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Effect of Bivalves' Sand Burial Capacity on Predation in the Invasive Blue Crab, *Callinectes sapidus*

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Abstract: In the Ebro Delta (Catalonia, Spain), the abundance of burrowing bivalves has dramatically decreased, with the blue crab, *Callinectes sapidus*, being blamed by shellfish collectors. Trends from 2010 evidence a decrease in the capture of clams (*Ruditapes* spp.) before 2016 (start of blue crab fisheries), although a further decline in both clams and cockles (*Cerastoderma glaucum*) occurred in 2018. In contrast, captures of razor clams (*Ensis siliqua*) have increased by 3.6-fold since 2016. Predation risk for these taxa, with contrasting burrowing capacities (1.7 ± 0.3 cm, 0.4 ± 0.2 cm, and 26.3 ± 0.1 cm, respectively), was assessed using predation preference (N = 5 tanks; 5 individuals of each species) and no-choice experiments (N = 5 tanks; 15 individuals of the same taxa) in the absence and presence of sand. The results showed that, in the absence of sand, razor clams were fully preyed upon in 24 h, clams in 96 h, and cockles reached 60% after 144 h. Conversely, when sand was present, only 4% of razor clams were predated, while clams and cockles reached 60–100% in 120–144 h. The no-choice results featured similar patterns, depending on substrate availability. Overall, clams and cockles appear to be greatly vulnerable to blue crab predation, whereas razor clams may escape thanks to their deeper burrowing capacity.

Keywords: *Ruditapes* spp.; *Cerastoderma glaucum*; *Ensis siliqua*; predation escape; Ebro Delta

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1. Introduction

The blue Atlantic crab, *Callinectes sapidus* Rathburn, 1896, is a marine decapod native to the western Atlantic region, from Maine to the Río de la Plata [1]. The species features euryhaline and eurythermal capabilities that allow it to colonize both coastal and freshwater habitats, coupled with high fecundity and aggressive behavior [2,3]. Since its accidental introduction to the Eastern Mediterranean Sea in 1948, blue crab abundances have progressively increased [4], impacting natural ecosystems and local fisheries [3,5,6].

Although the blue crab is regarded as a generalist omnivorous consumer feeding on a variety of food resources depending on availability and size [7,8], bivalves appear to be a favorite prey item for juveniles and adult individuals [9,10], thus becoming one of the most vulnerable taxa to predation. Previous experimental research with non-burying bivalves has reported important predation effects associated with factors such as prey density, attachment strength, and shell size and hardness, as well as distinctive nutritional features [11–14] that point to a large variability in predation vulnerability across species. A particular decisive aspect is the arrival at a critical upper threshold size—from >40 mm in the hard clam, *Mercenaria mercenaria* [11] to 80–90 mm for the ribbed mussel, *Geukensia demissa* [13]—at which not even large crabs can consume the prey, but such a size might not be attained [14]. However, for burying bivalves, protection from substrate, rather than prey

size, might reduce predation rates, depending on the relative burying capacities of both predator and prey and the sensory abilities to detect buried prey at various densities [15,16]. Blue crabs are tactile feeders, capable of extracting bivalves up to a maximum burial depth of ca. 10–15 cm of substrate [17]. In contrast, the burying ranges of bivalves might widely differ across species, from sub-superficial layers in *Donax* spp., *Ruditapes* spp. or *Cerastoderma* spp. [18] to over 1 m in razor clams [19], which could provide enhanced chances to escape from predation for species with greater digging capacities.

In the last two decades, the blue crab has experienced an expansion toward the western Mediterranean basin [5]. More specifically, in the Ebro Delta, the species was first reported in 2012 in the Tancada Lagoon [20] (Figure 1), and since then, it has become increasingly abundant [21,22]. Alongside this, the remaining local populations of *Cerastoderma* spp. and *Ruditapes* spp. in the Alfacs and Fangar Bays have virtually disappeared over the last years. Also, the hatchery production of the Japanese clam *Ruditapes philippinarum* in the Fangar Bay has closed because of high predation losses (Vongole 2000 S.L., pers. communication from the manager, P. López to I. Gairin). Presently, the only bivalve species that seems to be captured in large abundance in shallow habitats invaded by the blue crab is the razor clam, *Ensis siliqua*, according to data provided by the Catalan Research Institute for the Governance of the Sea (ICATMAR).

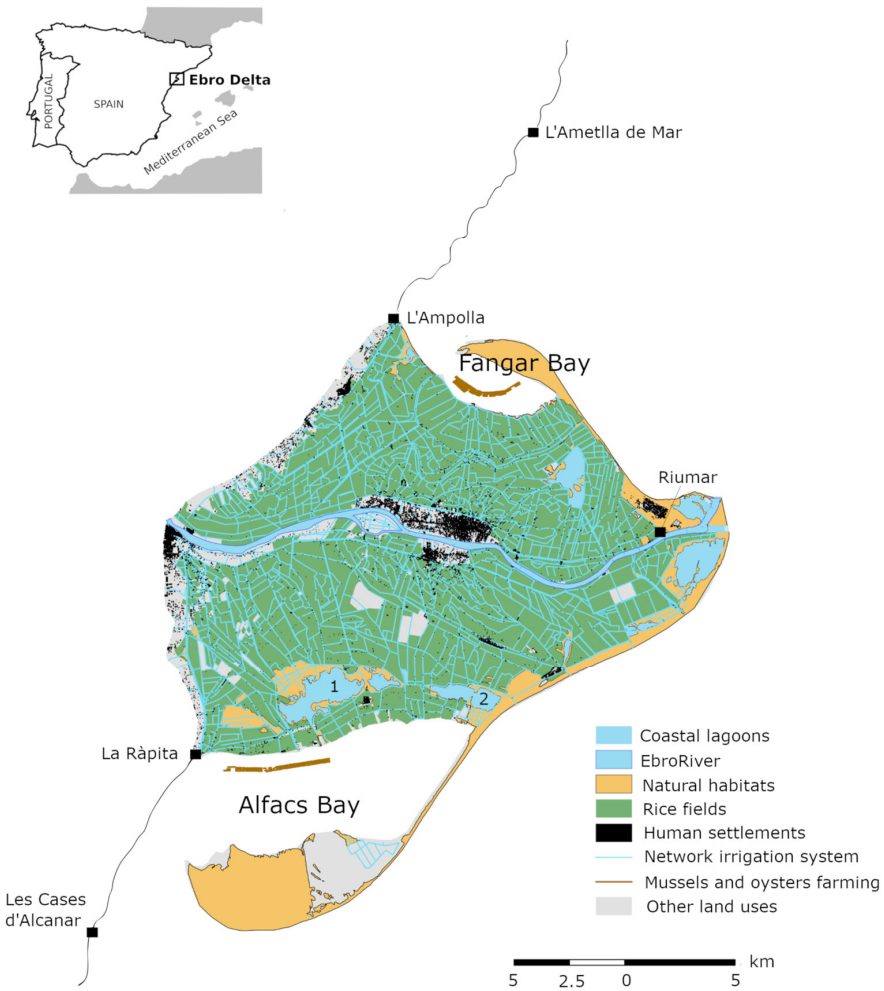

Figure 1. Map of the Ebro Delta, showing the location of the five fishermen's guilds included in the fisheries study and where experimental species were obtained (Riumar). The extension of rice fields, agricultural drainage channels, natural areas such as coastal lagoons (1: Encanyissada and 2: Tancada), bays (Alfacs and Fangar), wetlands and beaches, and the location of mussel and oyster farms are also shown.

In this context, the objective of the present work is two-fold. First, we conducted several manipulative experiments (multiple-choice and no-choice) aiming to assess preferential predation rates across the three taxa that commonly share a habitat with the blue crab, and with higher commercial interest (*Cerastoderma* spp., *Ruditapes* spp., and *E. siliqua*). Second, we aimed to evaluate and capture data from 2010 to 2023 from the different local fisheries across the Ebro Delta in order to assess possible patterns in bivalve trends associated with the increasing captures of blue crab, as proxies of local abundances.

2. Materials and Methods

2.1. Collection of Predators and Prey Items

Live blue crab individuals were bought from the fishermen's association of Riumar located in the town of Deltebre, close to the mouth of the Ebro River (Figure 1). Only males were used throughout the experiments in order to avoid sex-related differences in claw morphology leading to possible variability in predation efficiency [12]. Individuals with a medium size (185.5 ± 4.6 g WW, and carapace width with spines of 157.6 ± 1.9 mm) were selected as the most representative fishery size and were replaced after each experimental trial. Crabs were transported to IRTA facilities 24 h before experiments in order to allow for the acclimation of individuals and ensure non-feeding conditions during that period.

Live bivalve species from local catches in the Ebro Delta were bought from the Riumar fishermen's association (*E. siliqua, Ruditapes* spp. and *C. glaucum*). Individuals with comparable weights (including shells) were selected (*Ruditapes* spp.: 14.7 ± 0.3 g WW; *C. glaucum*: 14.5 ± 0.3 g WW; and *E. siliqua*: 14.3 ± 0.2 g WW) in order to avoid possible size effects in predation preferences. Individuals of each species were also brought to our facilities 24 h before each experiment, in order to allow for natural burying depths in sand substrate trials (see below). Additional individuals of each species (N = 5) were also used to assess burying variability (24 h after placement) across species using a 2 L graduated measuring cylinder made of transparent glass that allowed the positioning of the animal amidst the sand (only one individual per cylinder).

2.2. Predation Experiments

Multiple-choice experiments were first conducted with the three species of bivalves in order to assess predation preferences in the presence and absence of sand substrate. For no-substrate trials, N = 5 plastic tanks of 120 L, 50 cm diameter, and 100 cm height were used to host one blue crab and N = 5 individuals of each species (i.e., a total of 15 bivalves per tank). In the substrate trials, half of the tank was filled with sand (50 cm) and the remaining space with seawater; in the no substrate treatment, seawater was only filled up to 50 cm.

In the no-choice experiments (i.e., only one prey species available), N = 5 tanks hosting one blue crab individual were used for each bivalve species (N = 15 per tank), also in the presence and absence of sand. In all experiments (total of 10 tanks for multiple choice and 10 tanks per species (N = 3) for no-choice), daily predation rates were visually monitored for empty shells or possible fragments, until at least two of the three species were fully consumed or destroyed (usually 144 h).

Individuals of *Ruditapes* spp. and *C. glaucum* were usually opened by chipping the edges and exerting pressure with the claw until the abductor muscle was reached and torn (Figure 2a,b). In contrast, the predation of *E. siliqua* was facilitated by its very thin shell, which lead to easy fragmentation and the rapid death of individuals during manipulation, with the presence of unconsumed flesh remaining (see Figure 2c).

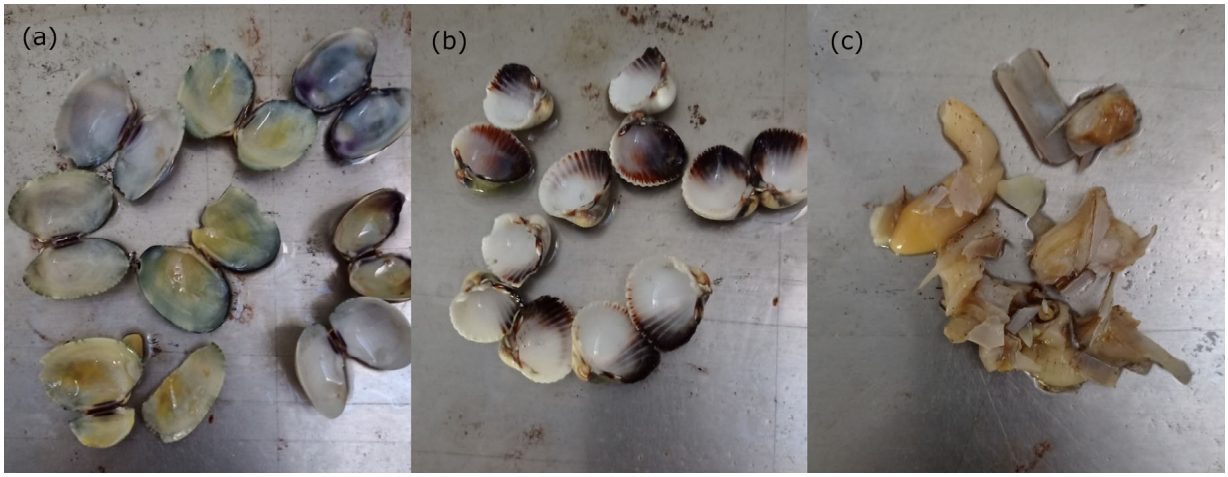

Figure 2. Bivalve species (aggregated from different tanks in no-choice experiments) predated by the blue crab *Callinectes sapidus*. (**a**) *Ruditapes* spp., (**b**) *C. glaucum*, and (**c**) *E. siliqua*. For razor clams, only large shell fragments of partially preyed individuals are shown.

2.3. Fishery Trends

Fishery landings communicated daily from fish markets to the Catalonian government were facilitated by ICATMAR. We selected data from fishermen's guilds around the Ebro Delta from 2010 to 2023 in order to assess patterns before and after the beginning of blue crab fisheries in August 2016. In that year, the species started to become abundant and fishing permission was granted by not including *C. sapidus* in the Spanish invasive species list [21]. From north to south, the included fishermen's guilds were as follows: L'Ametlla de Mar, L'Ampolla, Deltebre, La Ràpita, and Les Cases d'Alcanar, all of them operating both in Ebro Delta Bays (Alfacs and Fangar) and in the adjacent open sea (Figure 1). The selected bivalve species included those used in the predation experiments (*Ruditapes* spp., *C. glaucum*, and *E. siliqua*) that commonly occur in protected environments such as Ebro Delta bays. The wedge clam (*Donax* spp.) was used as a negative control, since it mostly occurs in exposed open-sea areas where the blue crab is not abundant [23]. Other locally present commercial species of Venus clams (*Venus casina*, *V. verrucosa*, and *Chamelea gallina*) were pooled together to assess the general effects on the remaining bivalve community.

Fisheries data were expressed as annual captures in kg and not in CPUEs, because of inadequate registration of effort for bivalves collected with manual methods (fictional groupings of shellfish collectors instead of individuals) by fishermen's guilds before 2019 (personal communication from ICATMAR to P. Prado). Yet, captures from 2010 to 2023 for each taxa were still significantly associated with the available reports on effort ($0.76 \leq R^2 \leq 0.96$ for bivalves and $R^2 = 0.98$ for blue crab) and were considered as an adequate proxy of field abundances.

2.4. Data Analysis

The experimental data on predation rates in terms of the number of predated individuals were transformed to percent cumulative predation for data analyses purposes. The results were analyzed with two-way repeated-measures analysis of variance (RM-ANOVA) using a generalized linear model, followed by Tukey post hoc testing to determine significant groupings. The validity of the F-statistic used in the RM-ANOVA was examined by performing Mauchly's test of sphericity. Since sphericity could not be assumed, the less conservative Huynh–Feldt criteria were applied. For all tests, a p-value of <0.05 was considered statistically significant.

The possible association between blue crab captures and those of the different bivalve taxa for the 2016–2023 period (N = 8) was investigated with regression analyses.

3. Results

3.1. Multiple Choice Experiments

RM-ANOVA showed significant time effects, with increasing cumulative predation throughout the experiment (144 h > 120 h > 96 h > 72 h = 48 h > 24 h > 0 h) (Table 1A; Figure 3a,b). However, predation rates over time were uneven across species, with *Ruditapes* spp. being preyed upon at a quicker pace than *C. glaucum*, both in the presence and the absence of sand, whereas predation on *E. siliqua* was the fastest in the absence of substrate and the slowest in the presence of sand (Table 1A; Figure 3a,b).

Table 1. Results of the 2-way repeated-measure ANOVA of cumulative predation rates of bivalve species (*Ruditapes* spp., *Cerastoderma glaucum*, and *E. siliqua*) using two different substrates (with and without sand). (A) Multiple-choice results with bivalve species offered simultaneously to each blue crab individual. (B) No-choice results for each bivalve species. Statistically significant results are indicated in bold.

(A) Multiple-Choice Experiments	**df**	**MS**	***F***	***p***	**Eta Square**
Between subjects					
Time (Ti)	4.33	32,677.58	196.38	**0.000**	0.891
Ti × S	4.33	1568.55	9.42	**0.000**	0.282
Ti × Sp	8.66	4207.57	25.28	**0.000**	0.678
Ti × S × Sp	8.66	1915.41	11.51	**0.000**	0.490
Error	103.98	166.39			
Within subjects					
Substrate (S)	1	31,697.14	42.12	**0.000**	0.637
Species (Sp)	2	15,716.19	20.88	**0.000**	0.635
S × Sp	2	45,274.28	60.17	**0.000**	0.834
Error	24	752.38			
(B) No-choice experiments	**df**	**MS**	***F***	***p***	**Eta square**
Between subjects					
Time (Ti)	3.57	50,233.04	577.15	**0.000**	0.960
Ti × S	3.57	2235.88	25.68	**0.000**	0.517
Ti × Sp	7.13	1839.54	21.13	**0.000**	0.638
Ti × S × Sp	7.13	1607.84	18.47	**0.000**	0.606
Error	85.67	87.03			
Within subjects					
Substrate (S)	1	44,200.84	217.32	**0.000**	0.901
Species (Sp)	2	19,663.06	96.67	**0.000**	0.890
S × Sp	2	26,469.41	130.14	**0.000**	0.916
Error	24	203.38			

There were also significant effects from the substrate, species, and their interactions. The presence of sand substrate significantly decreased the overall predation compared to bare substrate (68 ± 12.2% vs. 86.7 ± 6.7%, respectively). For species, predation rates were significantly higher in *Ruditapes* spp. (100% in all cases), followed by *C. glaucum* (80 ± 9.4%) and *E. siliqua* (52 ± 16.1%). The presence of sand substrate, coupled with a large burial depth capacity (mean of 26.3 ± 4.1 cm), was a key factor for the survival of *E. siliqua* (4 ± 4% vs. 100% predation, respectively, in the presence and absence of sand) (Figure 3a,b). In contrast, *Ruditapes* spp. and *C. glaucum*, with very shallow burial abilities (1.7 ± 0.3 and 0.4 ± 0.2 cm, respectively), showed either the same or even more predation in the presence of sand.

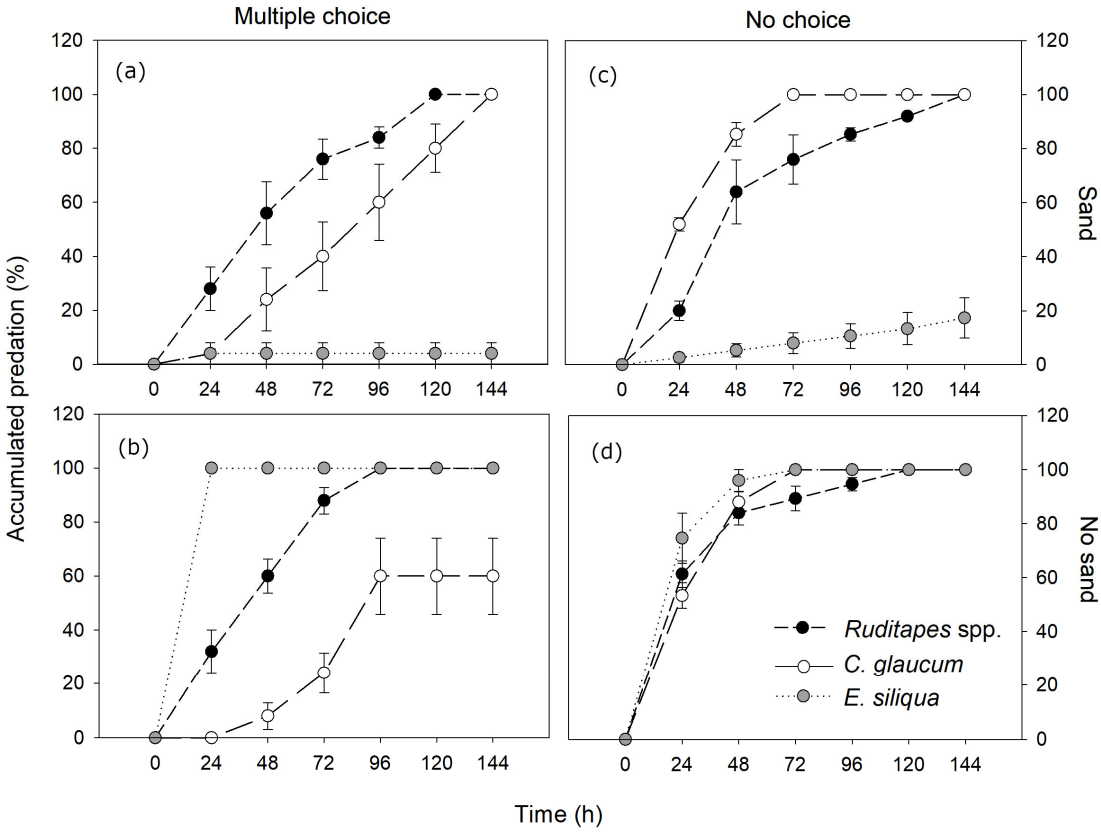

Figure 3. The results of blue crab predation experiments with the different species of bivalves. (**a**) Multiple preference with sand; (**b**) multiple preference without sand; (**c**) no choice with sand; (**d**) no choice without sand. Errors are SE.

3.2. No Choice Experiments

RM-ANOVA also showed increasing cumulative predation over the experimental period (144 h = 120 h = 96 h = 72 h $\geq$ 48 h > 24 h > 0 h), with significant interaction effects between the substrate and species (Table 1B; Figure 3c,d). Compared to the multiple-choice results, when substrate was present, blue crabs predated individuals of *C. glaucum* at a faster rate than those of *Ruditapes* spp., whereas a similar lower predation pattern was observed for *E. siliqua*. In contrast, in the absence of substrate and other bivalves, all prey species were preyed upon at a similarly high rate at all experimental times (Figure 3c,d).

The presence of sand also resulted in decreased predation compared to bare substrate (72.4 $\pm$ 10.6% vs. 100% predation). Furthermore, among species, there was a significantly higher predation of *C. glaucum* and *Ruditapes* spp. (100% in both of them) than *E. siliqua* (58.7 $\pm$ 14.2%). As in the multiple-choice results, the presence of sand was a central factor for the survival of E. siliqua (17.3 $\pm$ 7.5% vs. 100% predation), but this showed no effects for the other taxa (Figure 3c,d).

3.3. Fisheries Trends

The capture of cockles has dramatically decreased from ca. 12,000–14,000 kg in 2010–2011 to only 1755 kg in 2023. Furthermore, an abrupt decline with no further recovery was observed in 2018, shortly after an increase in blue crab captures (Figure 4), resulting in a significant association between both taxa (R^2 = 0.664, df = 7, F = 11.86, p = 0.013). For clams, abundances were already low in 2010 (3537.2 kg) and these have been jaggedly declining, reaching only 59.3 kg in 2023; however, no significant association with blue crab captures was observed due to the strong interannual variability (R^2 = 0.02, df = 7, F = 0.538, p = 0.490). In contrast, the abundance of razor clam has unevenly increased from 31,879 kg

in 2010 to up to 110,488 kg in 2023, particularly after 2019 (Figure 4), but no significant association with blue crab captures was observed (R^2 = 0.305, df = 7, F = 4.084, p = 0.089).

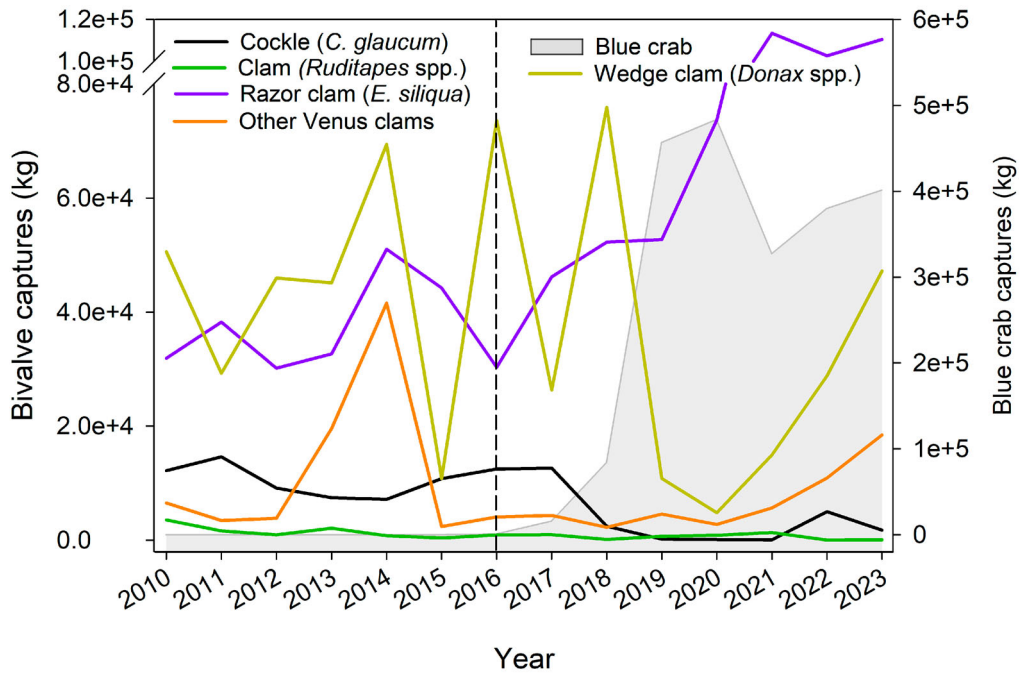

Figure 4. Fishery trends of the main bivalve species in the Ebro Delta (cockles, *Cerastoderma* spp.; clams, *Ruditapes* spp.; razor clams, *E. siliqua* and *S. marginatus*; the wedge clam *Donax* spp.; and several other species of Venus clams) before and after the beginning of blue crab captures in 2016 (dashed line).

The wedge clam displayed an extremely jagged pattern of capture over the previous years and, after the arrival of the blue crab, featured similar values in 2010 (50,594 kg) and 2023 (47,230 kg) (R^2 = 0.283, df = 7, F = 3.543, p = 0.096). For the pooled Venus clam taxa, there was a major peak in 2013–2014, with values increasing from ca. 3500–7000 kg to up to 41,779 kg and then decreasing again to similar values in 2015 (Figure 4). Later, in 2022–2023, captures increase again to the 10,000–20,000 kg range (R^2 = 0.135, df = 7, F = 0.860, p = 0.389).

4. Discussion

4.1. Patterns of Experimental Predation

Our results are in line with the findings of other studies reporting declining crab predation with increasing burying depth for other bivalve species such as *Paphies ventricosa* [15] and *Macoma balthica* [24]; such studies further demonstrate burying depth can act as a refuge from predation. However, we provide additional evidence that burial depth might be responsible for distinctive predation rates across coexisting bivalve species, contributing to shaping abundance patterns in invaded Mediterranean ecosystems.

We show that the razor clam, *E. siliqua*, featuring a burrowing depth range between 17.5 and 40 cm, is not efficiently extracted by the blue crab, with predation rates reaching maximum values of only 20–33% across the experiments. This burial range is lower than that described in natural media (up to 1 m; [19]), but it still exceeds the critical 10–15 cm depth indicated for the blue crab by Seitz et al. [17], suggesting that *E. siliqua* can still be exposed to a certain amount of predation, which might be related to their less evasive burrowing behavior following disturbance compared to other species in the genus [25]. In contrast, in the absence of substrate, predation on razor clam reached rates similar to or higher than the other species, possibly because of the effect of enhanced shell fragility on prey vulnerability [14], although we estimate that only ca. 70% of the flesh was consumed

(satiation might have occurred more rapidly). Furthermore, the predation rates in the multiple-choice experiments in the absence of substrate were also much higher in razor clams, pointing to a preferential attack, possibly because of manipulative easiness [14,26], since prey availability was kept alike in all experiments (ca. 76.4 ind.·m^{-2}). Other factors such as enhanced palatability or profitability alone do not seem to be a clear predictor of the blue crab's preference (see also Ebersole and Kennedy [27]) for razor clams, since, in the absence of substrate, the species was quickly attacked but largely unconsumed (Figure 1); this pattern was not observed for the other two bivalves.

Clams and cockles both featured similarly low burrowing capacities (<2 cm), lying within the crab excavating ability [17], and the presence of substrate did not result in enhanced protection from predation. However, predation rates during multiple-choice experiments were consistently higher and occurred at a faster pace in clams than in cockles (up to 100% vs. 60% in the absence of substrate), suggesting additional preferential predation. Microhardness (fracture toughness of the material) tests conducted on the shells of several Mediterranean species evidenced ca. 26% higher values in *Cerastoderma* than in *Ruditapes* [28], which could account for the observed differences in predation. Alternatively, cockles might also feature significantly lower protein and lipid contents than coexisting clams [29], and could be less preferred for nutritional reasons. Only when no-choice was available did predation on *C. glaucum* significantly increase (up to a 40%), reaching similar values to *Ruditapes* spp.

4.2. Bivalves' Fishery Patterns

Experimental patterns of blue crab predation were in accordance with trends in capture fisheries obtained from ICATMAR. The extraction of razor clams (mostly *E. siliqua* and, to a lesser extent, *Solen marginatus*) has increased outstandingly, by 3.6-fold, since the first captures of blue crab in 2016 [21,22] as a result of an increased fishing effort (R^2 = 0.554), which might partly obscure the predation effects. In contrast, the extraction of *Cerastoderma* spp. from natural banks has decreased since 2017 from over 12,000 kg to less than 2000 kg, despite lower fishing efforts on the species during this period and the concurrent sharp increase in blue crab captures. Furthermore, local populations in the Ebro have evidenced several infections by the parasite *Marteilia cochillia*, which was associated with summer mortalities with a prevalence that oscillated between 40% in 2008, 23.34% in 2010, and 33.34% in 2013 [30–32], but with further unknown effects due to a lack of monitoring. Yet, this could partly account for the overall dramatic decrease in captures (by >85%) from 2017 to 2023, since an up to 100% prevalence was reported during the fishery collapse in the Atlantic Spanish region in 2012 [33]. Also, there is an important small-scale fishery using mechanized dredges to extract clams along the Catalan coast [34], which has shown a significant negative effect on the subsequent settlement of the species [35]. For clams (*Ruditapes* spp.), a large decrease in captures was observed in 2018 (by ca. 12-fold of the average of the previous seven years), only two years after increasing abundances made the blue crab a commercial fishing target [21], and captures have reached minimums of only 2.3 and 59.3 kg in 2022–2023. In this case, predation appears to have played a major role that forced the closure of the last remaining cultivation company (Vongole 2000 S.L., pers. communication from the manager, P. López to I. Gairin). However, the production of *Ruditapes* spp. in shallow areas of the Alfacs and Fangar Bays reached values of over 250 tons in the late 90s [36] and crop values from 2010 to 2015 were also considerably higher (an average of ca. 1500 kg). Since over 75% of the Ebro Delta surface is devoted to rice cultivation, bays have been greatly exposed to agricultural pollution and feature anoxic sediments (P. Prado, personal observ.), impacting commercially exploited shallow natural banks and also affecting suspended cultures of mussels and oysters [37]. The extraction of other species of Venus clams was dominated by the thick-ridged Venus (*V. casina*; over 90% of total after 2015) and, to a lesser extent, by the striped Venus clam (*C. gallina*) and the warty Venus (*V. verrucosa*); these species occur in the open waters of the Ebro Delta [31,38]. In particular, the thick-ridged Venus is found at depths of over 120 m [39] which the blue

crab cannot reach; this species seems to have become an increasing alternative resource compared to other heavily exploited Venus clams such as the striped Venus [34]. In shallow, exposed, open-sea areas that are not frequented by the blue crab, the abundance of wedge clams (*Donax* spp.) is subjected to large interannual variability, possibly due to the effect of fishing pressure and/or natural density-dependent processes affecting spawning and recruitment [23,34]. In fact, recent research in the open waters of the Ebro Delta has found that bivalves are a minor component of the blue crab diet, which appears to feed at much higher trophic levels [40].

5. Conclusions

The evidence presented herein shows that the burrowing capacity inherent to each bivalve species is a major factor determining the predation rates of blue crab; species inhabiting shallow sands (<2 cm), such as *Ruditapes* spp. and *Cerastocerma* spp., are ca. 6 to 25 times more vulnerable than razor clams, which are capable of accessing deeper sand depths (>25 cm). Capture data from local fishery rates were used as a proxy of the field abundance of the different bivalve species; these data appear to be coherent with experimental top-down patterns, with razor clams being the only taxa that is still being captured in large quantities. However, other factors such as fishing pressure, pollution, or diseases [30,31,33] might also have greatly contributed to the collapse of cockle and clam captures in the Ebro Delta. Overall, urgent management measures are needed to recover the missing prosperity and diversity of bivalve resources that the region saw during the 90s and 00s [33].

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