Marine and Fishery Sciences 39 (3): 467-483 (2026)
https://doi.org/10.47193/mafis.3932026010707

ORIGINAL RESEARCH

Energy allocation and condition of adult female *Lithodes santolla* before molting and reproduction in central Patagonia

Neonila N. Kulisz[1, *], Carla A. Firpo[1], Karina A. Rodrigues[1], H. Pablo Lértora[1], Marta Estrada[1], A. Cecilia Mauna[1] and Gustavo J. Macchi[1, 2]

[1]Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo Nº 1, Escollera Norte, B7602HSA - Mar del Plata, Argentina. [2]Instituto de Investigaciones Marinas y Costeras (IIMyC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Mar del Plata (UNMdP), Juan B. Justo 2550, B7608FBY - Mar del Plata, Argentina.
ORCID *Neonila N. Kulisz* https://orcid.org/0009-0002-5564-4463, *Carla A. Firpo* https://orcid.org/0000-0002-9983-3111, *Karina A. Rodrigues* https://orcid.org/0000-0003-4407-3474, *H. Pablo Lértora* https://orcid.org/0000-0001-5651-9344, *A. Cecilia Mauna* https://orcid.org/0000-0003-3557-4330, *Gustavo J. Macchi* https://orcid.org/0000-0003-1821-5491

ABSTRACT. *Lithodes santolla* is a key benthic resource in the Patagonian region of South America, sustaining major fisheries in Chile and Argentina. Assessing population condition is essential, as it influences recruitment dynamics and informs sustainable management. This study evaluated energy allocation and physiological condition in adult females during the pre-reproductive period. Samples were collected during the austral spring of 2024 from the central Patagonian sector (43° 30′ S-48° 00′ S). Proximate composition (moisture, protein, and lipid contents) and energy density were determined in muscle, hepatopancreas, and ovary across three management zones: northern national waters (NN), southern national waters (SN) of 46° S, and San Jorge Gulf (GSJ). The ovary exhibited the highest energy density, followed by the hepatopancreas, while muscle showed lower values. Most females were in ovarian regression or post-ovigerous stages, indicating entry into a new molt-reproduction cycle. Consistent with this condition, the ovary exhibited high protein and lipid contents and showed no significant spatial variation. In contrast, females from SN sector tended to exhibit higher hepatopancreatic protein content, whereas females from NN sector showed higher muscle moisture and lower protein content. These findings provide new insights into tissue-level energy allocation patterns in female *L. santolla* and highlight the need for future studies encompassing additional stages of the reproductive cycle, which could contribute to a better understanding of temporal variation in energy allocation and reproductive physiology in the central Patagonian sector.

Key words: Lithodid crab, biochemical composition, energy density, hepatopancreas, ovary, muscle.

∗Correspondence:
nkulisz@inidep.edu.ar

Received: 19 March 2026
Accepted: 16 June 2026

ISSN 2683-7595 (print)
ISSN 2683-7951 (online)

https://ojs.inidep.edu.ar

Journal of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP)

This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License

Reservas energéticas y condición de hembras adultas de *Lithodes santolla* antes de la muda y la reproducción en el sector patagónico central

RESUMEN. *Lithodes santolla* es un recurso bentónico clave en la región patagónica Sudamericana, sustentando importantes pesquerías en Chile y Argentina. Evaluar el estado poblacional es esencial, ya que influye en la dinámica del reclutamiento y orienta el manejo sostenible. Este estudio analiza la asignación de energía y la condición fisiológica en hembras adultas previo a la temporada reproductiva. Las muestras se recolectaron en la primavera austral de 2024 en el sector patagónico central (43° 30′ S-48° 00′ S). Se determinó la composición proximal (humedad, proteínas y lípidos) y la densidad energética (DE) en músculo, hepatopáncreas y ovario en tres zonas de manejo: jurisdicción nacional al norte (NN), al sur (SN) de 46° S y el Golfo San Jorge (GSJ). El ovario presentó mayor DE, seguido por el hepatopáncreas, mientras que el músculo mostró valores más bajos. La mayoría de las hembras se encontraron en regresión ovárica o posovígeras, indicativo de un nuevo ciclo mu-

da-reproducción. En concordancia con esta condición fisiológica, el ovario presentó altos contenidos de proteínas y lípidos y no mostró variación espacial significativa. En contraste, las hembras del sector SN presentaron una tendencia mayor en el contenido proteico en el hepatopáncreas, mientras que las hembras del sector NN mostraron mayor contenido de humedad y menor contenido proteico en el músculo. Estos hallazgos aportan nuevos conocimientos sobre los patrones de asignación de energía en hembras de *L. santolla* y destacan la importancia de realizar estudios futuros que evalúen hembras del sector patagónico central durante otras etapas del ciclo reproductivo, lo que podría contribuir a una mejor comprensión de las variaciones temporales en la asignación de energía y la fisiología reproductiva de la especie en el sector patagónico central.

Palabras clave: Cangrejos litoideos, composición bioquímica, densidad de energía, hepatopáncreas, ovario, músculo.

INTRODUCTION

The southern king crab *Lithodes santolla* is one of the most valuable benthic crustaceans in the southern tip of South America and sustains important commercial fisheries in both Chile and Argentina. It is rank second in catch volume among exploited crustaceans in the Argentine Sea, after shrimp (SAGPYA 2025). Within the Argentine king crab fishery, four independent stocks have been identified: (1) Beagle Channel; (2) central Patagonian sector (CPS), which includes the San Jorge Gulf and adjacent waters; (3) southern Patagonian sector (SPS); and (4) Buenos Aires sector (Allega et al. 2020). The Beagle Channel supports an artisanal fishery that has been operating since the 1950s, with historical landings of approximately 250 t per year during the 1970s; however, catches declined markedly over time (Lovrich et al. 2017). The Buenos Aires sector currently has no active fishing operations, while the industrial fishery is concentrated in the CPS, exploited since 2004, and the SPS, which has been active since 2016. Together, both stocks landed 2,068 t during the 2024-2025 season (910 t in the CPS and 1,158 t in the SPS) with a value of USD 21,400 per ton (Firpo et al. 2025; Mauna et al. 2025). Historically, the CPS has represented the main zone of fishing effort concentration and in general the highest catch volumes (Wyngaard et al. 2016).

The king crab inhabits cold waters between 4 °C and 12 °C, at depths ranging from the intertidal zone to 700 m. It has an annual reproductive cycle closely linked to molting (Firpo et al. 2016). Juvenile males and females may molt several times per year; however, after reaching sexual maturity, females molt once annually in association with the reproductive cycle, whereas adult males also molt annually but during a different season (Firpo 2020). In the CPS, males molt mainly between May and July, and females between November and December. These events coincide with the mating period, during which a larger hard-shell male mate with a female that has already spawned and is close to molting. Copulation occurs after the female molts, and the male protects her during subsequent days. A new batch of eggs is then oviposited and fertilized, remaining attached to the pleopodal setae until hatching approximately 10 months later (Wyngaard et al. 2016; Firpo 2020).

In the context of reproductive studies of this species, determining the maternal condition is of great importance. This term refers to the overall health status of females, including their nutritional and energetic reserves (Peig and Green 2009; Schulte-Hostedde et al. 2005). Various approaches have been used to assess this condition, including morphometric indices (such as length-weight ratio or the K index), physiological indices (hepatosomatic index, HSI), and biochemical analyses (measuring lipids, proteins, and other components in various tissues). Biochemical evaluation is particularly accurate, as it allows for the estimation of available energy in each tissue, providing a better understanding of energy dynamics (Rätz and Lloret 2003; Hidalgo et al. 2008; Kulisz et al. 2025).

Energy reserves acquired through feeding are fundamental to physiological processes such as maintenance, somatic growth, and reproduction. In several species, population fecundity has been closely linked to the nutritional condition of females (Calow 1985; Sibly and Calow 1986; Schulte-Hostedde et al. 2005). Maternal condition influences energy allocation to reproduction, determining the quantity and quality of reserves transferred to the eggs during ovarian development. As these reserves constitute the only nutritional link between female king crabs and their offspring, they play a fundamental role in embryo quality, larval viability, and ultimately recruitment success (Sacristán et al. 2023). In *Lithodes santolla*, due to the commercial importance of males, biochemical indices have been used to evaluate muscle condition, in both raw and cooked tissue samples (Cocito et al. 2024), as well as in the hepatopancreas of captive males subjected to starvation (Comoglio et al. 2008). For females, egg production and quality have been assessed in the CPS (Militelli et al. 2019). Additionally, energy dynamics throughout a reproductive cycle have been analyzed in the ovaries of females from the Beagle Channel (Sacristán et al. 2023). However, the energy allocation of the organs involved in reproduction and molting processes have not yet been comprehensively evaluated, particularly in females from heavily exploited populations in the CPS.

In this context, understanding the status of the population under exploitation pressure is essential for proper assessment and sustainable management of the resource. The southern king crab fishery in the CPS is managed and monitored according to administrative borders. These boundaries do not necessarily reflect the biological organization of the population. Spatial heterogeneity in environmental conditions, benthic community structure, and trophic availability could generate areas of greater biological relevance (Firpo 2020; Gaitán et al. 2022), promoting the aggregation of individuals with distinct physiological and energetic characteristics. Assessing whether the observed differences among management zones reflect underlying biological processes is essential for achieving a more robust ecological interpretation of biochemical indicators and for strengthening spatially explicit management approaches. Within this framework, the present study aimed to evaluate the energy allocation associated with the maternal condition of adult female king crabs by determining the proximate composition of the pereopod muscle, hepatopancreas, and ovary before the molting and reproductive processes in the CPS.

MATERIALS AND METHODS

Sample collection

Samples were collected during a research survey conducted under the Benthic Crustacean Fisheries Program of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). The survey was carried out aboard the research vessel 'Víctor Angelescu' in Patagonian waters, between 43° 30′ S and 48° 00′ S, during the austral spring of 2024 (October and November). Sampling stations were spatially clustered within each management zone, reflecting the operational design of the research survey (Figure 1). Biological samples were obtained from hauls 2, 3, and 5 in national waters north of 46° S (NN); hauls 23 and 25 in national waters south of 46° S (SN); and hauls 8, 9, and 16 in the San Jorge Gulf (GSJ). While sampling effort was more evenly distributed between the northern and southern national waters, the GSJ was represented by fewer stations, which should be considered when interpreting spatial patterns.

Adult female king crabs were collected using baited traps following the methodology described by Lértora et al. (2025), in management areas comprising the CPS: NN, SN, and the jurisdictional waters of Chubut and Santa Cruz, all within the GSJ. A total of 70 adult females were selected from those captured in the traps during the survey. All individ-

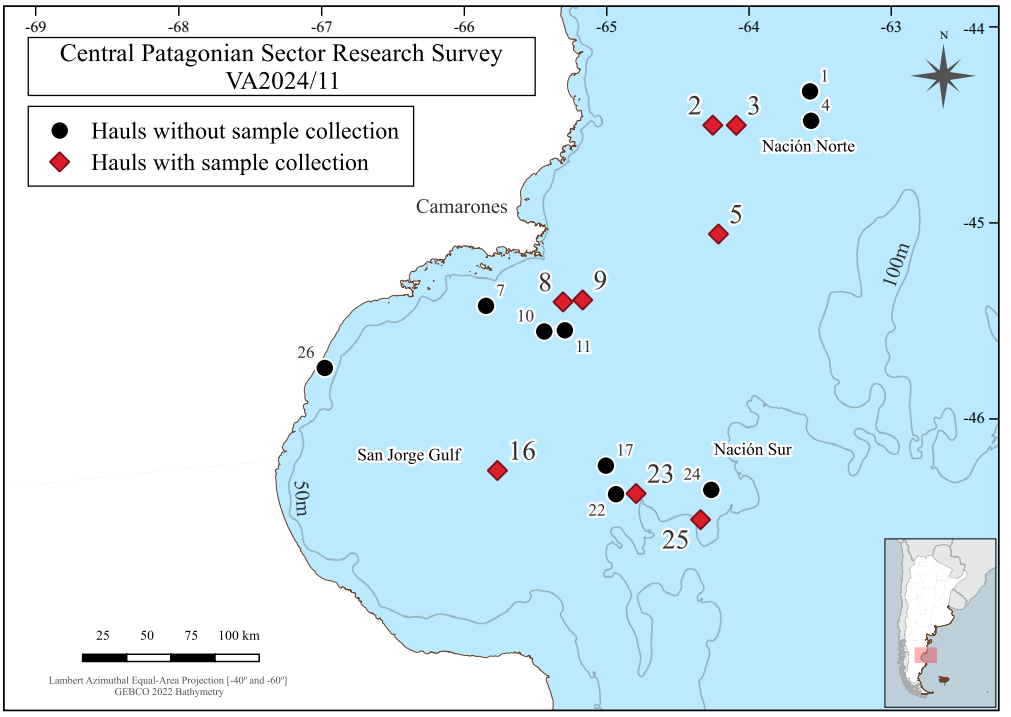


Figure 1. Map of the central Patagonian sector showing the geographic location of trap sets. Red diamonds indicate sets in which samples of *Lithodes santolla* females were collected for studies of condition, with identification numbers, corresponding to research survey VA2024/11.

uals were morphologically mature and exceeded the estimated size at first maturity (62.7 mm CL) reported for female *L. santolla* in the CPS (Firpo et al. 2017). In addition, exoskeleton condition (EC), reproductive condition (RC), and egg mass percentage (%E) were recorded following the criteria established by Mauna et al. (2022).

The EC was assessed based on carapace hardness, leg flexibility, and coxal wear as indicators of the time elapsed since the last molt. Individuals were classified into four categories: (0) recently molted, (1) flexible, (2) new and (3) intermediate. In adult females from the CPS, exoskeleton condition does not exceed category 3 because molting occurs annually and is tightly coupled with the reproductive cycle. The RC was classified into four categories: (1) females without eggs; (2) females with hatching egg masses; (3) females carrying remnants of egg masses, including few eggs with visible eyes and setae on the appendages; and (4) females without eggs but with setae on the abdominal appendages. The egg mass percentage (%E), equivalent to the clutch fullness index (CFI), was estimated visually as the proportion of the brood chamber occupied by eggs relative to the total cavity formed beneath the abdomen. Six categories were used: 0%, 25% (1-25%), 50% (26-50%), 75% (51-75%), 100% (> 75%), and > 100% (cavity full, with eggs extending beyond the abdominal cavity (Firpo et al. 2023).

Due to the high concentration of endogenous enzymes in lithodid crabs, tissues degrade post-mortem rapidly (Cocito et al. 2024). Therefore, individuals were preserved at -20 °C for 20 min immediately after capture and subsequently dissected to extract the target tissues. Muscle (without exoskeleton), ovary, and hepatopancreas were dissected from each specimen sampled and preserved frozen at -20 °C in aluminum foil envelopes until

their analysis in the laboratory. The selected tissues represent functionally distinct compartments: somatic muscle involved in locomotion, the hepatopancreas as the main metabolic and storage organ, and the ovary as the reproductive organ where energy is ultimately allocated (Sánchez et al. 2006) (Figure 2).

Biochemical composition and energy density

Samples were analyzed to determine moisture, protein, and lipid contents (expressed as a percentage of the tissue wet weight). Moisture content was determined by drying the samples for 24 h at 105 °C and weighing them at room temperature (AOAC 1995; moisture content: AOAC 925.10). Lipid content was determined following the extraction method of Folch et al. (1957) using chloroform: methanol solution (2:1 v/v) and gravimetric quantification. Protein content was determined from a tissue homogenate by constructing a standard curve using bovine serum albumin (BSA) at a concentration of 1 mg ml^{-1} and following the protocol described by Lowry et al. (1951). Energy density (ED, kJ g^{-1}) was estimated for the muscle, ovary, and hepatopancreas of each female as the sum of energy contributions from lipids and proteins, calculated by multiplying their contents (mg g^{-1} wet weight) by their respective energy equivalents (39.5 kJ g^{-1} for lipids and 23.6 kJ g^{-1} for proteins; Kleiber 1975). Carbohydrate content was not measured as it is generally low in marine species and contributes negligibly to total energy content (Anthony et al. 2000; Eder and Lewis 2005; Spitz et al. 2010). However, this assumption may not always hold in crustaceans, particularly during molting or periods of reduced feeding activity (Chang 1995).

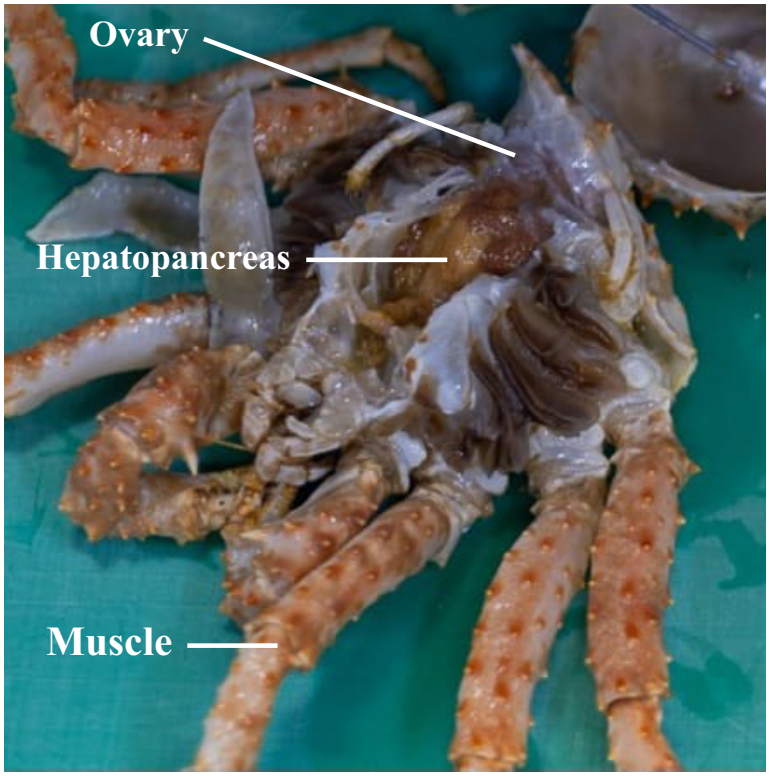


Figure 2. Dissected female southern king crab *Lithodes santolla* showing muscle, hepatopancreas, and ovary.

Statistical analysis

Linear regression analyses were used to assess the relationships among biochemical composition variables within each tissue or organ (muscle, ovary, and hepatopancreas). Differences in moisture, lipids and protein content, and energy density among zones were then statistically evaluated separately for each tissue using Kruskal-Wallis tests, followed by Dunn's multiple comparison test. Each tissue was analyzed separately by zone. These nonparametric methods were selected because the data did not meet the assumptions of normality or homogeneity of variance. Additionally, differences in carapace length (CL) among zones were evaluated using a one-way ANOVA followed by Tukey's multiple comparison test. All statistical analyses were performed using GraphPad Prism 8, with a significance level of $p = 0.05$.

RESULTS

To provide physiological context for the interpretation of biochemical composition and energy allocation, the external and reproductive condition of female *L. santolla* was first assessed. Females collected from offshore waters of the CPS during the spring exhibited hard exoskeletons and minimal wear at the coxae. Largest individuals were recorded in the NN sector where carapace length was significantly higher than in GSJ and SN (Tukey's test, $p < 0.05$) than in the other sectors (Table 1). In terms of reproductive condition, post-ovigerous females (RC4) predominated during this season in both the NN and GSJ areas (Table 1). Most females were classified as being in regression or post-ovigerous reproductive stages, suggesting that they were approaching the premating molt. This interpretation was reinforced by the presence of a second gelatinous carapace in most individuals, a well-known indicator of an imminent molt during the reproductive cycle of the species.

The analysis of proximate composition in samples of king crabs provided descriptive statistics of moisture, protein, and lipid percentages among sampling zones (Table 2). Considering all samples together, muscle tissue was characterized by a predominance of moisture (83.68%), followed by protein (17.13%) and lipids (0.89%), the latter representing the lowest value recorded among the three tissues and organs evaluated. In the hepatopancreas, moisture was also the main component

Table 1. Sample size (N), mean carapace length in millimeters (CL) (different letters indicate significant differences according to Tukey's test ($p < 0.05$)), and percentage of specimens with different exoskeleton condition (EC) and reproductive condition (RC), by sampling area. Areas include national waters north of 46° S (NN), national waters south of 46° S (SN), and San Jorge Gulf (GSJ). EC 2: new exoskeleton; EC 3: intermediate exoskeleton with signs of coxal wear. RC 1: without eggs, 3: spawning, 4: post-spawning (Mauna et al. 2022).

	Class	NN	SN	GSJ
N		20	21	29
CL		96.95[a]	84.33[b]	88.82[b]
EC	2	0%	29%	57%
	3	100%	71%	43%
RC	1	0%	14%	0%
	3	15%	38%	0%
	4	85%	48%	100%

Table 2. Minimum, maximum, mean, and standard deviation values of the proximate composition of different tissues (% wet weight) of adult female southern king crab, by geographic zones (national waters north of 46° S –NN, national waters south of 46° S –SN, and San Jorge Gulf –GSJ).

		Muscle			Hepatopancreas			Ovary		
Zones		Moisture	Proteins	Lipids	Moisture	Proteins	Lipids	Moisture	Proteins	Lipids
NN	Mean	85.38	14.81	0.83	71.88	17.90	6.86	47.79	34.76	20.16
	SD	2.65	3.46	0.52	4.56	2.56	3.21	4.87	2.82	3.21
	Max.	89.41	20.99	2.77	84.26	23.38	11.01	53.96	42.52	25.18
	Min.	81.10	8.53	0.45	59.21	13.13	3.76	42.53	24.51	13.13
SN	Mean	83.28	19.20	0.98	70.54	19.72	7.70	47.59	34.44	20.11
	SD	1.25	2.58	0.30	2.53	2.46	2.77	7.21	5.42	4.63
	Max.	85.53	22.60	1.99	76.01	23.87	11.67	69.33	40.45	23.91
	Min.	81.35	15.24	0.59	66.08	14.40	2.87	43.32	20.79	6.73
GSJ	Mean	82.80	17.24	0.87	70.78	17.46	7.19	45.91	35.65	21.15
	SD	1.85	1.93	0.22	3.08	2.64	3.38	3.00	4.36	2.59
	Max.	88.36	20.58	1.25	76.03	22.47	16.59	53.67	47.22	24.81
	Min.	79.15	13.46	0.40	64.36	12.82	2.66	41.98	26.32	14.16
Mean		83.68	17.13	0.89	71.02	18.26	7.25	46.95	35.03	20.55

(71.02%), followed by protein (18.26%) and lipids (7.25%). In contrast, the ovary exhibited the lowest moisture content (46.95%) and the highest proportions of protein and lipids (35.03% and 20.55%, respectively) compared with the other tissues and organs analyzed allowing comparison among groups. In addition, proximate composition analysis revealed a negative relationship between moisture and lipid content across all tissues, with the strongest associations observed in the ovary ($R^2 = 0.61$) and hepatopancreas ($R^2 = 0.48$). Similarly, linear regression analysis showed a significant negative relationship between moisture and protein content in both muscle ($R^2 = 0.42$) and ovary ($R^2 = 0.29$) ($p < 0.05$), whereas no significant association was detected in the hepatopancreas. Overall, these results indicated that increases in the concentration of organic compounds were associated with a reduction in tissue water content, particularly in the ovary and muscle (Figure 3).

Regarding spatial comparisons, the proximate composition analysis revealed that muscle moisture content in female king crabs was significantly higher from the NN than in the GSJ and SN sectors, while no significant differences were detected between the latter two zones (Dunn's test, $p < 0.05$) (Table 2). Muscle protein and lipid contents also showed spatial variation among zones (Dunn's test, $p < 0.05$). In both cases, females from the NN sector exhibited significantly lower values than those from the SN sector, whereas females from GSJ showed intermediate values that did not differ significantly from either zone (Figure 4). These spatial patterns in muscle composition provided a first indication of variability in tissue-level energetic traits among zones, which were further examined in metabolically active organs.

In the hepatopancreas, protein content was generally higher than lipid (Table 2). Its biochemical composition showed significant differences among zones only in protein content (Figure 5). Highest values of this component were recorded in the SN

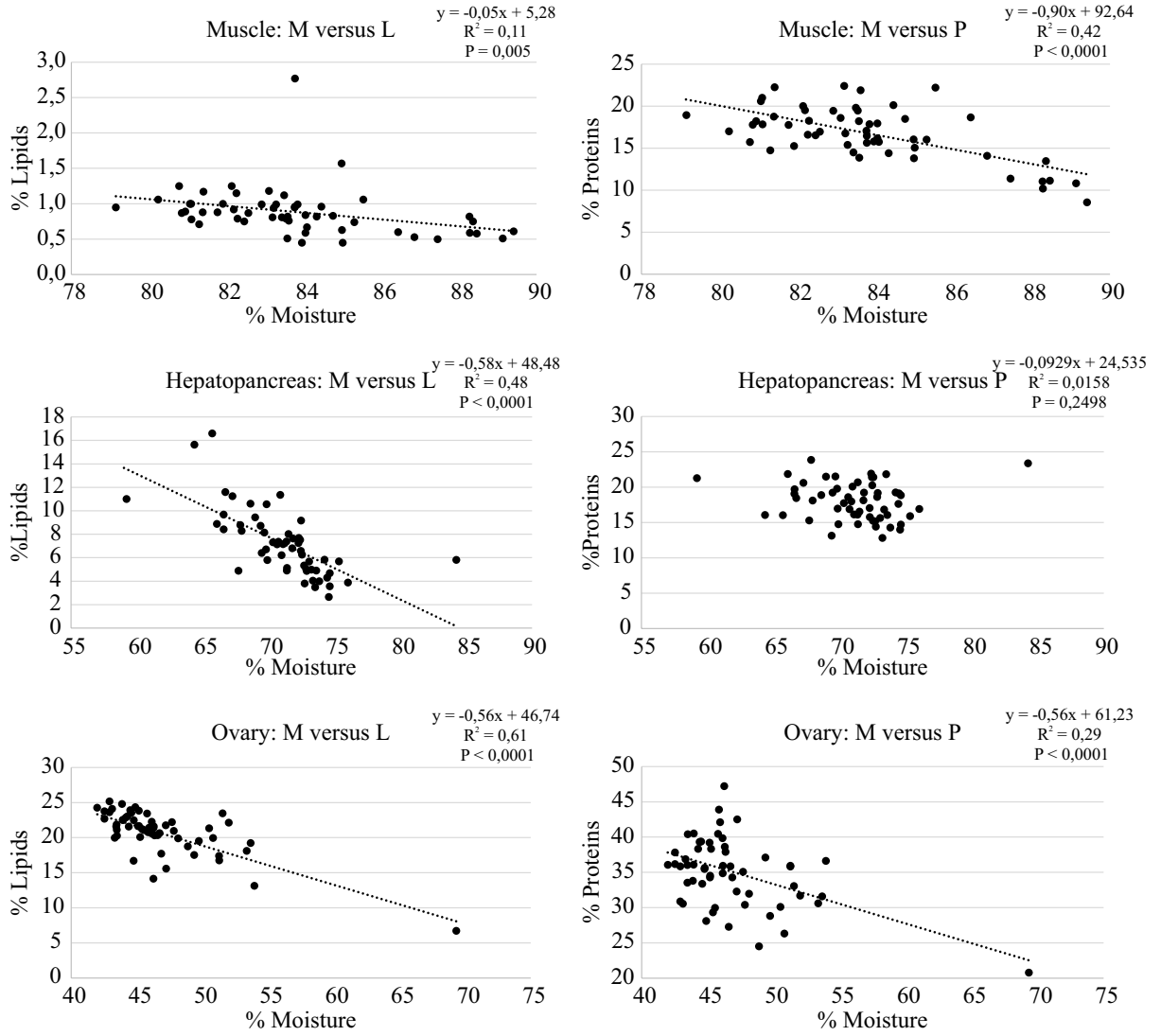


Figure 3. Relationships between moisture (M) content and lipid (L) and protein (P) contents (% wet weight) in muscle, hepatopancreas, and ovary of *Lithodes santolla* females, based on linear regression analyses (R^2 and $p < 0.05$).

sector. Multiple comparisons indicated significant differences between SN and GSJ, whereas NN exhibited intermediate values and did not differ significantly from either of the other two zones (Dunn's test, $p < 0.05$). Unlike what was observed in muscle and hepatopancreas, no significant differences were detected in the ovarian proximate composition among the zones analyzed (Dunn's test, $p > 0.05$) (Figure 6).

Regarding energy density, no significant differences were detected in the hepatopancreas and ovary among sectors (Dunn's test, $p > 0.05$). Mean energy density was 16.40 kJ $g^{-1} \pm 1.95$ in the ovary, and 7.25 kJ $g^{-1} \pm 1.40$ in the hepatopancreas (Table 2; Figure 7). In contrast, muscle energy density averaged 4.40 kJ $g^{-1} \pm 0.78$ and showed spatial variation among sectors. Females from the SN sector exhibited significantly higher values than those

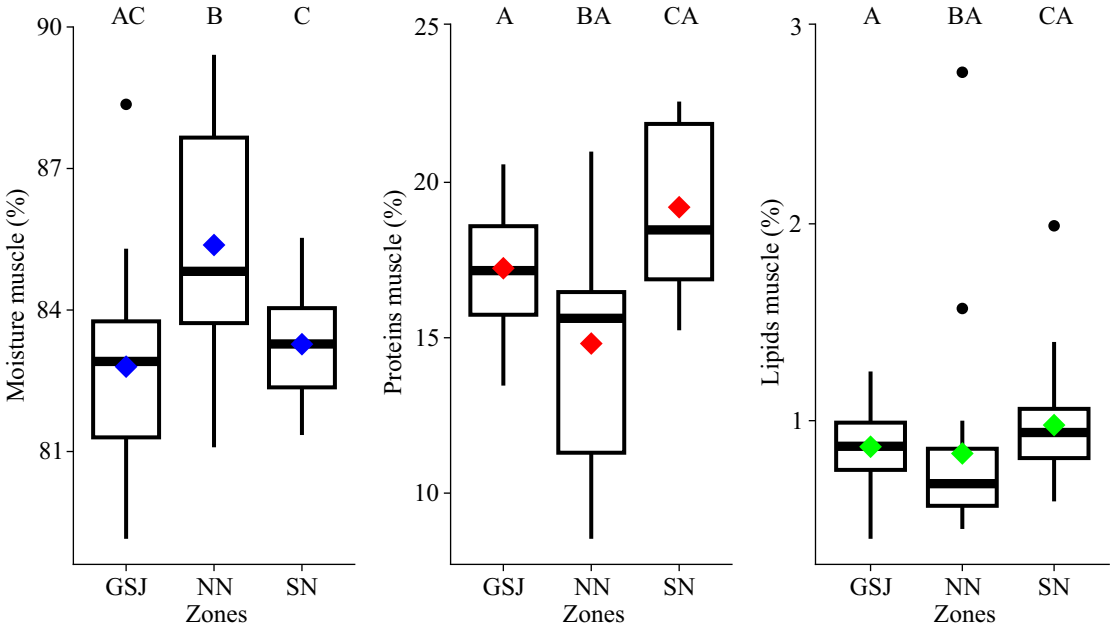


Figure 4. Moisture, protein and lipid content (% wet weight) in the muscle of *Lithodes santolla* females across different zones of the central Patagonian sector. Colored diamonds represent the mean value for each zone, and black circles indicate outlier values. Different letters denote significant differences according to Dunn's test ($p < 0.05$). GSJ: San Jorge Gulf; NN: national waters north of 46° S; SN: national waters south of 46° S.

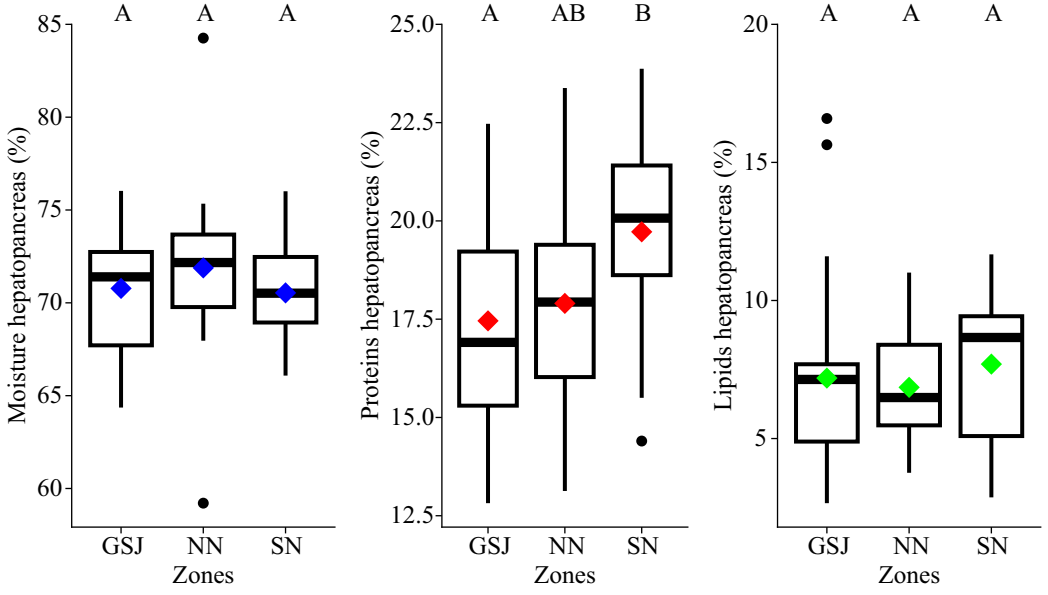


Figure 5. Moisture, protein, lipid content (% wet weight) in the hepatopancreas of *Lithodes santolla* females across different zones of the central Patagonian sector. Colored diamonds represent the mean value for each zone, and black circles indicate outlier values. Different letters denote significant differences according to Dunn's test ($p < 0.05$). GSJ: San Jorge Gulf; NN: national waters north of 46° S; SN: national waters south of 46° S.

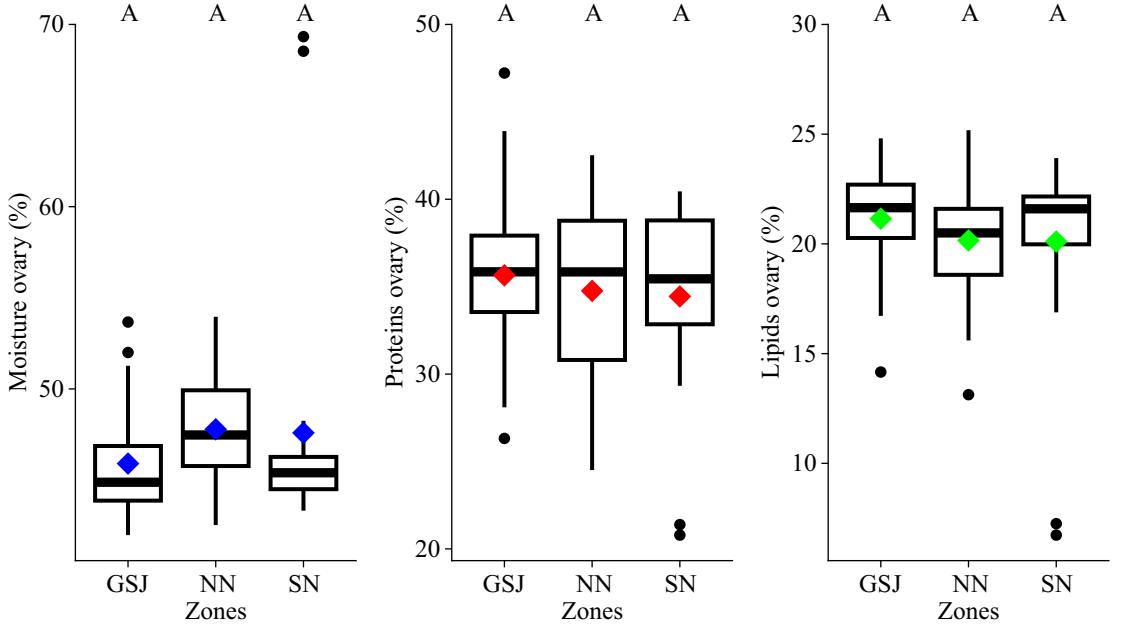


Figure 6. Moisture, protein and lipid content (% wet weight) in the ovary of *Lithodes santolla* females across different zones of the central Patagonian sector. Colored diamonds represent the mean value for each zone, and black circles indicate outlier values. Different letters denote significant differences according to Dunn's test ($p < 0.05$). GSJ: San Jorge Gulf; NN: national waters north of 46° S; SN: national waters south of 46° S.

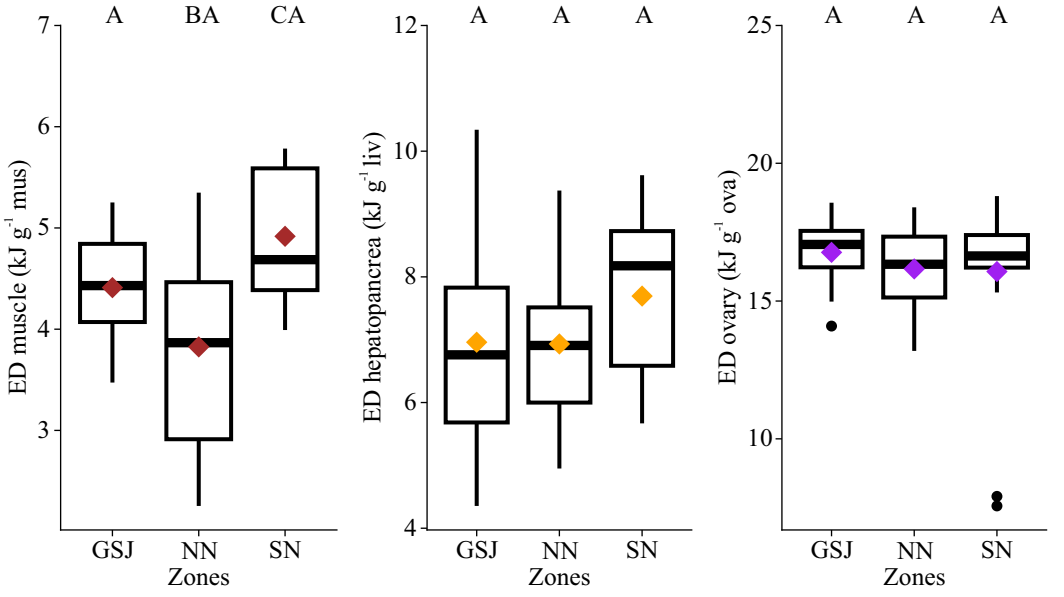


Figure 7. Energy density (ED, kJ g^{-1}) in the muscle, hepatopancreas and ovary of *Lithodes santolla* adult females across different zones of the central Patagonian sector. Colored diamonds represent the mean value for each zone, and black circles indicate outlier values. Different letters indicate significant differences according to Dunn's test ($p < 0.05$). GSJ: San Jorge Gulf; NN: national waters north of 46° S; SN: national waters south of 46° S.

from the NN sector (Dunn's test, $p < 0.05$), whereas GSJ showed intermediate values that did not differ significantly from either sector (Figure 7).

DISCUSSION

Most *L. santolla* females analyzed between October and November in the CPS were in regression or post-ovigerous stages, indicating that individuals were approaching the next molt event preceding copulation. This interpretation was supported by the presence of a second gelatinous carapace in most specimens, a characteristic associated with an imminent molt within the reproductive cycle of the species. This physiological context is particularly relevant because energy reserves and their allocation among tissues and organs vary according to ovarian development and proximity to of molting. In decapod crustaceans, offspring quality largely depends on the physiological condition of breeders, which is determined by factors such as maternal size and age, nutritional status, biochemical composition, reproductive history, and individual variability (Sacristán et al. 2023). The proximate composition of muscle, hepatopancreas, and ovary generally showed high moisture contents, followed by proteins and lipids. A negative relationship was also observed between moisture and both protein and lipid content in all analyzed tissues, indicating a decrease in water content as organic compounds increased. This pattern has been widely documented in marine organisms and supports the use of moisture as a rapid and indirect indicator of tissue energy reserves (Lambert and Dutil 2000; Dutil et al. 2003; Alonso-Fernández and Saborido-Rey 2011). The moisture, protein, and lipid values recorded in muscle were approximately 3% higher than those reported for raw meat from male king crabs collected in the GSJ during spring (Risso and Carelli 2012). Likewise, Comoglio et al. (2008) reported moisture, protein, and lipid contents of 76%, 7.33%, and 3.03%, respectively, for non-starved males from the Beagle Channel. Compared with those studies, the females analyzed here exhibited higher moisture and protein contents. These results suggest a greater accumulation of organic compounds, particularly proteins, in the analyzed females; however, differences in sex, reproductive condition, and sampling area should also be considered when interpreting these patterns. Furthermore, the low lipid content observed in muscle is characteristic of lean teleost fish and shrimp species, whose tissues generally contain less than 2% lipids (Huss 1995; Yeannes and Almandos 2003; Eder and Lewis 2005; Rodrigues et al. 2013; Leonarduzzi et al. 2014; Kulisz et al. 2025). In muscle tissue, proteins constituted the main contributor to energy density, consistent with the low lipid content recorded. Both proteins and lipids exhibited marked spatial variation, reaching their highest values in the SN sector, which was also reflected in a higher energy density of the tissue. This was the only area where females in reproductive stage RC1 were recorded, in addition to individuals in RC3 and RC4. Therefore, the greater energy reserves observed may be associated both with the reproductive structure of the sample and with spatial differences in resource availability. In this regard, Saborido-Rey and Macchi (2021) noted that individuals in early reproductive stages allocate proportionally more energy to somatic growth than to reproductive investment.

The hepatopancreas exhibited protein levels comparable to those observed in muscle, but substantially higher lipid contents. This organ constitutes the main center for digestion, absorption, and storage of energy reserves in decapod crustaceans, particularly lipids (López Greco et al. 2011; Serrano et al. 2016). The observed spatial variation was mainly associated with protein content, which was significantly higher in SN than in the GSJ, whereas the NN sector showed intermediate values. In contrast, moisture and lipid contents did not differ significantly among zones. The higher protein levels recorded in SN may be associated with differences in food availability or quality, suggesting some de-

gree of spatial heterogeneity in trophic conditions. Spatial patterns in prey availability have also been reported for the Argentine red shrimp by Souto et al. (2024), another commercially important decapod crustacean. Although benthic communities in the SN sector have not yet been characterized in detail, differences in prey composition and abundance could contribute to the variability observed in hepatopancreatic protein reserves.

Studies conducted on male *L. santolla* demonstrated that starvation induces changes in the biochemical composition of the hepatopancreas, mainly affecting protein reserves, whereas lipid content remains relatively stable (Comoglio et al. 2008). Consistent with these findings, only protein content exhibited significant spatial differences in the present study. This suggests that hepatopancreatic proteins may be more sensitive to recent variations in food availability or nutritional condition than lipid reserves. The absence of spatial differences in lipid content indicates that, despite differences in protein reserves, individuals maintained comparable energy levels during the sampling period. Feeding strategy directly influences both the quantity and quality of reserves accumulated by decapods, thereby affecting the success and duration of reproductive processes (Marciano 2022). Consequently, the differences observed in protein reserves could have implications for the energy available to support subsequent reproductive events.

The main energetic costs of reproduction are associated with vitellogenesis and embryo care (Fernández et al. 2000; Taylor and Leelapiyanart 2001; Silva et al. 2007; Oliveira et al. 2011; Simpson et al. 2015; Bert et al. 2016). In this context, the hepatopancreas plays a fundamental role as the primary source of lipids and glycogen used to meet these energetic demands (Marciano 2022). Since most females were in reproductive stages preceding molting (RC3 and RC4), a high accumulation of energy reserves in this organ was expected, as these reserves will subsequently be mobilized to the reproductive system during ovarian maturation (Sacristán et al. 2023). The ovary, in turn, exhibited high protein and lipid contents, reflecting the energetic investment allocated to reproduction. Unlike the patterns observed in muscle and hepatopancreas, no significant differences among zones were detected. This pattern is consistent with the physiological condition of females during post-ovigerous and previtellogenic phases, when the ovary reorganizes its reserves and accumulates the organic compounds required for subsequent reproductive events. Similar results were reported by Sacristán et al. (2023) for female *L. santolla* from the Beagle Channel during the same season, relating elevated protein and lipid levels to post-spawning ovarian reorganization and preparation for vitellogenesis. The absence of spatial differences suggests that reproductive organ was in a comparable physiological condition throughout the study area.

Overall, these results provide new information on energy allocation patterns in female *L. santolla* and highlight the importance of considering spatial variability when evaluating the physiological condition of populations subjected to fishing exploitation. The incorporation of biochemical indicators of energetic status improves our understanding of the reproductive dynamics of the species and may contribute to the development of ecosystem-based management strategies. Furthermore, the inclusion of different stages of the reproductive cycle in future studies will allow a more precise understanding of temporal variations in energy allocation among tissues and their relationship with the reproductive physiology of this commercially valuable species.

ACKNOWLEDGEMENTS

We thank the scientific and technical staff of the Benthic Crustacean Fishery Program and the crew of the BIPO ‘Víctor Angelescu’ for their considerable effort during the trap fishing operations, which made it possible to obtain the samples used in this study. This is INIDEP contribution no 2511.

Author contributions

Neonila N. Kulisz: conceptualization; formal analysis; methodology; investigation; writing-original draft preparation; project administration; visualization. Carla A. Firpo: writing-review and editing; methodology; formal analysis. Karina A. Rodrigues: writing-review and editing. H. Pablo Lértora: resources. Marta Estrada: formal analysis. A. Cecilia Mauna: writing-review and editing. Gustavo J. Macchi: resources; writing-review and editing, supervision; validation.

REFERENCES

Allega L, Braverman M, Campodónico S, Carozza CR, Cepeda, GD, Colonello JH, Derisio C, Di Mauro R, Firpo CA, Gaitán E, et al. 2020. Estado del conocimiento biológico pesquero de los principales recursos vivos y su ambiente, con relación a la exploración hidrocarburífera en la Zona Económica Exclusiva argentina y sus adyacencias. http://hdl.handle.net/1834/17370.

Alonso-Fernández A, Saborido-Rey F. 2011. Maternal influence on the variation of the reproductive cycle of *Trisopterus luscus* (Gadidae). Cienc Mar. 37: 619-632.

Anthony JA, Roby DD, Turco KR. 2000. Contenido lipídico y densidad energética de peces forrajeros del norte del Golfo de Alaska. J Exp Mar Biol Ecol. 248 (1): 53-78.

[AOAC] Association of official analytical chemists. 1990. Official methods of analysis. 15th ed. Arlington: AOAC.

Bert TM, Geiger SP, Gerhart SD, McCarthy KJ. 2016. Factors influencing reproductive attributes of stone crabs (Menippe) in Tampa Bay, Florida. J Shellfish Res. 35: 241-257.

Calow P. 1985. Adaptive aspects of energy allocation. In: Tytler P, Carlow P, editors. Fish energetics: new perspectives. London: Croom Helm. p. 13-31.

Chang ES. 1995. Physiological and biochemical changes during the molt cycle in decapod crustaceans: an overview. J Exp Mar Biol Ecol. 193 (1-2): 1-14.

Cocito LL, Permigiani S, Tapella F, Lattuca ME, Tomac A, Czerner M, Romero MC. 2024. Shelf-life of cooked meat of southern king crab (*Lithodes santolla*) and false king crab (*Paralomis granulosa*) during refrigerated storage. Heliyon. 10 (16): e36475. DOI: https://doi.org/10.1016/j.heliyon.2024.e36475

Comoglio L, Goldsmit J, Amin O. 2008. Starvation effects on physiological parameters and biochemical composition of the hepatopancreas of the southern king crab *Lithodes santolla* (Molina, 1782). Rev Biol Mar Oceanogr. 43 (2): 345-353.

Eder EB, Lewis MN. 2005. Proximate composition and energetic value of demersal and pelagic prey species from the SW Atlantic Ocean. Mar Ecol Prog Ser. 291: 43-52.

Dutil JD, Lambert Y, Chabot D, 2003. Winter and spring changes in condition factor and energy reserves of wild cod compared with changes observed during food deprivation in the laboratory. ICES J Mar Sci. 60: 780-786.

Fernández M, Bock C, Pörtner HO. 2000. The cost of being a caring mother: the ignored factor in the reproduction of marine invertebrates. Ecol Lett. 3: 487-494.

Firpo CA. 2020. Análisis de los patrones espacio-temporales de la distribución poblacional de centolla, *Lithodes santolla*, en el sector patagónico central [tesis doctoral]. Mar del Plata: Universidad Nacional de Mar del Plata. 255 p.

Firpo CA, Mauna AC, Mango VG, Lértora HP, Arenas MB, Munuce FN. 2025. Análisis de la temporada de pesca de centolla (*Lithodes santolla*) 2024-2025, en el Área Central. Inf Invest INIDEP Nº 153/2025. 28 p.

Firpo C, Militelli MI, Chaparro MAE, Mauna C, Lértora P. 2023. Clutch fullness index as an early indicator of overexploitation of the South-

ern king crab: implications for fisheries management. Ocean Coast Manage. 243: 106762.

Firpo C, Wyngaard J, Mauna C, Mango V, Lértora P. 2017. Estructura poblacional y condición reproductiva de las hembras de centolla (*Lithodes santolla*) en el sector patagónico central, temporada de pesca 2015-16. Inf Téc INIDEP Nº 21/2017. 16 p.

Folch J, Less M, Sloane GH. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J Biol Chem. 226: 497-509.

Gaitán E, Mauna C, Firpo C, Lértora P, Mango V. 2022. Captura potencial y efectiva de la fauna macro-bentónica asociada al Área Central (43° 30' S-48° S) de pesca de centolla (*Lithodes santolla*) en la Argentina. Mar Fish Sci. 35 (1): 19-37.

Gowland Sainz MF. 2018. Biología de la reproducción en la centolla *Lithodes santolla* del Canal Beagle: apareamiento y limitación espermática [tesis doctoral]. Córdoba: Universidad Nacional de Córdoba. 188 p.

Guzmán F, Bascur M, Olavarria L, Mora S, Riera R, Urzúa Á. 2020. Seasonal and interannual changes in reproductive parameters and eggs biochemical composition of the fishery resource *Pleuroncodes monodon* (Decapoda: Munididae) from the Humboldt Current System. Fish Res. 221: 105404.

Hidalgo M, Massutí E, Moranta J, Cartes J, Lloret J, Oliver P, Morales-NIN B. 2008. Seasonal and short spatial patterns in European hake (*Merluccius merluccius L.*) recruitment process at the Balearic Islands (western Mediterranean): the role of environment on distribution and condition. J Mar Syst. 71 (3-4): 367-384.

Huss HH. 1995. Quality and quality changes in fresh fish. In: Huss HH, editor. FAO Fish Tech Pap. 348. 195 p.

Jayasankar V, Tomy S, Wilder MN. 2020. Insights on molecular mechanisms of ovarian development in decapod Crustacea: focus on vitellogenesis-stimulating factors and pathways. Front Endocrinol. 11: 674.

Jimenez AG, Kinsey ST. 2015. Energetics and metabolic regulation, In: Chang, ES, Thiel M, editors. The natural history of Crustacea physiology. New York: Oxford University Press. p. 391-419.

Kleiber M. 1975. The fire of life: an introduction to animal energetics. New York: Krieger Publishing Company. 453 p.

Kruse GH. 1993. Biological perspectives on crab management in Alaska. In: Kruse GH, Eggers DM, Marasco RJ, Pautzke C, Quinn II TJ, editors. Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. Alaska Sea Grant College Program Report Nº 93-02. Fairbanks: University of Alaska Fairbanks. p. 355-384.

Kulisz NN, Fernández M, Rodrigues K, Militelli MI, Moriondo Danovaro P, Macchi GJ. 2025. Condición Nutricional de hembras adultas de langostino (*Pleoticus muelleri*) en diferentes zonas del sector patagónico. Inf Inv INIDEP Nº 4/2025. 16 p.

Lambert Y, Dutil JD, 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Can J Fish Aquat Sci. 57: 815-825.

Lee F, Chang C. 1997. The concentrations of vitellogenin and protein in hemolymph, ovary and hepatopancreas in different ovarian stages of the freshwater prawn *Macrobrachium rosembergii*. Comp Biochem Physiol. 117: 433-439.

Leonarduzzi E, Massa AE, Manca EA. 2012. Variación de la composición bioquímica en hembras de merluza común (*Merluccius hubbsi*) durante el ciclo reproductivo. Rev Invest Desarr Pesq. 21: 5-19.

Leonarduzzi E, Rodrigues KA, Macchi GJ. 2014. Proximate composition and energy density in relation to Argentine hake females (*Merluccius hubbsi*) morphometrics and condition indices. Fish Res. 160: 33-40.

Lértora HP, Firpo CA, Mauna AC, Mango VG, Ravalli C, Veccia MH, Epherra L, Rossi GE, Acevedo CD, Gonzalez S, et al. 2025. Campaña integral de centolla (*Lithodes santolla*) en el Área Central, a bordo del BIPO Víctor Angelescu. Inf Camp INIDEP Nº 8/2025. 39 p.

López Greco LS. 2013. Functional anatomy of the reproductive system. In: Watling L, Thiel M, editors. Functional morphology and diversity. Vol. 1. The natural history of the Crustacea. New York: Oxford Academic. p. 413-450. DOI: https://doi.org/10.1093/acprof:osobl/9780195398038.003.0015

López Greco LS, Tropea C, Sacristán HJ, Calvo NS, Stumpf L, Franco Tadic LM, Tomas AL. 2011. Estructura del hepatopáncreas de la langosta de agua dulce *Cherax quadricarinatus* (Decapoda, Parastacidae). Proceedings of Primeras Jornadas de Ciencias Morfológicas de las Sierras de Tandil, Argentina. https://bicyt.conicet.gov.ar/fichas/produccion/en/1231720.

Lovrich GA, Tapella F, Di Salvatore P, Gowland M, Diez M. 2017. Estado poblacional de las centollas *Lithodes santolla* en el Canal Beagle - 2016. Informe Convenio CONICET-UNTDF, Res. 361/15. https://www.researchgate.net/profile/Gustavo-Lovrich/publication/321168276_Estado_poblacional_de_la_centolla_Lithodes_santolla_en_el_Canal_Beagle_-_2016_--_Cluster_de_Pesca_Artesanal_de_Tierra_del_Fuego/links/5a12f178a6fdcc717b5226e7/Estado-poblacional-de-la-centolla-Lithodes-santolla-en-el-Canal-Beagle-2016--Cluster-de-Pesca-Artesanal-de-Tierra-del-Fuego.pdf.

Lowry OH, Rosebrough, NJ, Farr AL, Randall RJ. 1951. Protein measurement with the Folin phenol reagent. J Biol Chem. 193 (1): 265-275.

Marciano A. 2022. Esfuerzo reproductivo en el límite de la distribución geográfica: el cangrejo violinista *Leptuca uruguayensis* como modelo [tesis doctoral]. Buenos Aires: Universidad de Buenos Aires. 188 p.

Mauna AC, Firpo CA, Mango VG, Lértora HP, Arenas MB. 2025. Análisis de la temporada de pesca de centolla (*Lithodes santolla*) 2024-2025, en el Área Sur (48°-52° S). Inf Invest INIDEP Nº 92/2025. 26 p.

Mauna AC, Firpo CA, Mango VG, Lértora HP, Rodríguez D, Seco Pon JP, Arenas M. 2022. Protocolo de actividades para los asistentes a la investigación pesquera a bordo de buques centolleros. Inf Ases Transf INIDEP Nº 104/2022. 50 p.

Militelli, MI, Firpo C, Mauna AC, Rodrigues, KA, Macchi, GJ.2020. Reproductive potential of southern king crab (*Lithodes santolla*) in South Patagonian Sector (south 48° S), a new fishery area. Fish Res. 229: 105595.

Militelli MI, Firpo C, Rodrigues KA, Macchi GJ. 2019. Producción de huevos y validación de la escala de índices de plenitud de puesta de centolla, *Lithodes santolla*, en el sector patagónico central, Argentina (44°-48° S). Fish Res. 211: 40-45.

Oliveira GT, Hack C, Almerão M, Bond Buckup G, Dutra BK. 2011. Tissue composition and haemolymphatic metabolites during gonadal development in *Aegla platensis* (Crustacea, Decapoda) maintained in experimental culture. R Bras Bioci. 9: 64-71.

Peig J, Green AJ. 2009. Nuevas perspectivas para la estimación de la condición corporal a partir de datos de masa/longitud: el índice de masa escalado como método alternativo. Oikos. 118 (12): 1883-1891.

Peixoto S, Coman G, Arnold S, Crocos P, Preston N. 2005. Histological examination of final oocyte maturation and atresia in wild and domesticated *Penaeus monodon* (Fabricius) broodstock. Aquac Res. 36: 666-673.

Rätz HJ, Lloret J. 2003. Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. Fish Res. 60 (2-3): 369-380.

Risso SJ, Carelli AA. 2012. Nutrient composition of raw and cooked meat of male southern king crab (*Lithodes santolla* Molina, 1782). J Aquat

Food Prod Technol. 21 (5): 433-444.
Rodrigues KA, Macchi GJ, Massa AE, Militelli MI. 2013. Seasonal analysis of condition, biochemical and bioenergetic indices of females of Brazilian flathead, *Percophis brasiliensis*. Neotrop Ichthyol. 11: 153-162.
Rosset M, Militelli MI, Rodrigues KA, Fernández M. 2023. Condición y composición proximal de las hembras de *Pleoticus muelleri* en el área patagónica. Inf Inv INIDEP Nº 29/2023. 10 p.
Saborido-Rey F, Macchi GJ. 2021. Ecología reproductiva y pesquerías en el contexto iberoamericano. Vigo: Red Iberoamericana de Investigación para el Uso Sostenible de los Recursos Pesqueros (RED INVIPESCA).
Sacristán H, Di Salvatore P, Florentín O, Gowland-Sainz M, Greco LL, Lovrich G. 2023. Examination of female energy dynamics and larval quality in the southern king crab, *Lithodes santolla*: annual and interannual variability. Aquaculture. 576: 739819. DOI: https://doi.org/10.1016/j.aquaculture.2023.739819
[SAGPyA] Secretaría de Agricultura, Ganadería y Pesca. 2026. Desembarques. https://www.magyp.gob.ar/sitio/areas/pesca_maritima/desembarques/lectura.php?imp=1&tabla=especie_mes_2025.
Sánchez-Paz A, García-Carreño F, Muhlia-Almazán A, Peregrino-Uriarte AB, Hernández-López J, Yepiz-Plascencia G. 2006. Usage of energy reserves in crustaceans during starvation: status and future directions. Insect Biochem Mol Biol. 36 (4): 241-249.
Sasaki GC, Capuzzo JM, Biesiot P. 1986. Nutritional and bioenergetic considerations in the development of the American lobster Homarus americanus. Can J Fish Aquat Sci. 43: 2311-2319.
Schulte-Hostedde AL, Zinner B, Millar JS, Hickling GJ. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology. 86: 155-163.
Serrano Silvas SR. 2016. Caracterización morfológica, bioquímica y molecular de la vitelogénesis de las hembras del crustáceo subantártico centolla (*Lithodes santolla*) [tesis doctoral]. La Plata: Universidad Nacional de La Plata.102 pp.
Sibly RM, Calow. 1986. Physiological ecology of animals: an evolutionary approach. Oxford: Backwell Scientific Publications. 179 p.
Silva PV, Luppi TA, Spivak ED. 2007. Epibiosis on eggs and brooding care in the burrowing crab *Chasmagnathus granulatus* (Brachyura: Varunidae): comparison between mudflats and salt marshes. J Mar Bio Assoc UK. 87: 893-901.
Silvas S, René S. 2016. Caracterización morfológica, bioquímica y molecular de la vitelogénesis de las hembras del crustáceo subantártico centolla (*Lithodes santolla*) [tesis doctoral]. Valdivia: Universidad Austral de Chile. 125 p.
Simpson L, Ambrosio LJ, Guéron R, Mora N, Owen D. 2015. Reproductive investment in a phyletic giant, the Caribbean king crab *Damithrax spinosissimus*: exploring egg production costs in large brooding marine invertebrates. J Shellfish Res. 34: 1049-1056.
Souto V, López ME, Varisco M, Penoni M, Maldonado Montes De Oca E, Moriondo Danovaro P. 2024. Variabilidad especial de la dieta de juveniles y adultos del langostino *Pleoticus muelleri* a partir del análisis de contenido estomacal. Inf Inv INIDEP Nº 89/2024. 30 p.
Spitz J, Mourocq E, Leauté JP, Quéro JC, Ridoux V. 2010. Selección de presas por el delfín común: Satisfacer los altos requerimientos energéticos con alimento de alta calidad. J Exp Marine Biol Ecol. 390 (2): 73-77.
Subramoniam T. 2011. Mechanisms and control of vitellogenesis in crustaceans. Fish Sci. 77: 1-21.
Taylor HH, Leelapiyanart N. 2001. Oxygen uptake by embryos and ovigerous females of two intertidal crabs, *Heterozius rotundifrons* (Belliidae) and *Cyclograpsus lavauxi* (Grapsidae): scaling and the metabolic costs of reproduction. J Exp Biol. 204: 1083-1097.
Tsukimura B. 2001. Crustacean vitellogenesis: its role in oocyte development. Am Zool. 41: 465-

476.

Wyngaard JG, Iorio MI, Firpo C. 2016. La pesquería de centolla (*Lithodes santolla*) en la Argentina. In: Boschi EE, editor. Los crustáceos de interés pesquero y otras especies relevantes en los ecosistemas marinos. Tomo 6. El Mar Argentino y sus recursos pesqueros. Mar del Plata: Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). p. 229-250.

Yeannes MI, Almandos ME. 2003. Estimation of fish proximate composition starting from water content. J Food Compos Anal. 16 (1): 81-92.

Zar JH. 1996. Biostatistical analysis. 3rd ed. Upper Saddle River: Prentice Hall. 662 p.