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Trophic Ecology of Juvenile Southern King Crab Associated with Kelp Forest: Evidence of Cannibalism

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Abstract: The southern king crab, *Lithodes santolla*, is a well-known predator/scavenger species during its adult phase but its feeding strategy in early stages is less studied. This information is important to understand their role in ecosystems and to improve fishery management (i.e., stock enhancement). Based on stomach contents and stable isotope analysis, we determined variation in the composition of diet and niche overlap in vagile and cryptic phase collected within and outside a kelp forest, *Macrocystis pyrifera*, of Aguila Bay at the Magellan Strait in Patagonia, Chile. Results of juvenile stomach content analysis showed 60% dissimilarity between cryptic and vagile juvenile phases. Algae dominated the volumetric contribution in cryptic juveniles while crustacean dominated the diet in vagile phase. Exoskeleton of other king crabs occurred in 43% of juveniles with crustaceans in their stomach. This fact confirms cannibalistic behavior in the wild in this species, which is consistent with findings in massive laboratory cultures. There was no evidence of isotopic niche shift between cryptic and vagile juvenile phases. Overlapping isotopic niches of different-sized juveniles suggest that they exploit similar food resources. However, vagile individuals occupy a higher trophic position than cryptic individuals, which could suggest a switch in dietary preference, from detritivorous/herbivory within kelp forests to omnivory outside of kelp forests, and an increase in the level of cannibalism in vagile juveniles.

Keywords: Patagonia; *Macrocystis*; stable isotopes; stomach content; Decapoda; *Lithodes santolla*

1. Introduction

King crabs around the world have been a target of intensive fishery activity [1,2] and represent one of the most ubiquitous species in benthic non-tropical communities [3]. They are generalist, opportunistic epibenthic predators and scavengers, feeding on multiple food items from different trophic levels including algae, mollusks, echinoderms and crustaceans [4]. However, their diet has been principally described for adults, with less attention on early juveniles [5–7]. Under laboratory conditions, species such as the red king crab, *Paralithodes camtschatica* (RKC), and the southern king crab, *Lithodes santolla* (SKC), have been successfully maintained on carnivorous diets and juveniles exhibit high levels of cannibalism when they are held in high densities [8–10]. Therefore, king crab juveniles are assumed to have a carnivorous diet like adults.

In decapods, types of diet and relative importance of specific items can change during ontogeny, especially in cases when juveniles and adults use different habitats [7,11,12]. For

king crabs this could be especially true because they undergo three juvenile developmental phases related to habitat use: (1) Cryptic phase, where juveniles at age 0–1-years-old occur in complex and structured habitats; (2) Vagile phase, 1–2-year-old crabs enlarge their trophic niche moving to other habitats (i.e., outside kelp forest, such as mussel or algae beds) and (3) Gregarious phase, where older juveniles or pre-adults exhibit an aggregative behavior called "podding" [13].

Lithodes santolla is the most common king crab in Patagonian waters [14] and their juvenile ecology is one of the least known among the commercially important king crabs. However, information available [14–16] indicates that SKC seems to follow similar juvenile phases to those described by Stevens [13], but not necessarily with the same timing.

In *L. santolla*, larval settlement occurs at depths up to 40 m in complex habitats and is presumably associated with kelp forest, *Macrocystis pyrifera* [15]. This habitat is especially diverse, and their first juvenile stages would have a great environmental offer of prey including echinoderms, snails, amphipods, isopods, polychaetes and both fresh and decomposing algae [17–19]. Crabs in the cryptic phase inhabit inside of the holdfast of *M. pyrifera* and/or in spaces among plants, during the first years of life. Assuming the growth pattern at 9 °C [20], close to the mean temperature in the Magellan strait [21], cryptic phase individuals between 20 to 30 mm carapace length (CL) would be 3-year-olds. The vagile phase would correspond to larger juveniles who forage both inside and outside of kelp forests, potentially accessing other prey items. Finally, podding behavior has been documented for SKC [16], demonstrating that a gregarious phase is exhibited in this species. However, a larger size range of 34–75 mm CL was found participating in the pods and aggregations occur in the same habitat as the other stages (i.e., kelp forest). Therefore, in terms of habitat use and size, two phases (cryptic recruits and vagile juveniles) can be identified for SKC associated with kelp forest.

Stomach content analysis has been widely used in studies of diet and trophic habits because it represents the unequivocal consumption of individuals. However, stomach contents only represent a brief time period between ingestion and digestion [22,23] and does not identify the variability of components that are really assimilated by the organisms at different rates [24]. As such, the probability of underestimating the presence of some prey species (i.e., soft-bodied organisms) may be high.

An alternative to complement these analyses is the analysis of stable carbon and nitrogen isotopes in animal tissues. This technique uses the isotopic signatures of prey species reflected in the species that consume them and are transmitted all along the trophic web from producers to consumers [25]. Specifically, the isotopic values of $\delta^{15}N$ are indicators of the trophic level in species, given that $\delta^{15}N$ exhibits a slight enrichment of 2.5–5‰ in each trophic level [23,25,26]. Conversely, values of $\delta^{13}C$ vary little along the trophic web (close to 1‰), yet are good indicators of habitat, as they allow differentiation between the sources of primary production [27].

This study describes the trophic pattern of *L. santolla* juveniles associated with a kelp forest. Specifically, we investigate (1) if southern king crab juveniles shift their diet over the course of ontogeny, especially the relative importance of seaweed in their diet and (2) cannibalism in their natural environment.

2. Materials and Methods

2.1. Sample Collection

Samples were collected in summer 2018 in Aguila Bay (53°47′11″ S; 70°58′26″ W) in the Magellan strait, Chile, between 5 and 12 m depth. Samples were taken inside and outside of a kelp forest using an airlift device handle by two SCUBA divers to collect small mobile macrobenthic (>5 mm length) organisms [28]. Sampling was performed by haphazardly placing 5 square frames (0.25 m^2) and all the material and individuals contained within were suctioned with the airlift device into a 1 mm mesh size catch bag. Large individuals (>50 mm) were collected by hand.

2.2. Stomach Content Analysis

Carapace lengths (CL) of the southern king crabs collected were measured to the nearest 0.01 mm from the base of the rostral spine to the posterolateral margin of the carapace using a digital caliper. All crabs showed hard-shell condition and sex was not determined. All individuals were dissected, and their stomachs were removed and frozen at -20 °C until analysis was conducted. The stomach content estimation was performed using the modified [29–31] points method of Hynes [32]. This method registers the stomach fullness (Stomach Fullness Index SFI$_i$) on a scale of 0 (empty) to 16 (full) by visual examination using a stereomicroscope and categorizes the food items found as a percentage of total volume contribution to the diet. This method is very useful for invertebrates, or small organisms with little stomachs where the weight of the sample is difficult to estimate adequately. All food items were stored in 95% denatured ethanol.

Juveniles were categorized into two groups depending on their size: cryptic phase (<37 mm carapace length (CL)) and vagile phase (>50 mm and <100 mm CL).

2.3. Stable Isotope Analysis

Leg muscle tissue from each *L. santolla* was dissected, washed with MilliQ water and oven-dried at 60 °C for 48 h. The dried matter was ground to a homogenous powder using a mortar and pestle and rinsed with a 2:1 chloroform:methanol solution to remove lipids [33]. Then, the samples were divided into two portions. Calcium carbonate from the exoskeleton or cellular wall had to be removed to obtain unbiased δ^{13}C values [34,35]. As such, one of the subsamples was demineralized with 0.5 N hydrochloric acid (HCl) to eliminate remnants of calcium carbonate and the separate portion was used to measure δ^{15}N, given that the decarbonization treatment negatively affects ^{15}N [36].

Nitrogen and carbon isotope ratios were performed using a continuous flow isotope ratio mass spectrometer (Flash EA200 IRMS Delta Series, Thermo Scientific, Bremen, Germany). Stable isotope abundance is expressed in standard δ notation, relative to international standards: δ^{13}C = Vienna Pee Dee Belemnite and δ^{15}N = atmospheric nitrogen [37]. The precision for δ^{15}N was 0.18‰ and for δ^{13}C was 0.3‰. Isotopic estimation was performed at the Laboratory of Biogeochemistry and Applied Stable Isotopes (LABASI), Pontificia Universidad Católica de Chile (Santiago, Chile).

2.4. Trophic Position

The δ^{13}C and δ^{15}N values can vary significantly in primary producers over spatio-temporal scales. For this reason, two primary consumers were selected to define the baseline values, given that they generally present less variation in δ^{13}C and δ^{15}N, thus they may better represent an integrated spatio-temporal signal of primary producers within the system [38–40].

To determine the trophic position (TP) we used the Bayesian approach considering the equation proposed by Post, 2002 [41,42], which includes two different sources (one pelagic and one benthic). Our baseline TPs were calculated using δ^{15}N values of *Perumytilus purpuratus* a filter-feeder of phytoplankton collected from the same site as king crabs, and the benthic gastropod *Margarella violacea* (assuming that both occupy TP = 2). Furthermore, we used a trophic enrichment (δ^{15}N) of 3.4‰, which has been identified as an average trophic nitrogen fractionation for aquatic consumers [38,42].

2.5. Data Analysis

Stomach content: To compare crab diets in both stages, a PERMANOVA was performed on the matrix of volumetric contribution per item for each juvenile crab. Additionally, a similarity percentage analysis (SIMPER) was conducted to determine which prey species made the greatest contribution to dissimilarities in the diet between ontogenetic stages. Similarities among individuals were visualized by a principal coordinate analysis (PCO) using the Bray–Curtis similarity matrix [43]. All analyses were performed in PRIMER v7 [44].

Stable isotopes: The SIBER package [26,45] was used to assess the isotopic niche width ($‰^2$) of cryptic and vagile *L. santolla* juveniles. We used standard ellipse areas corrected for the small sample size (SEAc) to represent the core isotopic niche [45,46], and Bayesian standard ellipse areas (SEAb) to compare the niche width areas. This Bayesian modelling was done using 10^6 iterations to reduce the uncertainty of uneven and small samples [46]. Pairwise comparisons were considered meaningful when the probability of occurrence exceeded 95%.

Moreover, total trophic overlap was estimated between cryptic and vagile juveniles for a probabilistic niche region using nicheRover v1.0 [47]. This analysis is insensitive to sample size and evaluates the probability that the niche region of one species will overlap with that of another (i.e., A→B and B→A). The overlap index was generated after 10,000 Monte Carlo draws for a niche region (alpha = 0.95) using the predictor variables.

Finally, trophic position between juvenile phases was compared using an ANOVA test with permutation using the "lmPerm" package in R. This function tests a statistical hypothesis regardless of data distribution and it can be used for analyzing an unbalanced design.

3. Results

3.1. Stomach Content Analysis

A total of 35 individuals were processed and analyzed: 15 cryptic (17–36 mm CL) and 20 vagile (51–100.8 mm CL). All individuals collected, except one (vagile juvenile), showed material in their stomach (Table S1). Standardized volumetric contribution (%) and POC analysis showed a clear visual difference between the ontogenetic phases (Figure 1). The PERMANOVA corroborated these differences (Psedo-$F_{1,34}$ = 7.85; P_{perm} = 0.001, permutation = 999) and the SIMPER analysis showed a 60% dissimilarity between cryptic and vagile juveniles. Crustacean, bivalve and algae items were the prey that contributed most to differences between groups (20%, 14% and 11%, respectively) (Table 1). In fact, more crustacean items were consumed by vagile juveniles and very few by cryptic juveniles (Figure 2) and a high fraction (43%) of this category corresponded to king crabs body parts (Figure 3). The majority of carapace fragments were identified as *L. santolla* by presence of spines in the exoskeleton surface, which are absent in the other lithodid from the study area, the false king crab *Paralomis granulosa* [48]. Therefore, substantial levels of cannibalism were detected in vagile individuals. In the case of bivalves and algae, both items were more common in cryptic juveniles than vagile juveniles (Figure 2, Table 1).

Table 1. Contribution of principal food items (%) to dissimilarity in stomach contents between vagile and cryptic juveniles of Lithodes santolla associated with kelp forest. 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.

ITEMS	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
	Vagile	Cryptic				
Crustaceans	6.17	1.57	12	1.81	19.84	19.84
Bivalves	1.76	4.07	8.49	1.31	14.05	33.89
Algae	2.69	4.64	6.85	1.29	11.34	45.23
Sediment	3.61	2.55	6.65	1.18	10.99	56.22
Hydrozoans	1.62	2.07	5.02	1.14	8.3	64.52
Echinoderms	0.13	1.65	3.98	0.69	6.58	71.1
Average Dissimilarity = 60.46						
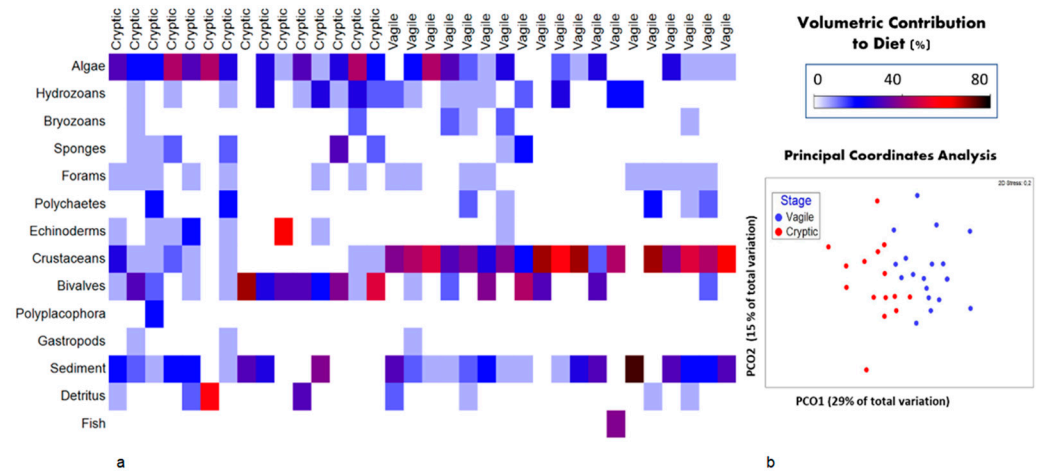
Figure 1. (**a**) Distribution of standardized volumetric contribution to diet (%) of 15 items for two juvenile ontogenetic phases of *Lithodes santolla*. (**b**) Ordination pattern of samples by principal coordinate analysis (PCA) on a resemblance matrix. An individual without stomach content was excluded from the analysis.
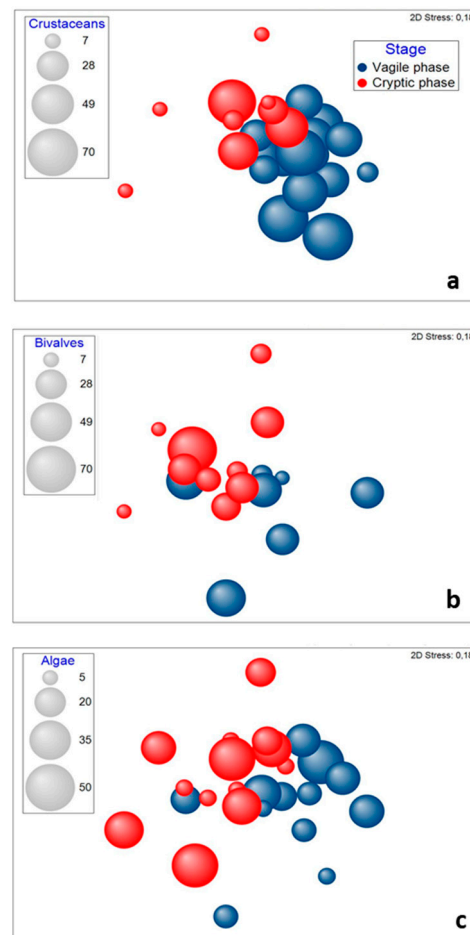
Figure 2. Standardized volumetric contribution to the *Lithodes santolla* diet (%) for three principal food items in the stomach content (SIMPER analysis). Resemblance similarities principal coordinate analysis (PCA). (**a**) Crustaceans contribution to diet; (**b**) Bivalves contribution to diet and (**c**) Algae contribution to diet.
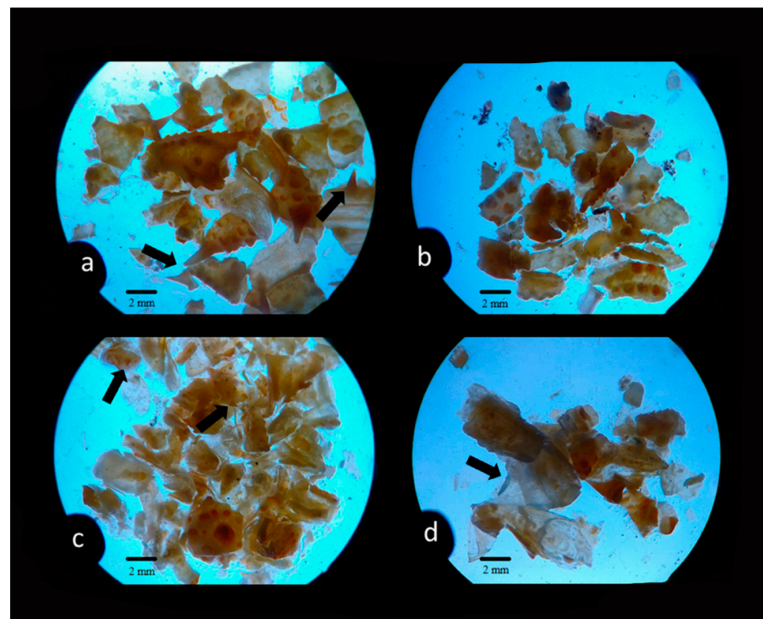
**Figure 3.** Examples of stomach contents showing a high volume of crustacean items, especially king crabs exoskeleton debris. Size of individuals (**a**) 88 mm CL, (**b**) 51mm CL, (**c**) 67 mm CL, (**d**) 63 mm CL. Arrows show the spines, characteristic of *Lithodes santolla*.

## 3.2. Trophic Niche Size and Overlap

A total of 26 juveniles were processed and analyzed: 11 cryptic (17–36 mm CL) and 15 vagile (55–100.6 mm CL) (Table S2). Bivariate standard ellipses (Figure 4a) indicated that the niche size of cryptic phase individuals (1.37 ‰^{2}) was greater than the niche size of vagile phase individuals (0.86 ‰^{2}). However, no significant differences in Bayesian standard ellipse area were found (SEAb [cryptic] < SEAb[vagile]; p = 0.14075) (Figure 4b). The probability of niche overlap was high among juveniles, with a higher probability of the vagile phase overlapping the trophic niche of cryptic individuals (80.3% at α = 0.95 probabilistic niche regions) than the cryptic phase overlapping the vagile trophic niche (59.2% at α = 0.95 probabilistic niche regions).
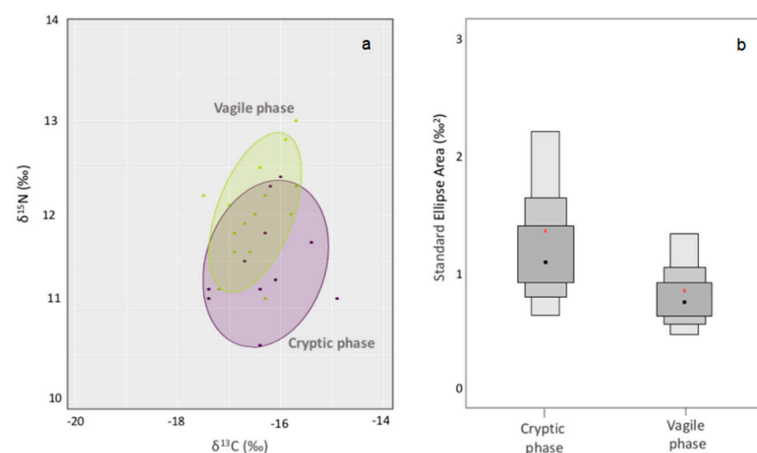
Figure 4. Isotopic niche areas of vagile and cryptic southern king crab juveniles sampled in Aguila bay. (**a**) Bivariate plot of δ^{13}C and δ^{15}N values showing standard ellipse area corrected for small sample size (SEAc). (**b**) Boxplots of model-estimated bivariate standard ellipse area (SEAb) for cryptic and vagile phase. Dark, medium and light gray boxes are respectively the 50%, 75% and 95% confidence intervals of the probability density function distributions of the model's solutions, and black dots are the modes of these distributions. Red dots are the SEAc values associated with each group.

3.3. Trophic Position

The average trophic position estimated for cryptic phase individuals was 2.52 ± 0.17, while for the vagile phase it was 2.73 ± 0.14, which is consistent with significant differences observed in the trophic position of the juvenile phases (permutation test, P_{perm} = 0.021, permutation = 4820) (Figure 5).
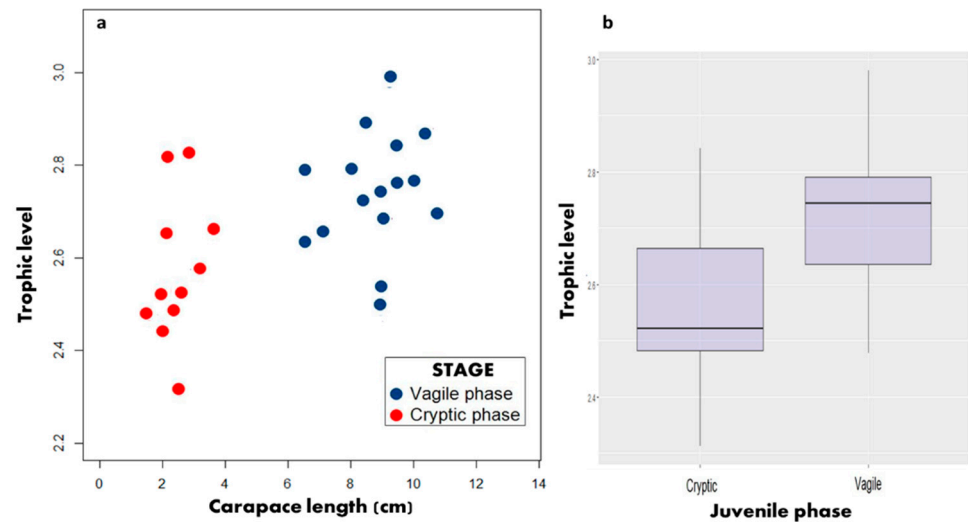
Figure 5. (**a**) Trophic position on a size gradient of *Lithodes santolla* juveniles. (**b**) Boxplot of cryptic and vagile juveniles' trophic levels.

4. Discussion

Southern king crab juveniles in the kelp forest showed changes in prey items across their ontogeny. Although a drastic switch of diet pattern was not found between juvenile phases, crustacean items appear as one of the principial and evident changes in prey consumption. The incorporation of king crab exoskeleton in stomachs by vagile juveniles suggests a dominance pattern by larger juveniles through inter-cohort cannibalism.

Cannibalism has been well described in general for king crab juveniles in a laboratory setting [9,49,50] and in SKC in particular [10,51], but evidence from wild animals has been more elusive [7,46]. Cannibalism has not been included in a seasonal assessment of wild *L. santolla* juvenile diet. Furthermore, *Paralomis granulosa*, a sympatric lithodid, showed no evidence of cannibalism in a field survey [52]. However, in this study direct evidence from stomach contents of juveniles indicates that inter-cohort cannibalism is an actual feeding behavior in nature, therefore, it is not an artefact of dense cultures of king crabs.

King crabs are active predators but also scavengers, therefore ingested individuals may already have been dead when they were consumed. This difference is important because in laboratories the intensity of cannibalism is density-dependent [51,53]. Active predation on early juveniles in nature could be an effective population control mechanism as it has been shown for other crab species [54]. Like many early benthic stages of decapods [55], including king crabs [56–58], SKC juveniles prefer complex habitats [59] to avoid predation, including cannibalism, as suggested here. The complex habitat provided by kelp forest, where cryptic juveniles can easily take refuge under boulders, cobbles or algae holdfasts and are protected by the kelp canopy, can be interpreted as a refuge for early ontogenetic benthic phases [15]. This habitat would improve the survival of younger juveniles. Furthermore, the great isotopic niche width indicates that the kelp forest provides food items from different carbon sources (pelagic and benthic), increasing the nutritional options for early juveniles. In fact, this is in line with the relatively high number of cryptic early juveniles inside of the kelp forest compared to those outside habitats (Pardo L.M., unpublished data).

Thus, the role of kelp forest habitat as nursery grounds for SKC seems to be plausible, but needs a rigorous comparison of survival and growth patterns among individuals from

multiple juvenile habitats. Moreover, the final evidence is the disproportional contribution of nursery habitat to the adult king crabs in comparison to other habitats of juveniles [60]. There is an urgent need to test the kelp forest nursery hypothesis for SKC, especially given the uncertain fate of kelp forests in the austral region facing climate change and harvesting possibilities in the future [61].

Although stomach content analysis in this study was limited to one season, the complementary use of prey species isotopic signatures provides quantitative insights into the trophic niche overlap/segregation between different phases of development [62]. This analysis suggests a change in the trophic position based on the size of individuals, where vagile juveniles can feed on organisms in a higher trophic position, including cryptic juveniles.

These findings agree with the behavioral ecology of the juvenile ontogenetic phases [13], when smaller juveniles (i.e., cryptic phase) have a reduced home range, foraging inside of the kelp forest habitat and preying on algae and bivalves (filter feeders), both sessile organisms with low trophic positions. On the other hand, larger juveniles (i.e., vagile and gregarious phases) have greater prey offer, especially with the addition of crustacean species to their diets, foraging both inside and outside of kelp forests. This ontogenetic shift in the diet seems to be coupled with better proteolytic enzymatic capacities, which appear in early juveniles, but increase towards adulthood with enhancing activities of endopeptidases such as trypsin and chymotrypsin [63].

Authors of a study performed on the Atlantic coast [7] also detected significant differences in the diet of small and large juvenile southern king crabs, but the shift in their diet was attributed to ophiuroids rather than crustaceans. On the other hand, a study in the Beagle Channel [64] reported gastropods as the principial food items which contributed to differences in the diet of large and small juveniles. More likely, different diets of SKC were associated with different habitat conditions. In any case, this research and previous studies confirm that juvenile southern king crabs are macrophages and opportunistic omnivorous predators [7].

Trophic niche breadth can be expected to increase with ontogeny, as species change habitat during their benthic life cycle and more potential prey becomes available. In addition, larger size of individuals improves accessibility to larger prey. However, in this study, we found a high overlap in the isotopic trophic niche among juveniles. Therefore, ontogenetic change in the diet seems to be only evident by observing the trophic position of juveniles, but this does not necessarily mean changes in the pattern of carbon source use. Similar results were found when comparing juvenile and adult red king crabs in Norway [65], where juveniles and adults showed a high overlap in the isotopic trophic niche, but adults had a higher trophic position. Other crabs such as *Chionecetes opilio* also showed a similar pattern [66]. A drastic habitat change such as bathymetric migration seems necessary to observe more evident changes in trophic niche breadth.

Southern king crab stocks demonstrate signs of overfishing in Chile and Argentina [67,68] probably due to male-only fishery management [69,70]. Therefore, stock enhancement, a feasible strategy to restore natural king crab populations [71], seems a management alternative for the near future. Along these lines, further studies should focus on differences in cannibalism levels among juvenile habitats, including kelp forests. Thus, restocking with early juveniles for population rehabilitation should take into account the size of juveniles released and habitat type with respect to cannibalism intensity.

Author Contributions: L.M.P.: Conceptualization, validation, field sampling, data analysis, writing—original draft, visualization. C.A.: Sampling analysis, visualization, writing—review and editing. L.Z.-D.: Sampling analysis, formal analysis, writing—review and editing. B.G.: Data curation, field sampling, data analysis, editing-review. C.R.: Sampling analysis, data curation, review. All authors have read and agreed to the published version of the manuscript.

Institutional Review Board Statement: The study was conducted according to the guidelines of Chilean law and organism were collected with fishing permits (Subsecretaria de Pesca y Acuacultura, Resolución Exenta No. 3747).

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available in Supplementary Materials.

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

References

1. Donaldson, W.E.; Byersdorfer, S.C. *Biological Field Techniques for Lithodid Crabs*; Alaska Sea Grant College Program—University of Alaska Fairbanks: Fairbanks, AK, USA, 2005; p. 76.

2. Otto, R.S. A history of King crab fisheries with special reference to the north Pacific Ocean: Development, maturity and senescence. In *King Crabs of the World: Biology and Fisheries Management*; Stevens, B.G., Ed.; CRC Press: Boca Raton, FL, USA, 2014; pp. 81–138.

3. Stevens, B.G.; Lovrich, G.A. King crabs of the world: Species and distributions. In *King Crabs of the World: Biology and Fisheries Management*; CRC Press: Boca Raton, FL, USA, 2014; pp. 1–30.

4. Stevens, B.G.; Jewett, S.C. Growth, molting and feedings of king crabs. In *King Crabs of the World: Biology and Fisheries Management*; CRC Press: Boca Raton, FL, USA, 2014; pp. 315–361.

5. Feder, H.M.; McCumby, K.; Paul, A.J. The food of post-larval king crab, *Paralithodes camtschatica* (Decapoda: Lithodidae), in Kachemak Bay, Alaska. *Crust* **1980**, *39*, 315–318. [CrossRef]

6. Tarverdieva, M.I.; Zgurovsky, K.A. On food composition of the deep-water crab species *Lithodes aequispina* Benedict and *Chionoecetes tanneri* Rathbun in the Bering and Okhotsk seas. In *International King Crab Symposium*; University of Alaska Sea Grant Program: Anchorage, AK, USA, 1985; pp. 319–329.

7. Vinuesa, J.H.; Varisco, M.A.; Balzi, P. Feeding strategy of early juvenile stages of the southern king crab *Lithodes santolla* in the San Jorge Gulf, Argentina. *Rev. Biol. Mar. Oceanogr.* **2013**, *48*, 353–363. [CrossRef]

8. Brodersen, C.C.; Rounds, P.M.; Babcock, M.M. Diet influences cannibalism in laboratory-held juvenile red king crabs (*Paralithodes camtschatica*). In Proceedings of the International Symposium on King and Tanner Crabs, Anchorage, AK, USA, 28–30 November 1989; Alaska Sea Grant College Program Report: Anchorage, AK, USA, 1989; Volume 90, pp. 377–382.

9. Stevens, B.G.; Swiney, K.M. Post-settlement effects of habitat type and predator size on cannibalism of glaucothoe and juveniles of red king crab *Paralithodes camtschaticus*. *J. Exp. Mar. Biol. Ecol.* **2005**, *321*, 1–11. [CrossRef]

10. Sotelano, M.P.; Lovrich, G.A.; Tapella, R. Cannibalism among *Lithodes santolla* (Molina 1782) juveniles: Effect of stocking density, stage and molt condition. *Aquac. Int.* **2016**, *24*, 1025–1037. [CrossRef]

11. Hines, A.H.; Lipcius, R.N.; Haddon, A.M. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **1987**, *36*, 55–64. [CrossRef]

12. Araújo, M.S.L.C.; Barreto, A.V.; Negromonte, A.O.; Schwamborn, R. Population ecology of the blue crab *Callinectes danae* (Crustacea: Portunidae) in a Brazilian tropical estuary. *An. Acad. Bras. Ciênc.* **2012**, *84*, 129–138. [CrossRef]

13. Stevens, B.G. (Ed.) Biology and ecology of juvenile king crabs. In *King Crabs of the World: Biology and Fisheries Management*; CRC Press: Boca Raton, FL, USA, 2014; Volume 636, pp. 261–284.

14. Lovrich, G.A.; Tapella, F. Southern king crabs. In *King Crabs of the World: Biology and Fisheries Management*; Stevens, B.G., Ed.; CRC Press: Boca Raton, FL, USA, 2014; Volume 636, pp. 139–210.

15. Tapella, F.; Lovrich, G.A. Asentamiento de estadios tempranos de las centollas *Lithodes santolla* y *Paralomis granulosa* (Decapoda: Lithodidae) en colectores artificiales pasivos en el Canal Beagle, Argentina. *Invest. Mar.* **2006**, *34*, 47–55. [CrossRef]

16. Cárdenas, C.A.; Cañete, J.I.; Oyarzún, S.; Mansilla, A. Podding of juvenile king crab *Lithodes santolla* (Molina, 1782) (Crustacea) in association with holdfasts of *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1820. *Invest. Mar.* **2007**, *35*, 105–110. [CrossRef]

17. Adami, M.L.; Gordillo, S. Structure and dynamics of the biota associated with *Macrocystis pyrifera* (Phaeophyta) from the Beagle Channel, Tierra del Fuego. *Sci. Mar.* **1999**, *63*, 183–191. [CrossRef]

18. Ríos, C.; Arntz, W.E.; Gerdes, D.; Mutschke, E.; Montiel, A. Spatial and temporal variability of the benthic assemblages associated to the holdfasts of the kelp *Macrocystis pyrifera* in the Straits of Magellan, Chile. *Polar Biol.* **2007**, *31*, 89–100. [CrossRef]

19. Kaehler, S.; Pakhomov, E.A.; Kalin, R.M.; Davis, S. Trophic importance of kelp-derived suspended particulate matter in a through-flow sub-Antarctic system. *Mar. Ecol. Prog. Ser.* **2006**, *316*, 17–22. [CrossRef]

20. Calcagno, J.A.; Lovrich, G.A.; Thatje, S.; Nettelman, U.; Anger, K. First year growth in the lithodids *Lithodes santolla* and *Paralomis granulosa* reared at different temperatures. *J. Sea Res.* **2005**, *54*, 221–230. [CrossRef]

21. Cárdenas, L.; Leclerc, J.; Bruning, P.; Garrido, I.; Détrée, C.; Figueroa, A.; Astorga, M.; Navarro, J.; Johnson, L.; Carlton, J.; et al. First mussel settlement observed in Antarctica reveals the potential for future invasions. *Sci. Rep.* **2020**, *10*, 5552. [CrossRef] [PubMed]

22. Peterson, B.J.; Fry, B. Stable isotopes in ecosystem studies. *Ann. Rev. Ecol. Syst* **1987**, *18*, 293–320. [CrossRef]

23. Hobson, K.A.; Clark, R.G. Assessing avian diets using stable isotopes II: Factors influencing diet-tissue fractionation. *Condor* **1992**, *94*, 189–197. [CrossRef]

24. Duffy, D.; Jackson, S. Diet studies of seabirds: A review of methods. *Col. Waterb.* **1986**, *9*, 1–17. [CrossRef]

25. DeNiro, M.; Epstein, S. Influence of diet on the distribution of carbon isotopes in animals. *Geoch. Cosmochim. Act.* **1978**, *42*, 495–506. [CrossRef]

26. Bearhop, S.; Adams, C.E.; Waldron, S.; Fuller, R.A.; Macleod, H. Determining trophic niche width: A novel approach using stable isotope analysis. *J. Anim. Ecol.* **2004**, *73*, 1007–1012. [CrossRef]

27. Fry, B. Using stable isotope tracers. In *Stable Isotope Ecology*; Springer: New York, NY, USA, 2006. [CrossRef]

28. Palma, A.T.; Pardo, L.M.; Veas, R.I.; Cartes, C.; Silva, M.; Manriquez, K.; Diaz, A.; Muñoz, C.; Ojeda, F.P. Coastal brachyuran decapods: Settlement and recruitment under contrasting coastal geometry conditions. *Mar. Ecol. Prog. Ser.* **2006**, *316*, 139–153. [CrossRef]

29. Brun, E. Food and feeding habits of *Luidia ciliaris* Echinodermata: Asteroidea. *J. Mar. Biol. Ass. UK* **1972**, *52*, 225–236. [CrossRef]

30. Fratt, D.B.; Dearborn, J.H. Feeding biology of the Antarctic brittle star *Ophionotus victoriae* (Echinodermata: Ophiuroidea). *Polar Biol.* **1984**, *3*, 127–139. [CrossRef]

31. Dearborn, J.H.; Ferrari, F.D.; Edwards, K.C. Can pelagic aggregations cause benthic satiation? Feeding biology of the Antarctic brittle star *Astrotoma agassizzi* (Echinodermata: Ophiuroidea). Biology Antarctic Seas XVII. *Antarct. Res. Ser.* **1986**, *44*, 1–28. [CrossRef]

32. Hynes, H.B.N. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* **1950**, *19*, 36–58. [CrossRef]

33. Folch, J.; Lees, M.; Stanley, G.H.S. A simple method for the isolation and purification of total lipids from animal tissues. *J. Biol. Chem.* **1957**, *226*, 497–509. [CrossRef]

34. Ogawa, N.; Ogura, N. Dynamics of particulate organic matter in the Tamagawa Estuary and inner Tokyo Bay. *Estuar. Coast. Shelf Sci.* **1997**, *44*, 263–273. [CrossRef]

35. Lorrain, A.; Savoye, N.; Chauvaud, L.; Paulet, Y.-M.; Naulet, N. Decarbonation and preservation method for the analysis of organic C and N contents and stable isotope ratios of low-carbonated suspended particulate material. *Anal. Chim. Acta* **2003**, *491*, 125–133. [CrossRef]

36. Bunn, S.E.; Loneragan, N.R.; Kempster, M.A. Effects of acid washing on stable isotope ratios of C and N in penaeid shrimp and seagrass: Implications for food-web studies using multiple stable isotopes. *Limnol. Oceanogr.* **1995**, *40*, 622–625. [CrossRef]

37. Bonde, A.L.; Jones, I.L. A practical introduction to stable-isotope analysis for seabird biologists: Approaches, cautions and caveats. *Mar. Ornithol.* **2009**, *37*, 183–188.

38. Post, D. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* **2002**, *83*, 703–718. [CrossRef]

39. Iken, K.; Bluhm, B.; Dunton, K. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2010**, *57*, 71–85. [CrossRef]

40. McMeans, B.C.; Rooney, N.; Michel, T.A.; Fisk, A.T. Food web structure of a coastal Arctic marine ecosystem and implications for stability. *Mar. Ecol. Prog. Ser.* **2013**, *482*, 17–28. [CrossRef]

41. Quezada, R.C.; Jackson, A.; Hayden, B.; Kahilainen, K.; Lopes, C.; Harrod, C. tRophicPosition, an R package for the Bayesian estimation of trophic position from consumer stable isotope ratios. *Met. Ecol. Evol.* **2018**, *9*, 1592–1599. [CrossRef]

42. Vander Zanden, M.J.; Rasmussen, J.B. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation; implications for aquatic food web studies. *Limnol. Oceanogr.* **2001**, *46*, 2061–2066. [CrossRef]

43. Clarke, K.R.; Somerfield, P.J.; Chapman, M.G. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *J. Exp. Mar. Biol. Ecol.* **2006**, *330*, 55–80. [CrossRef]

44. Clarke, K.R.; Gorley, R.N. *PRIMER v7: User Manual/Tutorial Plymouth*; PRIMER-E: Ivybridge, UK, 2015.

45. Jackson, A.L.; Inger, R.; Parnell, A.C.; Bearhop, S. Comparing isotopic niche widths among and within communities: SIBER— Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* **2011**, *80*, 595–602. [CrossRef]

46. Layman, C.A.; Arrington, A.; Montaña, C.G.; Post, D.M. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* **2007**, *88*, 42–48. [CrossRef]

47. Swanson, H.K.; Lysy, M.; Power, M.; Stasko, A.D.; Johnson, J.D.; Reist, J.D. A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology* **2015**, *96*, 318–324. [CrossRef]

48. Meyer, R.; Lochner, S.; Melzer, R.R. Decapoda—Crabs, shrimps & lobsters. In *Marine Benthic Fauna of Chilean Patagonia*; Häussermann, V., Försterra, G., Eds.; Nature in Focus: Santiago de Chile, Chile, 2009; p. 1000.

49. Borisov, R.R.; Epelbaum, A.B.; Kryakhova, N.V.; Tertitskaya, A.G.; Kovatcheva, N.P. Cannibalistic behavior in red king crabs reared under artificial conditions. *Russ. J. Mar. Biol.* **2007**, *33*, 227–231. [CrossRef]

50. Daly, B.; Long, W.C. Inter-cohort cannibalism of early benthic phase blue king crabs (*Paralithodes platypus*): Alternate foraging strategies in different habitats lead to different functional responses. *PLoS ONE* **2014**, *9*, e88694. [CrossRef]

51. Sotelano, M.P.; Lovrich, G.A.; Romero, M.C.; Tapella, F. Cannibalism during intermolt period in early stages of the Southern King Crab *Lithodes santolla* (Molina 1872): Effect of stage and predator-prey proportions. *J. Exp. Mar. Biol. Ecol.* **2012**, *411*, 52–58. [CrossRef]

52. Comoglio, L.I.; Amin, O.A. Feeding habits of the false southern king crab *Paralomis granulosa* (Lithodidae) in the Beagle Channel, Tierra del Fuego, Argentina. *Sci. Mar.* **1999**, *63*, 361–366. [CrossRef]

53. Takeshita, F.; Tamura, R. Optimal stocking density of juvenile red king crabs *Paralithodes camtschaticus* under cannibalism consideration. *Fish. Sci.* **2014**, *80*, 775–783. [CrossRef]

54. Moksnes, P.-O. Self-regulating mechanisms in cannibalistic populations of juvenile shore crabs *Carcinus maenas*. *Ecology* **2004**, *85*, 1343–1354. Available online: www.jstor.org/stable/3450176 (accessed on 2 October 2021). [CrossRef]

55. Pardo, L.M.; Palma, A.T.; Prieto, C.; Sepulveda, P.; Valdivia, I.; Ojeda, F.P. Processes regulating early post-settlement habitat use in a subtidal assemblage of brachyuran decapods. *J. Exp. Mar. Biol. Ecol.* **2007**, *344*, 10–22. [CrossRef]

56. Stoner, A.W. Habitat-mediated survival of newly settled red king crab in the presence of a predatory fish: Role of habitat complexity and heterogeneity. *J. Exp. Mar. Biol. Ecol.* **2009**, *382*, 54–60. [CrossRef]

57. Pirtle, J.L.; Eckert, G.L.; Stoner, A.W. Habitat structure influences the survival and predator-prey interactions of early juvenile red king crab *Paralithodes camtschaticus*. *Mar. Ecol. Prog. Ser.* **2012**, *465*, 169–184. [CrossRef]

58. Long, W.C.; Whitefleet-Smith, L. Cannibalism in red king crab: Habitat, ontogeny, and the predator functional response. *J. Exp. Mar. Biol. Ecol.* **2013**, *449*, 142–148. [CrossRef]

59. Tapella, F.; Sotelano, M.P.; Romero, M.C.; Lovrich, G.A. Experimental natural substrate preference of southern king crab *Lithodes santolla* larvae. *J. Exp. Mar. Biol. Ecol.* **2012**, *411*, 70–77. [CrossRef]

60. Beck, M.W.; Heck, K.L.; Able, K.W.; Childers, D.L.; Eggleston, D.B.; Gillanders, B.M.; Halpern, B.; Hays, C.G.; Hoshino, K.; Minello, T.J. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. *Bioscience* **2001**, *51*, 633–641.

61. Krumhansl, K.A.; Okamoto, D.K.; Rassweiler, A.; Novak, M.; Bolton, J.J.; Cavanaugh, K.C.; Connell, S.D.; Johnson, C.R.; Konar, B.; Ling, S.D.; et al. Global patterns of kelp forest change over the past half-century. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, 13785. [CrossRef]

62. Newsome, S.D.; del Rio, C.M.; Bearhop, S.; Phillips, D. A niche for isotopic ecology. *Front. Ecol. Envirom.* **2007**, *5*, 429–436. [CrossRef]

63. Saborowski, R.; Thatje, S.; Calcagno, J.A.; Lovrich, G.A.; Anger, K. Digestive enzymes in the ontogenetic stages of the southern king crab, *Lithodes santolla*. *Mar. Biol.* **2006**, *149*, 865–873. [CrossRef]

64. Comoglio, L.I.; Lovrich, G.A.; Vinuesa, J.H. Feeding habits of southern king crab, Lithodes santolla, and false king crab, Paralomis granulosa in the Beagle Channel. In Proceedings of the International Symposium on King and Tanner Crabs, Anchorage, AK, USA, 28–30 November 1989; Alaska Sea Grant College Program Report: Anchorage, AK, USA, 1990; Volume 90, pp. 315–325.

65. Fuhrmann, M.; Pedersen, T.; Nilssen, E. Trophic niche of the invasive red king crab *Paralithodes camtschaticus* in a benthic food web. *Mar. Ecol. Prog. Ser.* **2017**, *565*, 113–129. [CrossRef]

66. Divine, L.M.; Bluhm, B.A.; Mueter, F.J.; Iken, K. Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using.stomach contents and δ13C and δ15N stable isotopes. *Deep-Sea Res. II* **2017**, *135*, 124–136. [CrossRef]

67. Di Salvatore, P.; Sacristán, H.J.; Florentín, O.; Varisco, M.; Lovrich, G.A. Female reproductive output and potential recruitment of three fished southern king crab stocks from the Southern Atlantic Ocean. *ICES J. Mar. Sci.* **2021**, *78*, 2628–2692. [CrossRef]

68. Molinet, C.; Olguín, A.; Gebauer, P.; Díaz, P.A.; Díaz, M.; Matamala, T.; Mora, P.; Paschke, K. Upswing and expansion of the southern king crab (*Lithodes santolla*) fishery in Northwest Patagonia: Drivers, trends and opportunities for management. *Reg. Stud. Mar. Sci.* **2020**, *34*, 101073. [CrossRef]

69. Orensanz, J.M.; Ernst, B.; Armstrong, D.; Parma, A.M. Detecting early warnings of recruitment overfishing in male- only crab fisheries: An example from the snow crab fishery. In *Fisheries Assessment and Management in Data-Limited Situations*; Kruse, G.H., Gallucc, V.F., Hay, D.E., Perry, R.I., Peterman, R.M., Shirley, T.C., et al., Eds.; Alaska Sea Grant College Program: Fairbanks, AK, USA, 2005; pp. 267–287.

70. Pardo, L.M.; Riveros, M.P.; Fuentes, J.P.; Pinochet, R.; Cárdenas, C.; Sainte-Marie, B. High fishing intensity reduces females' sperm reserve and brood fecundity in a eubrachyuran crab subject to sex- and size-biased harvest. *ICES J. Mar. Sci.* **2017**, *74*, 2459–2469. [CrossRef]

71. Stevens, B.G. Is it possible to enhance king crab populations in Alaska? In *Alaska Crab Stock Enhancement and Rehabilitation: Workshop Proceedings, Kodiak, AK, USA, 14–16 March 2006*; Alaska Sea Grant College Program; University of Alaska Fairbanks: Fairbanks, AK, USA, 2006; pp. 5–8.