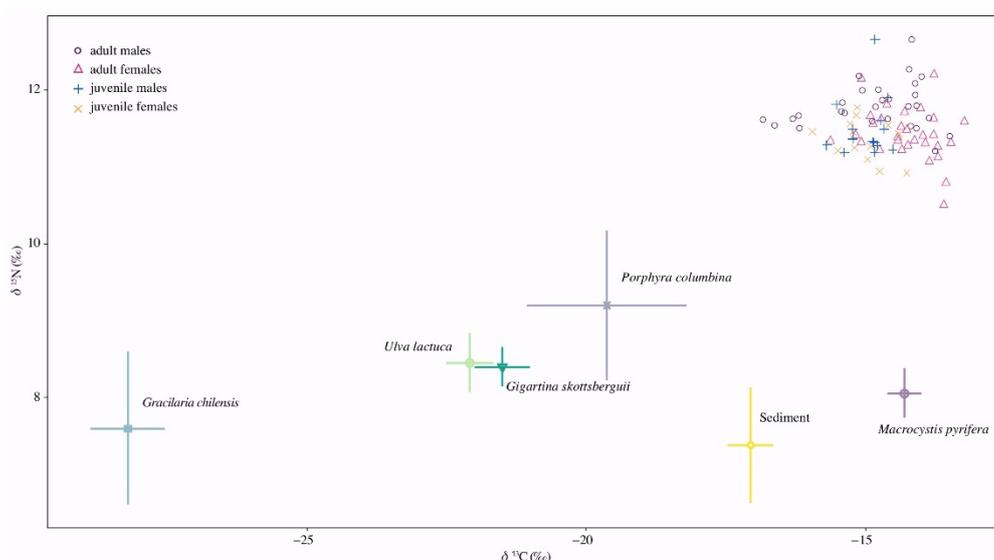
Figure 2. Isotope plot of mean δ^{13}C and δ^{15}N values (mean $\pm$ SD) for basal organic sources and southern king crab *Lithodes santolla* among sex and maturity stages, Nassau Bay, Cape Horn.

Among maturity stages, the mean δ^{13}C value of the late juveniles (-15.3‰) was significantly lower than in adults (mean -14.7‰) (Pseudo-F = 12.39; p = 0.001). The mean δ^{15}N value of adults (11.6‰) was significantly more enriched ^{15}N than the late juveniles (mean 11.4‰) (Pseudo-F = 4.67; p = 0.0355). Among sexes, the mean δ^{13}C value of the males (-15.1‰) was more ^{13}C depleted than the females (mean -14.8‰) but there were not significant differences (Pseudo-F = 3.39; p = 0.0509). The mean δ^{15}N value of males (11.7‰) was significantly higher compared to the females (mean 11.4‰) (Pseudo-F = 17.62; p = 0.0001).

Pairwise comparisons in δ^{13}C values among maturity stages and sexes revealed significant mean differences between adult females and late juvenile males, and between adult females and late juvenile females (p < 0.05). In δ^{15}N values, adult males were significantly different in relation to all the other groups (p < 0.05).

The Bayesian mixing models showed that the predominant basal carbon source that contributes to the diet of *L. santolla* population was the brown macroalgae *Macrocystis pyrifera*, with average values of 89.6% for males, 96.5% for females, 88.8% for adults, and 88.2% for late juveniles. The second carbon source contributing to *L. santolla* was the red algae *Porphyra columbina*, showing average values of 2.5% for males, 0.8% for females, 0.26% for adults, and 0.28% for late juveniles. The proportional contribution of sediment was 0.28% for males, 0.10% for females, 0.31% for adults, and 0.32% for late juveniles. The carbon primary sources such as macroalgae species *Gigartina skottsbergii*, *Gracilaria chilensis*, and *Ulva lactuca* contributed less than 0.20% to the nutrition of *L. santolla* (Figure 3).

Details of isotopic values for each basal source used in the model are shown in Table 2. There were significant differences in both δ^{13}C and δ^{15}N among basal sources (H = 18.23; p = 0.002 for δ^{13}C and H = 11.62; p = 0.002 for δ^{15}N). Among the sources, macroalgae *Porphyra columbina* and *Gracilaria chilensis* had the widest range in δ^{13}C. The highest mean δ^{13}C value was found for *G. chilensis,* and the highest mean δ^{15}N value was found for *P. columbina*. A mean δ^{13}C value of -15.59‰ and mean δ^{15}N value of 6.26‰ were for *Macrocystis pyrifera*. Sediment had mean δ^{13}C and δ^{15}N values of -18.35‰ and 5.58‰, respectively.
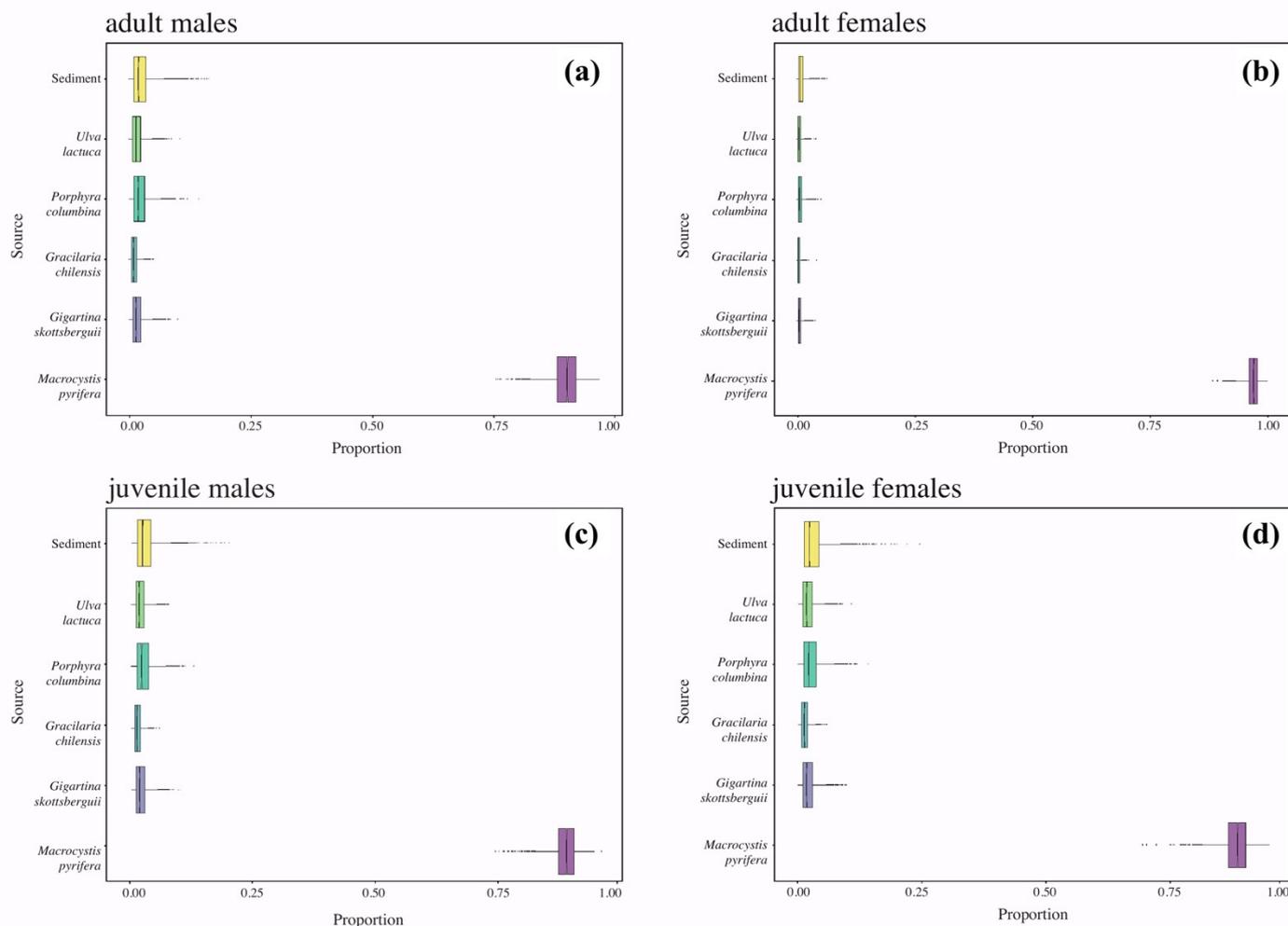
Figure 3. Results of SIMMR Bayesian mixing models showing proportional estimates of potential carbon sources (mean, 25% and 75% percentiles) to the diet composition of southern king crab *Lithodes santolla* by groups: (**a**) adult males, (**b**) adult females, (**c**) juvenile males, and (**d**) juvenile females.

3.3. Isotopic Niche and Overlap

The $\delta^{13}C$–$\delta^{15}N$ biplot with the standard ellipse area revealed intra-population niche differences for *Lithodes santolla* (Figure 4). *L. santolla* shows broader isotopic niches but they were marginally larger in adult males (SEAc = 0.85‰^{2}) than in adult females (SEAc = 0.61‰^{2}). Late juvenile males and females occupied relatively smaller isotopic niche spaces (SEAc = 0.49‰^{2} and 0.44‰^{2}, respectively) (Figures 4 and 5). The SEAc of late juvenile females was significantly smaller compared to the SEAc of adult males ($p < 0.05$) (Figure 5).

The niche overlap estimated with SIBER showed a high degree of overlap between late juvenile males and females (34.8%), while less overlap (<3%) was found for the rest of groups. The observed $\delta^{13}C$ of adult females were more enriched compared to late juvenile females, resulting in the lowest probability of niche overlap (0.8%) (Figure 4).

The nicheROVER analysis revealed that there is a high probability (95%) of southern king crab individuals to be found in the same niche region within the population, where the isotope niche of late juvenile females showed an extremely high probability to be found in the niche regions of adult males (98.2%), adult females (94%), and late juvenile males (91.4%). Similarly, the niche region of late juvenile males showed a high probability to be recorded in adult males and females niche regions (89.1% and 83.9%, respectively). Isotopic niches of adult females showed a high probability to be found in the niche region of adult

males (89.2%). Finally, the isotope niche of adult males was low in the niche regions of late juvenile females and males (54.8 and 53.4%, respectively) (Figure 6).
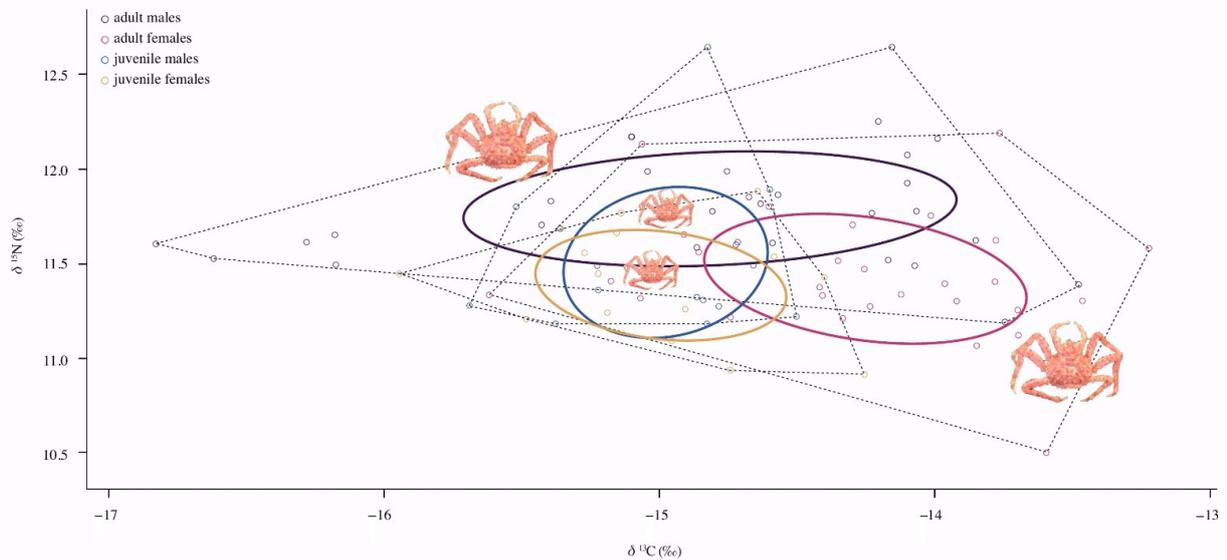

Figure 4. Isotopic niche widths of the southern king crab *Lithodes santolla* among sex and maturity stages in delta space. The standard ellipse areas (SEAs) are indicated by the solid lines, and convex hulls of the total area (TA) are indicated by the dashed lines estimated by SIBER analysis.
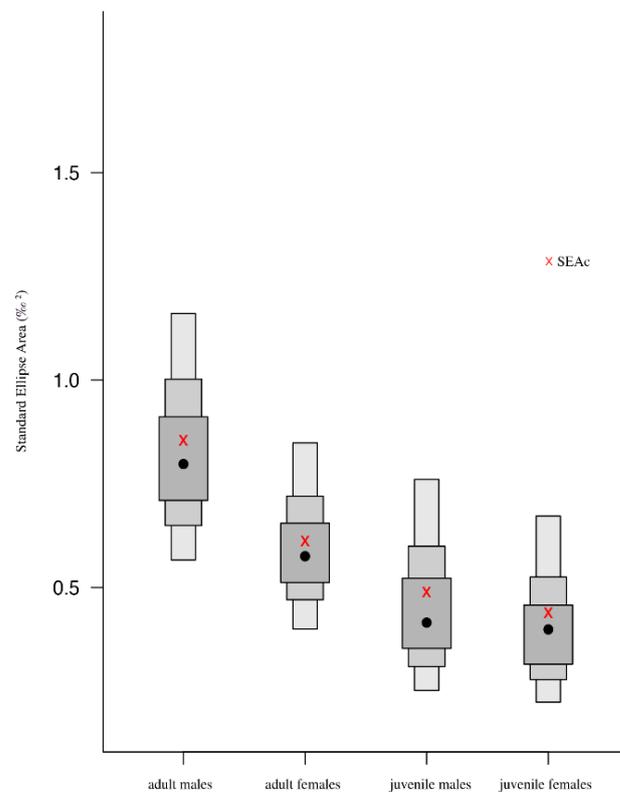

Figure 5. Bayesian density plots showing the credibility intervals (50%, 75%, and 95%) of the standard ellipse areas for the southern king crab *Lithodes santolla* groups estimated by SIBER analysis. Black points = mean standard ellipse area, red points = mean standard ellipse areas corrected for small sample size (SEA$_c$).
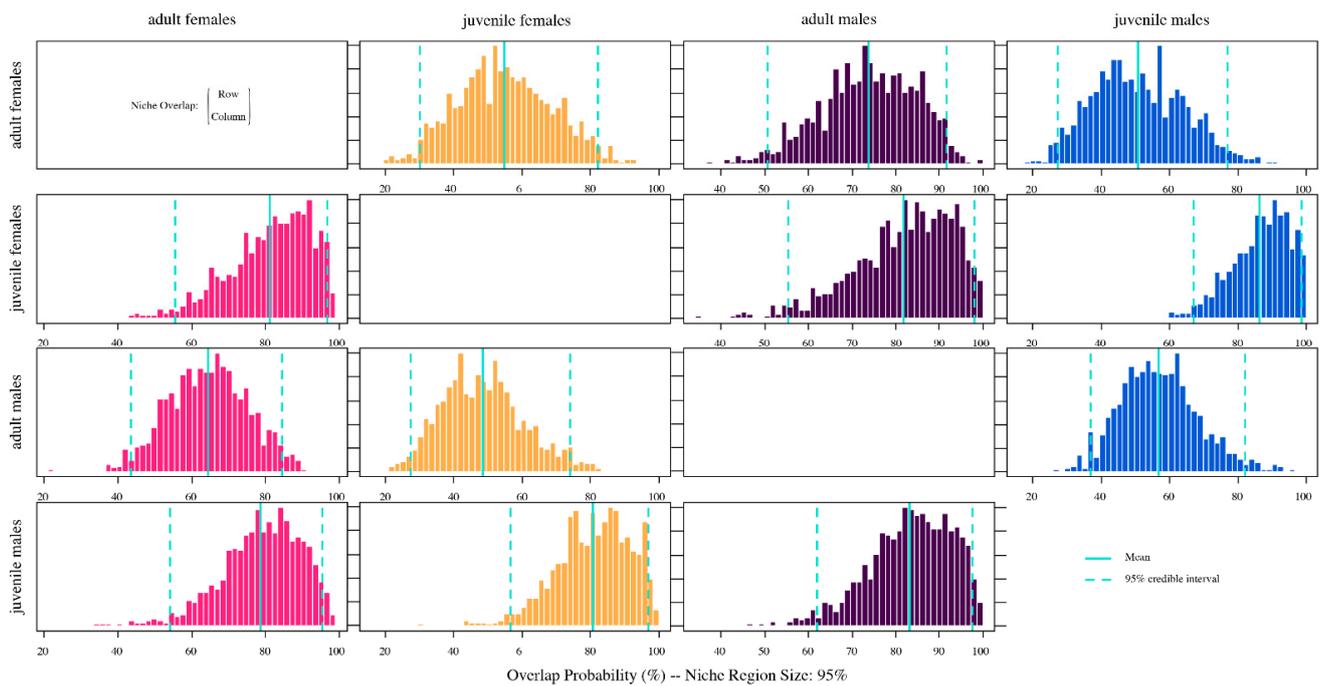
Figure 6. Bayesian plot of the posterior probability distribution of niche region metric (%) for the southern king crab *Lithodes santolla* groups estimated by nicheROVER analysis. The posterior means and 95% credible intervals are displayed in turquoise color.

3.4. Trophic Position and Ontogenetic Shift

Overall, the estimated mean trophic position for *L. santolla* was 3.3 (SD = 0.2; range 2.8–3.8). In relation to sex groups, in males the estimated mean trophic position was 3.4 (SD = 0.2; range 3.1–3.8) and for females 3.2 (SD = 0.1; range 2.8–3.6). Regarding maturity stage, in adults the estimated mean trophic position was 3.3 (SD = 0.2; range 2.8–3.8), and finally, for late juveniles it was 3.3 (SD = 0.2; range 3.0–3.8) (Table 6). The δ^{15}N of southern king crab indicated that individuals fed at a common trophic level representing secondary consumers. There were significant differences in trophic position among sex (Pseudo-F = 17.63, p = 0.0002) and maturity stages (Pseudo-F = 4.68; p = 0.034). When comparing all groups, adult males showed significant differences from all the other groups ($p < 0.05$).

3.5. Relationship between Body Size, Body Mass, TP and Isotopic Values of Lithodes santolla

There were significant positive relationships between body size (i.e., carapace length) with trophic position and δ^{15}N values of *L. santolla* ($p < 0.05$). In contrast, there was a significant negative relationship between body size and δ^{13}C (p = 0.005). Trophic position and δ^{15}N values increased significantly with individuals' body mass in all groups ($p < 0.05$), but a negative relationship with δ^{13}C was found (p = 0.004). The trophic position was not significantly related to δ^{13}C (p = 0.405) (Figure 7).

3.6. Community Niche Width and Food Web Length

The isotopic niche width of associated fauna and southern king crab indicated that the largest niche area hosts spider crab (*Eurypodius* sp.) with 1.67‰^{2}, followed by eelpout fish (*Bassanago* sp.) with 0.85‰^{2}, southern king crab (*L. santolla*) with 0.84‰^{2}, common fjord starfish (*Cosmasterias lurida*) with 0.75‰^{2}, hermit crab (*Propagurus gaudichaudi*) with 0.62‰^{2}, and southern octopus (*Enteroctopus megalocyathus*) with 0.54‰^{2}, being the smallest area of isotopic niche for false southern king crab (*P. granulosa*) with 0.39‰^{2} and piquilhue snail (*Adelomelon ancilla*) with 0.33‰^{2} (Figure 8). We found little niche overlap in almost all of the species within the southern king crab's niche, with the exception of the southern

octopus and the piquilhue snail where no overlap was found. The southern king crab showed some overlap with eelpout fish (0.33), common fjord starfish (0.28), false southern king crab (0.14), and spider crab (0.09) (Figure 8).
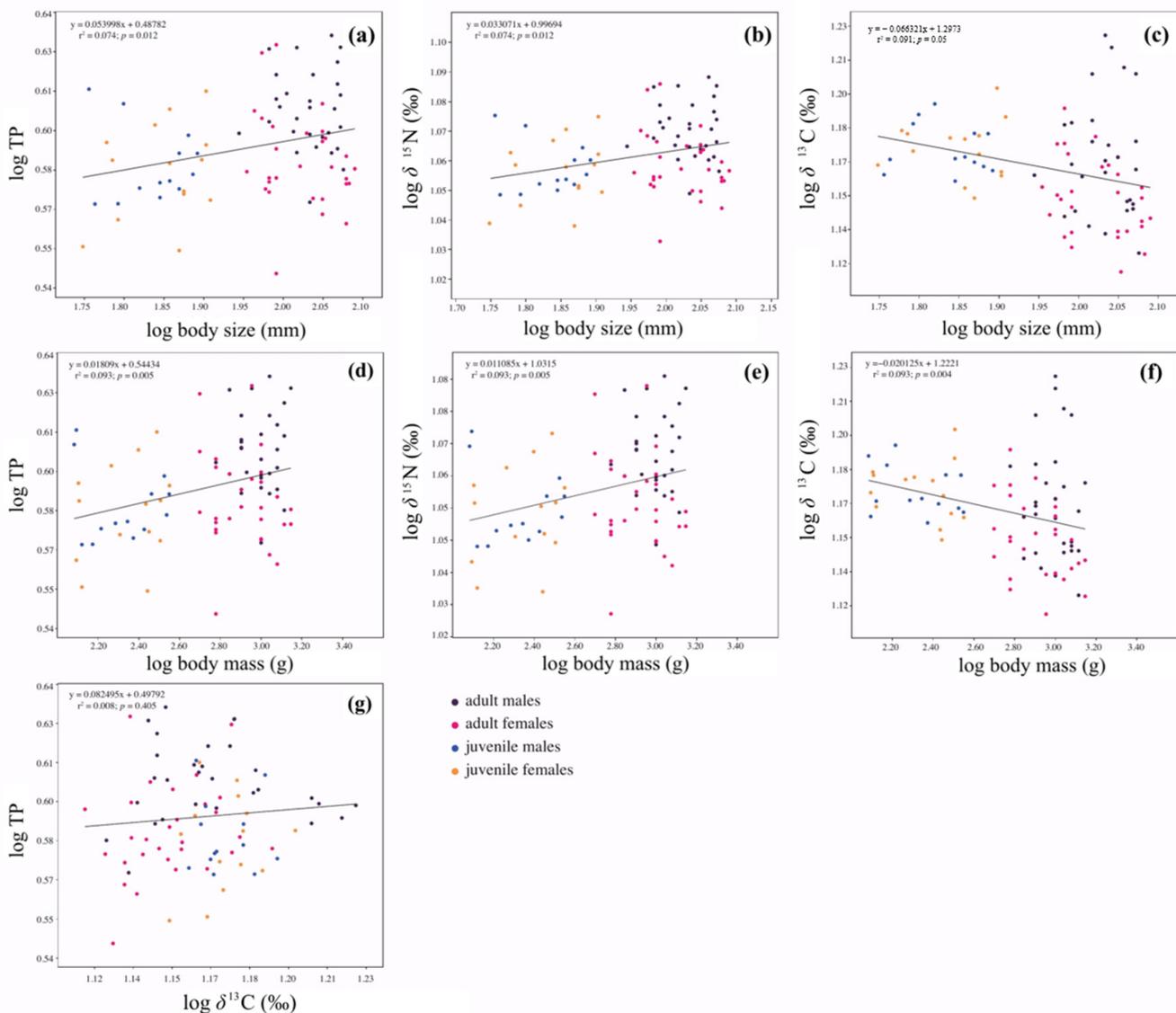

Figure 7. Relationships between: (**a**) body size vs. TP, (**b**) body size vs. δ^{15}N, (**c**) body mass vs. δ^{13}C, (**d**) body mass vs. TP, (**e**) body mass vs. δ^{15}N, (**f**) body mass vs. δ^{13}C, and (**g**) δ^{13}C vs. TP for all individuals of the southern king crab *Lithodes santolla*, Nassau Bay, Cape Horn.

With a TEF of 2.3‰, the estimated trophic position (TPs) for the associated fauna varied from 2.1 for the sponge *Haliclona* sp. positioned as a consumer of the first trophic level, to 4.2 for southern octopus as the highest predator in the benthic food web (Table 6). The community's isotopic niches revealed at least four trophic levels where the southern king crab was found positioned as an intermediate level consumer (trophic level = ~3).
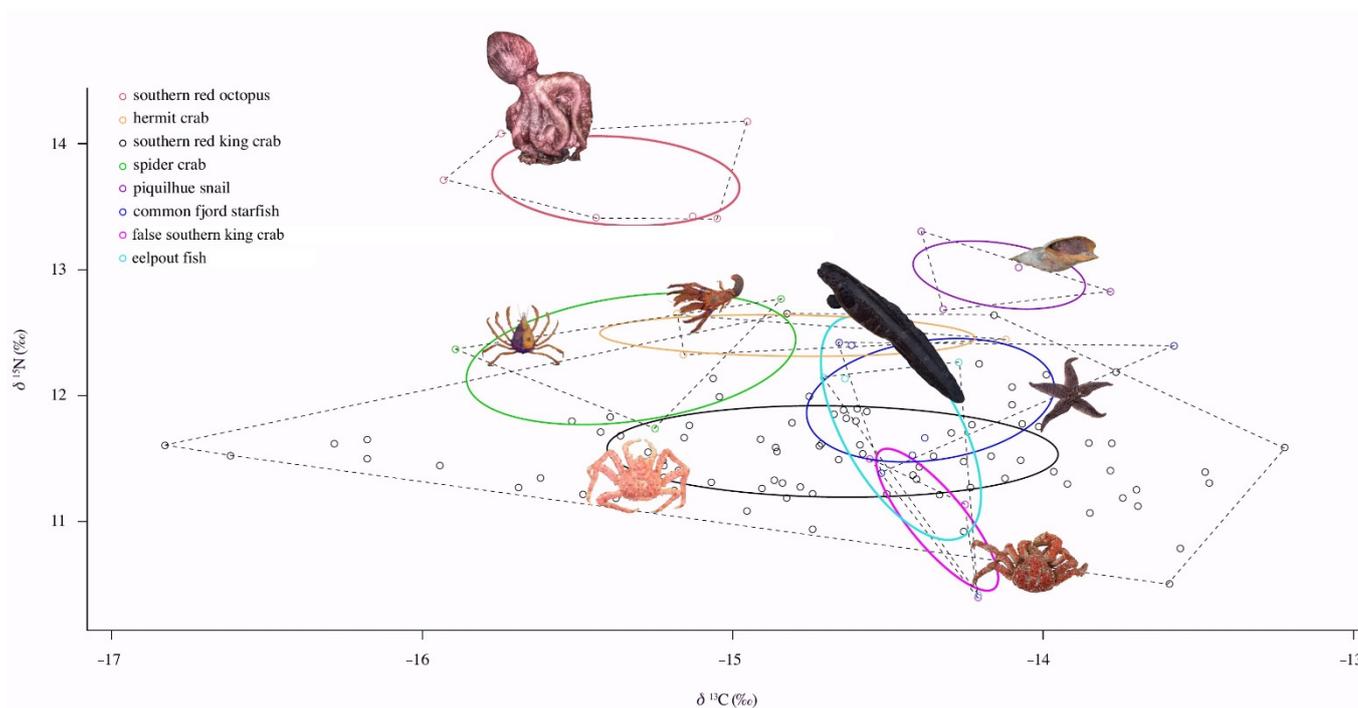
Figure 8. Community niche width output for the associated fauna species and the southern king crab *Lithodes santolla* using SIBER analysis. The standard ellipse area (SEA) represents the isotopic niche width of each species. SEA = solid lines and convex hulls of the total area (TA) = dashed lines.

4. Discussion

4.1. Diet Composition of Lithodes santolla

The stomach content data analyzed in the present study characterized Nassau Bay southern king crabs as omnivorous feeders that consume a great diversity of prey including crustaceans, hydrozoans, other small benthic invertebrates (e.g., bivalves and bryozoans), algae, among other prey. These findings corroborate previous studies of populations located in different regions and lead us to conclude that *L. santolla* has a generalist feeding strategy and the ability to exploit a wide variety of natural resources from coastal benthic waters [2–4,14,15,19,62,63]. Therefore, *L. santolla*'s foraging strategy should significantly influence trophic dynamics, as strategies that incorporate a more varied prey favor more complex energetic pathways in the local benthic food web [64].

Interestingly, studies of the diet composition of *L. santolla* based on stomach content analyses are mostly restricted to juveniles or adults, but they can shift their diets. For example, Comoglio and Amin [15] indicated that juveniles, between 40–70 mm CL from the Beagle Channel, consume mainly gastropod mollusks, crustaceans, bryozoans, and algae, finding a total of 20 different items. In early juveniles, that is, specimens between 8.40–49.04 mm CL from the Gulf of San Jorge, Argentina, Vinuesa et al. [14] identified a total of 27 different food items, being red algae, ophiuroids, echinoderms, isopods, bivalve mollusks, polychaetes and bryozoans the most consumed prey. In adults between 70–119 mm CL also from the Gulf of San Jorge, Balzi [42] recorded four main prey including fish, squat lobsters, echinoderms, and bivalve mollusks.

Our study shows significant differences in the feeding patterns of late juveniles and adults, whereby late juveniles consume more bivalves than any other group. Therefore, juveniles forage differently from adults, which is probably due to the availability of prey in the habitat which individuals use. Since southern king crabs' sexual maturity varies in relation to region or depth [5,40,65], care has been taken to assure the class sizes' accuracy between late juveniles and adults reflected in the population under study.

Furthermore, southern king crabs are also known to have similar food preferences between males and females [14,15]. Conversely, our study detected differences in diet composition between sexes in both adults that were mostly related to prey item percentage. This result could indicate variations in prey availability in the foraging areas that could probably be attributable to differences in sexual behavior and ontogenetic patterns of habitat use [66,67]. Indeed, some evidence indicates that in the early spring season, females and males of *L. santolla* migrate to shallow waters for molting and mating and then return to deeper waters in late spring [40,68]. Hence, foraging prey availability for *L. santolla* of both sexes may match within their habitat during this reproductive migration.

L. santolla also appears to have an opportunistic scavenging strategy since the proportion of fish registered in diet composition among sexes and maturity stages presumably relies on the fish bait used in the crab traps (e.g., southern hake). Similar results were recorded in other fishing areas, where *L. santolla* scavenges discarded fish, such as Argentine hake *Merluccius hubbsi*, from trawlers [42].

In general, *Lithodes santolla* feed throughout the year, except for a few weeks during the molting period, when feeding ceases or decreases in intensity [69]. This has been shown, for example, in *L. santolla* in the Beagle Channel, where a high percentage of empty stomachs were recorded during the spring period [15]. This may explain the results observed in our study, where although the number of entirely empty stomachs observed was minimal, a high percentage of stomachs were found only with traces of food.

On the other hand, the stomach content results provide evidence of intraspecific predation within the natural population of *L. santolla*. The presence of crab carapace fragments inside the southern king crabs' stomachs allows us to infer the possibility of cannibalistic behavior between juveniles and adults with unknown implications for this species' growth, fitness, and reproductive success. Indeed, Pardo et al. [19] reported cannibalism for this species in the wild, with 43% of exoskeleton crabs in the stomachs of early juveniles. In addition, Lovrich [17] observed that newly molted juveniles of *L. santolla* are eaten by adults. It has been observed in other juvenile crustaceans' species that a higher risk of predation associated with complex habitats, creates a conspecific predation bottleneck [69,70]. Further evaluation of species' habitats is needed to understand this particular characteristic, which may better describe the species' population dynamics [71].

In the present study, fragments of deteriorating algae had a relatively low volumetric contribution in the stomach content of *L. santolla* and may represent a direct and/or indirect intake of other prey such as epibionts bryozoans, gastropods, etc. These results are different from those reported by Vinuesa et al. [14], who observed a higher occurrence of red coralline algae on late juveniles of *L. santolla*. Here, bivalves and crustaceans were of major importance in the stomach contents of late juveniles. This may suggest that the relative abundance of prey availability and their quality could account for omnivorous feeding at different trophic levels [72,73].

Additionally, we also recorded the presence of microplastics in the stomach content of *L. santolla*, corresponding mainly to fibers between 0.05–5 mm in length. Fibers occur as both small strands, varying between blue and red, and in the form of a ball, ranging from transparent to black. Similar findings were reported by Andrade and Ovando [74]. They point out that the probable origin of this waste and its transport to the sampling area is due to fishing activities, domestic use materials, and/or synthetic clothing. The possible routes of ingestion of the plastics can be by direct consumption or indirectly by trophic transfer from the lower trophic level in the food chain [75]. Similar results of plastic ingestion have been found in other decapod crustaceans of commercial importance, such as Norway lobster *Nephrops norvegicus*, where plastic fibers' effects within the stomach contents caused a lower feeding rate and lower reserves [76]. Recently, the presence of plastic fibers in the stomach contents of *Paralithodes camtschaticus* has also been recorded, reaching 37.9% of 139 crabs analyzed [26]. At the moment, the potential toxicity is unknown and the mechanical or other detrimental effects caused by the ingestion of plastics by *L. santolla* or in the rest of the organisms that make up the food web in the Nassau Bay area.

For the first time, Cephalopoda were recorded in the stomach content of *L. santolla*, since octopus beaks were found in it. In general, cephalopods are active predators of crustaceans, mollusks, polychaetes, fish, and other cephalopods and constitute an important carnivore in marine ecosystems [77,78]. In the Magellan sub-Antarctic region, the presence of dead octopuses on the seabed has been anecdotally documented by fishermen during diving activities (Eduardo Almonacid, 2019, personal communication.). Most probably, *L. santolla* scavenges on octopus remnants, and such carrion prey availability can be beneficial to the *L. santolla*.

When comparing the diet of *L. santolla* to that of other decapod crustaceans from the northern hemisphere, similar findings are reported. For example, the opportunistic generalist Alaska red king crab *Paralithodes camtschaticus* fed on 69 food items, with bivalves and polychaetes being the most consumed items for both late juveniles and adults, followed by echinoderms and crustaceans. The analysis also showed that all the specimens contained algae in their stomachs, but lower than other items [26]. In addition, the omnivorous snow crab *Chionoecetes opilio*'s mainly preys on polychaetes, mollusks, echinoderms, and teleost fishes, although the latter two in smaller quantities for both late juveniles and adults (30–130 mm CW) [32].

4.2. Contribution of Kelp Carbon as the Major Source to Lithodes santolla

Our study significantly expands the knowledge on *L. santolla* trophic ecology studies since the stable isotope analysis provided a novel insight into resource use within a population across sex and maturity stage groups, trophic niche, overlap, trophic position, and interactions with crab trap-associated fauna. There is very little isotopic information on this species [19]. In general, the mean values of $\delta^{13}C$ and $\delta^{15}N$ of *L. santolla* are similar to those found in the Patagonian fjord ecosystem for this species [19,79], and they are within the range found for other species of omnivore crabs from high latitude ecosystems [26,32].

The carbon signal of *L. santolla* showed intermediate values in Nassau Bay, which reflected a nearshore ecosystem, where nearby kelp belts of *Macrocystis pyrifera* provide a predictable source of nutrition. Conversely, the mean values of $\delta^{13}C$ found in the *L. santolla* population presented a variation between –16.83‰ and –13.22‰, which corresponds to a food chain producer-based primary with a C_4 photosynthetic pathway (e.g., marine brown macroalgae [80]). The Bayesian mixing models confirmed that *M. pyrifera* was the most important basal carbon source for southern king crabs in Nassau Bay compared to the red algae *Porphyra columbina* and the sediment, whose contribution seems to be little.

The incorporation of kelp carbon into *L. santolla* body tissues may be from the direct and/or indirect consumption of *M. pyrifera*. Consequently, the transfer of energy and nutrients is mediated by abundant primary consumers such as herbivores and grazers relying on feeding on kelp [81–83]. Thus, the giant kelp *M. pyrifera* would be an important carbon donor throughout the benthic food web [84]. However, we cannot ignore that quantities of decomposed kelp material and macroalgal drift can be an important carbon source that enter the food chain through detrital pathways [85–87]. To disentangle these mechanisms of energy pathways, further isotopic information is required from other allochthonous and autochthonous carbon food sources and from other organisms inhabiting and consuming *M. pyrifera* in this high-latitude marine ecosystem. In addition, the spatio-temporal variability of basal sources should be considered, as their effects on the quantity/quality of available food for consumers are well known [88–91]. For instance, in sub-Antarctic marine systems, macroalgal carbon contributions sustain benthic food webs [92,93]. Large amounts of macroalgae-derived suspended particulate matter of kelp origin and resuspended kelp detritus represent significant nutrition sources for nearshore habitats [93,94]. The importance of kelp as an important trophic base for benthic food webs could also be due to the high polyunsaturated fatty-acid content [95] and probably, being of nutritional importance for the growth and reproduction of invertebrates, as many algae had been described to serve as high-quality food for invertebrates in other systems [96].

4.3. Intraspecific Niche Variation and Overlap of Lithodes santolla

The isotopic patterns observed show intraspecific trophic niche variation in the southern king crab. Niche size and region representations revealed a considerable dietary partitioning between sex and maturity, showing a greater tendency to forage different food items. It is perhaps forage intake that underpins differences in habitat use. The isotopic niches of individuals either overlapped or showed some levels of similar use and resource partitioning. The intraspecific niche variation observed in adult males/females indicated that their exploitation of trophic resources is more diversified than late juvenile males/females. These findings may be attributed to an ontogenetic shift linked to body size [97,98], age [99], seasonal migration [100], and sexual segregation [101], among others. However, spatial separation by migratory patterns in the life cycle of *L. santolla* [44,102,103] reinforces the idea that the high mobility of adults from both sexes, when migrating from shallow to deep waters, means they have more access to habitat foraging resources than the juveniles do. Therefore, the niche differentiation found in the southern king crab population allows the species to partition resources since they likely share the same ecological niche, which facilitates the coexistence of similar species [104]. The mechanism associated with this pattern in *L. santolla* has yet to be explored.

The narrower niche found in late juveniles from both sexes could indicate limited access to forage by the availability of food in the habitat and therefore can aid resource partitioning and a more specialized diet [105]. Consumer specialization shifts, for a particular resource or habitat use, are mostly related to ontogenetic changes in resource use in organisms [105,106]. For instance, evidence based on juvenile pods of *L. santolla* around kelp beds of *Macrocystis pyrifera* [8] supports the idea of juvenile specialization on kelp-associated prey (e.g., bivalves). Moreover, kelp forests and beds of *M. pyrifera* are common habitats, forming in shallow coastal ecosystems in the Magellan region [63,107], and smaller juveniles of *L. santolla* seem to occupy them as microhabitats to minimize the risk of predation or cannibalism [14].

Despite these findings, one also has to account for the influence when routing processes of isotopic data to estimate niche variation since outliers were included in our niche analysis to not underestimate the natural variability of organisms [67] as we do not have isotopic prey availability data.

On the other hand, the significant enrichment in δ^{15}N found in adult males enables them to forage on food sources higher in δ^{15}N than females and late juveniles in various habitats, including kelp beds, along a spatial gradient and also on prey sources, thus increasing their trophic position. Besides, adult females showed more enrichment of δ^{13}C, suggesting they are using other food sources more related to coastal waters (e.g., littoral benthic environment). Larger niche sizes in adults may also indicate a shift from a foraging behavior to scavenging [16], perhaps across a wide range of benthic habitats (e.g., nearshore and offshore). Given these characteristics in the complex feeding ecology of *L. santolla*, it would be useful to understand how ontogenetic changes affect an organism's resource use to optimize their energetic requirements and nutrition as they grow and when food resources are limited [96].

The overlapping of Bayesian ellipses provides a measure of the diversity of individual patterns in resource use [31] so that the results account for a broad use of trophic resources. There are similar resource requirements such as food and habitat, with varying degrees of overlap depending on the availability of the limited resources. It is possible that the overlapping of niches emphasizes the reported cannibalism for this species in their natural environment [19]. Indeed, cannibalism has been described as a common phenomenon among crustaceans [9,108,109].

4.4. Trophic Position of Lithodes santolla

According to our results, *L. santolla* has an intermediate trophic position belonging to a secondary consumer (relative trophic level = ~3), and its range reflects an intraspecific variation in diet (i.e., trophic level does not relate to δ^{13}C), which supports an omnivore-

based diet. Moreover, regression analyses indicated that as the *L. santolla* increased its body size and body mass, the isotopic niche moved along both axes, with a significant shift from late juveniles to adults, towards more enriched δ^{15}N values reflected in a higher trophic position. Therefore, these results suggest that southern king crab tissues assimilate ^{13}C- and ^{15}N-enriched food sources as they grow and develop [110–112]. Consequently, trophic positions increase with ontogeny. However, our data should be interpreted cautiously, as it does not fully reflect all *L. santolla* life stages. Hence, an extended sampling that incorporates early juveniles should be carried out. Recently, a published paper by Pardo et al. [20], focused on juveniles of *L. santolla*, found an ontogenetic shift where the vagile phase occupied a higher trophic position than the cryptic phase. In general, ontogenetic niche shifts through life history are common in aquatic consumers [97,99,113], particularly many crustaceans display ontogenetic dietary shifts related to body size increases [114–116].

The estimated trophic position for the southern king crab in this study (3.3) is higher compared to that reported by Pardo et al. [19] for other populations within the region, although the species showed a similar diet. These findings can be attributed to the basal carbon signature assimilated by *L. santolla* and to the availability of high-quality food in the environment. Another comparison can be made with the red king crab *Paralithodes camtschaticus* (3.1), a decapod from a different high latitude ecosystem [26], wherein both species represent a trophic role of a secondary consumer, also called the first-order predator, in the trophic structure.

4.5. Community Niche Width

Our study represents the first attempt to estimate the trophic niche overlap of *L. santolla* with associate fauna, as co-existing species, and their niche widths. Although there are many target fisheries in the area, the marine ecosystems and their trophic pathways' functioning remains poorly understood. Stable isotope analyses indicated that *L. santolla* overlap their isotopic niche, more or less, with some species of the associated fauna, such as false southern king crab, eelpout fish, and starfish, evidencing the sharing of food resources and habitat use. For example, *L. santolla* may share resources and habitat with *P. granulosa*. They present similar foraging behaviors and preys found in both species' diets (e.g., algae, mollusks, crustaceans, and echinoderms) [69]. The starfish, on the other hand, it may share gastropods and bivalves' prey, but also microhabitat since it is actively feeding in kelp *M. pyrifera* [82]. For eelpout fish, there is no information about its diet and these results might suggest that this species is a potential predator of the southern king crab as seen by the niche overlap. Moreover, eelpout fish has a similar niche size with southern king crab and may suggest both species share food sources and habitats.

In contrast, there is no evidence in our study of niche overlap within the community between *L. santolla* and the southern octopus and piquilhue snail. This is probably related to different habitats and preys, besides both species occupy a higher trophic position than *L. santolla.* In addition, the narrow niche size found in piquilhue snail seems to be a more specialist diet. In fact, Bigatti et al. [117] reported two dominant bivalve species in piquilhue snail stomach contents. Further research that includes more species interactions is necessary for improving the knowledge of the benthic food web.

The results of this study are relevant for ecosystem-based management in Nassau Bay. Therefore, it would be important to conduct long-term trophic studies to clarify whether the competing species are using the same habitats [97] and what the overlap niche effects are of multiple target fisheries in the abundance of food source availability.

5. Conclusions

The information presented here could be considered for the establishment of the regular monitoring of isotopic composition in southern king crab populations, as measures of niche and trophic position reflect the state of the populations summarizing the changes in a species' population dynamics [118]. Thus, our study could be considered a benchmark for future surveys of *Lithodes santolla* within and among populations since the increase or

decrease in trophic position and variation of trophic niche width could indicate changes in the availability of prey and the reduction of the adult fraction or an increase in juveniles of the population of *L. santolla*.

The feeding ecology complexity in *L. santolla* with its multiple features (foraging strategies, variation in habitat use, ontogenetic diet shifts, intraspecific/interspecific niche, partitioning of resources, among others) impact the efficiency of energy use, the requirements of the animal, and the secondary production [119]. It seems that being a generalist with an omnivorous diet is an advantage over other species since they can adjust their feeding preferences according to their fitness requirements by preying on less nutritious but abundant food and less but more nutritious food sources in variable proportions [120]. To improve the knowledge of foods' nutritional value, the fatty acid composition of *L. santolla* and their prey's abundance should be further investigated.

Finally, this study reinforces the urgency of research in this area to improve conservation management of southern king crab populations. Further studies are needed to assess the implications of habitat fragmentation enhanced by climate change and harvesting activities on the kelp forests, *Macrocystis pyrifera,* that play an essential role as a critical habitat and nutritious carbon food source for *L. santolla* and many other species.

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