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EDITED BY

Paolo Magni,
National Research Council (CNR), Italy

REVIEWED BY

Lucrezia Cilenti,
National Research Council (CNR), Italy
Sofia Reizopoulou,
Hellenic Centre for Marine Research
(HCMR), Greece

*CORRESPONDENCE

Cristina Munari
✉ cristina.munari@unife.it

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An integrated ecological and biochemical approach to the management of the invasive blue crab *Callinectes sapidus* in a Po Delta lagoon

Cristina Munari*, Annalisa Maietti and Michele Mistri

Department of Chemical, Pharmaceutical and Agricultural Sciences, University of Ferrara, Ferrara, Italy

To optimize management of the invasive blue crab *Callinectes sapidus* in Mediterranean lagoons, this study presents an integrated analysis of population dynamics, stock status, and biomass valorization in Valle Fattibello (Northern Adriatic Sea). Reproductive dynamics exhibited a marked seasonal pattern; while male-biased sex ratios suggest migratory behavior, the recording of high lagoon salinities (37 PSU) and a summer peak in ovigerous females (>25–33%) indicate potential *in-situ* reproductive success. Growth trajectories were found to be significantly sex-specific, with males exhibiting faster growth rates toward smaller asymptotic sizes compared to females. Fishery analysis over 116 days yielded 16 tonnes of biomass, yet Catch Per Unit Effort (CPUE) showed high temporal variability. We identified salinity as the primary driver of catchability, signaling that environmentally standardized assessments are critical for reliable stock monitoring. Complementing the ecological data, biochemical profiling revealed that proximate composition and fatty acid profiles are subject to significant seasonal and sex-related shifts. High n-3/n-6 PUFA ratios and substantial yields of astaxanthin, chitin, and proteins underscore a high-value biorefinery potential. Ultimately, these findings support a transition toward sex- and environment-aware management frameworks that integrate invasive species mitigation with the industrial valorization of blue crab resources in the Po Delta region

KEYWORDS

astaxanthin, *Callinectes sapidus*, fatty acids, growth parameters, invasive species, Po Delta lagoon

1 Introduction

Human-driven species redistribution is reshaping contemporary marine ecosystems, often causing profound alterations in community structure and ecosystem functioning, particularly in coastal zones. This phenomenon often results in profound modifications to community structure and ecosystem functioning, particularly in coastal zones (Bax et al., 2003). Enclosed and semi-enclosed seas, such as the Mediterranean, are especially prone to these dynamics. The convergence of intense maritime traffic, long-term shoreline alteration, and climate-mediated environmental shifts enhances both the frequency of species introductions and the likelihood of their persistence (Streftaris et al., 2006; Occhipinti-Ambrogi et al., 2011; Zenetos et al., 2012; Galil et al., 2014).

Within this invasion context, the Atlantic blue crab *Callinectes sapidus* Rathbun, 1896 represent a mature phase of marine biological invasion. It is characterized by wide spatial spread and multifaceted ecological and socio-economic consequences in recipient regions (Mancinelli et al., 2021; Tiralongo et al., 2024). Native to Atlantic, from Nova Scotia to Argentina (Kennedy and Cronin, 2007), the species possesses traits that favor successful establishment. These include a pronounced dispersal capacity, tolerance to broad salinity ranges, and flexible trophic strategies enabling the exploitation of heterogeneous habitats and prey (Hines et al., 1987; Eggleston et al., 1992).

While early occurrences in the Mediterranean during the mid-twentieth century were isolated and transient (Giordani Soika, 1951; Nehring, 2011), contemporary observations indicate a transition toward persistent populations. There is now clear evidence of rapid geographic expansion and sustained increases in abundance across large portions of the basin (Dulčić et al., 2011; Mancinelli et al., 2017; Galil et al., 2020; Castriota et al., 2024).

In the northern Adriatic lagoons, blue crab presence is relatively recent. The first record dates back to 1993 in the Venice Lagoon (Mizzan, 1993). Subsequently, a single male specimen was reported in 2014 in the Sacca di Goro, Po Delta (Manfrin et al., 2015), followed by two females observed in 2018 at Lido di Pomposa, the coastal stretch between the Sacca di Goro and the Valli di Comacchio (Munari and Mistri, 2019).

Following these initial sightings, the species rapidly expanded its distribution and abundance. This culminated in an unprecedented population outbreak during the summer of 2023, which caused substantial ecological and economic impacts across the northern Adriatic coastal systems, particularly in the Po Delta lagoons (Chiesa et al., 2025; Tiralongo et al., 2025). This rapid spread calls for management strategies that go beyond containment and control, embracing instead the principles of the circular economy.

The nutritional and commercial relevance of *C. sapidus* in its native range has been extensively documented (Farragut, 1965; Kennedy and Cronin, 2007). Economic responses to the species in the Mediterranean vary widely. Tunisia has integrated the crab into export-oriented processing chains, while Spain and France rely on high-value niche markets. Meanwhile, Greece and Turkey combine local consumption with exports to North America, where the species retains premium status (Marchessaux et al., 2024; UNEP/MAP-SPA/RAC, 2025).

Italy is currently facing an “economic paradox.” While the biomass available for commercialization is immense, with 2200 tonnes harvested in the Po River Delta alone in 2025 (ANMVI, 2026), the region lacks immediate industrial processing infrastructure. Furthermore, the collapse of the lucrative clam fishery caused by crab predation has resulted in a net economic loss for the coastal sector (Chiesa et al., 2025; Tiralongo et al., 2025).

Initial institutional responses were predominantly framed within a removal-oriented paradigm, where population containment was pursued through systematic biomass extraction followed by disposal. Within this framework, a sequence of four legislative measures enacted between 2023 and 2024 (MASAF 2023a, 2023b, 2024a, 2024b) established extraordinary interventions supported by

public funding. These measures allocated close to 10 million euros to compensate collection activities on a mass-based criterion, conditional upon the transfer of biomass to authorized land-fill facilities.

Notwithstanding a ministerial decree issued in January 2024 (MASAF, 2024c), which formally reclassified *C. sapidus* as a fishery resource of commercial interest, the predominant destination of harvested biomass from Po Delta lagoons remains disposal in landfills. Emerging supply chains generate modest revenues through domestic consumption and exports to the United States and Turkey (ANSA, 2025; BLUEAT, 2025). A public-private investment of 15 million euros will support a new processing facility in Goro, expected to be completed by 2027 (Bovenzi, 2026).

Nevertheless, the material balance associated with crab processing reveals a structural inefficiency. The edible fraction represents only a minor proportion of total biomass, while non-edible components (carapace, gastrointestinal system, gills, etc.) may account for over 80–85% of the mass (Baron et al., 2017). When conceptually reframed from waste to a secondary resource, this residual biomass becomes a strategic input for biorefinery-oriented valorization. This could enable the recovery of bioactive molecules with current or prospective relevance (Çelik et al., 2004; Küçükgülmez and Çelik, 2008; Khamassi et al., 2022; Arena et al., 2024; Tamburini, 2024).

A growing body of ecological information is becoming available at the Mediterranean scale concerning the blue crab, particularly regarding its spatial distribution, invasion processes, and feeding ecology. Studies on population dynamics have been carried out in several Mediterranean regions (Sumer et al., 2013; Türeli et al., 2016; Mehanna et al., 2019; Mancinelli et al., 2024). However, such investigations are entirely lacking in the area where *C. sapidus* has caused the most severe ecological disruption: the lagoon ecosystems of the Po River Delta.

To address this knowledge gap, we undertook a study on the blue crab population of Valle Fattibello, a lagoon within the Valli di Comacchio complex. During the 2024–2025 period, we conducted an integrated assessment of population abundance, size structure, sex ratio, and growth patterns. This work generates the fundamental knowledge required to support evidence-based management and control strategies. In parallel, we analyzed the biochemical composition of the carapace and edible tissues, framing population control within a sustainable valorization perspective aimed at the development of biorefinery and circular-economy pathways for the Po Delta blue crab.

2 Materials and methods

2.1 Study site and water parameters

Valle Fattibello (~7.3 km²) is part of the Valli di Comacchio lagoon system, adjacent to the town of Comacchio. The lagoon's name, “Fattibello” (“make yourself handsome”), reflects its historical role as a final water basin where fishermen would clean up before returning home. This dynamic lagoon hosts a mosaic of

aquatic and terrestrial habitats of high ecological value. Bottom substrates are predominantly muddy, with limited tidal excursions (~80 cm). Traditional lagoon fisheries, mainly using stationary gillnets, are still active.

Water column parameters were monitored using an OTT Manta+30A multiparametric probe, deployed on a fixed platform (*Stn Caldirolo*). The probe was configured to continuously measure water temperature, salinity, dissolved oxygen, and pH at a temporal resolution of 10 minutes, allowing for high-frequency monitoring of short-term variability and temporal trends in the water column.

2.2 Growth parameters and population dynamics

For the estimation of growth parameters and population dynamics, monthly sampling was conducted from February to November 2024. *Callinectes sapidus* were collected using rectangular crab traps (50 × 50 × 50 cm; 50-mm mesh; two entrances) baited with fish waste (e.g., *Chelon ramada*). At each sampling event, ten traps were deployed at fixed stations and left in the water for 24 h; specifically, the traps were arranged in a linear row perpendicular to the north-eastern shore of the Valle, spaced approximately 20 m apart. Each trap was individually marked with a surface buoy, a configuration that ensured reliable identification and retrieval even during days of low visibility or dense fog. All captured crabs were measured for carapace width (CW, mm) using vernier calipers and sexed. The proportion of ovigerous females was calculated as the percentage of ovigerous individuals relative to total females per sample. Size frequency distributions (10-mm classes) were analyzed using ELEFAN routines implemented in FiSAT II (Gayaniolo et al., 1995) to estimate Von Bertalanffy growth parameters (CW_{∞} and K). Growth performance index (Φ') was calculated according to Pauly and Munro (1984):

$$\Phi' = \log_{10}(K) + 2\log_{10}(CW_{\infty}).$$

where CW_{∞} is the asymptotic carapace width (mm) and K is the growth coefficient (year^{-1}). The theoretical age at zero length (t_0) was derived using Pauly's empirical equation (Pauly, 1979). Natural mortality (M) was estimated separately for males and females using Pauly's empirical temperature-dependent relationship, parameterized with sex-specific CW_{∞} (converted to cm) and K , and the mean annual temperature (T) for the Valli di Comacchio (*Stn Caldirolo*):

$$\log_{10}M = -0.0066 - 0.279\log_{10}CW_{\infty} + 0.6543\log_{10}K + 0.463\log_{10}T.$$

Exploitation scenarios were evaluated separately by defining light, medium, and heavy fishing mortality as fixed proportions of each group's estimated M (0.5 M , 1.0 M , and 2.0 M , respectively). Total mortality was computed as $Z = F + M$ and exploitation rate as $E = F/Z$ (FAO, 2016; ICES, 2022).

2.3 Harvest-based assessment of population stock

An intensive, harvest-based fishing activity was conducted during the period of highest blue crab abundance to support population stock assessment. During peak (May–November 2024), 60 additional baited traps were deployed. The experimental

design for crab sampling followed a systematic grid allocation to ensure uniform coverage of the study area. A total of 60 traps were deployed individually on the shallow bottoms (depth: 1.0–1.2 m), with each unit marked by a dedicated surface buoy. The traps were arranged in six parallel rows, with 10 traps per row. Within each row, traps were spaced approximately 20 m apart, while the distance between adjacent rows was maintained at roughly 50 m. The sampling grid was initiated at a distance of 60–70 m from the north-eastern embankment of the lagoon. This specific sector was selected as it is representative of the lagoon's dominant benthic environment, characterized by a homogenous silty-clay sediment profile. This standardized spatial arrangement was maintained throughout the study period to minimize catch variability associated with gear interference or habitat patchiness. Crabs were sorted into small ($CW < 50$ mm) and large ($CW \geq 50$ mm) classes, and the biomass of each size fraction was weighted to 2 g precision. Catch per unit effort (CPUE) was expressed as $\text{kg trap}^{-1} \text{day}^{-1}$. CPUE was calculated as:

$$\text{CPUE} = N / (T \times D).$$

where N is the total number of crabs captured per sampling event, T is the number of traps (60), and D is the soak time expressed in days.

Relationships between crab catches and environmental variables were analysed using generalized linear (GLM) and generalized additive models (GAM; Wood, 2017). Models were fitted with a Gamma error distribution and log link function, including salinity (PSU) and water temperature ($^{\circ}\text{C}$) as predictors. Fishing effort was constant (60 traps deployed for 24 h) and was therefore not included as an offset. GAMs used penalized regression splines, and model performance was evaluated using Akaike's Information Criterion (AIC). All analyses were conducted in R (R Core Team, 2024).

2.4 Biochemical characterization of blue crabs

For biochemical characterization, three additional traps were deployed at approximately monthly intervals from August 2024 to August 2025 following the same protocol described above. During each sampling campaign, five males and five females of comparable size were collected and transported to the laboratory, where they were euthanized by thermal shock (-20°C).

Whole-body wet weight was measured using a precision balance (Sartorius Entris). Carapace and muscle tissues (claws and lump) were separated, freeze-dried, and stored at -18°C .

Moisture content was determined gravimetrically. Exoskeletons were rinsed with distilled water, oven-dried at 75°C for 18 h, ground using a knife mill (GRINDOMIX GM 200; Retsch, Germany), and stored at -20°C until determination of proximate and fatty acids composition.

2.4.1 Proximate composition of blue crab tissues

Total ash content was determined by incinerating 1 g of dried sample in a muffle furnace (VELP Scientifica, Usmate, MB, Italy) at

TABLE 1 Water column parameters (annual mean, minimum, and maximum values).

Parameter	Mean	Min	Max
T (°C)	17.3	3.1	34.7
D.O. (%Sat)	82.3	0.8	198.9
Sal (PSU)	31.3	13.3	36.5
pH	8.2	5.1	9.1
Turbidity (NTU)	261.3	3.2	845.1

570 °C overnight, following Chiefa et al. (2024). Crude lipid content was measured in dried meat by Soxhlet extraction using diethyl ether as solvent (VELP Scientifica, Usmate, MB, Italy; extraction temperature 130 °C) and expressed as g 100 g⁻¹ wet weight after conversion from dry weight (Chiefa et al., 2024). Crude protein content in meat and exoskeleton was estimated from total nitrogen determined by the Kjeldahl method using a conversion factor of 6.25. For the exoskeleton, protein content (P) was calculated according to Naczek et al. (2004) as:

$$P = (S - C) \times 6.25.$$

where S is total nitrogen and C is nitrogen associated with chitin. Chitin was extracted from dried and ground exoskeletons following Longo et al. (2025) through sequential deproteinization (3% NaOH, 70 °C, 2 h), demineralization (1 M HCl, 1 h, room temperature), and decolorization (2.5% NaClO, 30 min), with intermediate washing steps to neutral pH and oven drying at 60 °C. Astaxanthin was extracted from exoskeleton powder by ultrasound-assisted extraction in methanol following Longo et al. (2025), with minor modifications. Extracts were obtained through two consecutive extraction cycles, pooled, concentrated under reduced pressure, resuspended in HPLC-grade methanol, and filtered prior to analysis. All procedures were conducted under dark conditions. Quantitative determination was performed using an HPLC system (Shimadzu VP Series, Shimadzu Italia, Milan, Italy) equipped with a UV-Vis detector and a C18 column (Force C18, 150 × 4.6 mm; Restek, USA), using an isocratic mobile phase of acetonitrile:methanol:2-propanol (85:10:5, v/v/v), a flow rate of 0.8 mL min⁻¹, and detection at 450 nm (Askera and Awad, 2019). Analyses were performed in duplicate, and astaxanthin was quantified using an external calibration curve (0.08–5 µg mL⁻¹; R² = 0.998).

2.4.2 Fatty acid composition of blue crab tissues

Fatty acid composition was determined as fatty acid methyl esters (FAMES) by GC-MS using a Varian 3900 gas chromatograph coupled to a Varian Saturn 2100 ion trap mass spectrometer (Varian, USA). Lipid extracts were transesterified in methanol and analyzed on a ZB-WAX capillary column (60 m × 0.25 mm, 0.25 µm; Phenomenex, Italy) with helium as carrier gas (1 mL min⁻¹). The injector temperature was set at 260 °C, and FAMES were separated using a temperature program from 100 to 200 °C. Mass spectra were acquired by electron ionization in full-scan mode (m/z 40–650), and compounds were identified by comparison with the NIST library, following Naczek et al. (2004) and Chiefa et al. (2024).

3 Results

3.1 Water parameters

As shown in Table 1, Valle Fattibello is a highly dynamic environment, characterized by pronounced and often extreme fluctuations in water column parameters. The lagoon displayed pronounced seasonal variability in temperature, salinity and dissolved oxygen, accompanied by marked fluctuations in pH and turbidity.

3.2 Growth and population dynamics

A total of 1245 blue crabs were captured from February to November 2024. Crabs varied from 16 to 234 mm CW. Figure 1 illustrates the demographic composition of the sampled population. Sex ratio (females:males) was 0.63 (481 females, 764 males), and showed marked temporal variation (Figure 1a), with the male component of the population consistently exceeding the female one, except in May, when the two sexes occur in similar proportions. During late summer and autumn, a pronounced decline in the female fraction is observed, likely related to the species' specific reproductive characteristics. Ovigerous females were observed from early June to mid-October, with a peak (approximately 33% of the female population) occurring between the second half of July and early August. From mid-October onwards, ovigerous females were no longer observed (Figure 1b).

Figure 2 shows length-frequency distribution with seasonal von Bertalanffy growth curves for both sexes (a: females; b: males; c:

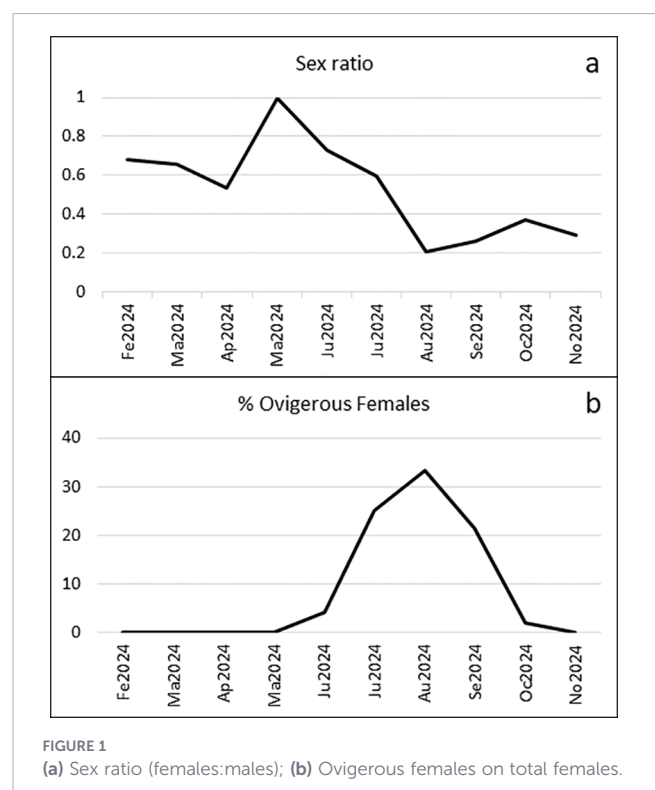


FIGURE 1 (a) Sex ratio (females:males); (b) Ovigerous females on total females.

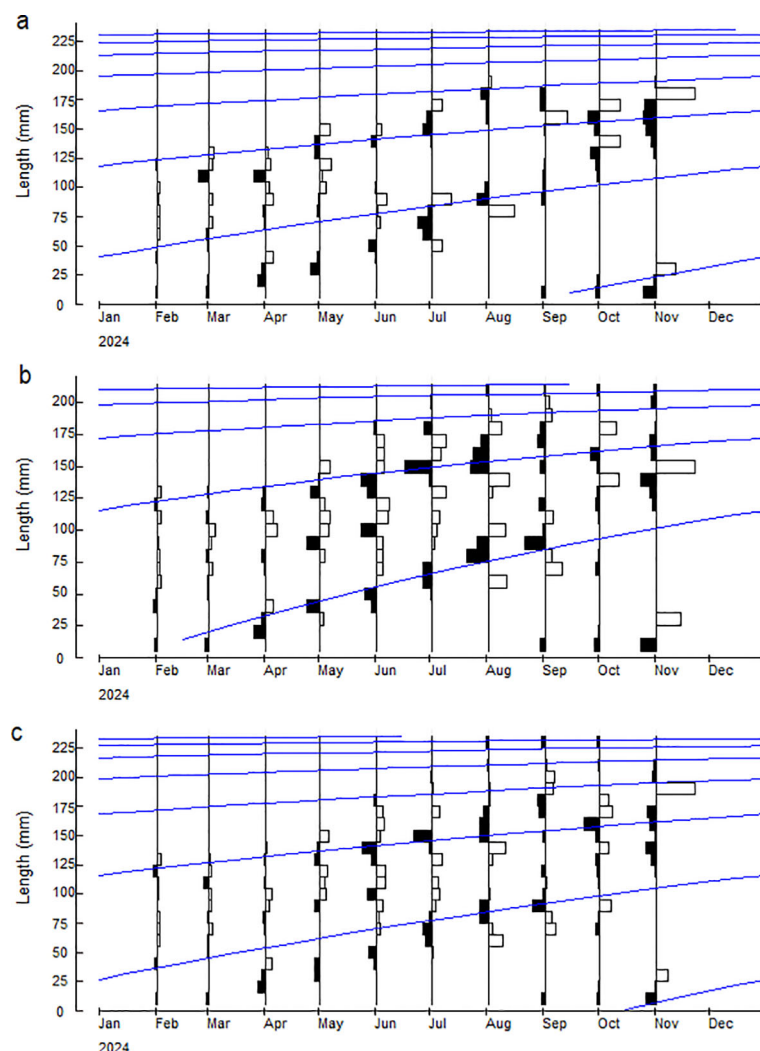


FIGURE 2

Length-frequency distribution with seasonal von Bertalanffy growth curves: (a) females; (b) males; (c) combined.

combined) of *C. sapidus*. Von Bertalanffy growth parameters differed by sex (Table 2). Females were characterized by a larger asymptotic size ($CW_{\infty}=241.5$ mm), and a lower growth coefficient ($K = 0.49 \text{ yr}^{-1}$), indicating slower somatic growth over a longer period. Males showed a smaller asymptotic size ($CW_{\infty}=220$ mm) but a higher growth coefficient ($K = 0.78 \text{ yr}^{-1}$), reflecting a faster approach to their maximum size. The growth performance index mirrors this pattern, being higher in males ($\Phi'=4.58$) than in females ($\Phi'=4.46$). Estimates for the combined sexes described an intermediate growth trajectory, with an asymptotic size similar to that of females and a growth rate ($K = 0.54 \text{ yr}^{-1}$) between those of males and females, resulting in a growth performance index that fell between the sex-specific values ($\Phi'=4.50$). The theoretical age at zero size (t_0) was negative in all cases, with only minor differences among groups. Table 2 summarizes Von Bertalanffy growth parameters for *C. sapidus* at Fattibello, together with those reported for other populations studied in the Mediterranean and elsewhere.

Sex-specific estimates of fishing mortality and exploitation rate revealed differences in absolute fishing pressure between males and females (Table 3). For a given exploitation scenario, fishing mortality was consistently higher in males than in females, reflecting their higher

estimated natural mortality. Exploitation rate increased predictably from light to heavy fishing scenarios, reaching high levels under heavy exploitation, while remaining moderate under light fishing pressure. Although exploitation rates were identical across sexes by design, the corresponding fishing mortalities differed substantially.

3.3 Stock assessment

From May to November 2024, a total of 16,047 kg of blue crabs were collected over 116 fishing days. Of this total, 12,322 kg consisted of “large” individuals ($CW>50$ mm), while 3,765 kg comprised “small” crabs ($CW<50$ mm). Small crabs were detected throughout the entire study period, although in variable amounts, with a marked increase in abundance from the second half of August and peak values observed between September and November (Figure 3). As illustrated in Figure 3, total catches were categorized into adults ($CW > 50$ mm) and juveniles ($CW < 50$ mm), with the non-homogeneous time intervals on the x-axis reflecting fishing days that were adjusted according to meteorological conditions. Crab catches varied widely across the sampling period, ranging from 23 to 375 kg per fishing event, corresponding to CPUE values of $0.38\text{--}6.25 \text{ kg}\cdot\text{trap}^{-1}\cdot\text{day}^{-1}$.

TABLE 2 Growth parameters for *C. sapidus* at Valle Fattibello, other Mediterranean lagoons, and native areas.

Area	Sex	Model	CW• (mm)	K (year ⁻¹)	t ₀ (year)	Φ'	Reference
Valle Fattibello (Italy)	Females	sVBGF	241.5	0.49	-0.188	4.460	This study
Valle Fattibello (Italy)	Males	sVBGF	220	0.78	-0.119	4.577	This study
Valle Fattibello (Italy)	Combined	sVBGF	241.5	0.54	-0.170	4.500	This study
Lesina Lagoon (Italy)	Females	sVBGF	237.8	0.63	0.530	4.550	Mancinelli et al. (2024)
Lesina Lagoon (Italy)	Males	sVBGF	232.6	0.36	0.750	4.390	Mancinelli et al. (2024)
Lesina Lagoon (Italy)	Combined	sVBGF	236.7	0.66	0.620	4.570	Mancinelli et al. (2024)
Beymelek Lagoon (Turkey)	Females	sVBGF	181.9	1.064	-0.850	4.520	Sumer et al. (2013)
Beymelek Lagoon (Turkey)	Males	sVBGF	230.1	0.86	-0.160	4.724	Sumer et al. (2013)
Yumurtalik Cove (Turkey)	Females	sVBGF	206.6	0.74	-0.240	2.499	Türeli et al. (2016)
Yumurtalik Cove (Turkey)	Males	sVBGF	209.5	0.5	-0.360	2.315	Türeli et al. (2016)
Yumurtalik Cove (Turkey)	Combined	sVBGF	201.6	0.81	-0.220	2.517	Türeli et al. (2016)
Bardawil Lagoon (Egypt)	Females	sVBGF	101.1	1.45	-0.150		Mehanna et al. (2019)
Bardawil Lagoon (Egypt)	Males	sVBGF	97.1	1.53	-0.140		Mehanna et al. (2019)
Bardawil Lagoon (Egypt)	Combined	sVBGF	99.6	1.42	-0.150		Mehanna et al. (2019)
North Carolina (USA)	Combined	VBGF	237.7	0.74	0.020		Eggleston et al. (2004)
Delaware Bay (USA)	Combined	VBGF	234.7	0.75	-0.100	4.741	Sumer et al. (2013)
Chesapeake Bay (USA)	Combined	VBGF	262.5	0.587	0.115	4.838	Sumer et al. (2013)
Chesapeake Bay (USA)	Combined	VBGF	240	0.7	0.110	4.760	Ju et al. (2001)
Hudson River (USA)	Combined	VBGF	151.1	0.75	-0.160	4.359	Sumer et al. (2013)
Coast of Louisiana (USA)	Combined	VBGF	175.9	1.45	0.130	4.491	Sumer et al. (2013)
Coast of Florida (USA)	Combined	VBGF	276	0.663	0.170	4.882	Sumer et al. (2013)

(mean = 2.30). Given that fishing effort was constant across all sampling events (60 traps deployed for 24 h), differences in catch and CPUE directly reflected temporal variability in crab availability. In the GLM (Gamma distribution, log link), salinity (Figure 4a) showed a significant positive effect on crab catches ($\beta=0.094$, $p=0.002$), indicating an estimated increase of approximately 9.9% in catch per 1 PSU increase in salinity (95% CI: 3.5–16.8%). Water temperature (Figure 4b) was not significantly associated with catches ($\beta=-0.013$, $p=0.257$). The GAM analysis confirmed a significant effect of salinity on crab catches (Wald $\chi^2 = 19.41$, $df=7$, $p=0.007$), whereas the smooth effect of temperature was not significant (Wald $\chi^2 = 4.08$, $df=7$, $p=0.77$). Model comparison based on AIC favored the GLM (AIC = 1250.68) over the GAM (AIC = 1258.49).

3.4 Biochemical characterization

3.4.1 Proximate composition of blue crab tissues

A total of 100 blue crabs (50 males and 50 females) were analyzed between August 2024 and August 2025, covering an almost complete annual cycle.

Detailed morphometric measurements and weights for the 100 analyzed crabs are provided in Supplementary Material (Supplementary Table 1). Two-way ANOVA, using month and sex as fixed factors, revealed that both variables significantly influenced body weight, muscle mass (claw and lump meat), and carapace weight ($p < 0.01$). A significant interaction between month and sex was observed for total body and carapace weight only ($p < 0.05$), while Levene’s tests confirmed homoscedasticity across the dataset.

The bulk biochemical composition of both sexes, including moisture, ash, protein, lipid, chitin, and astaxanthin, is reported in Supplementary Material (Supplementary Table 2). Carapace composition exhibited substantial seasonal and sex-related variation. Statistical analysis (Supplementary Table 3) showed that the month significantly affected ash, protein, chitin, and astaxanthin levels ($p < 0.001$). Furthermore, sex had a significant impact on all biochemical components ($p < 0.01$).

The interaction between month and sex was significant for ash and astaxanthin ($p < 0.01$), indicating that sex-based differences in these components fluctuated seasonally. In contrast, protein and chitin showed consistent sex patterns throughout the study.

TABLE 3 Fishing mortality (F) scenarios and exploitation rate (E).

Sex	Light (F) (yr ⁻¹)	Light (E)	Medium (F) (yr ⁻¹)	Medium (E)	Heavy (F) (yr ⁻¹)	Heavy (E)
Females	0.476	0.33	0.952	0.50	1.904	0.67
Males	0.662	0.33	1.324	0.50	2.648	0.67

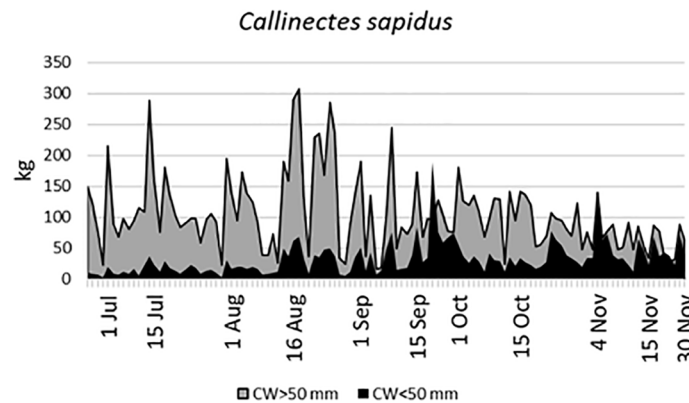


FIGURE 3

Total catches of blue crabs in Valle Fattibello (grey area: crabs with CW > 0 mm; black area: crabs with CW < 50 mm). Time intervals along the x-axis are not homogeneous, as they represent fishing days that varied according to meteorological conditions.

Specifically, ash content increased toward late spring and summer, with higher values generally observed in males. Protein content peaked from late winter to summer, maintaining stable sex differences. Chitin levels increased moderately in winter and summer compared to early autumn. Astaxanthin was highest during the

early months and declined thereafter, displaying pronounced sex-dependent differences. Overall, the carapace composition reflects a physiological shift from early-season enrichment in functional compounds toward the late-season accumulation of structural components.

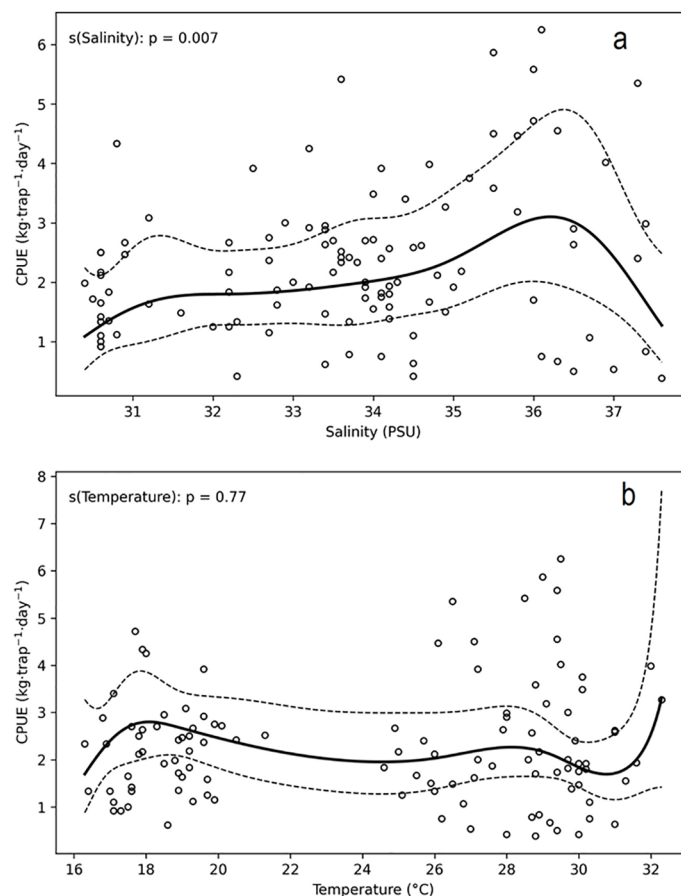


FIGURE 4

(a) Effect of salinity on crab CPUE. Crab catch per unit effort (CPUE; $\text{kg trap}^{-1} \text{day}^{-1}$) plotted against salinity (PSU). The solid line represents the fitted generalized additive model (GAM; Gamma distribution, log link), while dashed lines indicate 95% confidence intervals. Open circles represent observed CPUE values. The smooth effect of salinity was statistically significant ($p = 0.007$). (b) Effect of water temperature on crab CPUE. Crab catch per unit effort (CPUE; $\text{kg trap}^{-1} \text{day}^{-1}$) plotted against water temperature ($^{\circ}\text{C}$). The smooth effect of temperature was not statistically significant ($p = 0.77$).

Muscle composition also showed distinct seasonal and sex-related variation (Supplementary Table 2). Two-way ANOVA (Supplementary Table 4) indicated that the month significantly influenced ash ($p < 0.01$), protein ($p < 0.001$), and lipid content ($p < 0.001$). Sex also had a significant effect on all three muscle components ($p < 0.05$ for ash and protein; $p < 0.001$ for lipids).

No significant interactions between month and sex were detected in muscle tissue ($p > 0.05$), suggesting that males and females followed parallel seasonal trends. Ash content was highest in winter and decreased in summer, with slightly higher values in males. Protein content peaked during late summer and autumn, remaining consistently higher in males. Conversely, lipid content was highest in winter and early spring before decreasing toward summer, with females being consistently richer in lipids. These patterns highlight tissue-specific seasonal variations, where muscle composition reflects broader cycles of energy storage and growth.

3.4.2 Fatty acid composition of blue crab tissues

The complete fatty acid profile, ranging from C12:0 to C22:6 and including Σ SFA, Σ MUFA, Σ PUFA, Σ PUFA n3, Σ PUFA n6, and n3/n6, is presented in Supplementary Material (Supplementary Table 5). The analysis revealed distinct seasonal and sex-dependent patterns across all major fatty acid classes (Supplementary Table 6).

Saturated fatty acids (SFA) were significantly influenced by both month ($p < 0.001$) and sex ($p = 0.012$), though no significant interaction was observed. SFA levels peaked during the summer months and decreased toward winter, with males exhibiting slightly higher values than females. Monounsaturated fatty acids (MUFA) were affected by month ($p < 0.001$), sex ($p = 0.010$), and their interaction ($p = 0.03$), with the highest levels recorded in winter and spring, particularly among females.

Total polyunsaturated fatty acids (PUFA) varied significantly with the month ($p < 0.001$) and the month-sex interaction ($p = 0.02$). Seasonal peaks occurred in late winter and spring for males, while females showed higher concentrations in late summer. Similar trends were observed for n-3 PUFA (omega-3), which were significantly influenced by month ($p < 0.001$), sex ($p = 0.03$), and the interaction term ($p = 0.01$). In contrast, n-6 PUFA (omega-6) levels were significantly affected only by the month ($p < 0.001$), with no significant sex-related differences detected. Tukey *post-hoc* comparisons further highlight these distinct temporal allocations, suggesting that sex-dependent patterns are most pronounced for MUFA and n-3 PUFA. These results point to seasonal metabolic shifts and underscore the potential for timing-specific nutritional valorization.

The n-3/n-6 ratio remained within a nutritionally favorable range throughout the study period (Supplementary Table 5). In males, these values generally exceeded 1.4, with the highest ratios observed in late winter and summer. Females displayed a broader temporal pattern, with ratios increasing from mid-season to reach peaks above 3.3 in August. Overall, these values indicate a consistent dominance of n-3 over n-6 polyunsaturated fatty acids across the annual cycle, confirming the high nutritional quality of the blue crab biomass.

4 Discussion

Since the early 2020s, the Atlantic blue crab (*Callinectes sapidus*) has become highly invasive in the lagoon systems of the Po Delta (northern Adriatic Sea). Its rapid population expansion has caused severe ecological and socio-economic impacts in the region. In particular, the species has heavily affected the farming of the Manila clam (*Ruditapes philippinarum*), leading to economic losses estimated in the tens of millions of euros (Chiesa et al., 2025; Tiralongo et al., 2025).

This invasion has highlighted a striking “Italian paradox” (Mistri and Munari, 2026). Despite the availability of a large biomass with high commercial value elsewhere, such as in the United States, most blue crab harvested in Italy is currently discarded or sent to landfills. To date, there are only a few emerging attempts at commercial and industrial valorization.

Addressing this paradox requires a management-oriented perspective grounded in robust ecological knowledge. In lagoon-dominated systems like the Po Delta, where *C. sapidus* has established dense and persistent populations, effective management cannot rely solely on control or eradication. Instead, it requires an integrated understanding of population dynamics, size structure, and reproductive patterns to inform adaptive harvesting. Such knowledge is essential to transform this ecological threat into a usable resource. Ultimately, this approach aims to reduce both the environmental impacts on lagoon ecosystems and the socio-economic losses affecting local aquaculture.

4.1 Blue crab growth and population dynamics

In Valle Fattibello, the temporal patterns of sex ratio and ovigerous female occurrence provide key insights into local reproductive dynamics. Ovigerous females were absent from February to May, appearing in June and peaking between July and August, a trend consistent with other temperate populations (Millikin and Williams, 1984; Hines et al., 1987). During this peak period (July–September), the sex ratio became strongly male-biased, suggesting a seasonal reduction in female availability.

In many systems, ovigerous females migrate seaward to release larvae under oceanic salinity and circulation conditions (Epifanio, 2019), which typically reduces their vulnerability to lagoon-based fishing gear. However, salinity levels in Valle Fattibello frequently reached 37 PSU, indicating that lagoon conditions may locally support both egg incubation and larval release. The presence of ovigerous females under these high-salinity conditions suggests that a portion of the population may reproduce directly within the lagoon, as reported for other hypersaline transitional systems (Mancinelli et al., 2017).

These two strategies, seaward migration and in-lagoon reproduction, likely coexist, contributing to the observed temporal variability in sex ratio. From a management perspective, the summer decline in female abundance may therefore reflect temporary emigration rather than a true demographic shift in the population.

Growth analyses revealed sex-specific trajectories. Males grew faster toward a smaller asymptotic size, whereas females grew more slowly but attained larger sizes, reflecting contrasting life-history strategies. Pooling sexes produced intermediate growth parameters that obscure these biologically relevant differences. Comparison with the blue crab population from Lesina Lagoon, an extensively studied Adriatic population (Florio et al., 2008; Cilenti et al., 2015; Mancinelli et al., 2024), highlighted marked variability. Higher growth coefficients and growth performance indices in Lesina (Mancinelli et al., 2024) indicate a faster approach to asymptotic size relative to Valle Fattibello, consistent with temperature-mediated effects on crustacean growth (Hartnoll, 1982; Hines, 2007). Latitudinal thermal gradients likely contribute to accelerated growth in Lesina (41.886° N, 15.437° E) compared with Valle Fattibello (44.665° N, 12.200° E). Sex-specific growth patterns also differed between lagoons, with faster female growth in Lesina and faster male growth in Valle Fattibello. Such divergence, widely reported in blue crabs, reflects interactions between environmental drivers and sex-dependent life-history traits (Hines, 1982; Rugolo et al., 1991; Fogarty and Neiland, 1987; Hines, 2007).

Finally, sex-specific patterns in fishing mortality emphasize the need for sex-aware assessments. Higher fishing mortality in males likely reflects faster growth, higher natural mortality, and greater exposure to fishing gear, whereas female vulnerability may be seasonally reduced by reproductive movements. Consequently, identical exploitation rates may not correspond to equivalent demographic impacts between sexes (Motz Carvera et al., 2005). In lagoon systems characterized by spatial segregation and seasonal migration, management strategies based on pooled metrics risk misrepresenting population responses to exploitation, underscoring the need for site- and sex-specific approaches for managing this invasive species.

4.2 Blue crab stock assessment

Catch per unit effort (CPUE) is widely used as a proxy for relative abundance in fisheries and stock assessment, particularly in small-scale and lagoon fisheries where independent survey data are often unavailable (Hilborn and Walters, 1992; Maunder et al., 2006). In this study, crab CPUE showed pronounced temporal variability despite constant fishing effort, indicating substantial fluctuations in local availability and/or catchability. This variability is consistent with the highly dynamic nature of lagoon systems, characterized by strong environmental gradients and seasonal variability.

Among the environmental parameters monitored, salinity emerged as a significant predictor of CPUE variability, showing a positive correlation in both GLM and GAM analyses. Higher salinity levels were associated with increased catches even after standardizing for fishing effort, a pattern consistent with the role of salinity as a key structuring factor in transitional waters (Remane and Schlieper, 1971; Elliott and Whitfield, 2011). Although lagoon-dwelling crabs are typically euryhaline, higher salinities may influence gear vulnerability by enhancing metabolic activity, aggregation, or mobility, thereby increasing encounter rates with baited traps (Anger, 2003; Charmantier et al., 2009).

However, a cautious interpretation of these results is necessary. While salinity showed a statistical association with CPUE, it likely acts in concert with other unmeasured drivers. Our analysis relied on a specific set of environmental predictors and did not explicitly account for spatial heterogeneity within the lagoon, fine-scale behavioral patterns, or density-dependent catchability, where the efficiency of the gear may change non-linearly with crab abundance. From a fisheries perspective, this suggests that the observed fluctuations in CPUE reflect a complex interplay between environmental triggers and biological drivers. Consequently, periods of reduced freshwater input or enhanced marine water exchange may lead to elevated CPUE, which could result in an overestimation of stock size if these multi-factorial influences on catchability are not explicitly accounted for (Maunder and Punt, 2004).

The absence of a significant temperature effect on CPUE should be interpreted in light of the temporal scope of the assessment, which was limited to May–November, when temperatures were consistently high. Within this range, temperature likely exceeded the lower threshold for blue crab activity, reducing variability in temperature-driven behaviour. During colder months, blue crabs typically enter a state of reduced activity or lethargy, which strongly affects availability to fishing gear (Millikin and Williams, 1984; Hines et al., 1987). As winter conditions were not included in the analysis, temperature-related constraints on CPUE were likely minimal in our dataset. These results suggest a threshold-driven role of temperature, with strong effects during cold periods but limited influence once suitable thermal conditions are reached. Accordingly, temperature standardization may be less critical for warm-season CPUE, whereas year-round data would require explicit correction for temperature-driven catchability.

Overall, these findings highlight the importance of disentangling environmental and biological effects on catchability from true changes in population abundance (Harley et al., 2001). The application of GLM and GAM frameworks provides an initial approach for CPUE standardization (Maunder and Punt, 2004), though future models should aim to integrate spatial and density-dependent factors to increase robustness. From a management perspective, the influence of environmental variables on CPUE underscores the need to integrate hydrological processes into lagoon fisheries governance. Elevated CPUE observed under specific environmental conditions, such as high salinity, should be interpreted with caution when setting harvest levels, as it may reflect a temporary increase in the population's vulnerability to gear rather than a sustainable increase in total biomass. Incorporating broader environmental and spatial standardization into routine monitoring can help avoid overexploitation driven by environmentally enhanced catch rates.

4.3 Proximate composition of blue crab tissues

Seasonal and sex-related variation in crab biochemical composition from Valle Fattibello reflects coordinated physiological strategies with direct relevance for bio-refinery applications. In the carapace, the progressive increase of ash and chitin toward late winter–summer, particularly in males, likely reflects cuticle

TABLE 4 Comparative fatty acid profiles of blue crab populations across different Mediterranean regions, in comparison to other marine invertebrates, including crustaceans (shrimp), mollusks, echinoderms, and tunicates.

Organism / Tissue	SFA (%)	MUFA (%)	PUFA (%)	n-3 PUFA (%)	n-6 PUFA (%)	Reference
<i>C. sapidus</i> - Male meat (Po Delta)	33.16–55.85	27.03–34.17	10.00–30.26	7.20–20.90	2.80–10.29	This study
<i>C. sapidus</i> - Female meat (Po Delta)	34.01–50.99	22.73–39.22	12.81–31.10	7.07–24.34	5.18–9.69	This study
<i>C. sapidus</i> - Meat (NE Mediterranean)	24–35	20–22	40–45		5.34–7.80	Çelik et al. (2004)
<i>C. sapidus</i> - Meat & Shell (Adriatic Sea)	~24	~27	~49			Fuso et al. (2025)
<i>C. sapidus</i> - Male meat (Experimental diet)	32.7–34.1	24.5–29.1	29.1–30.7	30.65	6.85–23.52	Conti et al. (2024)
<i>C. sapidus</i> - Female meat (Experimental diet)	31.7–36.5	19.4–20.0	29.0–34.9	18.83–10.28	2.39–10.67	Conti et al. (2024)
<i>C. sapidus</i> - Meat (Mediterranean Coast)	26–31.8	20–29	39.7–41.6	24–27		Kuley et al. (2008)
<i>C. sapidus</i> - Male meat (Mediterranean)	33.72–35.23	20.84–21.49	43.24–48.51	EPA-DHA present	10.31–16.79	Brai et al. (2025)
<i>C. sapidus</i> - Female meat (Tunisian Med)			36.45–43.64	EPA 9.31–15.64, DHA 8.74–13.78	6.81–9.21	Khamassi et al. (2022)
<i>C. sapidus</i> - Body Meat (W Mediterranean)	29.5		34.9			Pulido-Rodriguez et al. (2024)
<i>C. sapidus</i> - eggs	34.85	28.77	30.34	EPA 7.71, DHA 12.19	0	Li et al. (2012)
<i>Penaeus kerathurus</i>	39.1–52.6	15.6–24.3	21.0–39.3	16.6	4.1–10.6	Passi et al. (2002)
<i>Portunus pelagicus</i>	23.3–27.2	23.3–26.7	42.4–44.5	31.7–35.4	8.8–11.0	Ayas and Ozogul (2011)
<i>Munida</i> spp.	16–18.2	16–17	50–55	EPA 16.9–19.9		García-Soto et al. (2017)
<i>Mytilus galloprovincialis</i>	25.66–29.19	15–24	50.7–55.8	22–32	15.9–19.8	Li et al. (2025)
<i>Paracentrotus lividus</i>		5–7		13–17	10–17	Martínez-Pita et al. (2010)
<i>Microcosmus sulcatus</i>	62.2		20–30			Pateiro et al. (2022)

mineralization and structural reinforcement, supporting efficient recovery of minerals and chitin-based biopolymers. Carapace protein content also varied seasonally and was consistently higher in males, indicating additional potential for protein valorization alongside structural fractions.

In contrast, astaxanthin showed an opposite temporal pattern, peaking in early months and displaying strong sex-dependent variation. As crustaceans are unable to synthesize carotenoids *de novo*, astaxanthin accumulation in blue crabs relies on the uptake of carotenoids synthesized by phytoplankton, which are transferred through the food web to higher trophic levels via filter-feeding bivalves and other crustaceans and scavengers that constitute the diet of the crab (Goodwin, 1984; Oninku et al., 2025). Seasonal changes in primary productivity and plankton availability are therefore likely drivers of the observed early-season peak (Fisher et al., 1954). In addition, astaxanthin plays key antioxidant and physiological roles, including protection against oxidative stress and functions related to molting and reproduction, which may further explain both seasonal and sex-specific differences (David et al., 2023; Oninku et al., 2025).

Muscle tissue exhibited complementary seasonal dynamics linked to energy allocation. Lipid content was highest in winter–early spring, consistent with pre-reproduction energy storage, while protein levels peaked later, reflecting growth and anabolic activity. These trends align with patterns reported in other decapod crustaceans, where lipids and proteins increase prior to reproductive events and decline during periods of high energetic expenditure (Anger, 2001; Rosa and Nunes, 2006). Sex-related differences in

muscle composition were consistent across months, suggesting parallel seasonal trajectories despite different allocation strategies.

Together, these findings highlight a tissue-specific seasonal partitioning of resources, with early-season enrichment in functional compounds such as astaxanthin and late-season accumulation of structural and energetic components. From a bio-refinery perspective, this supports seasonally optimized, sequential extraction strategies, targeting astaxanthin recovery early in the season, followed by chitin–mineral extraction from carapaces and lipid–protein recovery from muscle at later stages. Such an approach maximizes yield and selectivity while reinforcing the role of crab biomass in integrated, circular blue-economy models.

4.4 Fatty acid composition of blue crab tissues

The fatty acid composition of blue crabs from Valle Fattibello (Supplementary Table 5) highlights quite pronounced seasonal and sex-dependent variability. In our blue crabs, SFA ranged 33–56% in males and 34–51% in females, MUFA 27–34%/23–39%, PUFA 10–30%/13–31%, n-3 PUFA 7–21%/7–24%, and n-6 PUFA 3–10%/5–10%, depending on sex and month. The fatty acid profile of *C. sapidus* from Valle Fattibello falls within the range reported for other marine invertebrates (Table 4). SFA, MUFA, and PUFA proportions are comparable to those previously reported for blue crab from the Mediterranean and for other decapods such as *Portunus pelagicus* and penaeid shrimps. While total PUFA levels in blue crab are generally lower than in bivalves, which often exceed

45% PUFA, the relative contribution of n-3 PUFA is similar, indicating comparable nutritional quality. Compared with echinoderms and tunicates, which show either strong PUFA dominance or high SFA prevalence, blue crabs from Fattibello exhibit a more balanced fatty acid composition.

Our seasonal data revealed higher n-3 PUFA in winter–early spring and increased SFA in summer months, reflecting physiological cycles of energy storage, reproduction, and diet-mediated accumulation of plankton-derived lipids (Ayas, 2016; Ho et al., 2024). In Valle Fattibello, females showed slightly higher n-3 PUFA in early months, likely related to reproductive allocation, while males exhibited higher SFA in summer, possibly linked to structural energy reserves. These patterns are consistent with previous studies showing that PUFA content, particularly EPA and DHA, dominates crab lipids and varies with tissue, season, and diet (Brai et al., 2025; Khamassi et al., 2022). From a nutritional perspective, n-3/n-6 ratios above 1 are considered highly beneficial, as in a balanced diet they promote an anti-inflammatory lipid balance and are associated with reduced risk of cardiovascular, metabolic, and inflammatory diseases (Simopoulos, 2002; Calder, 2015). The ratios observed in blue crabs from Fattibello are substantially higher than those typically reported for terrestrial meats, which often show values below 0.1, and are comparable to, or higher than, those reported for many commercially important seafood species (Rosa and Nunes, 2004; Gladyshev et al., 2013). The pronounced seasonal peaks, particularly in late winter and late summer, suggest periods of enhanced nutritional quality, likely reflecting diet-driven accumulation of long-chain n-3 fatty acids such as EPA and DHA. Overall, the consistently elevated n-3/n-6 ratios observed in both sexes support the classification of blue crabs from Valle Fattibello as a high-value seafood from a human nutrition standpoint, with seasonal differences offering opportunities to optimize harvesting periods for maximal health benefits. These biochemical patterns, when viewed alongside the population dynamics and environmental drivers discussed previously, provide a multi-dimensional basis for refining current management strategies.

4.5 Integrating ecological observations and biochemical variability for adaptive management

The integration of population dynamics, environmental factors, and tissue-specific biochemical profiles provides a preliminary framework for the adaptive management of *C. sapidus* in the Po Delta. Our results suggest that the industrial value of this invasive biomass is not a static parameter; rather, it is a dynamic variable closely linked to the lagoon's ecological phenology. The observed seasonal fluctuations in nutritional and industrial compounds appear synchronized with the environmental cycles of Valle Fattibello.

For instance, the enrichment of astaxanthin and n-3 PUFAs during winter and spring likely reflects the diet-mediated accumulation of plankton-derived nutrients during periods of high primary productivity. Conversely, the late-summer increase in carapace mineralization and muscle protein coincides with both higher lagoon salinity and the maximum somatic growth phase identified

in our stock assessment. While these relationships require further validation across different lagoon systems, they suggest a strong “eco-biochemical” coupling.

From a management perspective, these findings indicate that invasive species control could benefit from transitioning from constant-effort removal toward more seasonally informed harvest models. Specifically, mass-removal interventions could be strategically aligned with identified “biochemical quality windows.” Early-season harvests could prioritize the extraction of high-value components like astaxanthin and n-3 fatty acids. In contrast, late-season biomass may be better suited for the recovery of chitin-based biopolymers and proteins.

Furthermore, by acknowledging how salinity might influence both crab catchability and physiological status, managers can better anticipate fluctuations in the economic return of fishing efforts under varying hydrological conditions. This integration of sex-specific growth trajectories also allows for a more nuanced approach to exploitation. Since males and females exhibit different allocation strategies and growth rates, harvest pressure could be tailored to specific demographic segments, depending on whether the objective is population suppression or biomass yield optimization.

Ultimately, by synchronizing harvesting schedules with the natural oscillations of the lagoon and the crab's physiological cycles, it is possible to move beyond a purely reactive management approach. This transition supports a proactive, circular-economy model that treats this biological invasion as a complex, but potentially valuable, secondary resource.

5 Conclusion

This study provides an integrated evaluation of population dynamics, stock status, and biochemical value of the invasive blue crab *Callinectes sapidus* in the lagoon system of Valle Fattibello. Reproductive patterns showed a summer peak of ovigerous females and seasonal male-biased sex ratios, likely linked to female reproductive movements. However, lagoon salinities reaching 37 PSU indicate that part of the population may reproduce directly within the lagoon, supporting the coexistence of alternative reproductive strategies. Growth analyses revealed clear sex-specific trajectories, with faster male growth toward smaller asymptotic sizes and slower female growth to larger sizes, differing from patterns observed in the southern Adriatic and likely reflecting interactions between life-history traits and environmental drivers.

Stock assessment results highlighted strong temporal variability in CPUE despite constant fishing effort, with salinity emerging as a significant environmental predictor of catchability within the parameters tested. This demonstrates that CPUE fluctuations in lagoon fisheries may reflect complex, environmentally driven changes in gear vulnerability, likely interacting with unmeasured spatial and density-dependent factors, rather than shifts in true abundance alone. Furthermore, sex-specific fishing mortality indicates that identical exploitation rates can have divergent demographic effects. These findings emphasize the necessity of adopting

more holistic, sex- and environment-aware assessment frameworks that account for the multi-factorial nature of catchability in transitional waters.

Seasonal and sex-related variation in proximate composition and fatty acid profiles further revealed the high biorefinery and nutritional potential of blue crab biomass. Early-season peaks in astaxanthin, late-season accumulation of structural and energetic components, and consistently high n-3/n-6 PUFA ratios support seasonally optimized harvesting and sequential extraction strategies. Overall, integrating environmentally informed stock assessment with sustainable biomass valorization offers a viable pathway for managing this invasive species while supporting circular blue-economy approaches in the Po Delta lagoons.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

CM: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. AM: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. MM: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2026.1803835/full#supplementary-material>.

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