

Article

Fisheries Biology and Basic Life-Cycle Characteristics of the Invasive Blue Crab *Callinectes sapidus* Rathbun in the Estuarine Area of the Evros River (Northeast Aegean Sea, Eastern Mediterranean)

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Abstract: The catch per unit effort (CPUE), population structure, sex ratio, and reproductive aspects of the invasive blue crab *Callinectes sapidus* Rathbun were studied in Monolimni Lagoon and the adjacent coastal waters in the estuarine area of the Evros River (Northeast Aegean Sea, Eastern Mediterranean). The CPUE varied both seasonally and spatially; higher values were recorded in summer and fall in the lagoonal stations characterized by shallow depth (<0.5 m) and a dense meadow of the angiosperm *Ruppia maritima*, whereas significantly lower CPUE was recorded in the adjacent coastal area. The bottom temperature was positively correlated with CPUE. Modal progression analysis estimated a three-modal size–frequency distribution for both sexes corresponding to the 0⁺, 1⁺, and 2⁺ age classes. Females attained a significantly larger size (carapace width (CW)) than males. Crab size decreased from the marine area to the lagoonal stations. The sex ratio was estimated at 2.45:1 (♂/♀). Males dominated in all months, except for October, when an equal sex ratio was observed. The mean size at maturity (L₅₀) of females was estimated at 124 mm CW. Females with mature ovaries were found from February to October. Ovigerous females were observed from May to October in the coastal area, where a spawning peak occurred in September. In the Evros River estuary, the American blue crab exhibits a life cycle that seems to conform to the general complex life-cycle pattern of the species along the mid-Atlantic coast.

Keywords: blue crab; *Callinectes sapidus*; invasive; CPUE; population structure; sex ratio; reproductive aspects; life cycle; Evros Delta; Aegean Sea; Eastern Mediterranean



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1. Introduction

The American blue crab *Callinectes sapidus* Rathbun (Decapoda, Brachyura) is native to the western Atlantic Ocean, with a broad distribution extending from Nova Scotia and the Gulf of Maine to northern Argentina, including Bermuda, the West Indies, and the Caribbean Sea [1,2]. It supports a large commercial fishery along the Atlantic and Gulf Coasts of the USA, with landings for 2021 estimated at 54,000 mt (NOAA 2022; <https://www.fisheries.noaa.gov/foss/f?p=215:200:988351972866>, assessed on 22 December 2022).

C. sapidus has been introduced accidentally or intentionally into both Asia and Europe [3,4]. In Europe, the blue crab was introduced to the Atlantic coast of France in 1900 through shipping [5]. In the mid-1930s, the blue crab appeared in the North Aegean Sea and,

subsequently, in other Mediterranean sites, most probably due to multiple introductions through ballast waters [6–8]. This invasive portunid crab was successfully established in the eastern basin along the coasts of the Levantine Sea and of the North Aegean Sea [9–11]. Holthuis [10] mentioned that “... well established colonies are found in Turkey and Greece and that *Callinectes sapidus* at present must be ranged among the ‘indigenous Crustacea of Europe’”. In the 1950s, a significant increase in population size led to significant commercial exploitation of the blue crab in the Thermaikos Gulf (Northwest Aegean Sea). However, due to an unknown reason or a combination of reasons involving pollution, habitat loss, disease, critical lethal water temperature, and overfishing, the blue crab stock collapsed in the mid-1960s, followed by a serious decline [7,12]. Afterwards, the blue crab was only sporadically recorded in the North Aegean Sea, and especially in the Thermaikos Gulf [7,13]. From 2007 onwards, population outbreaks of the blue crab occurred, and large populations have been observed along the coast of the North Aegean Sea, from the Evros Delta in the east to the Thermaikos Gulf in the west [12,14,15]. This was probably caused by a climate-driven change that resulted in a substantial increase in seawater temperature and the associated increase in blue crabs’ overwinter survival and growth. Satellite observations from the period 1985–2006 indicate that the temperature in the upper layer of the Eastern Mediterranean Basin has increased at an average (\pm sd) rate of $0.05 (\pm 0.009) ^\circ\text{C yr}^{-1}$ [16,17].

Furthermore, in the last decade, the species has exhibited a dynamic expansion into the Ionian and Adriatic Seas, e.g., [18,19], and in the western parts of the Mediterranean, e.g., [20,21], followed initially by population outbreaks in most cases [22], but also in the neighboring waters of the Black Sea and in the east Atlantic Ocean (e.g., [23–25]). Today, the blue crab forms the subject of economically important fisheries at a local scale in many areas within the Mediterranean Basin (e.g., [12,26,27]). Commercial landings from the North Aegean Sea for 2021, estimated at 13 mt, were significantly lower than the average (33 mt) of the period 2013–2021 (Auction Agency of Greece, 2022; <https://www.okaa.gr/statistika-alieumaton-okaa-ae/?rid=5>, assessed 20 December 2022). A drastic decrease in landings was also reported from Turkey, from 77 mt in 2009 to 1.5 mt in 2021 (Turkish Statistical Institute, <https://data.tuik.gov.tr/Kategori/GetKategori?p=tarim-111&dil=2>, assessed 20 December 2022).

The blue crab has been subject to broad scientific studies for more than 100 years, and general descriptions of its life history have been available since the early 20th century from the Middle and South Atlantic Bight and the Gulf of Mexico along the east coast of the USA (e.g., [28–30]). It has a complex life history, demanding both oceanic and estuarine habitats, and its patterns of habitat use vary by sex and ontogenetic stage. Mated females migrate from low-salinity waters to the polyhaline zones of lower estuaries to produce and incubate eggs prior to spawning. Subsequent to spawning, planktonic larvae are advected offshore to the continental shelf, after which early-stage crabs return inshore and ingress into estuaries (e.g., [3,30–36]). However, patterns in the life history of the blue crab may vary by region or even habitat, while the timing of life history events and lifespan appear to vary with latitude [35,36].

Biological invasions pose a leading threat to biodiversity worldwide (e.g., [37,38]). Through competition, predation, and habitat alteration, invaders can radically change both the species composition and functioning of native ecosystems [39]. The blue crab is a dominant opportunistic predator and scavenger in shallow estuarine and coastal waters throughout its range, capable of regulating benthic prey populations. The expansive dietary breadth of this species includes plant material, detritus, polychaetes, mollusks, crustaceans and fish [35,40–42]. Clavero et al. [22] pointed out that the blue crab is becoming a new keystone species in the invaded systems, and that it has the potential to induce radical changes in the composition and structure of coastal marine communities. However, the ecological impacts of the blue crab invasion within Mediterranean habitats are still largely unknown. Further research is urgently needed to quantify these impacts and find tools to prevent or mitigate them through effective control of blue crab populations and their spread [22,43]. As an initial step towards this goal, knowledge of the characteristics of the

blue crab life cycle is essential, given the complexities and variety of the invaded habitats along the east–west and north–south axes of the basin [44]. Furthermore, information on the biology, population dynamics, and fisheries of the species within the Mediterranean is still limited (e.g., [12,15,26,27,45–54]).

Taking into consideration all of the above, the aim of this work is to study the population and the basic life-cycle characteristics of the blue crab in an invaded Mediterranean coastal habitat, and to assess the relative abundance (as CPUE), population structure, sex ratio, and reproductive aspects of the species subjected to fishery exploitation in the Monolimni Lagoon and the adjacent coastal waters in the estuarine area of the Evros River, Northeast Aegean Sea, Eastern Mediterranean.

2. Materials and Methods

2.1. Study Area

Monolimni Lagoon is located in the Evros Delta (Northeast Aegean Sea, Eastern Mediterranean) (Figure 1). It is a poikilohaline, relatively enclosed Mediterranean brackish system. It occupies an area of about 112 ha and communicates with the sea mainly through an opening 15 m wide at its northwestern end with an average depth of about 2.5 m, but also through other, narrower entries. The maximum depth at the innermost northern part of the lagoon is about 0.5 m. The eastern entry and, to a lesser extent, the northwestern entry are influenced by the freshwater inflow of the eastern and western branches of the Evros River, respectively. An extensive macrophyte meadow (*Ruppia maritima* L.) almost completely covers the bottom of the northern part (and partially the southern part) of the lagoon. The macrozoobenthic community structure and the temporal variation in the population characteristics of *R. maritima* have been studied in Monolimni Lagoon by Kevrekidis [55] and Malea et al. [56], respectively.



Figure 1. Map of the study area indicating the sampling stations in Monolimni Lagoon, Evros River estuary (st. 1–st. 6), and in the adjacent coastal area (st. 7–st. 9). Stations’ depth: st. 1 = 0.5 m, st. 2 = 0.5 m, st. 3 = 0.5 m, st. 4 = 2.5 m, st. 5 = 0.5 m, st. 6 = 0.5 m, st. 7 = 1 m, st. 8 = 3 m, st. 9 = 6 m.

2.2. Sampling Procedure

From November 2020 to October 2021, fyke nets (10 pairs; mesh size 18–20 mm) were deployed monthly at 6 sampling stations in Monolimni Lagoon (st. 1–st. 6) and at 3 sampling stations in the adjacent marine coastal area (st. 7–st. 9) (Figure 1). Sampling took place according to the local fishery practice. The fyke nets were deployed in the morning and collected after about 48 h. None of the fyke nets contained bait. The bottom water temperature (°C), salinity (psu), and dissolved oxygen (DO) (mg/L) were recorded monthly with a Hack automatic recorder at each sampling station.

All of the collected *Callinectes sapidus* specimens were transferred to the laboratory, sexed according to the shape of their abdomen, and counted. Females were also separated into immature and mature depending on the shape of their abdomen. For each crab, the carapace width (CW)—including the lateral spines—was measured with a digital Vernier caliper to the nearest 0.01 mm. Crabs of CW < 60 mm were considered to be juveniles [57–59]. Every month from January to October 2021, visual inspection of ovarian stages was performed in a subsample of sexually mature females (ovigerous and non-ovigerous) according to the 5 ovarian stages (I–V) proposed by Hard [60]. In ovigerous females, the stage of egg development was based on the coloration of the egg mass and was classified into 5 stages—stage 1: bright orange, stage 2: pale yellow, stage 3: pale brown, stage 4: dark brown, stage 5 (advanced egg developmental stage): dark black.

2.3. Data Analysis

A one-way ANOVA (F) and a one-way Welch's ANOVA (F) were conducted to determine whether the temperature, salinity, and DO were significantly different between the sampling stations throughout the study period. Abundance was estimated as catch per unit effort (CPUE), i.e., the number of crabs collected by the 10 pairs of fyke nets (crabs/20 fyke nets). The effects of temporal (seasonal) and spatial variation on the (a) size (CW) and (b) CPUE of the population, and of each sex separately, were analyzed with the Kruskal–Wallis test (H). Subsequently, pairwise comparisons were performed using Dunn's (1964) procedure. A Bonferroni correction for multiple comparisons was also performed. The effect of seasonal variation on CPUE for females was tested with one-way Welch's ANOVA (F), and a Games-Howell pairwise test was applied.

The total sex ratio (σ/φ) and sex ratio per sampling month and station were assessed, and deviations from 1 were estimated applying a chi-squared (χ^2) test. The test was applied only for monthly samples of more than 50 crabs. Size–frequency distributions were calculated per 5 mm size (CW) class intervals for each sex separately to study the (a) population structure and (b) structure of the portion of the population selected in the lagoon and in the coastal area, separately. For each case, significant differences between female and male size distributions, mean ranks, and medians were tested with the two-sample Kolmogorov–Smirnov (z) test, Mann–Whitney (U) test, and independent-samples median test (T), respectively. The above tests were also used to assess significant differences between mature females (ovigerous and non-ovigerous) caught in the lagoon and in the coastal area. In the size (CW)–frequency analysis, only animals with intact spines were included. Modal progression analysis using the Bhattacharya method (1967), incorporated in the FISAT II package version 1.2.2 [61], was used to assess the modes for each sex separately using pooled abundance data per 5 mm size (CW) class interval. A Spearman's rank–order correlation was run to assess the relationships between (a) mean monthly temperature, salinity and DO, and mean monthly CPUE; and (b) the number of ovigerous females at the advanced egg development stage (stage 5) (only for September) and the depth gradient in the coastal area. Pearson's correlation was run to assess the relationship between the numbers of (a) females, (b) males, and (c) ovigerous females and the depth gradient in the coastal area. The Kruskal–Wallis (H) test was applied to examine whether significant differences existed in the size (CW) of females (ovigerous and non-ovigerous) according to the depth gradient in the coastal area. A one-way ANOVA (F) was conducted to determine whether significant size differences existed (CW) between ovigerous females with different stages of egg development and (a) males, (b) ovigerous females, and (c) ovigerous females at the advanced egg developmental stage (stage 5), according to the depth gradient.

In all of the above tests, the depth gradient was set to 1 m, 3 m, and 6 m, corresponding to st. 7, st. 8, and st. 9 sampling stations, respectively. All statistical analyses were performed using the SPSS software package. The mean size at maturity for females (L_{50}) was estimated with the package “Sizemat” in R (ver. 4.2.0), with RStudio.

3. Results

3.1. Physicochemical Parameters

The bottom temperature in the lagoon ranged from 6.1 °C (st. 2) in December 2020 to 27.0 °C (st. 3) in August 2021. In the marine area, the temperature ranged from 9.3 °C (January) at st. 7 to 26.6 °C at st. 8 in August. A one-way ANOVA showed that there were no significant differences in temperature between the sampling stations ($F = 0.055$, $p = 1$). Salinity varied significantly in the study area; in the lagoon, it ranged from 0.28 psu in April (st. 5) to 32.8 psu in December (st. 6), whereas in the coastal area it ranged from 30.05 psu in January (st. 8) to 36.7 psu in December (st. 9). The dissolved oxygen (DO) in the lagoon ranged from 3.75 mg/L at st. 4 to 16.5 mg/L at st. 1, both in October. In the marine area, DO ranged from 7.34 mg/L (st. 9) in August to 14.08 mg/L in February (st. 8). A one-way Welch's ANOVA showed that there was a significant difference in salinity ($F = 26.85$, $p = 0.000$) but no significant difference in DO ($F = 1.50$, $p = 0.19$) between the sampling stations.

3.2. Catch Per Unit Effort (CPUE)

The CPUE ranged from 0 to 204 crabs/10 pairs of fyke nets, with an overall mean (\pm SD) of 28.03 (± 46.25). The CPUE exhibited a significant spatiotemporal differentiation (Figure 2).

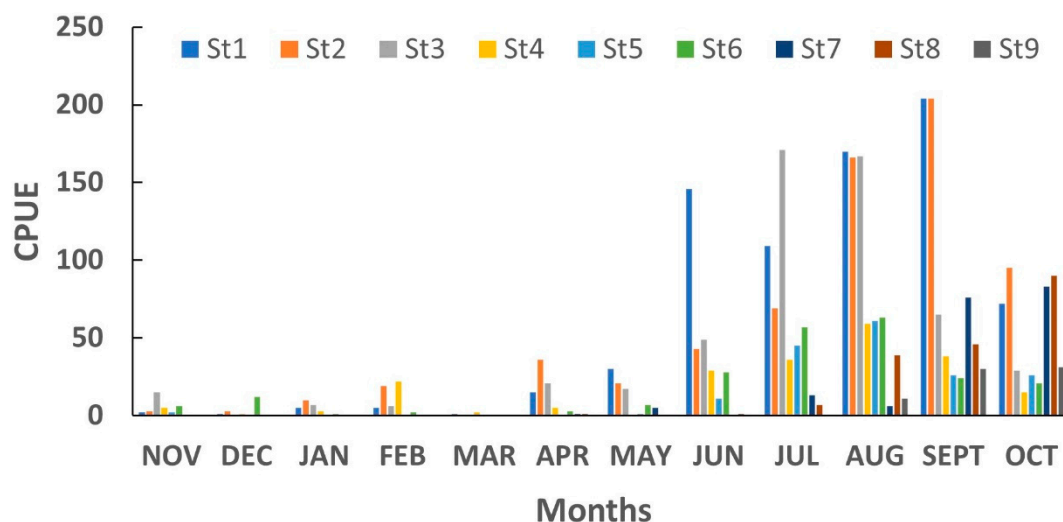


Figure 2. Catch per unit effort (crabs/10 pairs of fyke nets) of the blue crab *Callinectes sapidus* per station (st. 1–st. 9) and per month (November 2020–October 2021) in Monolimni Lagoon and the adjacent coastal area.

3.2.1. Seasonal Variation

The CPUE varied significantly with the seasons (Kruskal–Wallis test: $\chi^2_{(3)} = 21.784$; $p = 0.000$) (Figure 3a). Post hoc analysis revealed that mean CPUEs (\pm sd) in summer (172.89 ± 155.05) and in fall (134.22 ± 96.57) were not significantly different from one another ($p = 0.831$), whereas both CPUEs were significantly higher than the CPUEs in winter (10.78 ± 12.09) ($p = 0.001$ and $p = 0.000$, respectively) and spring (18.44 ± 22.18) ($p = 0.031$ and $p = 0.015$, respectively). The CPUEs in spring and winter were not significantly different from one another ($p = 0.662$). In males, the CPUE exhibited a significant seasonal differentiation (Kruskal–Wallis test: $\chi^2_{(3)} = 15.464$; $p = 0.001$); post hoc analysis revealed similar results for males and for the entire population. The CPUE for females also varied significantly with the seasons (one-way Welch's ANOVA: $F = 8.434$, $p = 0.000$). However, multiple comparisons with the Games–Howell test showed that the mean CPUE (\pm SD) was higher in fall (55.22 ± 45.46), but not significantly different in comparison to summer (37.22 ± 29.48) ($p = 0.754$); the CPUEs of both seasons were significantly different from

those in winter (1.67 ± 1.94) ($p = 0.031$ and 0.028 , respectively) and spring (3.33 ± 3.61) ($p = 0.037$ and $p = 0.035$, respectively).

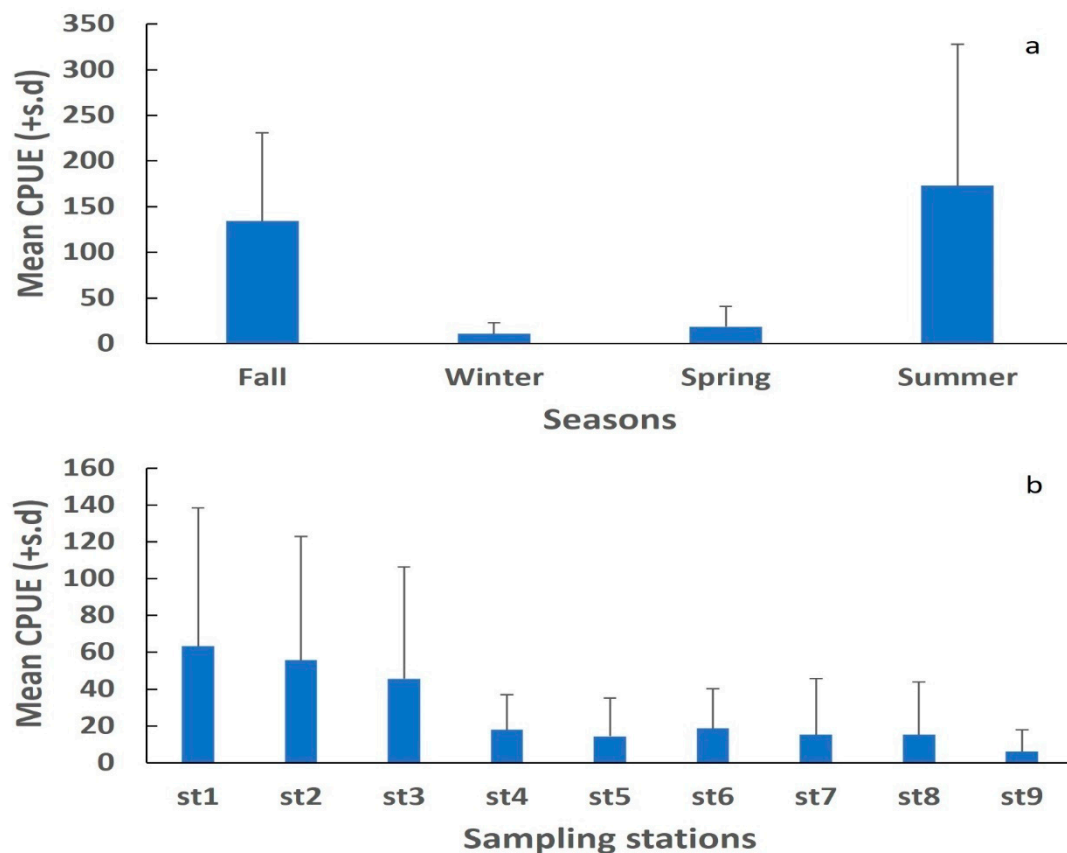


Figure 3. (a,b) Mean CPUE (\pm SD) of the blue crab *Callinectes sapidus* per season (November 2020–October 2021) (a) and per sampling station (st. 1–st. 6: lagoon; st. 7–st. 9: coastal area) (b) in Monolimni Lagoon and the adjacent coastal area.

During winter and spring, very low CPUEs (0 to 36 crabs/10 pairs of fyke nets) were recorded in the lagoon, especially from December to March, increasing slightly in April and May. The highest CPUEs were recorded in July and August—with 171 and 170 crabs/10 pairs of fyke nets, respectively—and in September, when a peak occurred (204 crabs/10 pairs of fyke nets). However, the highest monthly catch was recorded in August ($N = 686$), dominated by males. High abundance was also recorded in fall, with a gradual decrease from September to October, followed by an abrupt decrease in November, with the highest CPUEs in the latter two months estimated at 85 and 15 crabs/10 pairs of fyke nets, respectively. In the coastal area, crabs appeared in the catch in April and gradually increased in abundance from spring to fall, with a predominance of females; the highest CPUE was recorded in October, with 90 crabs/10 pairs of fyke nets. Thus, the bulk of the catches in the open sea was/were recorded in fall, when 81% of the total number of crabs were caught, with the number of crabs collected in October representing 46% of the total catch.

Spearman's rank-order correlation showed that for the entire blue crab population and for each sex separately there was (a) a significant strong positive correlation between temperature and CPUE, (b) a significant strong negative correlation between oxygen and CPUE, and (c) a significant strong positive correlation between salinity and CPUE, with the exception of the relationship between the CPUE of females and salinity, where the moderate correlation was not significant ($p = 0.1$) (Table 1).

Table 1. Spearman’s rank–order correlation results for the relationships (a) CPUE–temperature, (b) CPUE–salinity, and (c) CPUE–oxygen of the blue crab *Callinectes sapidus* in Monolimni Lagoon and the adjacent coastal area (ρ = Spearman’s correlation coefficient, * = significance at $p < 0.05$, n.s = non-significant).

Relationship	Blue Crab Population		Male Blue Crabs		Female Blue Crabs	
	ρ	p	ρ	p	ρ	p
CPUE–temperature	0.93	*	0.895	*	0.818	*
CPUE–salinity	0.629	*	0.594	*	0.497	n.s
CPUE–oxygen	−0.762	*	−0.720	*	−0.692	*

3.2.2. Spatial Variation

The CPUE was also significantly different between sampling stations (Kruskal–Wallis test: $\chi^2_{(8)} = 23.944$, $p = 0.002$) (Figure 3b). The highest mean values were recorded at the northern stations st. 1 (63.33 ± 75.04) and st. 2 (55.75 ± 67.23), followed by st. 3 in the southern part of the lagoon (45.58 ± 60.82 crabs/10 pairs of fyke nets). Significantly lower CPUEs (\pm SD) were observed in the coastal area, decreasing from st. 7 (15.33 ± 30.26) and st. 8 (15.33 ± 28.551) to st. 9 (6 ± 11.87). In the entries (st. 5 and st. 4) and the opening of the lagoon (st. 6) to the sea, the CPUEs were estimated at $14.33 (\pm 20.79)$, $17.92 (\pm 19.03)$, and $18.67 (\pm 21.49)$, respectively. Post hoc analysis revealed that the CPUEs at the stations located in the north (st. 1, st. 2) and the south (st. 3) of the lagoon were not significantly different from one another ($p = 0.68–0.95$). However, they were significantly different from those in the coastal area ($p = 0.001–0.035$). The CPUEs at the stations in the latter area were not significantly different from one another ($p = 0.387–0.987$). Moreover, Kruskal–Wallis tests showed that the CPUE was significantly different between the sampling stations for males ($\chi^2_{(8)} = 35.34$, $p = 0.000$), but not for females ($\chi^2_{(8)} = 9.144$, $p = 0.330$). Post hoc analysis revealed similar results for the CPUEs for males and for the entire population.

During the survey period, the number of blue crabs caught inside the lagoon ($N = 2587$) was significantly higher than the number caught in the coastal area ($N = 440$) and represented 85% of the total catch. Inside the lagoon, the highest CPUEs (204 crabs/10 pairs of fyke nets) were recorded at st. 1 and st. 2. The lowest CPUE at the above stations, with only 1 crab/10 pairs of fyke nets, was found at st. 1 in December and in March. From June to November, crabs were found at all stations inside the lagoon. During the survey, $\approx 56\%$ of the total catch came from stations st. 1, st. 2, and st. 3, whereas from June to October $\approx 23\%$ of the total catch was collected at st. 1. Almost 80% of the crabs caught in the lagoon were males. The CPUEs in the coastal area ranged from 0 to 90/10 pairs of fyke nets, with the highest CPUE recorded at st. 8. Almost 80% of the crabs caught in the open sea were females.

3.3. Sex Ratio

A total of 3027 individuals (2150 ♂ and 877 ♀) were collected in Monolimni Lagoon and the adjacent coastal area. The total sex ratio was estimated at 2.45:1 (♂/♀), with males outnumbering females in the population (Figure 4).

Males dominated in all months: February ($\chi^2 = 26.74$, $p < 0.001$), April ($\chi^2 = 38.24$, $p < 0.001$), May ($\chi^2 = 31.25$, $p < 0.001$), June ($\chi^2 = 19.88$, $p < 0.001$), July ($\chi^2 = 106.37$, $p < 0.001$), August ($\chi^2 = 450.25$, $p < 0.001$), and September ($\chi^2 = 56.66$, $p < 0.001$), with the exception of October when equality was assessed. The largest number of males against females was recorded in August, with 660 and 82 specimens, respectively, and with the sex ratio (♂/♀) estimated at 8.05.

Inside the lagoon, 2587 crabs were caught, with males ($N = 2059$) outnumbering females ($N = 528$) by a ratio of 3.89:1 ($\chi^2 = 907.59$, $p < 0.001$). At every station, males outnumbered females; st. 1: ($\chi^2 = 241.03$, $p < 0.001$), st. 2: ($\chi^2 = 171.02$, $p < 0.001$), st. 3 ($\chi^2 = 211.73$, $p < 0.001$), st. 4: ($\chi^2 = 44.88$, $p < 0.001$), st. 5: ($\chi^2 = 41.02$, $p < 0.001$), st. 6: ($\chi^2 = 33.01$, $p < 0.001$). On the other hand, in the coastal area, 440 crabs were caught; females

($N = 349$) outnumbered males ($N = 91$), with a ratio (σ/φ) of 0.26:1 ($\chi^2 = 151.28$, $p < 0.001$), and represented $\approx 79\%$ of all crabs caught in the coastal area. With the exception of April, when both sexes were equally exceptionally scarce, females dominated from May to October. Moreover, at every station, females outnumbered males (st. 7: $\chi^2 = 63.39$, $p < 0.001$; st. 8: $\chi^2 = 73.13$, $p < 0.001$; st. 9: $\chi^2 = 16.06$, $p < 0.001$). Pearson's correlation demonstrated a strong negative correlation for the abundance of males ($r = -0.98$) and females ($r = -0.90$), as well as an increasing sex ratio (σ/φ) (st. 7: 0.26, st. 8: 0.25, st. 9: 0.36) in favor of females, with increasing depth.

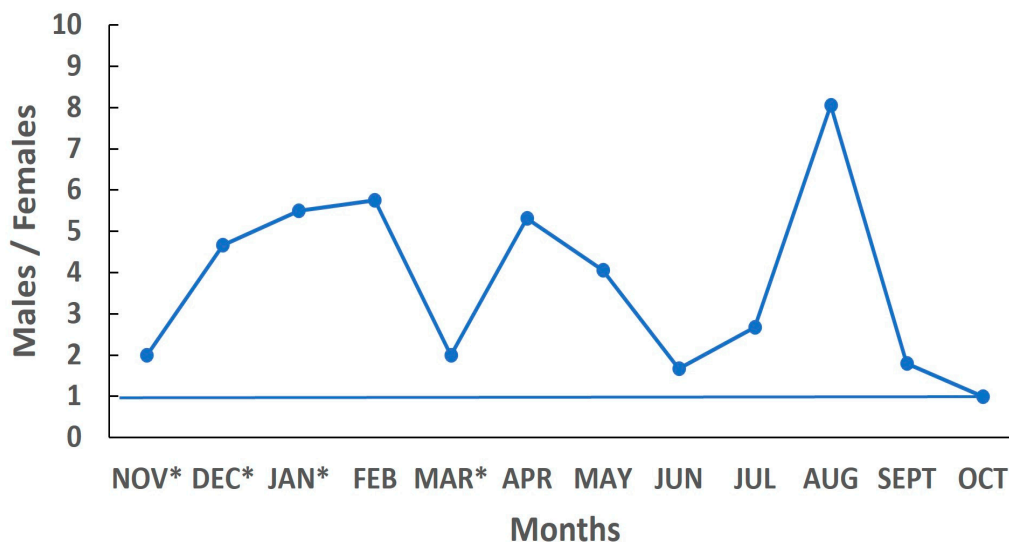


Figure 4. Sex ratio of the blue crab *Callinectes sapidus* in the period November 2020–October 2021 in Monolimni Lagoon and the adjacent coastal area. * Sex ratio was not tested (number of specimens collected <50 crabs).

3.4. Population Structure

3.4.1. Age Classes

Modal progression analysis estimated three modes corresponding to the 0^+ , 1^+ , and 2^+ age classes in both females and males. In males, the age class 1^+ was dominant and represented $\approx 90\%$ of the total number of males, whereas only ≈ 50 crabs belonged to the 0^+ and 2^+ age classes. In contrast, in females, the age class 2^+ dominated, with females in the age class 1^+ reaching $\approx 45\%$ of those belonging to age class 2^+ . Few individuals of both sexes with CW >175 mm were caught, probably belonging to the 3^+ age class ($N = 32$).

3.4.2. Size–Frequency Distribution

A total of 2984 ($\sigma = 2124$, $\varphi = 860$) crabs with intact lateral spines were caught in the survey and were analyzed for size–frequency distribution (Figure 5). Males exhibited a slightly wider size range than females and presented a higher frequency in the class 120–145 mm, whereas females were more frequent in the classes 100–120 and 135–160 mm. The mean CW (\pm SD) of males was 128.35 (± 18.26 mm) (range: 43.45–199.92 mm), whereas that of females was 130.33 (± 25.89 mm) (range: 53.87–205.26 mm). Only eight juveniles (0.27% of the population) were caught in the survey. Juveniles were caught for the first time in January, followed by February, May and, lastly, in July. Juveniles were caught only in the lagoon. The size–frequency distributions were significantly different between females and males (two-sample Kolmogorov–Smirnov test: $z = 5.975$, $p < 0.000$); the CW of females was significantly higher than that of males (Mann–Whitney test: $U = 1,014,456.00$, $z = 4.745$, $p < 0.000$), with females showing a greater median size than males (independent median test: $T = 27.608$, $p < 0.000$). However, when crabs caught in the lagoon and those caught in the coastal area were separated, different results were found for the size–frequency distributions of both sexes.

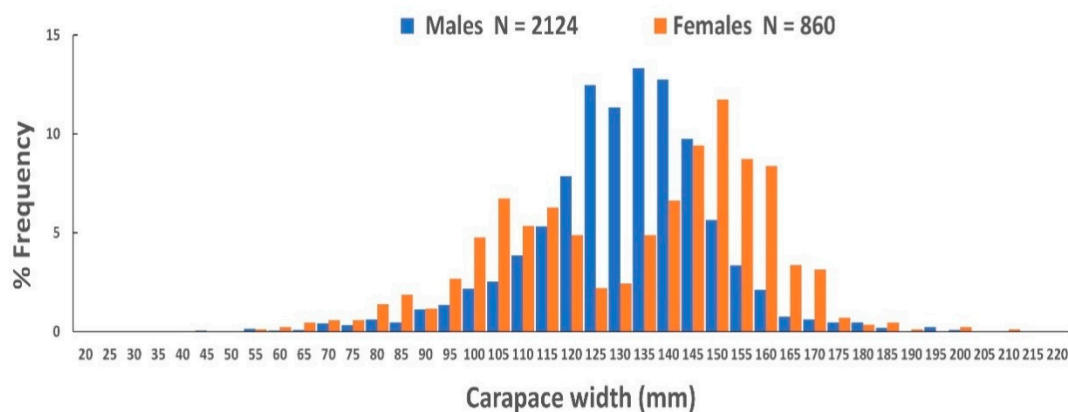


Figure 5. Size–frequency distributions of males and females of the blue crab *Callinectes sapidus* in the period November 2020–October 2021 in Monolimni Lagoon and the adjacent coastal area.

Inside the lagoon, 2034 males and 518 females were measured, with a mean CW (\pm SD) 128.09 (\pm 18.03) mm and 118.43 (\pm 25.49) mm, respectively. The size–frequency distributions were significantly different between females and males (two-sample Kolmogorov–Smirnov test: $z = 7.215$, $p < 0.000$). The CW of males was significantly larger than that of females (Mann–Whitney test: $U = 392,693.000$; $z = -8.958$, $p < 0.000$), with males having a greater median size than females (independent median test: $T = 55.66$, $p < 0.000$). In the coastal area, the number of females ($N = 342$) measured was significantly higher than that of males ($N = 90$); the mean CW (\pm SD) for males and females was 134.33 (\pm 17.06) mm and 148.30 (\pm 12.94) mm, respectively. The smallest crab was a male (CW = 92 mm), and the largest was a female (CW = 205 mm). The size–frequency distributions were significantly different between females and males (two-sample Kolmogorov–Smirnov test: $z = 3.86$, $p < 0.000$). Females were significantly larger than males (Mann–Whitney $U = 23,731.5$, $z = 7.915$, $p < 0.00$), with females having a greater median size than males (independent median test: $T = 47.214$, $p < 0.000$).

Crab size (CW) varied significantly between seasons (Kruskal–Wallis (H) test: $\chi^2_{(3)} = 254.247$; $p = 0.000$). Post hoc analysis showed that the mean CW (\pm SD) in summer (123.32 ± 20.46 mm) had the lowest value and was significantly different compared to all other seasons ($p = 0.000$ – 0.002). The size in winter (129.87 ± 23.66 mm) was different compared to that in spring (134.24 ± 23.75 mm) ($p = 0.047$) and fall (135.37 ± 18.25 mm) ($p = 0.012$), when the largest size was attained. However, the size in spring was not significantly different from that in fall ($p = 0.891$). Crab size (CW) also varied significantly between stations (Kruskal–Wallis (H) test: $\chi^2_{(8)} = 404.640$; $p = 0.000$), with crab size decreasing from st. 9 in the marine area to st. 1 in the lagoon. Post hoc analysis showed that the mean CW of crabs at the marine stations (range: 144.85–145.83 mm) was larger than the mean CW of crabs at all lagoonal stations (range: 123.3–129.8 mm) ($p = 0.000$ – 0.001 , in all cases), but they were not significantly different from one another ($p = 0.085$ – 0.101). Moreover, the size–frequency distributions of mature females (ovigerous and non-ovigerous) and the mean CW of males distributed in the coastal area stations were not significantly different in relation to depth, according to the Kruskal–Wallis test (H) ($\chi^2_{(2)} = 1.625$; $p = 0.444$) and one-way ANOVA ($F = 0.053$; $p = 0.949$), respectively.

3.5. Reproductive Aspects

Out of the 877 female crabs caught in the course of this study, sexually mature females made up 75% of the sample ($N = 656$). Immature females were caught only in the lagoon ($N = 221$), while sexually mature ones were caught both in the lagoon ($N = 308$) and in the coastal area ($N = 348$), including ovigerous females. Intact mature females ($N = 642$) ranged from 69.28 to 205.26 mm CW, with a mean (\pm SD) = 140.23 (\pm 20.54) mm, whereas intact immature females ranged from 53.87 to 127.66 mm CW (mean \pm SD: 101.06 \pm 15.80 mm). Intact mature females caught in the lagoon ($N = 300$) ranged from 69.28 to 200 mm CW,

with a mean (\pm SD) = 131.98 (\pm 23.57), whereas those in the coastal area (N = 342) ranged from 92.05 to 205.26 mm CW, with a mean (\pm SD) = 148.29 (\pm 12.89) mm. The size–frequency distributions of mature females in the lagoon and in the marine area were significantly different (two-way Kolmogorov–Smirnov test: $z = 4.577$, $p < 0.000$). Mature females collected in the marine area were significantly larger and had a greater median size than the females collected in the lagoon area (Mann–Whitney test: $U = 73,188.500$, $z = 9.335$, $p < 0.000$; independent median test: $T = 63.914$, $p < 0.000$, respectively).

3.5.1. Ovarian Stages

The frequency of monthly ovarian stages from January to October is shown in Figure 6. Females with mature ovaries (III) were observed for an 8-month period, from late winter (February) to mid-fall (October), with higher percentages found from late spring (April) to late summer (August); stage IV appeared only in September, and stage V peaked from June to October. Immature (I) and premature (II) ovaries were present throughout the study period, but mostly from late summer (August) to early fall and from late winter to early spring.

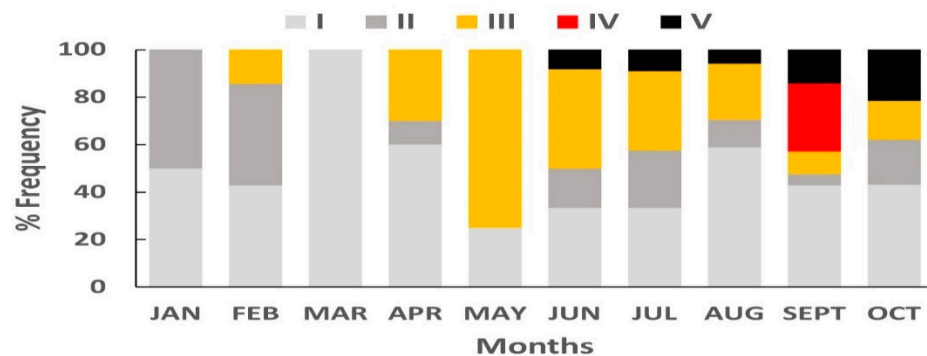


Figure 6. Monthly (January–October) ovarian stages (I–V, according to Hard [60]) of the blue crab *Callinectes sapidus* in Monolimni Lagoon and the adjacent coastal area.

3.5.2. Ovigerous Females

Ovigerous females (N = 116) were found only at all marine coastal stations (st. 7–st. 9) from May to October, with the exception of June. Their occurrence was very low in May (N = 4) and July (N = 5), increased slightly in August (N = 14), and peaked significantly in September (N = 92) (79% of total ovigerous females), whereas it decreased abruptly in October, when only one specimen was caught. Ovigerous females at the advanced developmental egg stage (stage 5) (N = 55) represented 47% of all ovigerous females. Although they were found in all months, they were predominant in September (N = 45), indicating one major spawning peak, followed by very low numbers in August (N = 5), July (N = 3), May (N = 2), and October (N = 1).

Ovigerous females appeared at st. 7, with their numbers decreasing with depth (st. 7, N = 55; st. 8, N = 35; st. 9, N = 26), resulting in a strong negative correlation between ovigerous females and depth (Pearson’s correlation, $r = -0.94$). However, whilst the highest number of ovigerous females was found at st. 7, the highest % frequency of ovigerous females at egg stage 5 was found at st. 9 (73%), followed by st. 7 (45%) and st. 8 (31%). When only September was considered, due to the large number of ovigerous females collected, a moderate non-significant negative correlation was found between the % frequency of ovigerous females at egg stage 5 and depth (Spearman’s rank–order correlation; $\rho = -0.5$, $p = 0.667$).

The size of ovigerous females and of ovigerous females at egg stage 5 ranged from 120.05 to 186.58 mm CW and from 120.73 to 176.08 mm CW, respectively, with a mean (\pm SD) = 147.26 (\pm 12.5) mm and 146.82 (\pm 11.24) mm, respectively. A one-way ANOVA showed that there were no significant differences in the mean CW of ovigerous females and of ovigerous females at egg stage 5 according to depth ($F = 1.717$, $p = 0.184$ and $F = 1.260$, $p = 0.290$, respectively). Moreover, no significant difference in mean CW was

found between ovigerous females at different developmental egg stages (one-way ANOVA: $F = 1.260$, $p = 0.290$).

3.5.3. Size at Maturity

The mean size at maturity for females (L_{50}) collected in the survey was calculated to be 124 mm CW, using both frequentist regression ($L_{50} = 123.9$ mm, $R^2 = 0.96$, confidence intervals = 122.1–125.5 mm) and Bayesian regression ($L_{50} = 123.8$ mm, $R^2 = 0.96$, confidence intervals = 122.1–125.5 mm) (Figure 7).

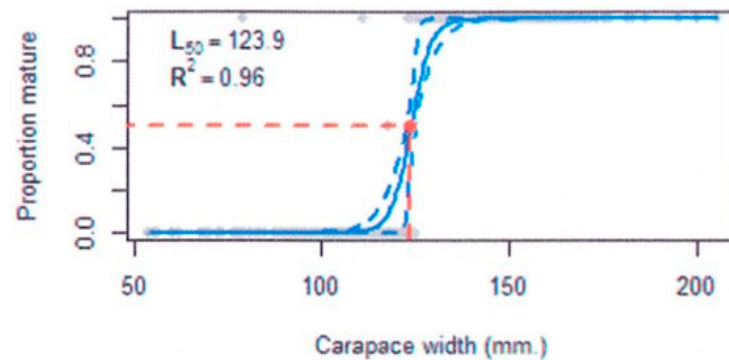


Figure 7. The mean size at maturity (L_{50}) of *Callinectes sapidus* females in the period November 2020–October 2021 in Monolimni Lagoon and the adjacent coastal area, according to frequentist regression.

4. Discussion

4.1. Physicochemical Parameters

The habitat selection of the blue crab is dependent on the particular physiological requirements of each life history in its complex life cycle, with blue crabs relying on estuarine habitats during most of their life cycle (e.g., [35,62,63]). However, within estuarine environments, species distributions are often limited by temperature and salinity tolerance, as estuaries are exposed to large diurnal, seasonal, and yearly fluctuations in salinity, temperature, and dissolved oxygen, e.g., [64,65]. Temperature is likely the key environmental parameter, and the blue crab life cycle is markedly affected by its seasonal cycle [35,63,66]. For juveniles and adults, there are minimum and maximum thermal tolerance limits (0–39 °C), but these are dependent on acclimation to temperature and salinity (e.g., [67]). One of the most remarkable features of the physiology of the blue crab is its ability to tolerate and indeed thrive in a broad range of environmental salinities, from almost freshwater to hypersaline environments (e.g., [68–70]). However, harsh winters (<3 °C, <8 psu) cause significant mortality in small juveniles and mature females [71]. Moreover, blue crabs can—at moderate water temperatures—survive at DO levels as low as 1.3 mg/L [72]. In the poikilohaline and typically shallow Monolimni Lagoon and the adjacent coastal area, the blue crab was subjected to seasonal fluctuations of the above major physicochemical parameters. However, at distinct stages of its life cycle, this portunid crab was able to overcome large-scale variations of these parameters in the estuarine area of the Evros River, which fluctuated within the species' tolerance range, i.e., temperature (6–27 °C), DO (3.75–16.5 mg/L), and especially salinity (0.28–37 psu), with its lowest value corresponding to freshwater conditions.

4.2. Catch Per Unit Effort (CPUE)

In the Monolimni Lagoon and the adjacent coastal waters, ≈90% of the total catch of the blue crab was fished in a 5-month period (June to October). High CPUE values were recorded from early summer to mid-fall, with a peak in September, whereas lower values were recorded from the end of fall to the end of spring—a pattern that was highly correlated with the bottom temperature. Annual variation in blue crabs' relative abundance and distribution is significantly affected by habitat and is correlated with salinity and temperature as environmental variables that are linked to broad climatic factors influencing

estuarine ecosystems [35,73]. Thus, blue crabs' abundance in higher-latitude estuaries typically exhibits a strong seasonal cycle, with very low to zero catches in winter and early spring, and higher catch densities by mid-summer [31,40,74], which reflects the natural behavior and demography of the blue crab [35]. Declining abundances during the cold season of the year have been also reported from other Mediterranean regions [12,26,50,52]. However, Sumer et al. [47] reported on aseasonally stable population in the Beymelek Lagoon. Moreover, the significant reduction in the blue crab's abundance during the cold period may be due to the burrowing behavior of the species into the substrate [75] of the lagoon for hibernation, and/or to the shift into deeper waters in the marine area. Thus, the high abundance trend observed in the coastal area in October possibly indicates a seasonal migration pattern of the species towards the sea for overwintering. Since the senescence of most blue crabs appears to result in death after about 2–3 years, the seasonal cycle of declining abundance may also reflect loss due to the death of older crabs [35].

A characteristic of lagoonal estuaries is the absence of extensive spatial variation in salinity, which may influence a variety of aspects of the blue crab's life history—such as population characteristics, which typically show relatively more temporal than spatial variation [76–78]. In Monolimni Lagoon—where a salinity gradient is absent—and in the adjacent coastal area, there was a significant strong positive correlation between the CPUE of males and of the entire population and salinity, whereas a non-significant moderate correlation was estimated between CPUE and females. However, according to Hines [35] and Jivoff et al. [78], salinity had a marked effect on the abundance of adult blue crabs because of sex-specific responses to salinity variation; male abundance was negatively correlated with salinity, whereas adult females were more abundant in high-salinity areas. Nevertheless, King et al. [79] reported that only 51% of the abundance variance of blue crabs was explained by salinity, watershed land use, and shoreline marsh habitat in 19 sub-estuaries of Chesapeake Bay. Therefore, further research is needed to establish the relationship between the relative abundance of females and salinity in the estuarine area of the Evros River. Moreover, a relatively strong negative correlation between relative abundance and DO was estimated in the study area. Blue crabs in Monolimni Lagoon experienced no episodic hypoxia (<2 mg/L) [80] during the survey period. However, low DO values (3.9–4.5 mg/L) coupled with high temperatures (>22.5 °C) were recorded at all stations in the lagoon from June to September—a period when the highest CPUEs were also attained.

CPUE also varied spatially, with higher values recorded at stations located in the northern and southern parts of the lagoon, whilst significantly lower CPUEs were derived from the marine stations. Thus, the bulk of the catch (%) was fished from the shallow-water (<0.5 m) stations st. 1, st. 2, and st. 3, and it was dominated by males. These stations are characterized by a high salinity variation (6–32 psu), silt substrate, and dense *Ruppia maritima* meadows [56]. Seagrass beds and marshes have been identified as important nurseries for the blue crab [81], and *R. maritima* in particular has been well recognized as a choice vegetation habitat, as it provides shelter for different stages of blue crabs. Small juveniles were abundant in *R. maritima*, possibly because of the high shoot density of *R. maritima* beds [82]. Moreover, the macrozoobenthic community in the Monolimni Lagoon was composed of 21 taxa and showed a rather homogeneous composition throughout the year, with the amphipod *Corophium orientale* and the gastropod *Ventrosia maritima* dominating the lagoonal benthic assemblages. Total abundance peaked (50,000 to 60,000 individuals m^{-2}) in mid–late fall. The macrozoobenthic community structure showed an almost-even seasonal periodicity [55], indicating that the Monolimni Lagoon is a preferred blue crab habitat. Moreover, recent research on the diet of the blue crab in Monolimni showed that the species fed mainly on polychaetes, crustaceans, and bivalves in the lagoon [83]. Therefore, a large portion of the population is segregated in the upper and the southern parts of the lagoon for most of the year—a fact that ensures higher survival rates and the growth of juveniles and adults, providing shelter and adequate food but also favorable conditions for molting and mating.

Abundance patterns differed between sexes. Males followed the same pattern as the entire population. In contrast, female abundance exhibited significant seasonal differences, with higher CPUEs obtained in fall, but no spatial variation. However, an increasing trend in abundance from spring to fall (September–October) was observed in the coastal area. This reflects migratory trends towards higher-salinity waters, mainly for spawning, because from May to October ovigerous females with eggs in all developmental stages were found only in the coastal area, along with mature females and a small number of males. A small number of fishermen in the study area use a large number of fyke nets targeting the blue crab—mainly males inside the lagoon, and for a period exclusively from early summer (June) to mid-fall (October). In this period, the fishing pressure applied to that portion of the crab population is intense. In the same period, no fyke nets were placed in the coastal area by the fishermen; thus, this portion of the population is rarely or not at all fished. In the present study, the bulk of the catch was derived from the age classes 1⁺ and 2⁺; however, males belonging to the age class 2⁺ accounted for only 1–2% of the total number of males, indicating that there is an intense fishing of males in that age class. Males comprised 80% of the crabs caught in the lagoon in the period June–September. The mean CPUE estimated in the present survey was lower than that in Methoni Bay in the period 2011–2012, where the mean CPUE was recorded at 21.72 crabs, as this value was estimated per 5 pairs of fyke nets soaked for 24 h with a 40 mm mesh size [12]. Within the Mediterranean, different fishing gears are used for blue crab fishing; however, fishing traps and fyke nets are the most commonly used. Differing fishing gear is used in different regions of the basin, making comparisons difficult for gear efficiency and the CPUE values reported (e.g., [26,46,52]).

4.3. Sex Ratio

The sex ratio is presumed to be balanced in most populations of blue crabs, especially in the juvenile stages [84]. However, quantitative assessment of sex ratio is difficult, because males and females partition the available habitats along the estuarine salinity gradient [31]. In the estuarine area of the Evros River, males dominated the population almost throughout the study period; in all monthly catches, males outnumbered females—with the exception of October, where equal numbers were recorded, as females contributed significantly to the catches in the coastal area. However, males' dominance varied seasonally; it was higher in winter and spring (>4:1) and lower in summer and fall (1–2.5:1)—except in August, when males' predominance was pronounced (8:1). In the Chesapeake Bay, migration of mated females to the higher-salinity waters for egg laying and hatching typically occurs throughout the summer and results in large skews in sex ratio [31].

In the survey period, males dominated at all stations inside the lagoon—and especially in stations st. 1–st. 3, from where the bulk of the catch of the blue crab originated. However, in June, the sex ratio (σ/φ) at the above stations was close to equality (1.5:1)—and especially at st. 1 (1.1:1). This was probably due to the initiation of mating taking place in early summer in these parts of the lagoon (see below in Reproduction). In the coastal area, females outnumbered males significantly from their first appearance in April through to October—and especially in September and October, with a ratio ranging from 1:3 to 1:9 (σ/φ), respectively. The number of males showed an increasing trend in that period, with the highest numbers recorded in September and October at stations st. 7 and st. 8. An increasing sex ratio with increasing depth was also observed in favor of females, implying that mature females (ovigerous and non-ovigerous) migrate deeper than males, probably indicating a preferable site or spawning depth. In Methoni Bay, a spatial divergence in sex ratio related to the spawning migration pattern of the species was also recorded, with females outnumbering males at greater depths [12].

The male dominance of blue crab populations has been reported in a variety of habitats along the Atlantic coast, e.g., [84,85]. In the Mediterranean Basin, male dominance in established blue crab populations has also been reported in Italian [50,86], Egyptian [52], and Croatian lagoons [26], as well as in Methoni Bay, where a 2:1 ratio in favor of males

was estimated [12]. However, divergence with respect to sex ratio results was reported from southern Turkish coast, where populations were found to be biased in favor of females [47,49].

4.4. Population Structure

Modal progression analysis of the blue crab population estimated a three-modal size–frequency distribution for both sexes, corresponding to the 0⁺, 1⁺, and 2⁺ age classes. However, Hines [35] stated that, based on long-term average size–frequency distributions in the Chesapeake Bay, the blue crab population typically exhibits a bimodal size–frequency distribution (0⁺ and 1⁺ age classes). This bimodal distribution derives from the seasonal pattern of summer–fall larval recruitment, retarded growth during cold winter months, and a 2–3-year life span [40,87]. At an even more northerly latitude of the species' distribution, Taylor and Fehon [36] confirmed the existence of the two distinct age classes in spring and summer, with males accounting for the majority of age 1⁺ crabs.

Hines [35] stated that in the Chesapeake Bay the 0⁺ age class grows from 80 to 90 mm during its first warm season of feeding in the sub-estuaries, and these juveniles reach the 1⁺ age class in their second summer, when they molt to maturity. In the present survey, crabs belonging to the 0⁺ age class grew to 80–85 mm in both sexes. However, only ≈80 crabs were assessed in the age class 0⁺, as the fyke nets were size-selective, with very few juveniles caught in the lagoon. Females in the age class 1⁺ had a mean CW = 110.85 mm, whereas males attained a mean CW = 133.75 mm. The age class 1⁺ was numerically dominant, with males accounting for the majority of age class 1⁺ crabs. In contrast, females were dominant in the age class 2⁺. They grew to 150 mm CW and were numerically much higher than males, which grew to 175 mm CW. Very few large crabs of both sexes >175 mm (probably belonging to the age class 3⁺) were caught; these large crabs made up a small proportion (1%) of the population. Hines [35] stated that most blue crabs are thought to die after a life span of about three years; however, there is some debate as to whether death ensues from senescence or from their high rate of fishing capture.

Size–frequency distributions showed that, in the classes 125–130 mm, females presented an unusually low frequency; these size classes were just or just over the size at first maturity (see below in Reproduction), and to some extent a significant number of females belonging to these classes had probably undergone their final molt through summer, when high CPUEs were recorded, making them vulnerable and, thus, immobile and under shelter, so were not caught in the fyke nets.

Hines [35] stated that, in Chesapeake Bay, blue crab males attain a larger size than females, with mature females reaching up to 180 mm CW and mature males typically larger (from 180 to 200 mm, but occasionally some grow to >250 mm) [88]. In the study area, females attained a greater mean size than males; it is noticeable that in the fished population the largest crab caught was a female (CW = 205 mm). However, in Methoni during the study period 2011–2012—which coincided with the early years of fishery exploitation of the species in the bay, with fishermen targeting mostly males and discarding ovigerous females—the mean size (CW) and size–frequency distributions were not significantly different between sexes [12]. This implies that a significant variation in population structure exists among blue crab populations that are found at the same latitude and neighboring geographical areas, but in different habitats and under different fishing intensities and durations.

In the Monolimni Lagoon and the adjacent coastal area, a significant spatial variation in size was observed between sexes; males were significantly larger than females when caught inside the lagoon, whereas females were larger than males in the coastal area. Moreover, the mean size of the crabs decreased gradually from st. 9 to st. 1 (st. 9 >> st. 1) indicating that the population inside the lagoon consists of significantly smaller crabs compared to those in the coastal area for both sexes, probably due to the intense fishing pressure imposed on that portion of the population, but also due to migratory movements for spawning and/or overwintering. Small crabs of both sexes caught at stations st. 1–st. 2 (mean CW range: 123–126 mm), where the population is mostly segregated, probably belonged to crabs that belonged to or had just exceeded the 1⁺ age class, indicating that these sites are

probably the nurseries of the blue crabs in the lagoon, where juveniles mature to adults. This is also supported by the fact that immature females were caught only in the lagoon in lower-salinity waters, where it is well known that mating takes place, e.g., [89]. Moreover, despite the small number of large males caught in the lagoon, these also migrated into the coastal area, mainly from August to October. Similar results were obtained from Methoni, where increasing crab size was observed at greater depths (3.5 and 5 m) than at <1 m [12].

Throughout the survey period, males dominated the catches in the lagoon and were larger in size than females. However, females attained a larger mean size than males in the entire population. The reduction in the size of males appears to be attributable to intense fishing, resulting in the removal of larger crabs—especially those from the lagoon; thus, the number of males in the 2⁺ age class was significantly lower than that of females. During the same period of intense fishing pressure in the lagoon, the portion of the population in the marine area was not at all fished. Therefore, in the coastal area, females outnumbered and were significantly larger than males, contributing to the final mean size estimation of the two sexes in the population, with females ending up larger than males. Moreover, males and females of >150 mm CW caught inside the lagoon and in the adjacent coastal area represented only 8% and 25% of the total number of each sex, respectively.

Moreover, it is suggested that the observed decrease in crab size in summer was the consequence of a shift in size–frequency distribution resulting from the recruitment of the 0⁺ and especially the 1⁺ classes into the population and in the catch, respectively, reflecting the main seasonal entry of new recruits to the fished population, together with the migratory trends of the species. In Methoni Bay, significant differences in mean size were also detected seasonally, with smaller specimens caught in July [12]. Subsequently, as the temperature rose significantly during the growing season in the study area (temperature range: 22–27 °C), size increased gradually towards fall. However, another decrease in size was observed in winter, which may also be attributable to the natural mortality of old and large crabs >175 mm, as fishing does not occur during this period in the lagoon and the coastal area. In the mid-Atlantic, a large decrease in the proportion of adult crabs between October and April of the following year was evident, suggesting the possibility of overwintering mortality in larger crabs [85].

4.5. Reproductive Aspects

An extensive reproductive period of the blue crab has been observed in the estuarine area of the Evros River. Sexually mature females made up ≈20% of the catch; females with mature ovaries (stage III) were observed for an 8-month period, from late winter (February), ready for producing broods early from spring—probably for those females that have stored sperm the previous summer—to October (mid-fall). Stage IV peaked in July, and stage V appeared from June to October. Immature (stage I) and premature (stage II) ovaries were present throughout the study period, but mostly from late summer (August) to early fall and from late winter to early spring. In the warmer Levantine Sea, mature ovaries of female blue crabs were present throughout the year, with the highest percentages recorded from August to October, whereas immature stages peaked in July [49].

In temperate areas such as the Chesapeake Bay and other estuaries in the mid-Atlantic, mating takes place almost throughout the estuary in hyposaline waters during the summer, although most females do not produce their first brood of eggs until the following spring or summer, using sperm stored for at least one year or more, depending on the longevity of the females (e.g., [63]). In the present survey, it seems that mating was probably initiated in June in the northern (st. 1–st. 2) and southern (st. 3) parts of the lagoon, where an almost 1:1 sex ratio was observed in that period; the population probably congregates in these shallow (0.5 m depth), hyposaline waters (≈17 psu) as they are warming up (>21 °C), characterized by the presence of *R. maritima* meadows and increased zoobenthos richness. Thus, these areas provide shelter and feed for the newly molted and post-copulatory females, which remain in the mating areas to feed, recover from molting, and begin to accumulate nutritional stores during summer and early fall. Tagatz [90] found that

spawning in northeastern Florida usually occurred one or two months after mating during spring and summer.

One well-known feature of blue crabs' behavior is the migration undertaken by recently mated females to the higher-salinity waters near the mouth of the Chesapeake Bay for egg laying and hatching, e.g., [32]. According to Tankersley et al. [89], migration from the mating area to spawning regions occurs in two phases: in phase I, inseminated females move to the lower estuary, where they subsequently produce and incubate broods; in phase II, ovigerous females migrate near or out of the mouth of the estuary in shallow marine waters to hatch their eggs, releasing larvae into the water column. Development of larvae progresses in the ocean, followed by migration of megalopae and young crabs back into estuarine waters to mature into adults.

In the present survey, an increasing trend in the abundance of females towards the sea was observed from April to October, with a peak in September and October related to the spatiotemporal migration of females from the lagoon into the marine area for spawning. The timing of brood production is influenced by environmental conditions, and there is a temporal and spatial variation in the timing and duration of the spawning season, with spawning initiated earlier in the spring at lower latitudes [3,35,63]. In the coastal area of the Monolimni Lagoon, based on the presence of ovigerous females caught, spawning occurred from May to October, with a peak in September. Additionally, the first occurrence of an ovigerous female in advanced egg stage 5 in May, and the last one in October, indicates at least a 6-month spawning period of the blue crab. Moreover, 80% of the total number of the ovigerous females (in all developmental stages) found in the present survey, as well as 82% of the ovigerous females with broods in advanced egg developmental stage 5, were caught in September, confirming that the spawning peak occurred in early fall at temperatures $> 21^{\circ}\text{C}$ in the marine area. In Iskenderun (Alexandretta) Bay, the highest numbers of ovigerous females were observed in July and August [49], whereas in the Beymelek Lagoon they appeared in the population in February and peaked in August and September, with the spawning period lasting between July and September [47]. Moreover, in the present survey, ovigerous females—including ovigerous females with eggs at stage 5—were found only in the adjacent coastal marine area. However, from observations conducted in the next period (2021–2022), ovigerous females were also found inside the lagoon (Kevrekidis K. et al., unpublished data). This indicates that phase I of female migration, as proposed by Tankersley et al. [89], was also evident in the study area.

The mean CW of the ovigerous females and of those at egg stage 5 was not significantly different between depths. Thus, all sizes of ovigerous females were distributed along a depth gradient. Ovigerous females appeared first at st. 7 and were present at that depth from May to September, whereas they were first found at st. 8 and st. 9 relatively late, in August and September, respectively. In October, only one specimen was found at st. 9. Moreover, as time proceeded towards the peak of spawning in September, the highest percentage of ovigerous females at egg stage 5 was found at st. 9. In that period, no significant differences in the ranges of the physicochemical parameters between depths were recorded (temperature: $21.1\text{--}21.4^{\circ}\text{C}$; salinity: 36.1–36.4 psu, DO: 8.01–8.5 mg/L). However, temperature, salinity, and DO increased gradually at greater depths (6 m), and it seems that ovigerous females at egg stage 5 migrate deeper into the sea to spawn, implying a preference for a certain spawning depth. Similarly, Ramach et al. [91] reported that ovigerous female habitat use varied by the developmental stage of the eggs. However, the above authors referred to a high-salinity and shallow embayment, where females with late-stage eggs were found closer to the embayment's entrance and at significantly shallower depths than females with early-stage eggs.

Geographic latitude, along with environmental variation, may affect the size at sexual maturity. Moreover, fishing intensity may also affect the meansize of mature females in a population. Significant differences in the range and the mean size of mature and ovigerous females were observed between the present study and that carried out in the Iskenderun Bay, with significantly lower mean values recorded in the latter area [49]. However, aside

from the effects of latitude and the temperature variation in these two areas, this difference may also be attributed to the different habitats and fishing gear used in the two studies. The mean size at maturity (L_{50}) for females collected in this survey (124 mm) was higher than the size range (114–118 CW mm) reported from the Levantine Sea [47,49]. A significant variation in L_{50} has been reported from different habitats along the Atlantic coast. In Maryland's coastal bays, it was estimated at 116 mm CW [85]; in the Chesapeake Bay, it ranged from 108 to 118 mm CW, as L_{50} decreased from 118.4 mm between 1988 and 1991 to 107.9 mm CW between 1992 and 2000 [92]. In Florida's estuaries, L_{50} ranged from 116.5 to 129.5 mm CW [93]. Lower values (102–103.3 mm CW) were estimated on the southern coast of Brazil [94,95].

A high population abundance of the Atlantic blue crab *Callinectes sapidus* has been observed in the last 15 years along the coast of the North Aegean Sea, which is considered to be one of the main fishing grounds of the invasive species within the Mediterranean Sea. Thriving populations of the species have been observed in a variety of habitats (coastal marine waters, bays, lagoons, estuaries, etc.) in the area. This portunid crab has been recognized as a “new” valuable resource and has become a target species. Thus, crab fishing has been developed at a local scale and gained a new perspective in the fisheries in the North Aegean. During these years, its price has tripled (1.5 EUR/kg), and the blue crab has become a motivation for young unemployed people to enter the fishing sector.

The blue crab has successfully invaded and become established in the extended deltaic area of the Evros riverine system, and a thriving population of the species can be found in the Monolimni Lagoon and the adjacent marine coastal area. Because the geographical distribution of the blue crab is extensive, ranging from temperate to tropical waters, patterns in the life history of the species may vary by region or even by habitat [85]. However, in the estuarine area of the Evros River, the blue crab exhibits a life cycle involving spatiotemporal migratory movements between the Monolimni Lagoon and the adjacent coastal area, which seems to conform to the general complex life-cycle pattern that has been studied thoroughly in temperate waters along the mid-Atlantic coast—and especially in the Chesapeake Bay (e.g., [30–32,35,63,87,96,97]). Thus, it is suggested that as juveniles mature into adults in the Monolimni Lagoon, and after mating takes place in suitable sites in the upper and southern parts of the lagoon—characterized by the presence of dense *R. maritima* meadows and high abundance of macrozoobenthos—inseminated females become catadromous by the end of spring through fall; they then migrate to the mouths of the lower lagoon, produce broods, incubate eggs and, finally, reach higher-salinity and shallow marine waters to spawn and hatch their eggs. According to Epifanio [30], larval release and subsequent development occur mostly in the open waters of the continental shelf, followed by migration of megalopae back into lagoonal waters to mature into adults. Unlike females, mature males tend to remain dispersed in the upper lagoon from spring through fall, with the exception of a small portion that can be found in the sea. Thus, the above life-cycle pattern generates significant spatiotemporal variability in blue crab population abundance in the study area. Moreover, it is suggested that any blue crab population that inhabits small water bodies of estuarine areas—such as the Monolimni Lagoon, where ongoing intense fishing is evident—will ultimately end up to be very small in number, either by reducing the spawning stock (since females will represent an increasing percentage of the catch as a result of a decreasing supply of males) or by overfishing of larger males which, in turn, will lead to a minimization or loss of sperm transfer to females. Thus, in the present survey, only a few male specimens were caught belonging to the age class 2⁺, and the mean size of females was larger than that of males in the population. Observations throughout the following year (2021–2022) confirmed a significant reduction in CPUE, but also in the spawning stock, based on the very low number of ovigerous females caught.

Nevertheless, this species is known to produce some considerable negative effects in artisanal fishing, whereas its ecological impacts are still largely unknown in the invaded habitats within the Mediterranean Sea. Therefore, the European Union (Regulation 1143/2014) designates the blue crab as an invasive species with a high risk of biodiversity

loss within the Mediterranean, and actions are required to prevent its further establishment and thoroughly control its population explosions, either by eradication and/or radical minimization of its populations in Southern European countries. However, today, the species has extended its distribution throughout the Mediterranean Basin, and fisheries of local importance have been reported to target this new resource. Therefore, for more than a decade, artisanal fisheries have continued to intensively exploit the blue crab along the North Aegean coast, and somehow the question imposed by Mancinelli et al. [43] “time to turn a threat into a resource?” has been answered by the ongoing commercial exploitation of the invader. Furthermore, as no legislative measures have been imposed on the fishing of the invasive blue crab in Greece, it is highly probable that population outbreaks will be affected by fishing intensity—especially on the spawning stock. Moreover, FAO recognizes the blue crab as a valuable resource—especially for North African countries—and the necessity to manage blue crab fisheries and maintain sustainable fishing. FAO initiatives (Recommendation GFCM/42/2018/7 and Scientifically Advisory Committee 22/2021/6) seek to obtain all necessary information so as to evaluate the population status in different habitats and maintain sustainable fisheries that could act as a tool to keep them at a non-expanding level, thereby minimizing their effects on native habitats.

However, all of the above actions towards the maintenance of sustainable fisheries or eradication require very good knowledge of the biology, ecology, and life-cycle pattern of the species in the different habitats of its new environment in the Mediterranean, along with quantitative information on its functional impacts on invaded ecosystems. With this aim, the present study contributes to our knowledge on the population and of the basic life-cycle characteristics of the blue crab from a lagoonal environment in the Northeastern Mediterranean, where this invasive species has been established and is under exploitation. This knowledge will be helpful in the near future for possible implementations and decisions that will be made as to the actions that should be taken for the management of the populations of this species with its peculiar biological characteristics within the Mediterranean Basin.

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