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Living Along Distribution Margins: Differences in the Body and Biochemistry of Red Squat Lobster Morphotypes (*Grimothea monodon*) from the Humboldt Current System

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Abstract: *Grimothea monodon*, an important fishery resource in the Humboldt Current marine ecosystem (HCE), present two contrasting morphotypes (PM, pelagic morphotype; BM, benthic morphotype). The fishery management of *G. monodon* is focused on understanding only fishery aspects that apply to a limited area, and there are currently no studies that evaluate the nutritional status of these morphotypes. This study evaluated the biological performance of PM and BM, analyzing the body (size, CL; weight, W; condition factor, Kn) and biochemical condition (glucose, G; proteins, P; lipids, L; fatty acids, FAs). The results reveal that *G. monodon* showed differences in CL and W between morphotypes, with higher values in BM than PM. The Kn was different between morphotypes with a tendency of isometric growth. In turn, the G contents were higher in PM than BM, while the contents of P, L, and FAs showed an opposite tendency, with higher contents recorded in BM than PM. Our findings suggest that the Kn should be included to strengthen the biological parameters and their relationships used in fishery management models. Differences in the biochemical condition between morphotypes can be considered potentially adaptive, in response to the combined effect of environmental factors that vary in the HCE.

Keywords: decapod crustaceans; nutritional condition; environment; Southeast Pacific Ocean; fishery

Key Contribution: *Grimothea monodon* adults showed notable differences in size, weight, and biochemical condition between morphotypes. The combined effect of temperature, food availability and oxygen could be modulating the capacity of ectothermic invertebrates to store energy for physiological processes.

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1. Introduction

On a global level, marine ecosystems provide various habitat mosaics that support vast biodiversity and provide multiple services to the planet [1,2]. However, these ecosystems are currently one of the most commercially exploited worldwide [3]. Anthropogenic activities (e.g., fisheries, aquaculture, shipping), and especially coastal fisheries, have a direct impact on the growth, abundance, and geographic distribution of resource species [4,5]. Furthermore, along with overfishing [6], abrupt and increasingly frequent variations in environmental and/or climatic conditions have been reported [7], which directly influence the performance of species and their interactions with others in the marine food web at different spatial/temporal scales [8]. For example, changes in predator feeding strategies due to a decrease in the abundance and/or absence of their prey [9] can influence the condition and sustainability of resources, ultimately affecting fishery management and exploitation activities [10]. Ectothermic marine invertebrates, such as decapod crustaceans, are characterized by having extended distribution ranges [11]. Considering the current context of climate change characterized by variation in seawater temperature, their life history traits, such as body condition (measured in terms of biomass and biochemical constituents), trophic habits (detritivores, filter feeders) and lifestyles (pelagic, benthic) could play an important role in energy transfer and the functioning of marine food webs [5,12].

The Humboldt Current marine ecosystem (HCE) comprises a large area (4° S–42° S) that is one of the most important marine systems worldwide due to the large pelagic fisheries it supports [13]. In particular, the HCE presents variations in oceanographic conditions (such as sea temperature, dissolved oxygen, marine currents, marine upwellings), as well as geomorphological changes along the continental shelf [13]; these variations are very abrupt when comparing the boundary zones and/or distribution margins of the HCE, and therefore, they can modulate the nutritional condition of the organisms that inhabit these areas [14]. In this context, the environmental and oceanographic conditions (temperature, food, oxygen level, and upwelling) that predominate in these areas can influence not only the body morphology and size that ectothermic marine invertebrates reach, but also their biochemical condition [15]. The variability in nutrient availability (in terms of quantity and quality) especially influences the content of important biomolecules (such as lipids, proteins, and carbohydrates) involved in important biological processes [16]. Therefore, species must adjust their functional responses (at the physiological–structural level) to carry out important processes within their life cycle, such as survival and reproduction, which subsequently modulate the stability of their populations [16,17].

Among the widely distributed and commercially important crustaceans in the HCE, our model species is the red squat lobster *Pleuroncodes monodon* (H. Milne Edwards, 1837; and recently renamed *Grimothea monodon* [18]) (Decapoda: Munididae), which is the main target species of the demersal crustacean fisheries in the HCE [19]. Furthermore, it is an important marine bioresource due to its attributes and biotechnological properties (i.e., its high content of axtasanthin and chitosan), which are in increasing commercial demand by the medical and food industries [20,21]. With respect to its biology and fishery, it is important to know: (i) the reproductive seasonality of this species is characterized by the presence of ovigerous females from March to September [22], (ii) the genetic structure and differentiation between morphotypes (mitochondrial DNA studies) indicates that the haplotypes of individuals with different morphotypes (pelagic vs. benthic) do not present genetic differentiation [23], and (iii) the capture gear used (purse seiners and trawling with other fishing resources (anchovy, hake)) and landings [21]. Its geographic distribution in the HCE (Perú-Chile) ranges from Isla Lobos de Afuera in Perú (5° S) to Chiloé in Chile (41° S) [24]. Throughout this wide geographic area, *G. monodon* has specific distribution margins where the fisheries mainly operate, known as the Southern Fishery Unit-Chile: V–VIII Region [21]. Within these margins, adult individuals of *G. monodon* present two morphotypes and/or lifestyles that are easily distinguishable by eye [23]: pelagic and small size (~15° S: Pisco, Perú) vs. benthic and large size (~35°: Faro Carranza, Chile). These morphotypes were used as a comparative reference for this study. In this context, the presence of contrasting adult morphotypes (pelagic vs. benthic) in their distribution margins could be strongly influenced by their dispersal potential or, conversely, by the degree of isolation or distance between their populations [11]. It could also be related to the spatial/temporal variations in food availability, together with abrupt geomorphological changes in the habitat and the biogeographic barriers present in the HCE [25]. All of the above could modulate the health and/or condition of these individuals throughout their wide distribution range.

In exploited marine species (e.g., fish and crustaceans) [26,27], condition status can be assessed through the length–weight relationship [28]. This tool establishes the relative condition factor (Kn) and is considered an indirect indicator of the body health status and/or body condition of the individual, and of the population in its natural habitat [29–31]. In turn, the Kn can reflect the quantity and quality of food available in the environment [32]; it is also highly influenced by exogenous variables (e.g., abiotic factors, oceanographic phenomena) and endogenous variables (e.g., feeding rate, growth, sexual cycle) [13,33,34]. Therefore, the Kn plays an important role in the assessment and management of marine resources, helping to understand the strategies and/or adaptations that species carry out for their survival [35]. A consistently high Kn value (≥1) indicates that the resource is in good condition, which indirectly reveals that there is a high abundance of prey in its habitat, and that consequently it has large amounts of biochemical and/or energy reserves stored in its tissues and/or organs for growth and reproductive cycles [32]. However, its generalized use to assess the status of a population can be inaccurate, because an increase of the condition of individuals could reflect a decrease in the population abundance [36].

Also, the condition status of decapods can be directly assessed at the biochemical and/or energetic level (measured as the content of lipids, proteins, carbohydrates, and fatty acids) because these biomolecules play an important role as an energy source to sustain fundamental physiological processes (metabolism, growth, reproduction) [37,38]. Recently, it has been described that these biochemical constituents vary not only at the sexual level (males vs. females) [39], but can also vary significantly at the spatial level throughout the geographic distribution in the HCE. In this spatial context, it has recently been reported that juvenile individuals of the benthic morphotype living in two nursery areas on the coast of Chile (Coquimbo vs. Concepción) present a different nutritional condition, which is linked to habitat characteristics [40]. Quantifying the nutritional status of the juvenile stock has made it possible to explain fluctuations in recruitment rates as well as generate some conservation and management strategies for the juvenile populations of this species on the central–southern coast of Chile [40,41].

As previously mentioned, throughout its wide geographic distribution range in the HCE *G. monodon* is exposed to various abiotic factors that determine habitat characteristics [11] and can consequently influence the phenotypic traits displayed by its populations [42]. However, to date, it is unknown whether habitat characteristics together with the contrasting phenotypic traits and lifestyles present in the adult individuals of *G. monodon* that inhabit diverse distribution margins may also induce potential differences in their body condition and biochemistry. Due to the ecological and commercial importance of *G. monodon* in the HCE [21,22], it is necessary to integrate fundamental information regarding its physiology and its interaction with the habitat, in order to develop appropriate tools for the sustainable management of these fisheries under an ecosystemic approach [32].

Despite ecological evidence indicating the ecosystemic relevance between the habitat of *G. monodon* and fishery production, the management of this resource is currently focused on understanding only biological/fishery aspects (size at first sexual maturity, fecundity, sexual radius) to establish the limited closed seasons (December–January) that apply to a limited area of HCE (the central–southern coast of Chile). Therefore, there are currently no studies that evaluate the nutritional status (measured as body and biochemistry condition) of the two morphotypes of *G. monodon* in their geographic distribution margins in the HCE. Thus, the "temperature size rule for ectothermic organisms" proposed by Atkinson in 1994 is followed [42]. We hypothesize that adult squat lobsters that live in cold environments grow slowly; therefore, they reach larger body sizes, have higher biochemical and/or energy reserves stored and live longer in the benthos (benthic morphotype) than those in warm environments, which grow faster, and consequently reach smaller body sizes, have lower biochemical reserves stored and live shorter lives in the pelagos (pelagic morphotype). Therefore, it is expected that the nutritional status differs between pelagic and benthic morphotypes due to the environmental and geomorphological variability of their respective habitats. Finally, this work aims to evaluate the biological performance and/or condition of the pelagic and benthic morphotypes of the red squat lobster by analyzing the body and biochemical condition of adult individuals from two very distant geographical areas of the HCE, with contrasting environmental characteristics.

2. Materials and Methods

2.1. Collection of Samples

Adult male and female specimens of *G. monodon* were obtained from the fishing fleet operating in historical catch areas (fishing grounds) off the coasts of Pisco (13°10.8′ S 76°47.5′ W) in Perú (pelagic morphotype: PM) and Faro Carranza (35°26′ S 75°29′ W) in Chile (benthic morphotype: BM), in late October of the year 2021 (Figure 1). Due to the beginning of fishing ban periods in the south–central zone of Chile (that includes the sampling area of Faro Carranza) there was a low number of samples available for this area (N = 34). The size of the captured individuals, the historical catch areas and the fishing gear (purse seine in Perú and trawl fishing in Chile) allows the catching of specimens of different sizes, which are representative of each population [21]. The sampling areas have consistently been characterized by their contrasting oceanographic and geomorphological conditions. For example, in Pisco, Perú, the continental shelf begins to disappear, while in Faro Carranza, Chile, the continental shelf reappears [43]. In addition, marine upwellings and changes in nutrient availability are frequent and intense throughout the year in Pisco, Perú, while in Carranza, Chile, they are seasonal [13,44]. In turn, abiotic factors such as the availability of dissolved oxygen and surface temperature vary significantly between these two areas (<5 mL/L vs. >5 mL/L; 20 °C vs. 15 °C; Pisco vs. Faro Carranza, respectively) [45]. The squat lobsters were transported by plane in boxes with dry ice to the laboratory of ecology at Universidad Nacional de San Agustin de Arequipa-Perú and to the hydrobiological resources laboratory at Universidad Católica de la Santísima Concepción in Chile, where their sex, sexual maturity, size, wet weight, and intermolt stage (C1) were recorded [46,47].

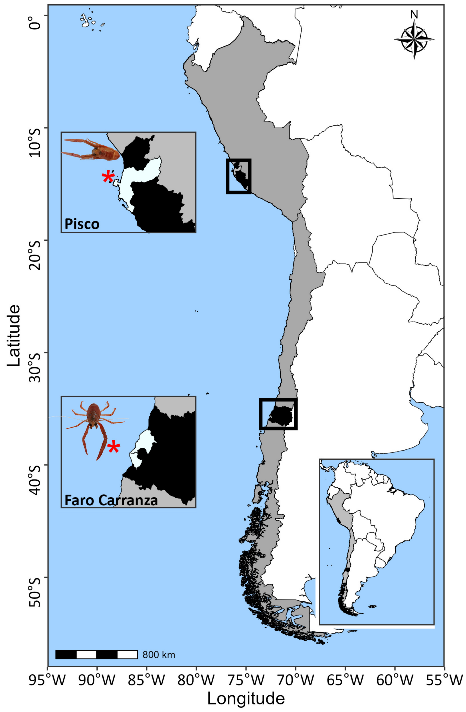

Figure 1. Sampling area of *G. monodon* in the HCE. Two contrasting morphotypes in their geographic distribution margins: (i) PM, pelagic morphotype (~15° S: Pisco, Perú) vs. (ii) BM, benthic morphotype (~35° S: Faro Carranza, Chile); captured in late October (non-reproductive period: indicated by the absence of ovigerous females in the field) of the year 2021. Black color zones and red asterisks represent reference points of sampling areas (Pisco, Ica Region; Faro Carranza, Maule Region).

2.2. Body Condition (Length, Weight, Relative Condition-Kn)

The body condition of male and female squat lobsters of the two morphotypes from the study areas were measured based on; (i) the length vs. weight ratio [28], and (ii) the relative condition factor [31]. This morphometric data, including cephalothorax length (CL, from eye orbit to posterior border of cephalothorax), were obtained by means of a vernier caliper with a precision of 0.001 mm, and the weight (W) of the individuals was quantified using a digital balance with a precision of 0.001 gr. In turn, a potential order regression analysis was used to analyze CL and W to obtain the constants "a" and "b" which are necessary to evaluate the relative condition factor-Kn, following the formula: $Kn = \frac{W}{aCL^b}$ [31], where Kn is the comparison between the weight of an individual and their theoretical weight at length; here, values above 1 are considered as 'good' condition, and below 1 as 'bad' condition. This indicates the body condition of the species and its potential degree of adaptation to the habitat [48].

2.3. Biochemical Condition (Glucose, Protein, Lipids, Fatty Acid Profile)

The biochemical condition of the individuals was evaluated based on the main biochemical constituents (glucose, protein, lipids, fatty acid profile), which are sources of metabolic energy in decapods [49]. For this, the muscle tissue from the tail of the red squat lobster (the body part where the energy for growth is deposited and commercially processed for human consumption [50]) was extracted, and each of the extracted muscle tissue samples were freeze-dried (FDU-7012, Operon) at −80 °C for 48 h. Due to the fact that the morphotypes have completely different sizes according to their geographical origin (see Figure 2), to standardize a common sample weight and statistically compare morphotypes, a total common sample of 20 mg of the dry weight of each morphotype (PM, BM) was used for the corresponding biochemical analyses.

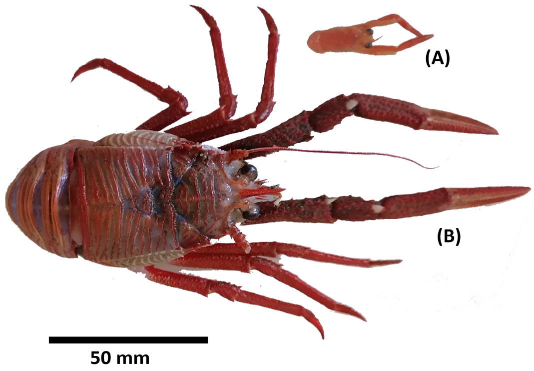

Figure 2. Adults of *G. monodon* in the HCE. Two contrasting morphotypes in their geographic distribution margins: (A) PM, pelagic morphotype (~15° S: Pisco, Perú) vs. (B) BM, benthic morphotype (~35° S: Faro Carranza, Chile). Scale bar 50 mm.

2.3.1. Glucose Content

The glucose content was quantified using the IVS Glucose-LQ glucose determination kit [39]. Each 20 mg sample was homogenized with 500 µL of ultrapure water, 10 µL of the sample was removed into a new Eppendorf tube, and 1 mL of reagent R was added. Subsequently, the standard reagent was prepared with 1 mL of reagent R and 10 µL of the glucose standard (Glucose Cal). Then, 200 µL of each sample was added to a 96-well microplate together with the glucose standard and a blank (reagent R only). Finally, the samples were incubated for 20 min at room temperature, after which the absorbance was measured with a BIOTECK spectrophotometer (ELx808) at a wavelength of 490 nm. The glucose concentration was obtained from the division between the sample (with blank correction) and the glucose standard.

2.3.2. Protein Content

For total protein quantification, the method described by Lowry et al. [51] was used with a colorimetric protein quantification kit (Bio-Rad DC Protein Assay, Hercules, CA, USA), which contains a solution of reagent A, reagent B, reagent S and a standard protein (bovine serum albumin). The lyophilized sample was homogenized in 500 µL of ultrapure water, and then placed in an ultrasonic bath (AC-120H) for 10 min. Subsequently, 5 µL of each sample was transferred to a 96-well microplate, where 20 µL of reagent A′ (A′ = 20 µL of reagent S and 1 mL of reagent A) and 200 µL of reagent B were added to each sample. For protein reading, a BIOTECK multiplate spectrophotometer (ELx808) was used at a wavelength of 750 nm, and its quantification was obtained using a protein calibration curve based on different dilutions of serum albumin (0.2–1.2).

2.3.3. Lipid Content

Lipid extraction was performed using the gravimetric method developed by Folch et al. [52] and modified by Cequier-Sánchez et al. [53] and Urzúa and Anger [54]. Each 20 mg sample was immersed in an amber glass bottle with a 5 mL dichloromethane–methanol solution (2:1 *v*/*v*). Then, ultrasonication was carried out (AC-120H equipment, MRC) for 15 min. Subsequently, 4 mL of 0.88% KCl (potassium chloride) was added and centrifuged for 5 min at 1500 rpm (FASCIO TG1650-S). The lower phase of the liquid containing the lipids was extracted, and subsequently dried with an injection of nitrogen gas (GLAS COL 109A YH-1), after which it was weighed on a balance (SARTORIUS LA230S) with an accuracy of 0.1 mg.

2.3.4. Fatty Acids Profile

For the determination of the fatty acids profile (FAs: saturated, monounsaturated, polyunsaturated) the method of Urzúa and Anger [55] was used, measured as FAs methyl esters (FAMEs). 1 mL of the lipid sample was extracted and then esterified with 2 mL of methanolic sulfuric acid (1%) and incubated at 70 °C (Thermo-Shaker MRC model DBS-001) for 1 h. Three washes were performed with n-Hexane in three volumes (6 mL, 3 mL and 3 mL, respectively). In each wash, the upper phase was extracted and placed in a new amber glass tube, and then dried with an injection of nitrogen gas. N-hexane was added again to obtain a volume of 1 mL in a 1.5 mL amber vial. FAMEs were determined by gas chromatograph (GC: Agilent, model 7890A, Santa Clara, CA, USA) equipped with DB 225 column (J and W Scientific, 30 µm length, 0.25 internal diameter and 0.25 mm film). For this, the temperature program for sample injection suggested for the GC column was used. Briefly, the oven temperature was initially set at 100 °C for 4 min, then increased at 3 mL/min to 240 °C for 15 min. For individual identification of fatty acids present in the samples, chromatographic software (B.0402.SP1, Agilent ChemStation, Santa Clara, CA, USA) was used and compared with a marine fatty acid standard (Supelco 37 FAME mix 47885-U) and quantified by the response factor of the internal standard (23:0 FA, which was incorporated before transmethylation) [56].

2.4. Statistical Analysis

Statistical analyses of the data were performed using standard methods (parametric, non-parametric, and multivariate tests) with a significance level <0.05 described by Zuur et al. [57]. To statistically verify significant differences in body condition and biochemistry between morphotypes (pelagic: PM; benthic: BM) and sexes (male, female) from the study areas, a two-way ANOVA was performed after meeting the assumptions of parametric statistics (independence, normality, heteroscedasticity [57]). To evaluate the contingency among the parameters analyzed (CL, W, Kn, glucose, proteins, lipids) a correlogram of the correlation matrix was performed [58]. In turn, for the statistical analysis of fatty acids, a multivariate PERMANOVA test and a principal coordinates analysis (PCoA) were performed through the Euclidean distance. Subsequently, to see the contribution of the main FAs present in the tail muscle of the two morphotypes and sexes, a SIMPER analysis (similarity percentage) was performed. Finally, to confirm the variability between the FA profiles, an ANOSIM (similarity analysis) was performed. For each of the analyses, the morphotype (PM, BM) and sex (male, female) were considered as fixed factors and the morphometric parameters (LC, W) and biochemical constituents (glucose, protein, lipids, FAs) were considered as response variables. All of these analyses were performed using Primer v7 software and the R platform.

3. Results

3.1. Body Condition

Adult individuals of *G. monodon* presented conspicuous differences in size and weight between the pelagic morphotypes of Pisco (PM) and benthic morphotypes of Faro Carranza (BM) (Figure 2). The CL of the PM was 15.61 ± 0.23 mm CL, with a weight of 0.52 ± 0.03 g, while the CL of the BM was 42.79 ± 1.67 mm, with a weight of 21.53 ± 2.86 g (Figure 3).

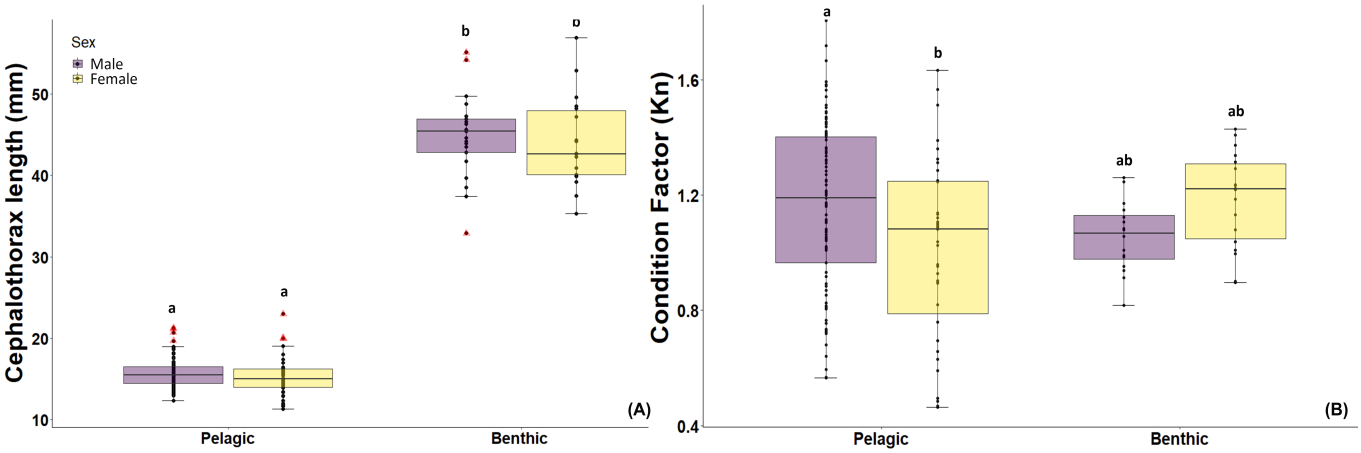

Figure 3. Male and female individuals of *G. monodon* in the HCE. Two contrasting morphotypes in their geographic distribution margins: (i) PM, pelagic morphotype (~15° S: Pisco, Perú) vs. (ii) BM, benthic morphotype (~35° S: Faro Carranza, Chile). (**A**) Cephalothorax length (CL) and (**B**) Condition Factor (Kn). Lowercase letters represent significant differences at 95%.

Although the notable differences between the *G. monodon* morphotypes from distinct distribution margins in the HCE were the focus of this study, comparisons of LC and W were also made within each morphotype and as a function of sex (male vs. female). Within the PM, males and females presented similar average CL values ($F_{1,154} = 0.876$, $p = 0.351$). A similar trend was observed for the BM, with similar CL values between males and females ($F_{1,37} = 0.227$, $p = 0.636$) (Figure 3A). In turn, the W of PM presented similar average values between sexes ($F_{1,154} = 1.052$, $p = 0.307$). Also, the W of BM presented similar average values between sexes ($F_{1,37} = 0.058$, $p = 0.8117$).

The Kn obtained from the general relationship (CL vs. W; Figure S1) showed significant differences (Figure 3B). In the MP, males (1.17 ± 0.29) had a slightly better Kn compared to females (1.01 ± 0.33) (MP-Sex: $F_{1,138} = 7.64$, $p = 0.0065$). In the MB, females (1.18 ± 0.17) had a slightly better Kn than males (1.05 ± 0.12) (MB-Sex: $F_{1,32} = 6.453$, $p = 0.0161$). These variations indicated significant differences in the morphotype*sex interaction ($F_{1,170} = 6.79$, $p = 0.00996$) and in the sex factor ($F_{1,170} = 3.913$, $p = 0.0495$), but not in the morphotype factor ($F_{1,170} = 0.003$, $p = 0.954$). In turn, sex between morphotypes was not statistically significantly different (Table S3). Finally, the Kn analysis reveals that the population of *G. monodon* (both morphotypes) have a growth positive allometric (b = 3.61) (Figure S1) and that, in each population morphotype, the males and females from the PM showed isometric growth (b = 3), while only females from the BM showed almost isometric growth (b = ~3). For detailed comparisons, see Tables 1 and S1–S3.

Table 1. Length–weight relationship parameters in males and females of *G. monodon* off the coast of Pisco in Perú (pelagic morphotype) and Faro Carranza in Chile (benthic morphotype).

Morphotype	Sex	N	b	a	R^2
Pelagic	Male	101	3.1547	0.00008	0.64
	Female	39	3.2338	0.00006	0.81
Benthic	Male	16	1.8479	0.0169	0.86
	Female	18	2.9806	0.0003	0.91

N: number of individuals, a and b: regression coefficient parameters, R^2: correlation coefficient. Small black letters represent significant differences between males and females.

3.2. Biochemical Condition

3.2.1. Glucose Content

The average glucose content recorded in male and female individuals was significantly higher in PM than the BM (morphotype: $F_{1,55}$ = 38.873, $p < 0.05$) (sex: $F_{1,55}$ = 5.484, $p = 0.0228$), but not in the interaction (morphotype*sex: $F_{1,55}$ = 0.043, $p = 0.8357$) (Figure 4A). In turn, according to sex between morphotypes, PM male specimens presented higher glucose contents than BM males ($F_{1,31}$ = 16.31, $p = 0.0003$). A similar trend was observed in females, with higher glucose values recorded in PM females than BM females ($F_{1,20}$ = 29.24, $p = 0.00002$). In turn, when comparing within each morphotype, in PM, the male specimens presented higher glucose contents than females ($F_{1,15}$ = 1.17, $p = 0.297$). A similar trend was observed in BM, with higher glucose values recorded in males than females (K-W: $H_{1,39}$ = 1.83, $p = 0.176$). For detailed comparisons, see Tables 2 and S3.

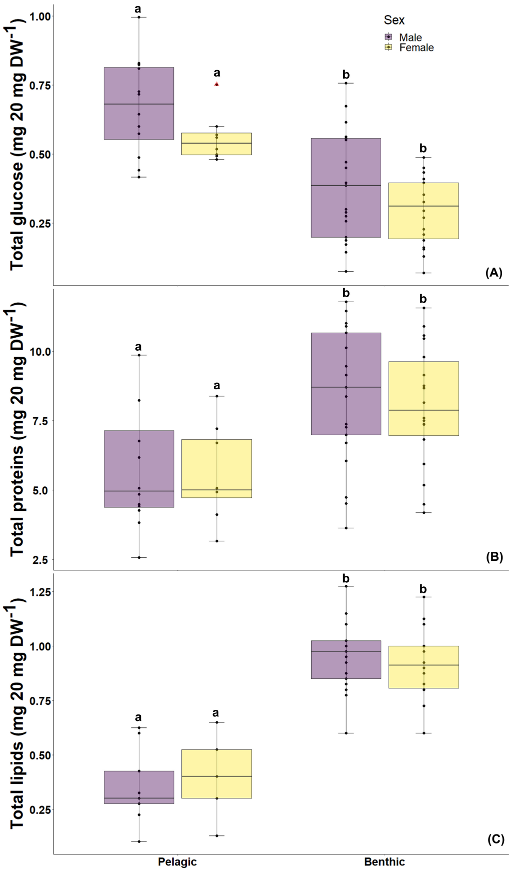

Figure 4. Male and female individuals of *G. monodon* in the HCE. Two contrasting morphotypes in their geographic distribution margins: (i) PM, pelagic morphotype (~15° S: Pisco, Perú) vs. (ii) BM, benthic morphotype (~35° S: Faro Carranza, Chile). Biochemical constituents (contents of (**A**) glucose, (**B**) proteins, and (**C**) lipids). Lowercase letters represent significant differences at 95%.

Table 2. Biochemical condition (contents of glucose, proteins, and lipids) in males and females of *G. monodon* off the coast of Pisco in Perú (pelagic morphotype) and Faro Carranza in Chile (benthic morphotype).

Biochemical Condition (mg 20 mg Dry Weight^{-1})	Morphotype	Male		Female	
		N	X ± DS	N	X ± DS
Glucose	Pelagic	12	0.67 ± 0.18 ^{a}	8	0.56 ± 0.09 ^{a}
	Benthic	21	0.39 ± 0.20 ^{b}	18	0.29 ± 0.12 ^{b}
Protein	Pelagic	12	6.02 ± 2.67 ^{a}	8	5.56 ± 1.73 ^{a}
	Benthic	21	8.42 ± 2.45 ^{b}	18	8.03 ± 2.18 ^{b}
Lipid	Pelagic	12	0.33 ± 0.04 ^{a}	5	0.43 ± 0.16 ^{a}
	Benthic	21	0.72 ± 0.06 ^{b}	18	0.87 ± 0.17 ^{b}

N: number of samples, X: mean, DS: standard deviation. Superscript letters represent significant differences.

3.2.2. Protein Content

The protein content showed an opposite trend to that observed for the glucose content. Here, comparisons between morphotypes revealed that male and female individuals from BM showed a higher protein content than individuals from PM (morphotype: $F_{1,55} = 13.954$, $p = 0.0004$), although not in the interaction (morphotype*sex: $F_{1,55} = 0.002$, $p = 0.963$) and sex ($F_{1,55} = 0.446$, $p = 0.507$) (Table 2, Figure 4B). In turn, in comparisons between morphotypes according to sex, males of both morphotypes (PM and BM) showed a slightly higher protein content than females; BM males in particular had the highest protein content (8.42 ± 2.45 mg 20 mg dry weight^{-1}) (male: $F_{1,31} = 6.87$, $p = 0.0135$; female: $F_{1,24} = 7.91$, $p = 0.0096$). In comparisons within each morphotype, males of both morphotypes (PM and BM) showed a slightly higher protein content than females; BM males in particular had the highest protein content (8.42 ± 2.45 mg 20 mg dry weight^{-1}) (PM: $F_{1,15} = 0.143$, $p = 0.711$; BM: $F_{1,37} = 0.27$, $p = 0.606$) (Table S3).

3.2.3. Lipid Content

The lipid content showed a similar trend to that observed in proteins. Comparisons between morphotypes consistently showed BM individuals with a significantly higher protein content than individuals from PM (BM: males (0.95 ± 0.15 mg 20 mg dry weight^{-1}), females (0.90 ± 0.18 mg 20 mg dry weight^{-1}); vs. PM: males (0.35± 0.15 mg 20 mg dry weight^{-1}), females 0.40 ± 0.20 mg 20 mg dry weight^{-1})) (morphotype: $F_{1,52} = 136.37$, $p < 0.05$) (sex: $F_{1,52} = 0.196$, $p = 0.660$) (morphotype*sex interaction ($F_{1,52} = 0.916$, $p = 0.343$)) (Table 2, Figure 4C). In comparisons between morphotypes according to sex, MB females had higher lipid content than MP females ($F_{1,21} = 27.62$, $p = 0.0000329$). In males, a similar the trend was observed, with higher lipid values recorded in BM than PM ($F_{1,31} = 124.54$, $p < 0.05$) (Table 2, Figure 4C). In comparisons within each morphotype, PM females had a higher lipid content than males ($F_{1,15} = 0.35$, $p = 0.563$), while in BM, the trend observed was the opposite, with higher lipid values recorded in males than females ($F_{1,37} = 0.762$, $p = 0.388$) (Table S3).

According to the contingency analyses among the parameters analyzed (CL, W, Kn, glucose, proteins, lipids) of *G. monodon*, the correlogram indicated that Kn showed a positive and significant correlation with glucose ($R = 0.49$, $p < 0.05$) and a negative and significant correlation with lipids ($R = -0.51$, $p < 0.05$). Consistently, W and CL showed a positive and significant correlation with lipids (Figure S2).

3.2.4. Fatty Acid Profiles

The FA profiles revealed that PM had a lower number of fatty acids (6 FAs in males and females) compared to BM (12 FAs in males and females). In both morphotypes, saturated fatty acids (SFAs) represented the most prominent fatty acid (FA) detected, with values higher than 50% of the total recorded (Table 3). In turn, the monounsaturated fatty acids (MUFAs) of the BM showed a lower percentage (~20–22%) with respect to the percentage of total polyunsaturated fatty acids (PUFAs) (~26–31%). On the other hand, in PM, a higher percentage of MUFAs was recorded with respect to PUFAs (~30% vs. ~18%), except in male individuals that presented slightly lower MUFA values (22.59%) with respect to PUFAs (23.53%). Signals of n6 chain polyunsaturated fatty acids were recorded only in BM (Table 3).

Table 3. Fatty acids profile in males and females of *G. monodon* off the coast of Pisco in Perú (pelagic morphotype) and Faro Carranza in Chile (benthic morphotype).

		Pisco				**Faro Carranza**			
		Male		**Female**		**Male**		**Female**	
FA		**Mean ± SD**	**%**	**Mean ± SD**	**%**	**Mean ± SD**	**%**	**Mean ± SD**	**%**
SFA	C14:0	0.98 ± 0.01	14.16	0.97 ± 0.00	13.45	1.09 ± 0.11	7.42	1.08 ± 0.11	7.95
	C15:0					0.58 ± 0.04	3.92	0.53 ± 0.15	3.88
	C16:0	1.63 ± 0.26	23.60	1.72 ± 0.10	23.81	3.24 ± 0.43	22.06	3.22 ± 0.39	23.72
	C17:0					0.54 ± 0.15	3.71	0.54 ± 0.14	3.99
	C18:0	1.12 ± 0.08	16.12	1.10 ± 0.05	15.22	1.50 ± 0.09	10.24	1.55 ± 0.07	11.44
Total SFA		3.37 ± 0.33	53.88	3.79 ± 0.34	52.48	6.96 ± 1.04	47.35	6.91 ± 1.02	50.98
MUFAs	C16:1			0.63 ± 0.04	8.69	0.64 ± 0.04	4.33	0.69 ± 0.06	5.11
	C18:1n9	1.56 ± 0.09	22.59	1.52 ± 0.09	21.02	2.40 ± 0.29	16.36	2.35 ± 0.38	17.33
Total MUFAs		1.56 ± 0.09	22.59	2.14 ± 0.44	29.71	3.04 ± 0.88	20.68	3.04 ± 0.78	22.44
PUFAs n6	C18:3n6					0.59 ± 0.02	3.98	0.57 ± 0.02	4.24
	C20:2n6					0.68 ± 0.00	4.61		
	C20:3n6					0.73 ± 0.02	4.97	0.79 ± 0.04	5.83
Total PUFAs n6						1.99 ± 0.07	13.56	1.36 ± 0.11	10.06
PUFAs n3	C20:5n3	0.77 ± 0.09	11.05	0.68 ± 0.40	9.43	1.43 ± 0.52	9.75	1.19 ± 1.13	8.79
	C22:6n3	0.86 ± 0.13	12.48	0.60 ± 0.34	8.38	1.27 ± 0.45	8.66	1.05 ± 0.94	7.73
Total PUFAs n3		1.63 ± 0.12	23.53	1.28 ± 0.35	17.81	2.70 ± 0.49	18.41	2.24 ± 1.03	16.52
Total PUFAs		0.163 ± 0.38	23.53	1.28 ± 0.35	17.81	4.70 ± 0.51	31.97	3.61 ± 0.95	26.58
Total FA		6.93 ± 0.38	100.00	7.22 ± 0.49	100.00	14.69 ± 0.92	100.00	13.57 ± 1.01	100.00

FA: fatty acid, SFA: saturated fatty acid, MUFAs: monounsaturated fatty acids, PUFAs: polyunsaturated fatty acids, SD: standard deviation, %: percentage of fatty acid.

The results evaluated with the two-way PERMANOVA showed no significant statistical differences in the interaction of morphotype*sex in the study areas (PERMANOVA, pseudo-$F_{1,51} = 2.528$, $p = 0.069$) and sex (PERMANOVA, pseudo-$F_{1,51} = 2.1687$, $p = 0.107$); differences were only observed at the level of morphotype (PERMANOVA, pseudo-$F_{1,51} = 22.125$, $p = 0.001$). This finding is confirmed through the ANOSIM test, which showed an R = 0.367, indicating that there are different groups at the morphotype level (see paired test, Table 4).

Table 4. Pairwise test of ANOSIM (analysis of similarity) (global R: 0.367; $p < 0.01$), comparing the morphotype*sex interaction of *G. monodon* off the coast of Pisco in Perú (pelagic morphotype) and Faro Carranza in Chile (benthic morphotype).

Groups	**R Statistic**	**Significance Level %**
Pelagic-Male, Benthic-Male	0.654	0.001
Pelagic-Male, Pelagic-Female	0.193	0.069
Pelagic-Male, Benthic-Female	0.631	0.001
Benthic-Male, Pelagic-Female	0.443	0.003
Benthic-Male, Benthic-Female	0.014	0.276
Pelagic-Female, Benthic-Female	0.431	0.002

Through the principal coordinates analysis (PCoA) (Figure 5), it was possible to verify the differentiation and/or grouping between the fatty acid profiles of the pelagic and benthic morphotypes, which indicate that this variability is explained by 80.5% (sum of the % of the PCO1 and PCO2 axis (Figure 5)). Finally, the SIMPER test revealed that FAs contributed the most to this variability, ranging from 8% to 40% (see Table 5).

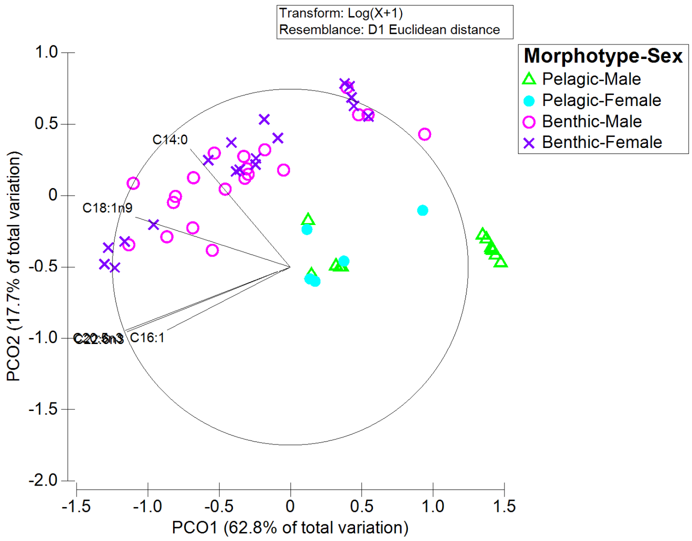

Figure 5. Male and female individuals of *G. monodon* in the HCE. Two contrasting morphotypes in their geographic distribution margins: (i) PM, pelagic morphotype (~15° S: Pisco, Perú) vs. (ii) BM, benthic morphotype (~35° S: Faro Carranza, Chile). Principal coordinates analysis (PCoA) of fatty acids profile. Main fatty acids: C14:0, C16:1, C18:1n9, C20:5n3, C22:6n3.

Table 5. Contribution percentage of the main fatty acids in males and females of *G. monodon* off the coast of Pisco in Perú (pelagic morphotype) and Faro Carranza in Chile (benthic morphotype), using the SIMPER test (similarity percentage), through Euclidean distance.

Morphotype	Fatty Acid	Av. Value	Av. Sq. Dist	Sq. Dist/SD	Contrib %
Pelagic	C14:0	0.185	4.55E-02	0.42	8.77
	C20:5n3-EPA	0.31	8.41E-02	0.58	16.21
	C22:6n3-DHA	0.314	9.87E-02	0.57	19.02
	C18:1n9	0.548	0.205	0.54	39.55
Benthic	C16:1	0.199	6.36E-02	0.57	9.44
	C22:6n3-DHA	0.631	0.176	0.5	26.17
	C20:5n3-EPA	0.683	0.211	0.5	31.33

Av. Value: mean value, Av. Sq. Dist: average square distance, Sq. Dist/SD: square distance, Contrib %: contribution percentage.

4. Discussion

Our findings reveal that the lifestyles of *G. monodon*, together with their body and biochemistry conditions, are linked to the environmental characteristics of their habitats, thus revealing the functional morphological capacity of the body of *G. monodon* and its relationship with the use of resources and/or nutrients available in the environment [25]. In this context, the HCE presents two large areas of nutrient upwelling, the first area where the reduction or disappearance of the continental shelf in Perú begins (~15° S, near Pisco) and the second area where the continental shelf reappears and begins to extend down the Chilean coast (~35° S, near the Carranza Lighthouse) [59]. In both study areas, the highest intensity of upwelling during a cycle occurs in the spring season [60,61]. These upwelling dynamics, the habitat geomorphology, and also the ecological interactions that *G. monodon* displays in the HCE (as a keystone species in the food chain: see Yapur-Pancorvo et al. [21]) can modulate their phenotypic responses (contrasting size morphotypes: PM vs. BM) [62] and physiological responses (variations in body and nutritional condition). Together, these can be considered as potentially adaptive biochemical traits, as revealed in the present study [51].

Although *G. monodon* adults in the study areas have comparatively varied sizes and lifestyles, this species converges as an important marine bioresource in the HCE [21]). In Perú, it is essential for the biotechnology industry, as the main marine source of carotenoid pigments, omega 3 oils and chitin/chitosan compounds [20,21]. In Chile, it is the main resource of industrial crustacean fisheries that are destined for human consumption, as an excellent source of marine protein [19,24]. In addition, in both areas, this species plays an important ecological role as a key link in the marine trophic structure [63]. The variations in adult size observed between the two morphotypes (pelagic vs. benthic) could be due to sea temperature, as a regulatory factor of the growth and lifestyle of these organisms, as established in Bergman's rule for ectothermic marine invertebrates from temperate regions [64]. In our findings, it seems that this ecological rule of size is fulfilled, since adult individuals of *G. monodon* from colder regions (Faro Carranza, average temperature 13 °C) had a larger size (CL 32.9–56.9 mm) and weight (11–52 g), compared to those from warmer regions (Pisco, average temperature 20 °C), which had a smaller size (11.23–23 mm) and weight (0.05–1.82 g). These morphometric variables (size and weight) alone could explain the differences in lifestyle presented by this species (pelagic vs. benthic). However, to avoid misinterpretations, these variables must be integrated to consider a standardized relationship such as the relative condition factor (Kn), which in our study present significant differences in the morphotype*sex interaction. This could indicate that other environmental factors, reproductive seasonality, and ecological relationships could be influencing the notable size differences observed in *G. monodon,* such as food availability, reproductive period (i.e., from autumn-March, through winter-June, and to early spring-September), and interspecific relationships (e.g., competition and predation) that occur in the habitat of this species, and which together subsequently impact its growth rates [62].

The Kn is an appropriate indicator to determine the quality and/or nutritional status of a species that lives in heavily exploited marine environments, as is the case of our model species [24]. In this context, since the assessment models of crustaceans exploited by fisheries in the HCE [21,22] only consider the variables of weight and size separately (i.e., not combined), the Kn, which integrates both biological variables, could estimate the health status of individuals in each population. However, the relative condition factor is an indicator at the individual scale, and its use to assess the state of population can be inaccurate in some cases [36,65]. For example, if the population abundance strongly decreases, the competition between individuals within the population also decreases, and therefore, the availability of prey will increase, generating good conditions for the individuals of the population [21,22]. In our results, both adult morphotypes of *G. monodon* (MP from Pisco and MB from Faro Carranza) showed isometric growth (b constant close to or equal to 3 [31,66]) and a Kn value close to or greater than 1, which indicates the healthy development of this species. This reveals that *G. monodon* (as a resource species), in both morphotypes, presents a good condition factor that allows it to develop optimally in its respective environments. Similar Kn trends to those observed in our study have also been reported in the Kn of decapod crustaceans of the Munididae family off the coast of Colombia (*Antillimunida evermanni*, *Babamunida forceps*), which showed isometric growth and Kn values close to 1, confirming a healthy condition for these species [67]. In the present study, the Kn was also able to consistently reflect the biochemical condition of individuals, revealing variations in the content of the main biochemical constituents (in a standardized sample) of both morphotypes.

Variations were found in the carbohydrate contents (measured as glucose) of the two morphotypes. Specifically, where PM was higher than BM, this could be due to the fact that the pelagic lifestyle requires a greater amount of available energy to be used immediately for movement through the water column than life in the benthic zone [68]. Also, according to Wang et al. [69], a pelagic lifestyle in decapods generates a high demand for carbohydrates, mainly glucose, which are necessary in the molting process that determines their growth rates [70]. Carbohydrates are an important source of energy for decapods to produce chitin [71], and an essential element to produce their exoskeleton [70,71]. In our study, we postulate that a higher carbohydrate content could explain the higher frequency and rates of molting that have been mostly recorded in BM [72,73]. This biochemical constituent could be stored both in the hepatopancreas and in the tail muscle [74], to be used in molting processes, which occur in the PM throughout the year, while in the BM they take place only during the summer season [39,69].

Proteins are important biomolecules, forming part of the cellular structure of tissues [39,75]; after carbohydrates and lipids, they are considered the third most relevant energy source and/or metabolic substrate in decapods [76]. In our study, a higher concentration of proteins in BM compared to PM could be due to the development of energy storage strategies influenced by environmental conditions, such as food availability, which, due to the effect of the intense seasonal spring upwelling that occurs in south–central Chile (Faro Carranza study area) [61], can affect the quality of food in the habitat, and consequently influence the amount of proteins stored in the muscle of *G. monodon* [38]. Proteins are particularly important for females during the spring season. At this time, there is a high availability of food in the system, which allows them to synthesize and store more proteins during growth and, therefore, have sufficient proteins to ensure their reproduction and the transfer of these essential biomolecules for successful embryonic development and the subsequent hatching of viable larvae [77].

Lipids, key biomolecules with a high energy content, are stored in the body of crustaceans as their main nutritional source, and can vary due to intrinsic factors (growth, reproduction, competition) and extrinsic factors (temperature, upwelling, habitat biogeochemistry) [62,78,79]. It has been reported that crustaceans can vary intra-specifically depending on the size and weight of the organism, as well as the habitat and trophic lifestyle [78]. In our study, the high presence of lipids in the tail muscle of BM compared to PM is mainly due to a high food availability due to the high spring seasonal upwelling that occurs at the Carranza lighthouse [60,61]. This greater food availability could determine the quality and quantity of energy stored by *G. monodon* [80]. In the case of BM, they need this increased energy to sustain their extensive reproductive period (from early autumn to late spring), characterized by successive egg laying (3–4 years), and the subsequent successful hatching of numerous planktotrophic larvae [80,81]. Furthermore, the significant correlations between morphometric parameters (W, CL, Kn) and biochemical constituents (glucose, lipids) of *G. monodon* could explain its energetic or nutritional condition, and consequently reveal the possible causality of some ecological interactions and environmental factors (e.g., competition, food availability) that occur in its habitat [36].

Fatty acids are important lipid biomolecules involved in many physiological processes including reproduction, muscle contraction, buoyancy, brain and eye development, all of which are key processes for the growth and survival of marine invertebrates [79,82,83]. In our findings, the predominance of saturated fatty acids (SFAs) in both morphotypes is a characteristic biochemical attribute of this species, which stores this type of FA in the tail muscle, establishing the nutritional palatability of this fishery resource for humans [50]. Also, differences in the proportions of certain types of FAs may represent some degree of rigidity (SFA) or fluidity (PUFA) of cell membranes which, when compared in two distant latitudinal zones (present study: 15° S vs. 35° S), may be modulated by water temperature [84,85]. In our findings, the presence of essential fatty acids (polyunsaturated fatty acids-PUFAs), such as DHA (C22:6n3) was recorded only in BM from cold water, which in its functional ecological role (through the homeoviscous adaptation mechanism) allows BM to face the membrane rigidity generated by low and/or cold temperatures [84]. These differences in the FA compositions between morphotypes can be considered as a response and/or adaptive biochemical mechanism that *G. monodon* presents between its morphotypes, depending on the water temperature [84,86].

The condition factor is an important index that reflects the vital interaction between biotic and abiotic factors on the physiological performance of marine organisms and can be used as an index of health and/or condition status [87]. In the case of fishery resources, such as *G. monodon*, this index is essential for the management and conservation of natural populations within an ecosystem approach that allows for their adequate exploitation [88,89]. In addition, the condition factor can strengthen the fishery biological parameters used in fishery management models and their estimates. These results suggest the importance of future studies establishing whether these morphotypes, lifestyles and physiological processes (e.g., molt and gonadal cycle) of *G. monodon* adults (pelagic vs. benthic) maintain themselves or vary along the latitudinal gradient. In future research, it is also necessary to explore information on latitudinal variations in the integrated bioenergy status of this resource, considering its wide geographic distribution in the HCE, particularly along the coasts of Perú and Chile, where it is commercially exploited by fisheries.

5. Conclusions

In conclusion, the red squat lobster *G. monodon* in its distribution margins in the HCE is exposed to highly contrasting environmental [13] and geomorphological [44,90,91] conditions. In response to these contrasting habitat conditions, *G. monodon* adults present different lifestyles (pelagic vs. benthic), which are highly noticeable in their phenotype (size and shape: small and compact vs. large and elongated), and can be considered a functional morphological trait adapted to the type of environment. In turn, considering a standard comparative parameter that integrates the size and weight relationship for both morphotypes, such as the relative condition factor (Kn), our findings reveal significant differences between morphotypes; they both presented a tendency of isometric growth. Therefore, our hypothesis regarding the variability of the relative condition factor is accepted. In turn, our hypothesis indicating differences in the content of biochemical constituents between morphotypes of different habitats is accepted. These biochemical responses can be considered potentially adaptive in response to the combined effect of key environmental factors (temperature, food availability) that vary at the latitudinal level in the HCE, and that could be modulating the capacity of ectothermic invertebrates to store energy for fundamental physiological processes that occur during their ontogeny, such as reproduction and growth.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes9110445/s1, Figure S1: Length–weight relationship of *G. monodon* individuals captured in the HCE during late October of the year 2021. Figure S2: Correlogram among the parameters analyzed (CL, W, Kn, glucose, proteins, lipids) of *G. monodon* individuals captured in the HCE during late October of the year 2021. Asterisk in red (*) shows significant differences. Table S1: One-way analysis of variance on size (cephalothorax length), weight and relative condition (Kn) between males and females within each morphotype (pelagic and benthic) captured at the locations of Pisco in Perú and Faro Carranza in Chile. Table S2: Two-way analysis of variance in the relative condition factor (Kn) and biochemical condition (glucose, protein and lipid) between morphotypes (pelagic, benthic) and sexes (male, female) captured in the localities of Pisco in Perú and Faro Carranza in Chile. Table S3: One-way analysis of variance between morphotypes (pelagic vs. benthic) according to sex (males, females) in relation to their relative condition factor (Kn) and biochemical condition (glucose, proteins, and lipids) in individuals captured in the localities of Pisco in Perú and Faro Carranza in Chile.

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