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Article

Morphometrics of the Blue Crab *Callinectes sapidus* Rathbun, 1896 in a Northern Adriatic Saline Marsh Under Environmental Stress

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Abstract

The Atlantic blue crab (*Callinectes sapidus*) has rapidly expanded across the Mediterranean, raising concerns over its ecological and economic impacts. This study examines the morphometric characteristics and environmental influences on *C. sapidus* populations in the Palud-Palù swamp (western Istrian coast) from 2022 to 2024. A total of 203 specimens were analyzed for carapace width, length, depth, and body mass, alongside monthly measurements of temperature, salinity, oxygen saturation, and pH. Statistical analyses (*t*-tests, ANOVA, PCA, and RDA) revealed pronounced sexual dimorphism, with males consistently larger than females. Interannual differences in size distribution showed larger individuals in 2022, followed by a decline in 2023 and 2024, likely due to environmental stressors (e.g., salinity, temperature, hypoxia) and increased anthropogenic pressures (e.g., trapping and illegal harvesting). RDA identified temperature, oxygen saturation, and pH as key abiotic drivers of morphometric variation. These findings suggest that while *C. sapidus* demonstrates physiological plasticity, enabling its persistence in estuarine environments, its growth and invasive potential may be constrained under extreme or suboptimal local conditions. This study highlights the importance of long-term monitoring and integrated management to mitigate ecological disruption in sensitive coastal ecosystems.

Keywords: decapods; invasive species; crustacean morphometry; length–weight relationship; population structure; size distribution

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1. Introduction

The Atlantic blue crab (*Callinectes sapidus* Rathbun, 1896) is a prominent example of an invasive species in the Adriatic Sea (Figure 1). Originally native to the western Atlantic, from Nova Scotia to Argentina, the species was first described by Mary Jane Rathbun in 1896. This species is highly adaptable to new environments, resilient to climate change, and possesses a high reproductive capacity, all while lacking natural predators. These factors contribute to its recognition as one of the 100 most invasive species in the Mediterranean [1].

The introduction of the blue crab into the Mediterranean is attributed to three main hypotheses: its natural arrival due to strong swimming capabilities, transfer through ballast water from extensive maritime traffic, and intentional introduction for commercial purposes [2]. A comprehensive database detailing its distribution in both native and non-native ranges confirmed numerous records in the Mediterranean Sea, indicating that the species can now be considered "virtually ubiquitous" [3,4]. Its first confirmed record in northern Adriatic dates back to 1949 from the Grado Lagoon in the Gulf of Trieste when it was identified as *Neptunus pelagicus* [5]. The accurate identification was confirmed in 1993 after the discovery of two males in the Venice Lagoon during 1991 and 1992 [6]. The blue crab was often misidentified as *Neptunus pelagicus*, *Portunus segnis*, or *Portunus pelagicus* [7]. The abundance of this invasive species has recently escalated in the Po River Delta, disrupting local fisheries where devastating effects have been observed on clams, mussels, and oysters' farms [8] as well as on several commercial fish species [9]. On the eastern coast of the Adriatic Sea, it was first observed at the mouth of the Neretva River in 2004 and has successively been documented along the entire coast [7,10,11]. The blue crab (*Callinectes sapidus)* has been present in the northern Adriatic, particularly along the western part of Istria, since at least 2013 (pers. observations, Neven Iveša and Paolo Paliaga). Its presence has become increasingly established in recent years, and since 2021, it has been regularly recorded in coastal lagoons characterized by fluctuating salinity—most notably in the Palud-Palù salt marsh. Located in western Istria, the Palud-Palù special ornithological reserve is a protected area of high ecological value. This unique wetland, connected to the sea via an artificial channel, provides critical habitat for numerous bird species, including those protected under the European Union's Birds Directive (Directive 2009/147/EC).

Figure 1. The Atlantic blue crab (*Callinectes sapidus* Rathbun, 1896).

The first confirmed observation of the blue crab in the reserve dates back to summer 2021. Since then, its establishment has raised ecological concerns due to potential negative impacts on the native fauna. These include indigenous decapod species such as *Eriphia spinifrons*, *Xantho* sp., and *Maja crispata*, as well as various fish species like *Diplodus vulgaris*, *Diplodus puntazzo*, and *Sparus aurata* [12–14]. The introduction of this invasive predator into a fragile and biodiversity-rich ecosystem such as Palud highlights the need for further ecological research, especially regarding its interactions with native species and the potential for long-term ecological shifts.

Studies by Mancinelli et al. [15] using international databases revealed extensive records of blue crab occurrences in both native and invaded areas, reflecting its wide scientific study over 125 years. The species' northward migration within its native range is driven by global warming, with warming coastal waters facilitating its spread [16]. Predictive maps indicate suitable conditions across the entire Mediterranean basin for sustaining *C. sapidus* populations under all considered warming scenarios [17].

Morphometric analysis serves as a valuable tool in population studies, offering complementary insights alongside genetic and environmental methods for stock identification [18]. They are indicators in crustacean biology, facilitating the assessment of reproductive maturity [19,20], ontogenetic development [21], sexual dimorphism [22], and shape transitions across life stages [23]. Length–weight relationships are instrumental in translating linear growth models into weight-based equations, which are essential for integration into stock assessment frameworks [24,25]. These relationships are particularly significant for estimating stock biomass and, consequently, guiding sustainable exploitation. For crustaceans, length–width/weight models are considered especially effective in evaluating population parameters [25]. Morphometric and length–weight characteristics are commonly applied in assessments of commercially exploited species, aiding in the evaluation of population dynamics and stock assessment [26]. Moreover, morphometric traits can serve as effective indicators of population-level differentiation, supporting stock delineation efforts. Variations in overall body shape often reflect underlying morphological divergence within a species [27]. Pronounced morphological changes occur during the shift from juvenile to adult stages, particularly in sexually dimorphic structures such as the pleon, chelipeds, and gonopods [28]. These characteristics have significant ecological implications, as they directly influence reproductive output and overall fitness [29], and are therefore often prioritized in morphometric research.

The morphological differentiation observed throughout ontogeny is predominantly a result of adaptive responses to ecological and environmental pressures [30], with genetic determinants playing a foundational role in shaping phenotypic outcomes [31]. These integrated factors modulate organismal performance and influence how individuals respond to natural selection [32]. In this regard, morphometric analyses provide a rigorous quantitative framework for examining the interplay between environmental variability, genetic inheritance, and phenotypic plasticity [32].

Given the increasing densities of *C. sapidus* populations and the potential ecological advantages associated with rising seawater temperatures, this species has been identified as a promising candidate for targeted commercial exploitation in European waters [33]. The implementation of such initiatives necessitates a thorough understanding of population dynamics, for which morphometric approaches and length–weight relationships remain standard and reliable methodologies [26,34]. These techniques are essential not only for characterizing extant populations, but also for informing sustainable management strategies and evaluating species' adaptability in novel environments.

The aim of this study is to investigate the morphometric characteristics of the blue crab (*C. sapidus*) within a small coastal marsh in the northern Adriatic, a habitat characterized by pronounced seasonal fluctuations in temperature and salinity. These extreme and dynamic abiotic conditions have the potential to significantly influence the structure, morphology, and population dynamics of this invasive species. As a keystone species that connects multiple trophic levels and exerts substantial ecological pressure on invaded environments, the blue crab's presence in such a variable habitat warrants detailed investigation. Understanding its biology and ecological responses under these stress conditions is essential for effective monitoring and management, and the data obtained will contribute to a more comprehensive assessment of its ecological impact on transitional coastal systems.

2. Materials and Methods

2.1. Study Area

This study was conducted in the Croatian part of northern Adriatic. Sampling was performed in the special ornithological reserve Palud-Palù, located on the western Istrian coast, eight kilometers southeast of Rovinj-Rovigno (Figure 2).

The reserve's diverse ecosystem provides a habitat for various species, including the invasive *C. sapidus*. Palud-Palù, declared a special ornithological reserve in 2001, is the only protected area of its kind in Istria County, covering about 18 hectares. The wetland formed in a natural depression due to the accumulation of waters leaching from the surrounding hills and a northern spring. In 1906, a 200 m canal was dug to connect the wetland to the sea and prevent malaria. Palud-Palù is known for its high biodiversity and numerous bird species [35]. The reserve includes an inner marsh area and a canal extending to the sea. About 30 m from the marsh area, there is a sluice gate that regulates water flow, acting as a dam. Beyond the sluice gate, the canal ends at a grated structure that prevents large debris entry and optimizes water flow. Behind the grate is a concrete tunnel leading to a basin that communicates with the sea through channels between large stone blocks (Figure 3).

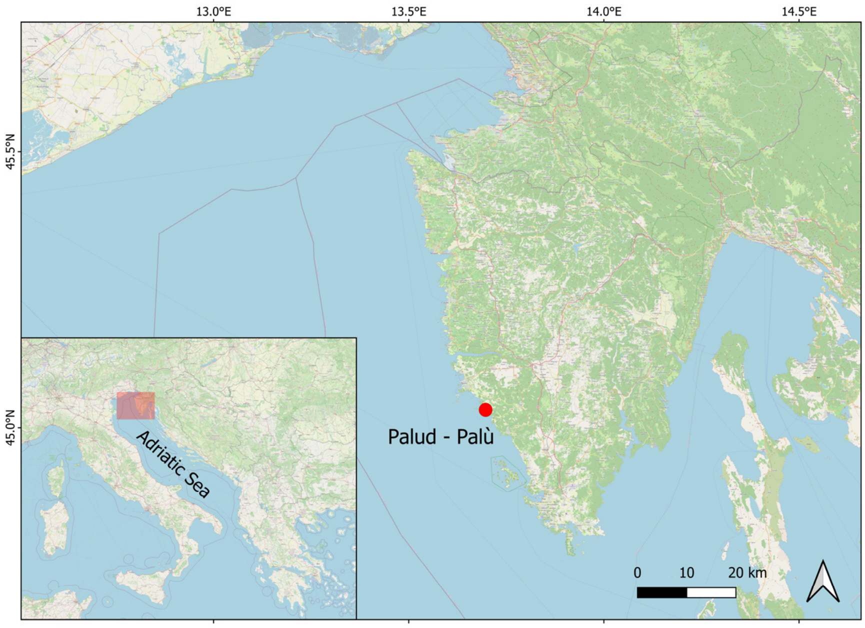

Figure 2. The sampling location, Palud-Palù, on the western Istrian coast in the northern Adriatic Sea.

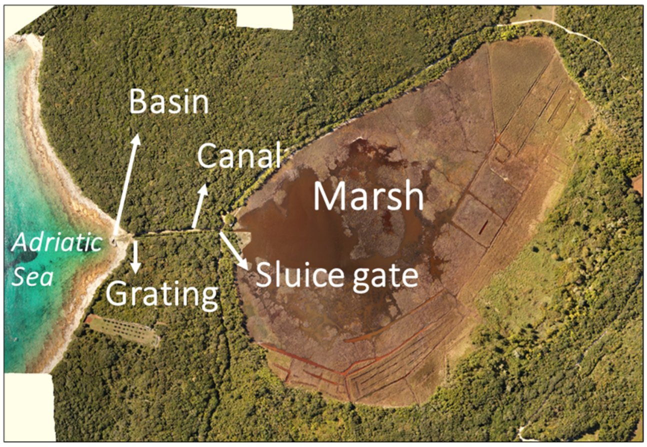

Figure 3. Configuration details of the Palud-Palù study area.

2.2. Sample Collection, and Abiotic and Morphometric Measurements

Specimens of *C. sapidus* were collected from the Palud-Palù area during the period from April to December from 2022 to 2024. This time frame was selected based on the 2022 monitoring results, which showed that the species can only be reliably found in the area during these months. In winter, due to low temperatures, the crabs are either buried in the sediment or absent from the site. The collection of crabs was performed using a hand net and baited fishing traps during both day and night. Immediately after collection, the specimens were transferred to portable coolers with ice to reduce metabolic intensity, and then frozen at −20 °C. A total of 203 specimens were collected and analyzed. Abiotic parameters were recorded monthly from April to December over a three-year period (2022–

2024). Surface water temperature (T), oxygen saturation (O_2 [%]), salinity (S), and pH were measured monthly in situ at two stations (P and S) using a multiparameter probe (Hanna ™ Instruments, USA.). Station P was positioned within the marsh, while Station S was located in the sea in its close proximity (Figure 4). Station S served as a control station, representing baseline coastal marine conditions.

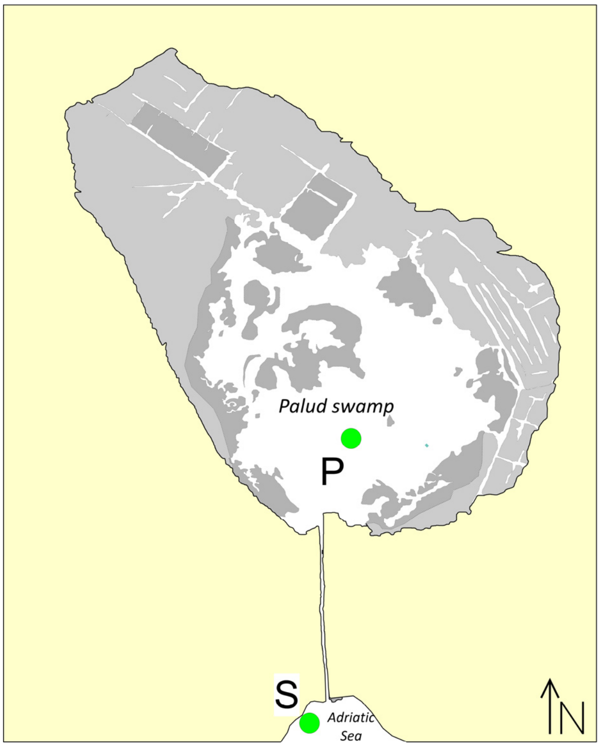

Figure 4. Sampling locations for surface water temperature, oxygen saturation, salinity, and pH.

For all specimens, measurements were taken of carapace width (CW) in cm, carapace length (CL) in cm, carapace depth (CD) in cm (Figure 5), and body mass in grams. The sex of each crab was noted, and Fulton's condition factor (K%) was calculated to assess the overall condition of the specimens.

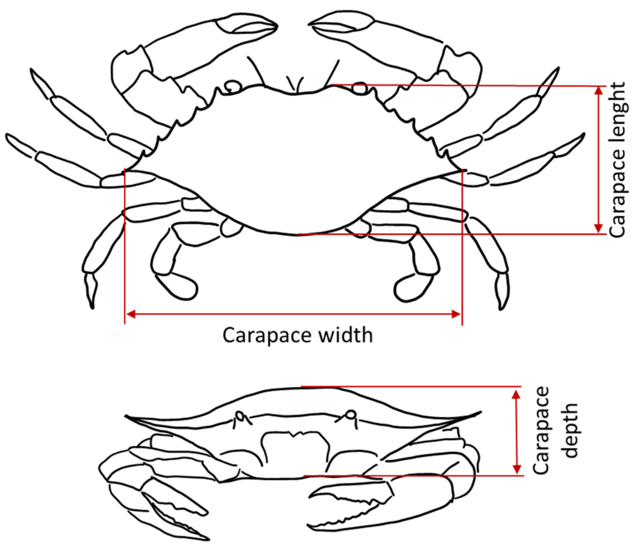

Figure 5. Measurement of carapace width (CW), length (CL), and depth (CD).

Fulton's condition factor (K%) is expressed using the following formula:

$$K\ (\%) = W/CW^3 \times 100 \quad (1)$$

where

K (%) = value of the condition factor
W = blue crab weight (g)
CW = carapace width (cm)

2.3. Statistical Analysis

The data were analyzed using statistical methods in R version 4.4.2 [36]. Descriptive statistics (mean, median, minimum, maximum, and standard deviation) were calculated for each morphological characteristic. To explore sexual dimorphism, *t*-tests or Mann–Whitney U tests were used to compare the measurements between male and female crabs. For annual variation, ANOVA or Kruskal–Wallis tests were conducted to examine differences in size between crabs measured in 2022, 2023, and 2024. Histograms and boxplots were generated to visualize the distributions of each characteristic by sex and year.

Principal component analysis (PCA) was performed using the prcomp function in R to identify the main axes of variation in crab morphology. The first two principal components were used to visualize morphometric variation, with individuals grouped by sex and sampling year. The PCA biplot was enhanced by coloring points according to sex and drawing 95% confidence ellipses around years to explore patterns of morphological differentiation.

To assess the differences in morphological traits between male and female *Callinectes sapidus*, a series of statistical tests were conducted. Welch's two-sample *t*-test was used to compare the means of weight (g), carapace width (CW), carapace length (CL), and carapace depth (CD) between males and females. This test was chosen due to the unequal variances between the two groups. Additionally, Wilcoxon rank-sum tests were performed to confirm the results from the *t*-tests, providing a non-parametric approach for comparison.

Correlation analysis was performed to assess relationships between weight, carapace width (CW), carapace length (CL), and carapace depth (CD) in *Callinectes sapidus*. The correlation matrix was calculated using the cor function, and a correlation plot was generated using the corrplot package in R.

To assess whether the morphometric characteristics of *Callinectes sapidus* varied across years, a multivariate analysis of variance (MANOVA) was conducted. The response variables included weight, carapace width (CW), carapace length (CL), and carapace depth (CD), with the year as the independent variable. Prior to analysis, data were checked for missing values and normality assumptions. The analysis was performed using the manova function in R.

A redundancy analysis (RDA) was performed using the vegan package in R to assess the multivariate relationship between crab morphometry (weight, CW, CL, CD) and abiotic factors (temperature, salinity, pH, dissolved oxygen), along with sampling year as a categorical factor. The morphometric variables were standardized to ensure their equal contribution to the analysis. The significance of the model and canonical axes was tested with permutation ANOVA (999 permutations). Individual environmental predictors were also tested to assess their contribution to explaining morphological variation.

3. Results

3.1. Abiotic Parameters

Monthly measurements of surface water T, S, pH, and O_2 [%] were recorded at two stations, Station P (within the marsh) and Station S (coastal sea). The data reveal seasonal and spatial variability, with notably higher salinity and temperature extremes at Station P, particularly during summer months, accompanied by lower O_2 [%] levels and pH compared to the control site (Table S1). The hydrographic data show that the swamp became progressively warmer over the investigated period, with average temperatures rising from 21.6 ± 7.2 °C in 2022 to 22.1 ± 7.8 °C in 2023 and reaching 24.2 ± 8.8 °C in 2024. The adjacent sea also exhibited a warming trend, though more modestly, increasing from 20.1 ± 4.7 °C in 2022 to 21.3 ± 5.1 °C in 2024. Swamp salinity remained similar in 2022 (38.0 ± 8.4 ‰) and 2023 (39.0 ± 6.8 ‰), but surpassed 40‰ in 2024 (40.4 ± 9.5 ‰), with peaks of 56.7‰ in July. In contrast, the sea salinity slightly increased from 36.5 ± 0.8 ‰ in 2022 to 36.8 ± 0.7 ‰ in 2023 before dropping to 35.4 ± 2.4 ‰ in 2024. Interestingly, a marked drop in swamp salinity was recorded in May 2024 (24.9‰), possibly indicating freshwater input. Average swamp oxygen saturation remained around 72.2 ± 22.4% in 2022 and 72.8 ± 17.5% in 2023 but dropped significantly to 62.6 ± 25.4% in 2024, with extreme lows (~23–27%) in the summer. Meanwhile, the sea maintained high oxygen saturation, ranging between 98.8 ± 5.6% and 99.6 ± 3.9%. Swamp pH values were stable at around 7.90 ± 0.1 in 2022 and 7.90 ± 0.1 in 2023 but declined to 7.76 ± 0.3 in 2024. In contrast, sea pH showed a slight increase from 8.19 ± 0.0 to 8.23 ± 0.0. Overall, the swamp showed increasingly extreme summer conditions, with elevated temperatures, salinity, and oxygen depletion, highlighting its growing environmental stress and sensitivity compared to the adjacent sea.

3.2. Morphometric Measurments

A total of 203 individuals of *C. sapidus* were collected from the swamp from 2022 to 2024. Among the collected specimens, the majority were males, with only a smaller proportion being females. For each individual measurement of carapace width (CW), carapace length (CL), carapace depth (CD), and body mass were recorded. Carapace width varied between 7.13 cm and 15.40 cm, while carapace length ranged from 3.60 cm to 7.10 cm. Carapace depth ranged from 2.19 cm to 4.60 cm. Body mass of the specimens ranged from 34.00 g to 240.60 g (Table 1).

Table 1. Morphometric measurements and body mass of all collected *Callinectes sapidus* individuals from the Palud-Palù swamp (count—number of collected individuals, SD—standard deviation).

Variable	Count (n)	Average	Median	Min	Max	SD
Weight (g)	203	111.08	100.00	34.00	240.60	45.79
CW (cm)	203	11.14	11.00	7.13	15.40	1.73
CL (cm)	203	5.30	5.26	3.60	7.10	0.68
CD (cm)	203	3.16	3.13	2.19	4.60	0.40

Males were predominant in samples and made 82% of all collected crabs. They generally exhibited greater carapace width and mass compared to females, although some overlap in size was observed between the sexes. The largest individuals were primarily males, with the average carapace width recorded at 11.31 cm and the average body mass at 118.54 g. Females, while generally smaller, showed considerable variation, with the average carapace width of 10.36 cm and an average body mass of 77.64 g.

The results show the overall weight distribution of all collected crabs and most individuals weighed between 50 g and 150 g, with the highest frequency around 100 g (Figure 6).

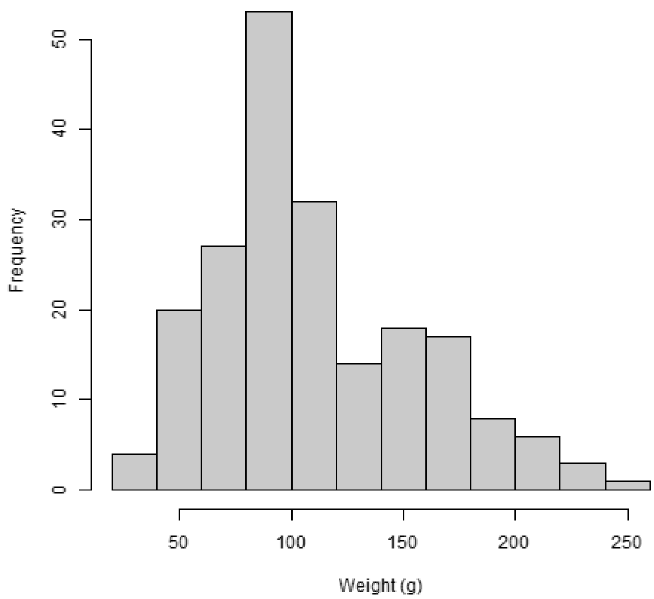

Figure 6. Histogram of weight distribution for all crabs.

3.3. Sexual Dimorphism in Morphometric Traits

The analysis revealed significant sexual dimorphism in the morphological traits of *Callinectes sapidus* collected from the investigated area. For weight, males exhibited significantly higher values than females. The mean weight for males was 118.54 g, while for females, it was 77.64 g. The Welch's *t*-test revealed a significant difference between the two groups ($t = -6.1821$, $p < 0.001$), with the 95% confidence interval for the difference in means ranging from −54.1 g to −27.7 g.

A similar pattern was observed for carapace width (CW). Males had a larger average carapace width (11.31 cm) compared to females (10.36 cm). The Welch's *t*-test showed that this difference was statistically significant ($t = -2.6737$, $p = 0.01031$), with the 95% confidence interval for the difference in means ranging from −1.67 cm to −0.24 cm.

Carapace length (CL) also differed significantly between the sexes. Males had an average carapace length of 5.40 cm, while females had an average of 4.86 cm. The Welch's *t*-test revealed a significant difference ($t = -4.2653$, $p < 0.001$), with the 95% confidence interval for the difference in means between −0.80 cm and −0.29 cm.

Finally, a significant difference was observed in carapace depth (CD), with males having an average of 3.21 cm, while females had an average of 2.95 cm. The Welch's *t*-test indicated a significant difference between the sexes ($t = -3.5254$, $p = 0.0008997$), with the 95% confidence interval for the difference in means ranging from −0.41 cm to −0.11 cm.

Overall, these results highlight clear and statistically significant differences in size between males and females, with males exhibiting larger carapace width, length, depth, and body mass across all measured traits.

3.4. Interannual Variation in Morphometric Traits

All the measurements (weight, carapace width, carapace length, and carapace depth) show statistically significant differences across the years (all *p*-values < 0.001). The F values suggest that year-to-year variations in these measurements are substantial. The results of the statistical analyses indicated significant differences in size measurements between the years

2022, 2023, and 2024. The one-way ANOVA results for the weight (g) of crabs across years showed a significant effect of year (F (1, 201) = 107.6, $p < 2 \times 10^{-16}$). Similarly, significant differences were observed for carapace width (CW) (F (1, 201) = 85.54, $p < 2 \times 10^{-16}$), carapace length (CL) (F (1, 201) = 54.68, $p = 3.75 \times 10^{-12}$), and carapace depth (CD) (F (1, 201) = 52.55, $p = 8.82 \times 10^{-12}$), suggesting that these size measurements also increased in 2022 compared to 2023 and 2024. Boxplots for each of the size variables (weight, CW, CL, and CD) across the years are shown, and the visual inspection of these plots revealed clear differences in the distribution of size metrics among years, with noticeable larger values for the year 2022 (Figure 7). Both the statistical analyses and visualizations suggest that the crabs measured in 2022 were significantly larger than those measured in 2023 and 2024.

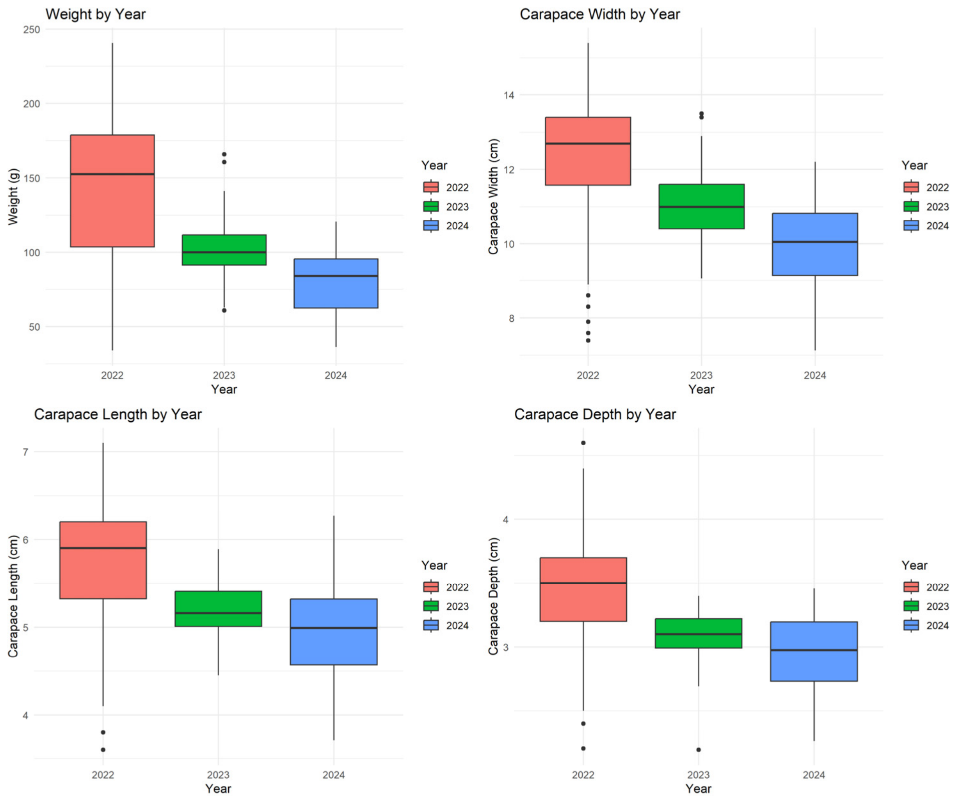

Figure 7. Boxplots of crab size measurements (weight, carapace width, carapace length, and carapace depth) across the years 2022, 2023, and 2024.

The MANOVA results revealed a highly significant effect of year on the combined morphometric traits of *C. sapidus* (Pillai's trace = 0.433, F (4, 198) = 37.85, $p < 2.2 \times 10^{-16}$), indicating differences in overall body morphology across sampling years.

3.5. Multivariate Analysis of Morphometric Variation

Principal component analysis (PCA) was performed on three morphometric traits of *Callinectes sapidus*—carapace width (CW), carapace length (CL), and carapace depth (CD)—to explore patterns of variation among individuals. The first principal component (PC1) accounted for 94.2% of the total variance, indicating a strong underlying gradient common to all three variables. The second component (PC2) explained an additional 4.3% of the variance. All three morphometric variables loaded strongly and positively on PC1, suggesting that PC1 primarily reflects overall crab size. PC2 showed contrasting loadings among the variables, potentially capturing variation in body shape independent of size. Together, PC1 and PC2 explained roughly 98.5% of the total variation, justifying the use of a two-dimensional ordination plot for visualizing morphometric patterns by sex and year (Figure 8).

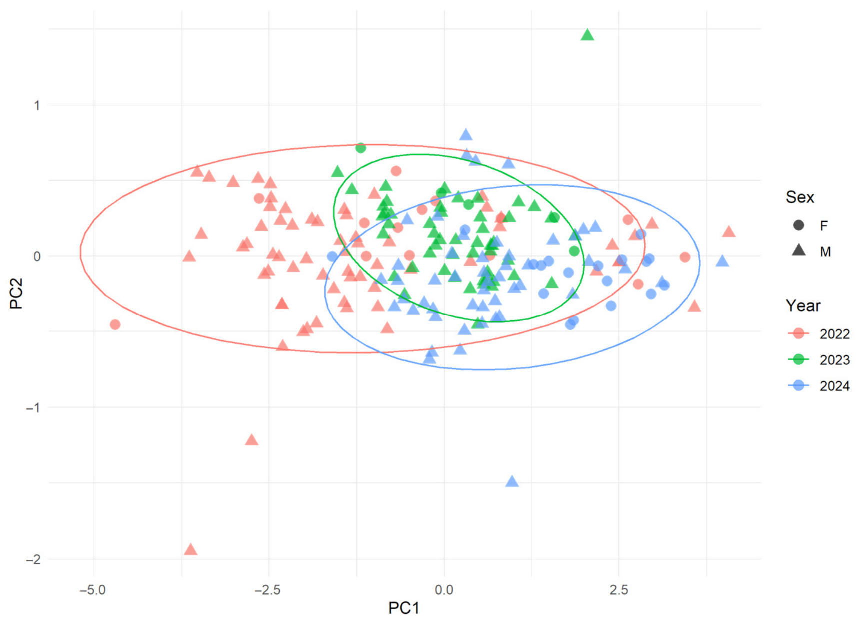

Figure 8. Principal component analysis of blue crab morphometry, grouped by sex and year.

The correlation analysis showed strong positive correlations between weight and all morphometric traits (CW: 0.92, CL: 0.93, CD: 0.87). Carapace width, length, and depth also exhibited high correlations with each other (CW-CL: 0.94, CW-CD: 0.87, CL-CD: 0.92), indicating a common growth pattern (Figure 9).

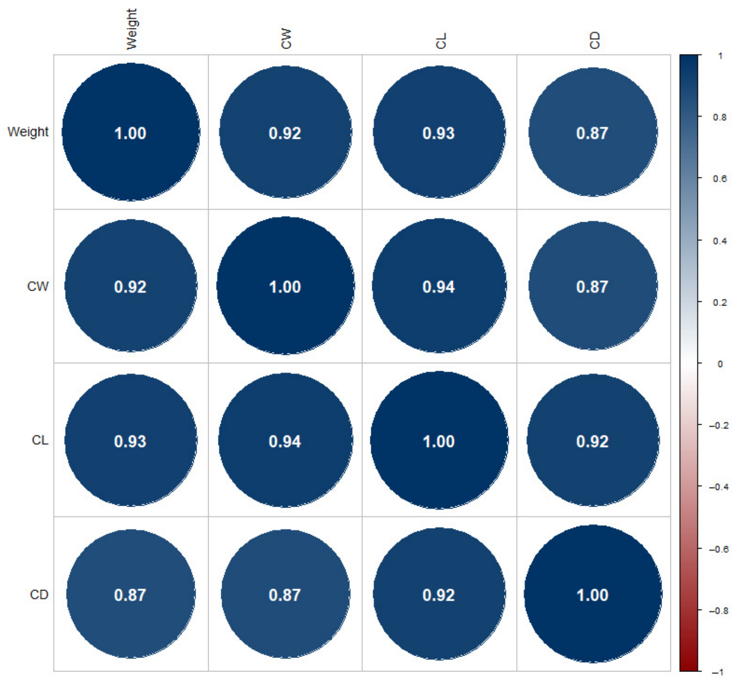

Figure 9. Correlation matrix of morphological traits and weight in *Callinectes sapidus* from the Palud-Palù area.

The log–log regression analysis revealed a significant relationship between carapace width and body mass (R^2 = 0.88). The scatter plot illustrates the growth pattern of *C. sapidus*, with a positive correlation between the variables. The plot also highlights the distribution by year, with separate colors for 2022, 2023, and 2024, and shapes distinguishing males and females. The year 2022 had a higher proportion of larger individuals, while the size distribution was more varied in subsequent year (Figure 10).

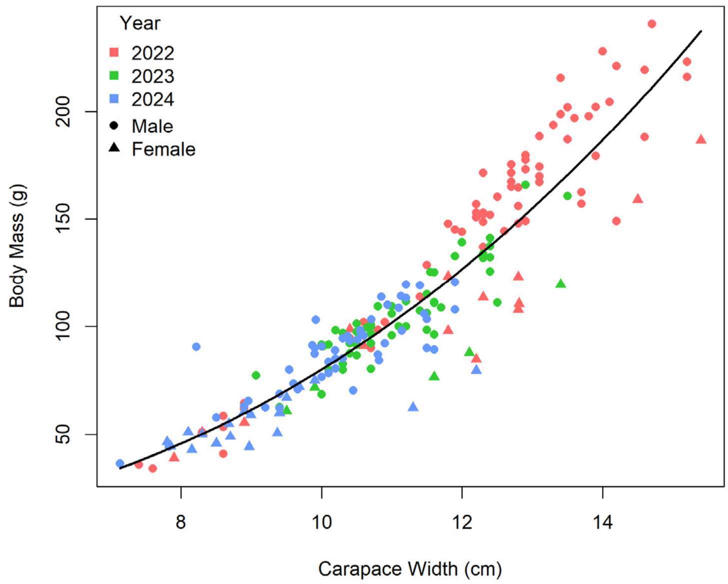

Figure 10. Length–weight relationship by year and sex for *Callinectes sapidus* (Palud-Palù area, 2022–2024).

3.6. Condition Factor Analysis

The calculation of condition factor (K%) by sex revealed visible differences in the distribution of K values between male and female crabs (Figure 11). Female crabs showed a wider range of K values, while males generally had slightly higher median values, suggesting potential variation in condition between sexes. The ANOVA test revealed a statistically significant difference in mean K between sexes ($p < 0.001$), suggesting that sex has a notable effect on the condition factor of blue crabs in the sample (Table 2).

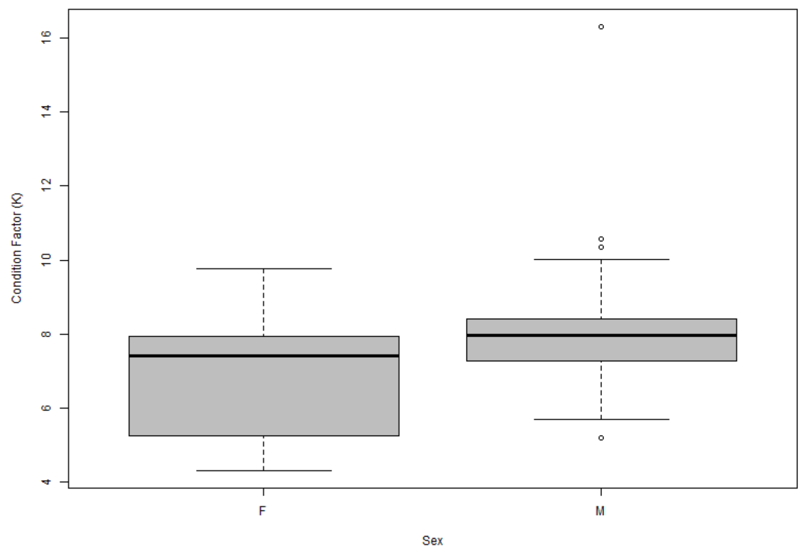

Figure 11. Boxplot of condition factor (K) by sex (F—female, M—male).

Table 2. One-way ANOVA results for the effect of sex on Fulton's condition factor (K) in blue crabs.

Source	df	Sum of Squares	Mean Square	F-Value	*p*-Value
Sex	1	27.21	27.209	18.29	<0.001
Residuals	201	298.94	1.487		

3.7. Environmental Influences on Morphometry

The RDA model explained approximately 38.4% of the variance in blue crab morphometry, indicating a moderate influence of abiotic conditions and sampling year on size and shape traits. The first canonical axis (RDA1) accounted for nearly 99% of the explained variation, suggesting a strong primary gradient in the data. Morphometric traits (CW, CL, CD) showed distinct correlations with environmental variables, with temperature and oxygen saturation appearing as important drivers. The ordination plot revealed that larger carapace dimensions were positively associated with higher temperatures and oxygen levels, while other parameters such as salinity and pH showed weaker relationships. Sampling year contributed to variation, reflecting temporal changes in environmental conditions and crab morphology (Figure 12). The redundancy analysis (RDA) model demonstrated a significant relationship between blue crab morphometry and abiotic factors, including sampling year (ANOVA permutation test: $p = 0.001$). The first canonical axis (RDA1) was highly significant ($p = 0.001$), capturing the primary gradient of environmental influence on crab morphology, while subsequent axes were not significant. Individual variable testing revealed that temperature ($p = 0.001$), pH ($p = 0.001$), and year ($p = 0.001$) significantly contributed to explaining variation in morphometric traits. In contrast, salinity and dissolved oxygen saturation were not significant predictors ($p > 0.3$). These results indicate that temporal variation and specific abiotic conditions, especially temperature and pH, play important roles in shaping the morphometric characteristics of blue crabs.

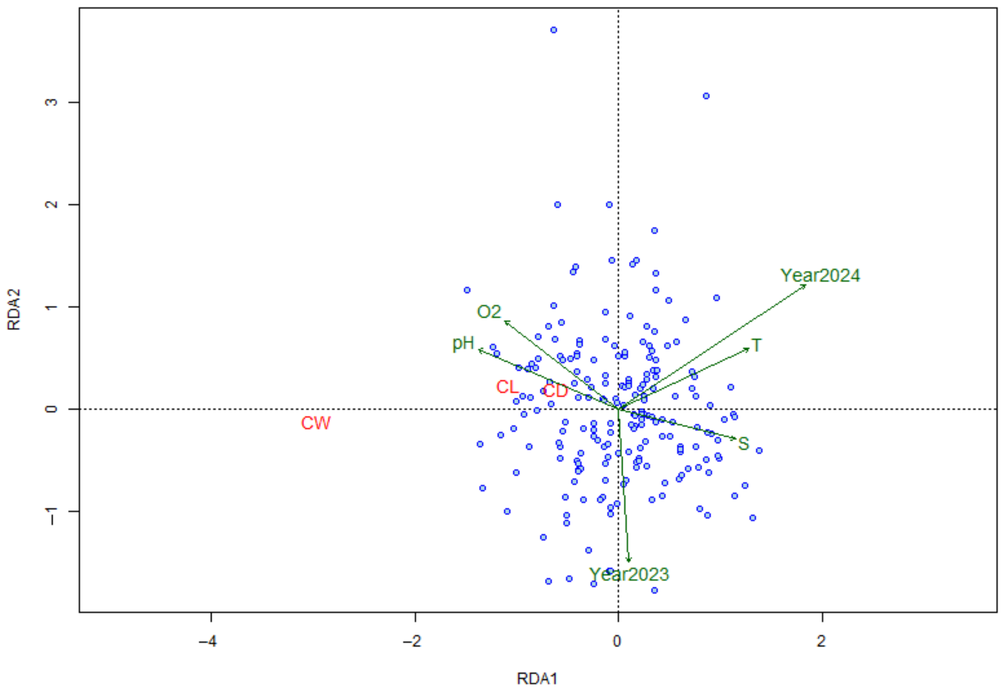

Figure 12. Redundancy analysis (RDA) of *Callinectes sapidus* morphometry in relation to abiotic parameters and sampling year.

4. Discussion

The study on *Callinectes sapidus* populations in the Palud-Palù salty swamp provides an insight into the relationships between abiotic environmental conditions, morphometric characteristics, sexual dimorphism, and temporal variations in growth patterns. The findings highlight the influence of environmental factors and sex-specific differences on crab morphology and condition, with implications for ecological understanding and fisheries management. Across the sampling years, a variation in the size distribution of the individuals was noted. In 2022, most specimens were larger in size and mass compared to those collected in 2023 and 2024, where smaller and younger crabs were more frequently recorded. This trend suggests the possibility of different recruitment events or seasonal variability in population structure over the years. The overall dataset provides valuable insight into the population structure and size distribution of *C. sapidus* in the studied areas, reflecting the continued presence and spread of this non-native species in the region.

Our findings reveal pronounced seasonal and spatial differences in key abiotic parameters, particularly temperature, salinity, and oxygen saturation. The marsh exhibited extreme salinities and temperatures during summer months, coupled with lower oxygen saturation and pH compared to the more stable adjacent coastal environment. These abiotic stresses likely impose physiological challenges that constrain crab growth and condition. Furthermore, salinity fluctuations can impact osmoregulatory energetics, potentially reducing the energy available for somatic growth [37]. This is consistent with prior research indicating that temperature influences metabolic rates and growth in crustaceans, while low oxygen levels can constrain energy allocation for growth [38]. High salinity, as observed in the marsh, may also affect osmoregulation, potentially diverting energy from growth to physiological maintenance [39]. *C. sapidus* showed a significant osmoregulatory capability, facilitating its invasive success in various aquatic habitats. Gender differences are evident in osmoregulation, with females showing greater sensitivity to osmotic stress compared to males, which presented a more consistent response across different salinity levels. In general, the hydrographic conditions of the swamp, although oscillating within the ecological valence for *C. sapidus* (0 to 40 °C for temperatures and 0–64 PSU for salinities) [40], were far away from the optimal salinity conditions (18 PSU) and close to the upper temperatures that allow the crab's growth (30 °C). On the other hand, swamp waters had oxygen levels which were well above the threshold of 0.6 mg/L (approximately 9% saturation) at 24 °C, which in laboratory conditions cause specimen mortality within 24 h [41]. The reason that the swamp can maintain tolerable summer conditions for *C. sapidus* can be ascribed to the periodic tidal exchanges which lower T and S every six hours, bring oxygen to the system and prevent pH from decreasing excessively. During low tides, bottom waters in the inner parts of the swamp become very hypoxic (6–8% O_2 [%]), hypersaline (60 PSU) and can reach 37 °C (pers. observations Paolo Paliaga), and this is why the majority of the specimens is concentrated in the channel and the adjacent portion of the swamp, where tidal influence is strongest.

In addition to salinity, temperature, and oxygen, pH represents an important abiotic stressor shaping blue crab ecology in the swamp environment. Our measurements show that swamp waters exhibit lower and more variable pH values than adjacent coastal zones, particularly during summer stagnation and low-tide periods, when tidal flushing is limited. Such episodes of local acidification are common in shallow estuarine wetlands and result from high rates of organic matter decomposition and CO_2 accumulation [42,43]. Although *C. sapidus* demonstrates some tolerance to moderate acidification, experimental studies suggest that reduced pH can impair larval development or slow growth, especially under extreme or fluctuating conditions [44]. Low pH can also increase the metabolic cost of acid–base regulation in decapod crustaceans, diverting energy from growth and reproduction to physiological maintenance [45]. These costs may be compounded under synergistic stress from high temperature and acidification [46], conditions documented in the inner parts of the swamp during summer. While periodic tidal exchange likely mitigates extreme acidification and maintains conditions within the species' ecological tolerance, the observed spatial segregation of crabs toward better-flushed channels suggests behavioral avoidance of the most stressful low-pH, hypoxic, and hypersaline zones. Such dynamics underscore the importance of pH variability as a potential constraint on recruitment success, growth rates, and overall population resilience in invaded estuarine habitats.

The physiological plasticity of *C. sapidus* provides a competitive advantage over native species, enhancing its successful invasion [47]. These findings suggest that estuarine habitats may pose unique challenges or opportunities for blue crab growth, depending on seasonal conditions. The ecological dominance of *C. sapidus* in the Palud-Palù reserve underscores its role as a keystone species capable of altering trophic dynamics. Its omnivorous feeding habits, which include predation on native mollusks, fish, and crustaceans, can lead to cascading effects on local food webs, potentially reducing biodiversity and disrupting ecosystem services [48]. The observed increase in crab size in 2022 may reflect favorable environmental conditions, which enhance metabolic rates and growth but could also exacerbate competitive interactions with native species [4]. These interactions highlight the need for adaptive management strategies, such as targeted removal programs or habitat restoration, to mitigate the crab's impact. For instance, studies in other invaded regions have shown that sustained trapping efforts can reduce *C. sapidus* populations, thereby alleviating pressure on native fauna [49]. Integrating such approaches with real-time environmental monitoring could enhance their effectiveness in the Palud-Palù ecosystem.

Consistent with some previous studies on *C. sapidus*, males were more abundant and exhibited larger body sizes than females across all morphometric traits [50,51]. Sexual dimorphism in blue crabs is typically attributed to differences in reproductive strategies and behavior, with males investing in larger size for territorial defense and mating success, while females prioritize energy allocation toward reproduction [52,53]. The strong positive correlations observed among morphometric variables reflect coordinated allometric growth patterns, which are common in crustaceans [26,53]. The significant interannual differences in crab size, with larger individuals recorded in 2022 compared to 2023 and 2024, suggest fluctuating environmental conditions or resource availability influencing growth. Such year-to-year variation has been reported in other *C. sapidus* populations and linked to factors including temperature variability, food supply, and fishing pressure [54]. The log–log regression of carapace width and body mass demonstrated consistent growth allometry but with clear shifts in size distribution between years, reinforcing the role of environmental fluctuations in shaping population structure. Principal component analysis (PCA) showed that the primary axis of variation was associated with overall size, while secondary axes captured shape differences, such as trade-offs between carapace dimensions. The strong correlations among morphometric traits indicate a coordinated growth pattern, consistent with allometric scaling in crustaceans [53]. These patterns suggest that sexual dimorphism in blue crabs is not only a function of size, but also of subtle shape differences that may reflect ecological or reproductive roles.

Statistical analyses confirmed that year-to-year differences in crab morphometry were significant, likely driven by annual differences in environmental conditions such as temperature, salinity, or food availability. Milder winters due to climate change are expected to enhance winter survival and support faster growth and brood production. However, elevated temperatures may also lead to higher juvenile mortality and a decrease in size at maturity [55]. These findings align with studies showing that blue crab populations exhibit high interannual variability in response to environmental fluctuations [56]. The observed temporal patterns underscore the importance of long-term monitoring to disentangle the effects of climate variability and other ecological factors on population dynamics.

A comparison of our morphometric data with other studies from the region confirms significant spatial variability in the size structure and body condition of *Callinectes sapidus* populations. While our study revealed a strong male predominance and moderate size range across individuals, other regional studies have documented populations with more balanced sex ratios and overall larger body dimensions. For example, Glamuzina et al. [11] reported significant size differences between males and females, with males consistently larger and heavier, though females were more numerous. Mancinelli et al. [57] noted marked growth differences and sex-specific growth trajectories in the Lesina Lagoon, and Tiralongo et al. [58] highlighted spatial variation, with coastal populations exhibiting far larger sizes than their riverine counterparts. Compared to these populations, the individuals recorded in our study appear smaller and less variable in size, particularly in the latter years. This trend may be partly attributed to environmental constraints specific to the Palud-Palù swamp, such as elevated salinity, extreme summer temperatures, and periodic hypoxia, which can impair growth and condition. However, alternative explanations must also be considered. An actual trapping program was initiated after 2022, coordinated by the public institution Natura Histrica that manages the area, which deployed baited traps in targeted areas. It is plausible that the largest crabs were captured early on through this program, potentially removing the biggest individuals from the population and thereby contributing to the observed decline in average size in subsequent years [59]. A further hypothesis is that, in more recent years, local harvesting pressure on larger individuals increased, possibly due to rising awareness among fishers of the blue crab's market potential. This is supported by observations of increased illegal fishing activity in the area in the last two years (pers. observations Paolo Paliaga). If larger crabs were selectively removed by fishers, this could have contributed to the observed shift in size distribution. Unregulated harvesting pressure could have intensified, with fishers further targeting the largest crabs for their commercial value, a pattern well documented in blue crab fisheries [60]. Such size-selective removal can shift population structure toward smaller and younger individuals, independently of environmental drivers, while density-dependent competition and recruitment dynamics can further shape these patterns [51,61]. Taken together, these factors suggest a complex interplay of ecological pressures, anthropogenic influences, and sampling biases, all of which likely shape the morphometric trends observed in the population. Such dynamics underscore the need for integrated management approaches that consider both biological and socio-economic dimensions of the blue crab invasion.

The condition factor analysis indicated differences between sexes, with males generally showing higher condition values and females displaying greater variability. This could reflect reproductive demands in females, such as energy allocation to egg production, which may lower their condition during certain periods [62]. The condition factor is a valuable metric for assessing physiological health and environmental suitability, as it reflects energy reserves and growth efficiency [63]. Differences in condition between sexes suggest potential variations in fitness or resilience, which could influence population dynamics and reproductive success. These findings have implications for fisheries management, as condition can affect the sustainability of harvested populations.

The RDA results demonstrate that abiotic factors significantly shape the morphometric variation observed in blue crab populations. Temperature and oxygen saturation emerged as key environmental drivers, consistent with the physiological demands of crustaceans that influence growth and development. The notable proportion of variance explained by year highlights the importance of temporal environmental fluctuations, possibly related to climatic variability or habitat changes. These findings suggest that blue crab morphometry is sensitive to local abiotic conditions, which could have implications for population dynamics and management. This supports earlier findings that environmental parameters are key drivers of morphometric variation in estuarine crustaceans [64,65]. Moreover, the integration of morphometric data with ecological modeling can improve predictions of invasion dynamics under future climate scenarios. For example, predictive models suggest that warming Mediterranean waters will likely expand the number of suitable habitats for *C. sapidus*, potentially intensifying its ecological impacts [17,66]. Such insights are critical for developing proactive management plans, including stakeholder engagement with local fishermen to balance ecological conservation with economic interests [67,68]. Future studies should incorporate finer-scale temporal and spatial data and explore the causal mechanisms underlying these patterns. With climate change projections indicating increases in temperature and salinity variability [69], understanding these morphometric responses is critical for anticipating shifts in growth patterns and population viability [70].

The interplay of abiotic factors, sexual dimorphism, and temporal variation highlights the complexity of *C. sapidus* ecology in coastal and estuarine systems. The significant influence of temperature suggests that climate change, which is likely to alter these parameters, could impact blue crab populations. Increasing temperatures and hypoxia in estuaries may reduce growth and survival, as noted in studies of crustaceans in estuarine and coastal environments [55,71].

5. Conclusions

This study on the invasive Atlantic blue crab (*C. sapidus*) in the Palud-Palù ornithological reserve in the northern Adriatic, highlights its significant ecological impact and morphometric variability from 2022 to 2024. Although this study does not statistically model invasion mechanisms or predict ecological risk, the observed morphometric patterns, environmental correlations, and potential anthropogenic influences offer a valuable foundation for future research aimed at understanding the invasion dynamics of *C. sapidus* in the northern Adriatic. Morphometric analyses revealed pronounced sexual dimorphism, with males consistently larger than females across carapace width, length, depth, and body mass. Interannual differences, with larger crabs in 2022, suggest environmental influences as key drivers of morphometric variation. These may include extreme salinity and temperature fluctuations, hypoxia, and suboptimal habitat conditions within the swamp environment, which impose physiological stress and limit growth. Strong correlations among morphometric traits indicate coordinated growth patterns, while condition factor differences reflect sex-specific reproductive demands. However, recent anthropogenic factors, such as the introduction of trapping programs and increased fishing pressure, may also be contributing to the observed shifts in size distribution. It is plausible that larger individuals were selectively removed either through trapping or unregulated harvesting, particularly in recent years as public awareness of the species' edibility and commercial value increased. These alternative explanations, together with climate-related changes, underscore the complex and multifactorial nature of morphometric variability in invasive populations. Along with the recorded size of individuals over three consecutive years, this may suggest that the *C. sapidus* populations in the Palud-Palù area are not exhibiting the typical patterns associated with strong invasiveness, as some authors have previously questioned [72]. The findings of this study highlight that, under the influence of abiotic stressors and spatial conditions, such as high salinity fluctuations, limited spatial range, and possible resource scarcity specific to the Palud salt marsh, the population growth and invasive potential of this species may be constrained. This also emphasize the necessity of continuous monitoring and targeted control measures to mitigate ecological disruptions in this protected ecosystem. Long-term studies integrating environmental data, fishery activity, and population dynamics are needed to clarify causal mechanisms and inform future conservation strategies. As climate change alters abiotic conditions, understanding these dynamics is crucial for developing effective management strategies to ensure the sustainability of local fisheries and the preservation of native species in the Adriatic Sea.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/app15147990/s1, Table S1: Monthly in situ measurements of surface water temperature (T), salinity (S), pH, and oxygen saturation (%O_2) at Station P (marsh) and Station S (sea) from April 2022 to December 2024.

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