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Posted Date: 3 May 2024

doi: 10.20944/preprints202405.0152.v1

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## Article

# Effects of Sand Burial Depth on Bivalve Species Predation by the Invasive Blue Crab, *Callinectes sapidus*

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**Abstract:** In the Ebro Delta, 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 further decline of both clam and cockle (*Cerastoderma glaucum*) occurred in 2018. In contrast, captures of razor clam (*Ensis siliqua*) have increased by 3.6-fold since 2016. Predation risk for these taxa with contrasting burrowing capacities ( $1.7 \pm 0.3$  cm,  $0.4 \pm 0.2$  cm, and  $26.3 \pm 0.1$  cm, respectively), was assessed using predation preference (N= 5 tanks; 5 individuals of each species) and no-choice experiments (N= 5 tanks; 15 individuals) in the absence and in the presence of sand. Results showed that in the absence of sand, the razor clam, was fully preyed in 24h, clams in 96h, and cockles reached 60% after 144h. Conversely, when sand was present, only 4% of razor clams were predated, while clams and cockles reached 60-100% in 120-144h. No-choice results featured similar patterns depending on substrate availability. Overall, clams and cockles appear to be greatly vulnerable to blue crab predation, whereas the razor clam may escape thanks to its deeper burrowing capacity.

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

## 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 been 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 to factors such as prey density, attachment strength, shell size and hardness, and as well as to distinctive nutritional features [11–14] that point to a large variability in predation vulnerability across species. A particular decisive aspect is the arrival to 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 size might not be attained [14]. However, for burying bivalves, the protection of 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 preys 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, 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 to species with greater digging capacities.

In the last two decades the blue crab has experienced an expansion of towards the Western Mediterranean basin [5]. Specifically, in the Ebro Delta, the species was first reported in 2012 from the Tancada Lagoon [20], and since then, it has become increasingly abundant [21,22]. Alongside, 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), and presently, the only bivalve species that seems to be captured in large abundance in shallow invaded blue crab habitats is the razor clam, *Ensis siliqua*, according to data provided by the Catalan Research Institute for the Governance of the Sea (ICATMAR).

In this context, the objective of the present work is two-fold. First, we conducted several manipulative experiments (multiple choice and no choice) aimed to assess preferential predation rates across the three taxa commonly sharing habitat with the blue crab, and with higher commercial interest (*Cerastoderma* spp., *Ruditapes* spp., and *E. siliqua*). Second, we aimed to evaluate 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 to the increasing captures of blue crab, as proxies of local abundances.

## 2. Materials and Methods

### 2.1. Collection of Predators and Prey Items

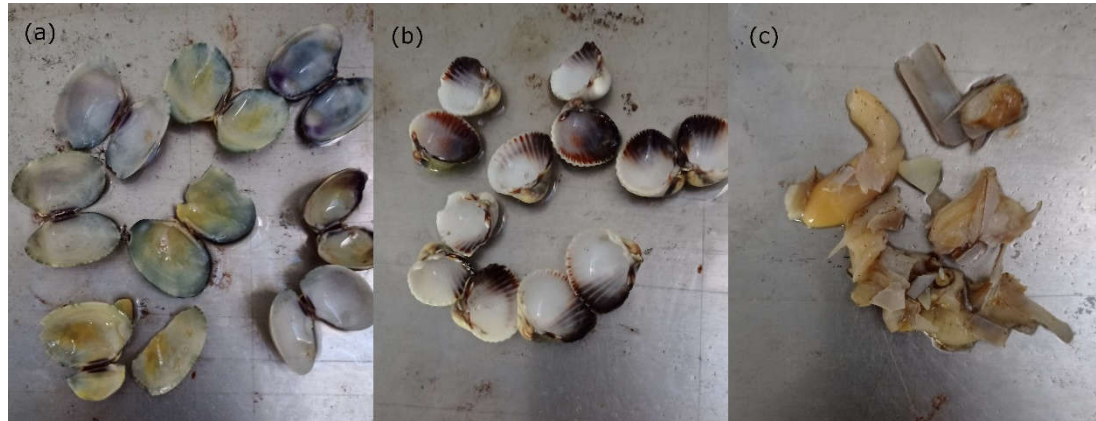
Blue crab individuals were bought alive from the fishermen's association of Riumar located in the town of Deltebre, close to the mouth of the Ebro River. Only males were used throughout the experiments in order to avoid sex-related differences in claw morphology leading to possible variability in predation efficiency [12]. Individuals with a medium size (150–250 g WW) were selected as the most representative fishery size and replaced after each experimental trial. Crabs were transported to IRTA facilities 24 h before experiments, in order to allow for acclimation of individuals and ensure non-feeding conditions during that period.

Bivalve species from local catches in the Ebro Delta were bought alive at the Riumar fishermen's association (*E. siliqua*, *Ruditapes* spp., and *C. glaucum*). Individuals (including shells) were selected with comparable weights (*Ruditapes* spp.:  $14.7 \pm 0.3$  g WW; *C. glaucum*:  $14.5 \pm 0.3$  g WW; and *E. siliqua*:  $14.3 \pm 0.2$  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 across species using a 2 L glass graduated measuring 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 in the absence of sand substrate. For each trial, 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 no choice experiments, N= 5 tanks hosting one blue crab individual were used for each bivalve species (N= 15 per tank) also in the presence and in the absence of sand. In all experiments, 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 exerting pressure with the claw until both valves were slightly ajar and then prying until the abductor muscle was torn (Figure 1a,b). In contrast, predation of *E. siliqua* was facilitated by a very thin shell, which led to easy fragmentation and rapid death of individuals during manipulation with possible presence of unconsumed flesh remains (see Figure 1c).



**Figure 1.** Blue crab-predated individuals of each bivalve species. (a) *Ruditapes* spp., (b) *C. glaucum*; and (c) *E. siliqua*.

### 2.3. Fisheries Trends

Fisheries landings communicated daily from fish markets to the Catalanian government were facilitated by ICATMAR. We selected data from 2010 to 2023 in order to assess patterns before and after the beginning of blue crab fisheries in August 2016, after the species started to become abundant and fishing permission was granted by not including *C. sapidus* in the Spanish invasive species list [21]. Selected bivalve species included those used in the predation experiments (*Ruditapes* spp., *C. glaucum* and *E. siliqua*) and the wedge clam (*Donax* spp.) 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 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 to available reports of effort ( $0.76 \leq R^2 \leq 0.96$  for bivalves and  $R^2 = 0.98$  for blue crab) were considered as an adequate proxy of field abundances.

### 2.4. Data Analysis

Experimental data on predation rates in number of predated individuals were transformed to percent cumulative predation for data analyses purposes. 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 was 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.

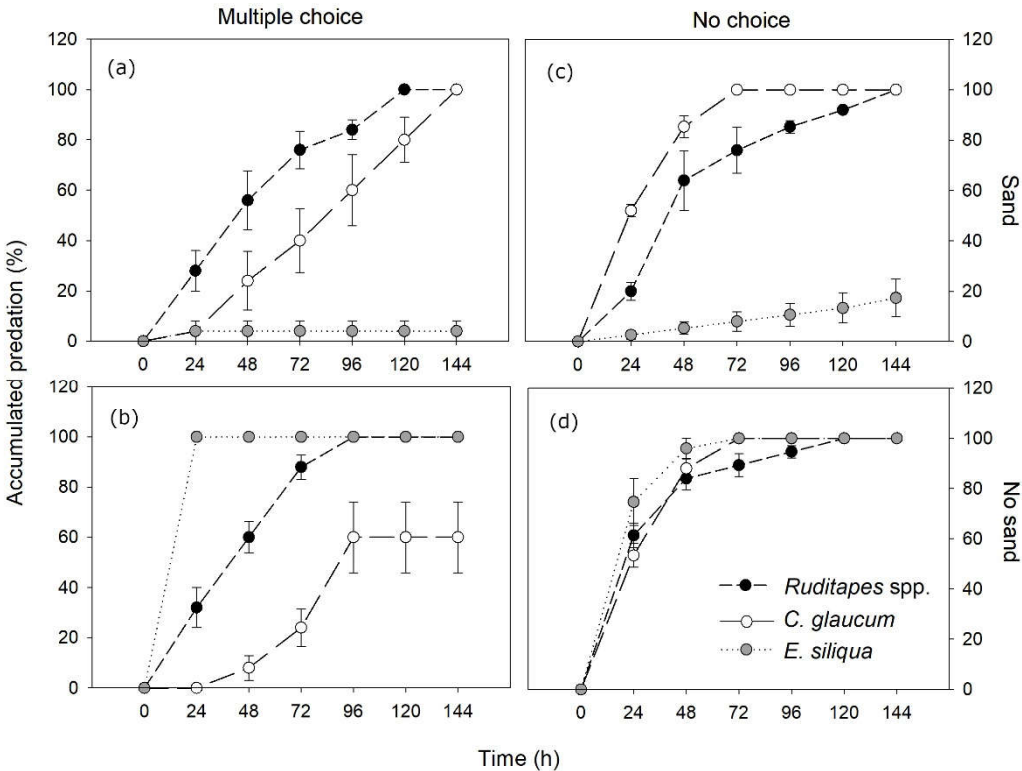


3. Results

3.1. Multiple Choice Experiments

RM-ANOVA showed significant time effects, with increasing cumulative prey predation along the experiment (144 h > 120 h > 96 h > 72 h = 48 h > 24 h > 0 h) (Table 1a; Figure 2a,b). However, predation rates over time were uneven across species, with *Ruditapes* spp. being preyed 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 2a,b).

There were also significant effects of 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 *E. siliqua* (4 ± 4% vs. 100% predation, respectively in the presence and in the absence of sand) (Figure 2a,b). In contrast, *Ruditapes* spp. and *C. glaucum* featuring a very shallow burial (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 2.** 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.

**Table 1.** Results of the 2-way repeated measures ANOVA of cumulative predation rates bivalve species (*Ruditapes* spp., *Cerastoderma glaucum*, and *Ensis 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	32677.58	196.38	<b>0.000</b>	0.891

Ti x S	4.33	1568.55	9.42	0.000	0.282
Ti x Sp	8.66	4207.57	25.28	0.000	0.678
Ti x S x Sp	8.66	1915.41	11.51	0.000	0.490
Error	103.98	166.39			
Within subjects					
Substrate (S)	1	31697.14	42.12	0.000	0.637
Species (Sp)	2	15716.19	20.88	0.000	0.635
S x Sp	2	45274.28	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	50233.04	577.15	0.000	0.960
Ti x S	3.57	2235.88	25.68	0.000	0.517
Ti x Sp	7.13	1839.54	21.13	0.000	0.638
Ti x S x Sp	7.13	1607.84	18.47	0.000	0.606
Error	85.67	87.03			
Within subjects					
Substrate (S)	1	44200.84	217.32	0.000	0.901
Species (Sp)	2	19663.06	96.67	0.000	0.890
S x Sp	2	26469.41	130.14	0.000	0.916
Error	24	203.38			

3.2. No Choice Experiments

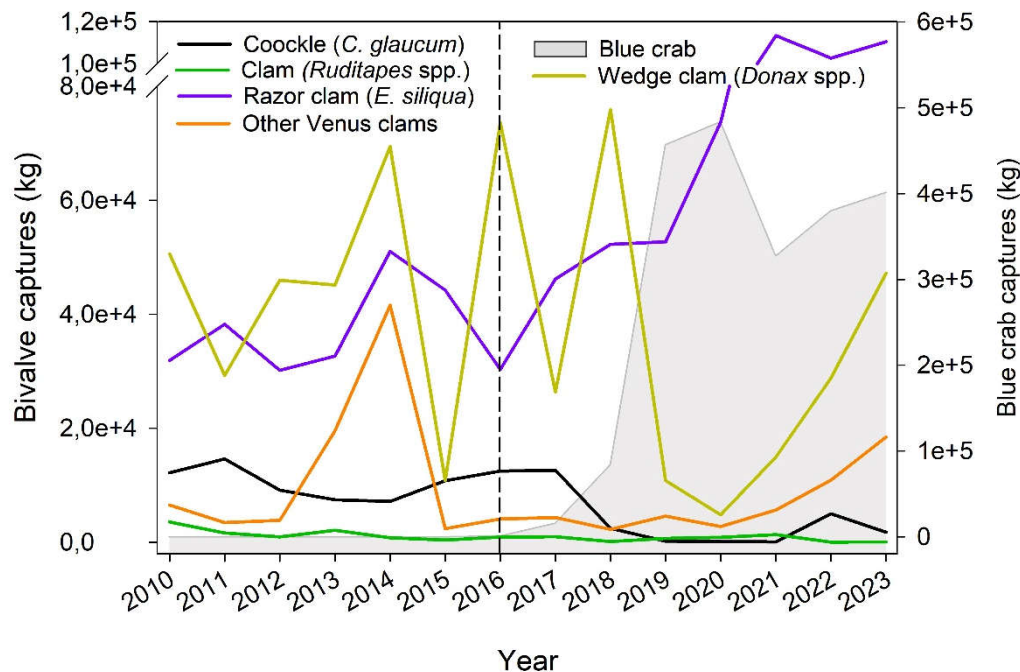
RM-ANOVA also showed increasing cumulative predation over the experimental period (144 h= 120 h= 96 h= 72 h≥ 48 h> 24 h> 0h), with significant interaction effects with substrate and species (Table 1b; Figure 2c,d). Compared to multiple choice results, when substrate was present, blue crabs preyed individuals 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 at a similar high rate at all experimental times (Figure 2c,d).

The presence of sand also resulted in decreased predation compared to bare substrate (72.4 ± 10.6% vs. 100% predation). Besides, among species there was significantly higher predation of *C. glaucum* and *Ruditapes* spp. (100% in both of them) than *E. siliqua* (58.7 ± 14.2%). As in multiple choice results, the presence of sand was a central factor for the survival of *E. siliqua* (17.3 ± 7.5% vs. 100% predation), but showed no effects for the other taxa (Figure 2c,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. Besides, an abrupt decline with no further recover was observed in 2018, shortly after an increase of blue crab captures (Figure 3), resulting in a significant association between both taxa ( $R^2= 0.664$ ,  $df= 7$ ,  $F= 11.86$ ,  $p= 0.013$ ). For clams, 2010 abundances were already low (3537,2 kg) and have been jaggedly declining until reaching only 59,3 kg in 2023 but no significant association with blue crab captures was observed due to 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 3), but no significant association was either observed ( $R^2= 0.305$ ,  $df= 7$ ,  $F= 4.084$ ,  $p= 0.089$ ).

The wedge clam displayed an extremely jagged pattern of captures over the years previously and after the arrival of blue crab, featuring 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. 3,500-7,000 kg to up to 41,779 kg and then decreasing again to similar values in 2015 (Figure3). Later, in 2022-2023, captures increase again to the 10,000-20,000 kg range ( $R^2=0.135$ ,  $df=7$ ,  $F=0.860$ ,  $p=0.389$ ).



**Figure 3.** Fisheries trends of the main bivalve species in the Ebro Delta (cockles, *Cerastoderma* spp.; the clams, *Ruditapes* spp.; the 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).

## 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] buried at different depths, and further demonstrate that it 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 and contribute to shaping abundance patterns in invaded Mediterranean ecosystems.

We show that the razor clam, *E. siliqua*, featuring a burrowing depth range between 17.5 to 40 cm, is not efficiently extracted by blue crab, with predation rates reaching maximum values of only 20-33% across the experiments. This burial range is lower than that described in the natural media (up to 1 m; [19]) but still exceeds the critical 10–15 cm depth indicated for blue crab by Seitz et al. [17], suggesting that *E. siliqua* can still be exposed to certain predation, which might be related to a less evasive burrowing behavior following disturbance compared to other species in the genus [25]. In contrasts, in the absence of substrate, predation on razor clam reached similar or higher rates than the other species, possibly because of the effect of enhanced shell fragility on prey vulnerability [14]. Besides, in the absence of substrate, predation rates in multiple-choice experiments were also much higher on razor clam, 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<sup>-2</sup>). Other factors such as enhanced palatability or profitability alone do not seem to be a clear predictor of blue crab preference (see also Ebersole and Kennedy [27]) for razor clam, since in the absence of substrate, the

species was quickly attacked but largely unconsumed (Figure 1), while 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 on *Cerastoderma* than in *Ruditapes* [28], which could account for 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, predation on *C. glaucum* was significantly increased (up to a 40%) and reached similar values to *Ruditapes* spp.

#### 4.2. Bivalves' Fisheries Patterns

Experimental patterns of blue crab predation, were in accordance with trends in capture fisheries obtained from ICATMAR. The extraction of razor-clam (mostly *E. siliqua*, and to a lesser extent *Solen marginatus*) has been outstandingly increased by 3.6-fold since the first captures of blue crab in 2016 [21,22] as a result of an increasing fishing effort ( $R^2=0.554$ ), which might partly obscure predation effects. In contrast, the extraction of *Cerastoderma* spp. from natural banks has decreased from over 12,000 kg to less than 2,000 kg since the arrival of blue crab, coupled with decreasing capture effort during this period. Besides, local populations in the Ebro have been undergoing repeated infections of the parasite *Marteilia cochillia* [30] with an unknown evolution forecasting due to a lack of monitoring. Also, there is an important small-scale fishery using mechanized dredges to extract clams along the Catalan coast [31], which has been shown a significant negative effect on the subsequent settlement of the species [32]. For clams (*Ruditapes* spp.), a large decrease in captures was observed in 2018 (by ca. 12-fold of the average of the previous 7 years), only two years after increasing abundances made of 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 [33] and crop values from 2010 to 2015 were also considerably higher (an average of ca. 1,500 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.), that impact commercially exploited shallow natural banks and also affecting suspended cultures of mussels and oysters [34]. 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*), that occur in open waters of the Ebro Delta [31,35]. In particular, the thick-ridged venus, is found at depths over 120 m [36] that the blue crab does not reach, and seems to have become an increasing alternative resource compared to other heavily exploited Venus clams such as the striped venus [31]. In shallow exposed open sea areas that are neither frequented by the blue crab the abundance of wedge clam (*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 [23,31]. In fact, recent research in open waters of the Ebro Delta, has found that bivalves are a minor component of the blue crab diet, which appears to be feeding at much higher trophic levels [37].

## 5. Conclusions

The evidence presented herein shows that the burrowing capacity inherent to each bivalve species, is a major factor determining predation rates of blue crab; species inhabiting shallow sands (<2 cm) such as *Ruditapes* spp. and *Cerastoderma* spp. being ca. 6 to 25 times more vulnerable than



razor clam capable of accessing to depth sands (>25 cm). Capture data from local fisheries rates as a proxy of field abundance of the different bivalve species appear to be coherent with experimental top-down patterns, razor clam being the only taxa that is still being captured in large quantities. However, the undergoing of other factors such as fishing pressure, pollution, or diseases [30,31,33] might have also 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 in the region during the 90s and 00s [33].

**Author Contributions:** Conceptualization, P.P., and S.F.; Data curation, P.P.; Formal analysis, P.P., and S.F.; Investigation, P.P.; Methodology, P.P., and I.G.; Study design, P.P., and S.F.; Data analysis, P.P.; Resources, P.P., and S.F.; Supervision, P.P.; Visualization, P.P., I.G., and S.F.; Writing—original draft, P.P.; Writing—review and editing, S.F., and I.G. All authors have read and agreed to the published version of the manuscript.

**Funding:** Predation experiments were supported by the Spanish Government (Ministry of Science and Technology) under the ECESIS project (PID2020-118476RR-C21) to P. Prado and S. Falco.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** We encourage all authors of articles published in MDPI journals to share their research data. In this section, please provide details regarding where data supporting reported results can be found, including links to publicly archived datasets analyzed or generated during the study. Where no new data were created, or where data is unavailable due to privacy or ethical restrictions, a statement is still required. Suggested Data Availability Statements are available in section “MDPI Research Data Policies” at <https://www.mdpi.com/ethics>.

**Acknowledgments:** P. Prado was contracted under the INIA-CCAA research program for postdoctoral incorporation from the Spanish National Institute for Agricultural and Food Research and Technology (INIA). We thank C. Alcaraz for advise with the experimental design of the predation experiments. We are very grateful to the ICATMAR institution for providing the fisheries data on blue crab and bivalve species used in this study.

**Conflicts of Interest:** The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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