

Article

Behavioural Responses of *Cerastoderma edule* as Indicators of Potential Survival Strategies in the Face of Flooding Events

Tiago Verdelhos ¹, Helena Veríssimo ^{1,*}, João Carlos Marques ¹ and Pedro Anastácio ² 

¹ Marine and Environmental Sciences Centre, Department of Life Sciences, Calçada Martim de Freitas, University of Coimbra, 3000-456 Coimbra, Portugal; tverdelhos@uc.pt (T.V.); jcmimar@ci.uc.pt (J.C.M.)

² Marine and Environmental Sciences Centre, Departamento de Paisagem, Ambiente e Ordenamento, Escola de Ciências e Tecnologia, Universidade de Évora, Rua Romão Ramalho, 59, 7000-671 Évora, Portugal; anast@uevora.pt

* Correspondence: helena.verissimo@uc.pt; Tel.: +351-968-768-949

Abstract: According to climate change scenarios the incidence of extreme events, such as flooding, is expected to increase worldwide. In the current climate change context, understanding behavioural responses of marine species to such stressors is essential, especially for species of high ecological and economic interest such as bivalves, which can be quite useful for future management and conservation actions. In this study, a laboratory experiment using different salinity conditions was undertaken to assess potential behavioural responses of cockles (*Cerastoderma edule*), as a survival strategy facing low-salinity stress during riverine flood events. Results showed consistent patterns of burrowing/emergence of cockles facing salinity variation: with high salinities the individuals were observed buried in the sediment; when salinity decreased, organisms were observed to actively emerge, and when salinity was <10, cockles were found exposed at the sediment surface. These behavioural changes may be a strategy for the survival of this species in response to flooding: once at the sediment surface, hydrodynamics may transport organisms towards areas that are more suitable

Keywords: wild cockles; salinity changes; riverine flooding events; climate change; estuarine and coastal habitats



Citation: Verdelhos, T.; Veríssimo, H.; Marques, J.C.; Anastácio, P. Behavioural Responses of *Cerastoderma edule* as Indicators of Potential Survival Strategies in the Face of Flooding Events. *Appl. Sci.* **2021**, *11*, 6436. <https://doi.org/10.3390/app11146436>

Academic Editor: Paola Grenni

Received: 9 March 2021

Accepted: 30 June 2021

Published: 12 July 2021

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Global climate change is one of the main challenges the world faces, seriously affecting coastal ecosystems. In particular, the increasing occurrence and intensity of extreme climatic events (e.g., floods, droughts and heat waves) often lead to abrupt changes in temperature, salinity and hydrodynamic conditions [1]. This results in impacts on organisms (e.g., physiological processes, behaviour, and mortality), leading to changes in population abundance, community structure and ecosystem functioning [2]. Since this trend is expected to continue, further impacts on aquatic ecosystems are predictable [3,4]. As such, understanding how biological communities respond to these scenarios is essential for coastal ecosystem management.

Bivalves are key species of estuarine and coastal macrofaunal communities, since they usually are: (i) long-lived and large-sized species dominating the assemblage biomass [5]; (ii) highly abundant and productive [6]; (iii) economically valuable as a food resource, being frequently harvested and produced in aquaculture [7–9]. Moreover, they perform essential ecological functions in the ecosystem, as they influence the benthic-pelagic interface through sediment reworking, resuspension and filtration activities, promoting nutrient regeneration and contributing to water column purification [9–11]. As such, they play a key role in the ecosystem food web [12].

The cockle *Cerastoderma edule* (Linnaeus, 1758) is a common species along the NE Atlantic Ocean and through the Baltic, Mediterranean and Black seas—Latitude: 70° N to 16° N [7,13,14]. It usually inhabits intertidal and subtidal muddy/sand or sand banks on

semi-sheltered coastal and estuarine systems [7,14,15], preferentially on higher salinity areas located downstream [7,16,17]. *C. edule* is a suspension feeder that burrows just below the sediment surface and filters water above the sediment/water interface [14,18,19]. It feeds on phytoplankton, zooplankton, suspended organic matter and microphytobenthos [18,20–23] and is usually preyed on by crustaceans, fishes, and wading birds, being a link between primary producers and consumers [19]. Additionally, it is extensively harvested and produced in aquaculture for human consumption throughout its range [7,24–26] having a large economic interest [9,25,26].

C. edule is usually subjected to great physiological stress related to high gradients and variability of abiotic factors, typical of transition habitats [27,28]. Salinity is a key physical factor for estuarine bivalves and determine the limits of their geographic distribution and biological features [16,29,30]. As an euryhaline species, *C. edule* can survive in a wide range of salinities, being commonly found in habitats where salinity changes regularly (e.g., estuaries) with daily tidal cycles and seasonal freshwater inflows driven by precipitation. However, the increasing frequency and intensity of extreme climatic events is additionally demanding for these organisms [30–33], which must endure augmented osmotic stress [27,28]. Short-term (tidal) and long-term (rain periods) salinity changes generate an osmotic gradient between the ambient medium and the organisms, often leading to behavioural and physiological responses [34–36] and ultimately to mortality episodes [8,19,37].

In a previous laboratorial experimental study, Verdelhos et al. [16] showed that *C. edule* is negatively affected by low salinities, being particularly vulnerable to floods. One of the main observations was the absence of burrowing behaviour on salinity treatments <10 [16]. At first, this could be considered as a simple protection strategy: organisms submitted to low salinity close their valves and suspend their activity, shielding themselves from the osmotic stress. However, *C. edule* specimens in nature were observed at the sediment surface during a period of high freshwater inflow–low salinity (personal observation), which suggests an emergent movement from the sediment towards the surface. These in situ observations raised a question that motivated the present study: does *C. edule* have a behavioural strategy to cope with salinity declines during riverine flooding events? This work aimed to evaluate *C. edule*'s burrowing/emergence patterns when subjected to salinity variations, observing if the individuals: (a) burrow in the sediment at higher salinity; (b) emerge with decreasing salinity; (c) re-burrow when salinity increase; (d) show consistent behaviour when salinity variation is repeated.

2. Materials and Methods

2.1. Study Site and Sampling

The Mondego estuary (8.6 km²) is a warm-temperate intertidal ecosystem on the Atlantic coast of Portugal (40°08' N, 8°50' W). It comprises two arms separated by an alluvium-formed island (Figure 1) and has a mean water flow of 79 m³.s⁻¹, which in rainy years can reach above 140 m³.s⁻¹, dropping to 27 m³.s⁻¹ in dry years [38]. Freshwater outflow moves mainly via the northern arm, while in the southern arm water circulation is more dependent on tides and on the freshwater input from the Pranto River, a small tributary with a flow controlled by a sluice. Over the last few decades, there was an increase in the occurrence and intensity of flooding events characterized by intense freshwater flow, increased turbidity and abrupt salinity declines, with impacts on bivalve populations and macrobenthic communities [15,38].

C. edule is mainly distributed in downstream areas, specifically on an intertidal sandflat on the South arm [16,17,39] and subtidal areas on both arms [38]. Salinity is usually high in these areas, ranging between 30 and 34, during high tide, although they may be subjected to lower salinity values during low tides (ranging between 10 and 30) and high riverine freshwater flow. Adult specimens (average length 29.63 ± 1.82 mm) were collected by hand, at low tide during Spring (Water temperature = 19.2 °C; Water salinity = 20.7), on the South arm intertidal sandflat (composed by 72% fine sand and 23% medium sand,

with ~0.8% organic matter content [39]). They were transported in cooled boxes with local water (salinity ~18–22; practical salinity scale), acclimated to laboratory conditions for 48 h (temperature = 20 °C; salinity = 20; 12 h light/dark; continuous aeration) and kept in starvation to equalize the hunger state among individuals [40]. Sediment was collected at the site, transported to the laboratory and litter, shells, boulders and large biological structures were removed by hand and sediment was sieved through a 4 mm mesh. Seawater (salinity ~33–35) was collected, transported to the laboratory, and filtered using GC-50 glass fiber membrane filters.

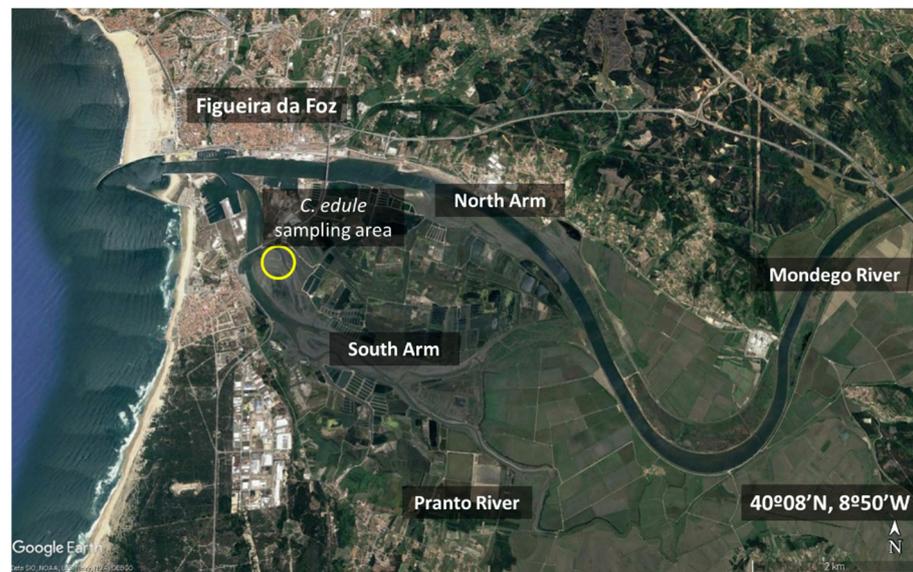


Figure 1. Mondego estuary, located on the south eastern Atlantic coast of Europe near Figueira da Foz (Portugal), and location of the intertidal sampling area.

2.2. Experimental Procedures and Statistical Analysis

A laboratorial experiment was conducted to assess *C. edule*'s burrowing vs. emergence response under different salinity conditions, simulating low-salinity stress during riverine flood events. Specimens ($N_{\text{total}} = 180$) were exposed to different salinity variation treatments at 20 °C for 156 h (Table 1). In the Control treatment (Treatment C), salinity was constant during the test (= 20), but the water in the tank was changed every 12 h. In Treatments A and B, organisms were submitted to each salinity level for 12 h, starting at salinity = 20 and varying 5 units each time the water in the tank was changed (12 h). Treatment A consisted on: (i) initial salinity decrement from 20 to 5 (0 to 48 h); (ii) salinity increase from 5 to 20 (48 to 84 h); (iii) decrease from 20 to 5 (84 to 120 h); (iv) maintenance at 5 until 156 h. Treatment B comprised: (i) initial salinity decrement from 20 to 5 (0 to 48 h); (ii) salinity increase from 5 to 20 (48 to 84 h); (iii) decrease from 20 to 5 (84 to 120 h); (iv) final increase up to 20 until 156 h. For further analysis of the results obtained in Treatment A and Treatment B “salinity variation cycles” will be considered, i.e., in Treatment A we consider a 1st cycle from 0 to 84 h consisting on a salinity decrease/increase, followed by a 2nd cycle from 84 to 120 h with a salinity decrease (until 120 h), remaining = 5 until 156 h (“salinity maintenance”); in Treatment B we consider two cycles of salinity decrease/increase: the 1st from 0 to 84 h and the 2nd from 84 to 156 h.

For each treatment (Treatment A, Treatment B and Control) three runs were performed, using two tanks per run. Each tank (26 × 36 × 22 cm) contained a 5 cm layer of sediment and 15 L of water (filtered seawater was diluted with distilled water to reach the correct salinity). In each tank, 10 specimens were individually placed in submerged perforated cups that allow water flux and enable salinity balance between the water and the sediment (Figure 2). Every 12 h the specimens' burrowing condition (e.g., buried in the sediment vs. at the surface) was observed and registered (cockles were considered burrowed when

they had totally or partially (more than 2/3) burrowed into the substratum). Tanks were continuously aerated; salinity and temperature values were monitored and adjusted if needed to maintain constant conditions; and specimens were fed daily ad libitum (with “Ocean Nutrition Microplankton” composed by phyto and zooplankton, diluted in the experimental water).

Table 1. Experimental setup (e.g., treatments; runs; number of individuals) and salinity conditions throughout the experiment: Treatment A—Variable salinity | T = 20 °C; Treatment B—Variable salinity | T = 20 °C; Control—Constant salinity = 20 | T = 20 °C (for more details on the experimental conditions of Treatment A, Treatment B and Control, please see Section 2.2).

	Runs (n°)		Tanks/Run (n°)		N _{tank} (N° Individuals/Tank)					N _{treatment} (N° Individuals/Treatment)				
Treatment A	3		2		10					60				
Treatment B	3		2		10					60				
Control	3		2		10					60				
					N _{total}					180				
Time (h)	12	24	36	48	60	72	84	96	108	120	132	144	156	
Salinity														
Treatment A	20	15	10	5	10	15	20	15	10	5	5	5	5	
Treatment B	20	15	10	5	10	15	20	15	10	5	10	15	20	
Control	20	20	20	20	20	20	20	20	20	20	20	20	20	

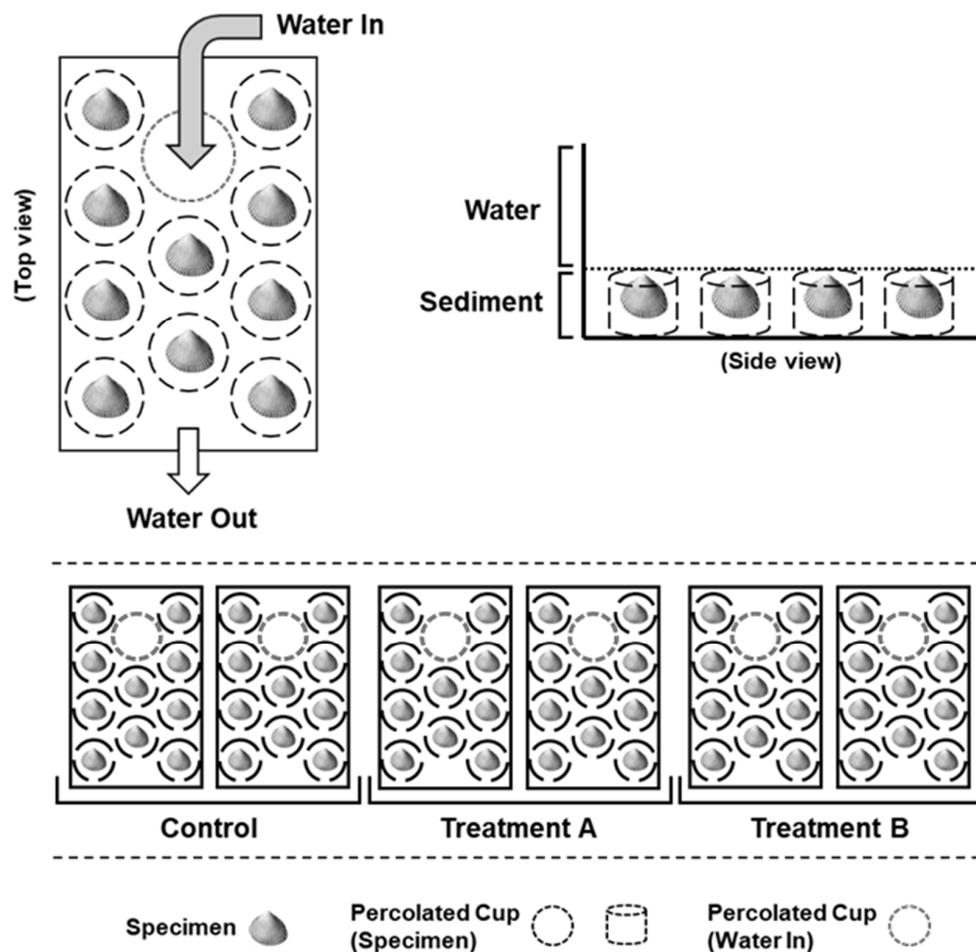


Figure 2. Experimental setup: top and side views of the tanks. Treatment A—Variable salinity | T = 20 °C; Treatment B—Variable salinity | T = 20 °C; Control—Constant salinity = 20 | T = 20 °C (for more details on the experimental conditions of Treatment A, Treatment B and Control, please see Section 2.2).

A one-way analysis of variance (ANOVA) with repeated measures was performed for each treatment to test for significant differences on the observed burrowing response (dependent variable) between the different salinity levels (independent variable), using IBM SPSS Statistics 19.0. To avoid pseudoreplication issues, since individuals in the tank are not totally independent (pseudoreplicates), analysis was performed considering each tank as a replicate and the proportion of buried individuals in each tank (i.e., $p = 1$, if all the individuals were buried; $p = 0.5$ if five individuals were buried). Thus, six replicates were considered on each treatment (n° tanks per treatment), taking into account that the experimental conditions on each tank and each run were the same. Sphericity was tested using Mauchly's test as part of the GLM Repeated Measures procedure, and after a significant F test, differences among means were identified using the Bonferroni *post hoc* procedures. Moreover, the relationship between the % of buried cockles and salinity levels was estimated using a linear regression. Shapiro–Wilk and Levene tests were used to check for the normality of the data and homogeneity of the variances, respectively.

3. Results

Control (treatment C) showed constant values of salinity (=20); moreover, burrowing % was high (> 90%) during the 156 h (Table 2, Figure 3C), and the registered mortality was ~5%.

Table 2. Results of Treatment A, Treatment B and Control during the experiment (156 h), showing: Salinity conditions; Burrowed %-considered the % of burrowed individuals/treatment ($N_{\text{treatment}} = 60$) at each 12 h observation moment; Δ Burrowed every 12 h and per salinity variation cycle (for more details on experimental conditions of Treatment A, Treatment B and Control, please see Section 2.2 and Table 1).

Time (h)	12	24	36	48	60	72	84	96	108	120	132	144	156
Treatment A													
Salinity	20	15	10	5	10	15	20	15	10	5	5	5	5
Burrowed (%)	98	100	56	17	40	82	97	97	75	33	18	3	3
Δ Burrowed		+2	−44	−39	+23	+42	+15	0	−22	−42	−15	−15	0
Δ Burrowed [on Each Salinity Variation Cycle]		1st Cycle				2nd Cycle				Maintenance			
		Decrease [0–48 h]			Increase [48–84 h]			Decrease [84–120 h]			Increase [120–156 h]		
				−81			+80			−63			−30
Treatment B													
Salinity	20	15	10	5	10	15	20	15	10	5	10	15	20
Burrowed (%)	96	98	60	12	38	88	96	95	74	38	59	88	93
Δ Burrowed		+2	−38	−48	+26	+50	+8	−1	−21	−36	+21	+29	+5
Δ Burrowed [on Each Salinity Variation Cycle]		1st Cycle				2nd Cycle				Increase			
		Decrease [0–48 h]			Increase [48–84 h]			Decrease [84–120 h]			Increase [120–156 h]		
				−84			+84			−58			+55
Treatment C													
Salinity	20	20	20	20	20	20	20	20	20	20	20	20	20
Burrowed (%)	90	93	100	100	100	100	100	100	100	96	95	91	90
Δ Burrowed		+3	+7	0	0	0	0	0	0	−4	−1	−4	−1

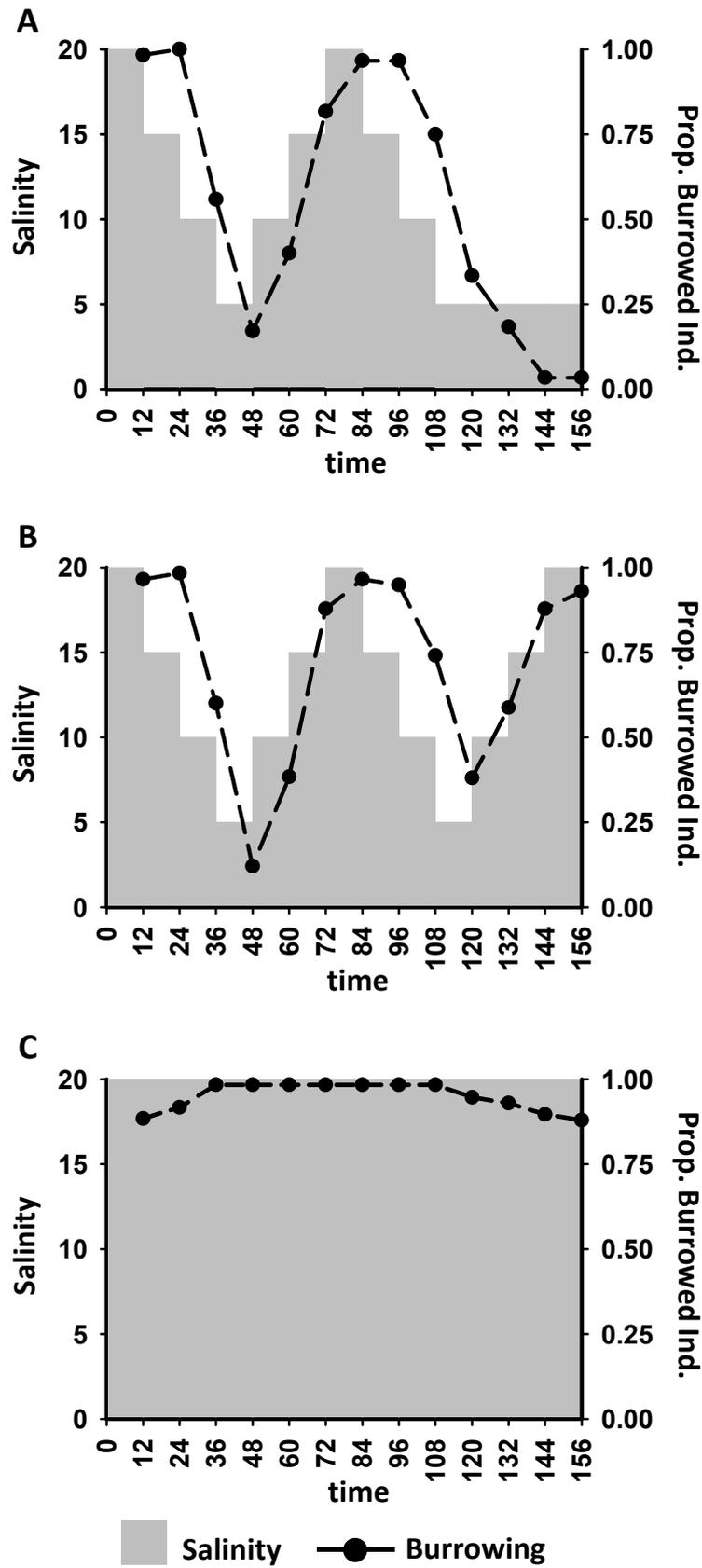


Figure 3. (A–C). Salinity variation and proportion of burrowed individuals *per* treatment, over the experiments duration time (156 h)—Treatment A (plot A.), Treatment B (plot B.) and Control (plot C.).

Treatment A: (i) during the 1st salinity variation cycle the percentage of buried individuals was ~100% at salinity 20 (12 h) and 15 (24 h), (Table 2, Figure 3A), decreasing to 56% at salinity 10 (36 h) and <20% at salinity 5 (48 h), and then it increased with salinity increment to 40% at salinity 10 (60 h), ~80% at salinity 15 (72 h), and ~100% at salinity 20 (84 h); (ii) during the 2nd cycle (salinity decrease/maintenance), burrowing percentage followed a similar pattern, decreasing to 75% at salinity 10 (108 h), ~30% at salinity 5 (120 h), ultimately reaching 3% after 144 h. At the end, almost all individuals were at the surface and the registered mortality was ~3%.

Treatment B: (i) during the 1st salinity variation cycle, the percentage of buried individuals was ~100% at salinity 20 (12 h) and 15 (24 h), (Table 2, Figure 3 B), decreasing when salinity was reduced to 60% at salinity 10 (36 h) and ~10% at salinity 5 (48 h), and it increased again when salinity rose, reaching ~40% at salinity 10 (60 h), ~90% at salinity 15 (72 h) and ~100% at salinity 20 (84 h); (ii) on the 2nd cycle, a similar burrowing pattern was observed, decreasing with salinity reduction to ~75% buried at salinity 10 (108 h) and <40% at salinity 5 (120 h), and increased when salinity rose, reaching ~60% at salinity 10 (132 h) and ~90% after 144 h. At the end of the test <10% individuals were at the surface and mortality was ~3%.

Burrowing differences between the distinct salinity levels in each treatment were assessed using an ANOVA test with repeated measures. As our data did not meet the sphericity assumption (Mauchly's test with $p < 0.05$), values with a Greenhouse–Geisser correction were considered (Table 3). Overall, the percentage of buried individuals was significantly different between salinity levels on treatments A and B (Table 3): (a) higher values (>80%) at salinity levels 20 and 15; (b) medium values (38% to 75%) at salinity 10; (c) lower values (<38%) at salinity 5. Pairwise comparisons using post hoc tests (Bonferroni correction) revealed no significant differences ($p = 1$) on the burrowing percentage observed between salinity levels 20 vs. 15, while significant differences ($p < 0.05$) were found between salinity levels 20 vs. 5 and 15 vs. 5, both on treatments A and B. Additionally, the observed burrowing percentage showed linear relationships with salinity (Figure 4A,B) on Treatment A ($R^2 = 0.8565$; $p < 0.001$) and B ($R^2 = 0.792$; $p < 0.001$). On both treatments, normality of the data (Treatment A: $p = 0.201$; Treatment B: $p = 0.375$) and homogeneity of the variances (Treatment A: $p = 0.578$; Treatment B: $p = 0.921$) were verified.

Table 3. Summary of the one-way analysis of variance (ANOVA) with repeated measures results for treatments A and B.

Treatment A			
Mauchly's Sphericity	W	Sig	
	0	<0.05	
Greenhouse–Geisser	ϵ		
	0.196		
	df, df error	F	Sig
	2.354, 11.769	61.414	<0.05
Treatment B			
Mauchly's Sphericity	W	Sig	
	0	<0.05	
Greenhouse–Geisser	ϵ		
	0.241		
	df, df error	F	Sig
	2.890, 14.451	39.516	<0.05

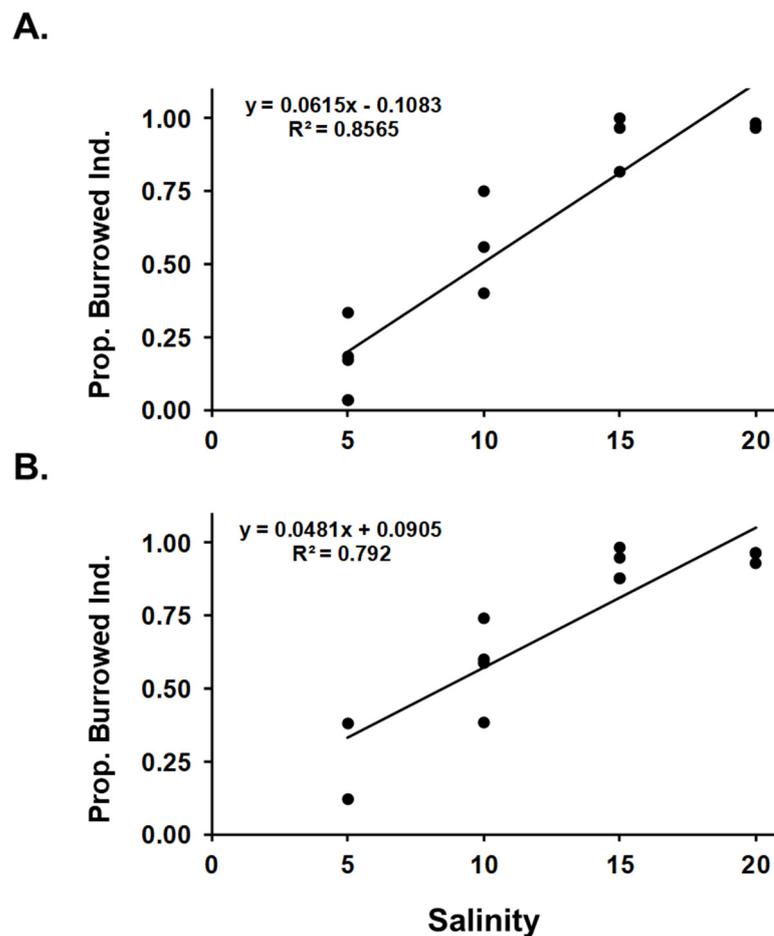


Figure 4. (A,B). Regression equations between salinity and proportion of buried individuals for treatments A (plot A.) and B (plot B.).

4. Discussion

Cerastoderma edule exhibited a burrowing vs. emergence pattern when subjected to salinity variations: (a) at the initial experimental salinity (= 20) individuals burrowed in the sediment, quite swiftly in some cases; (b) they displayed an emerging response during decreasing salinity trend; (c) specimens showed a burrowing response in the course of salinity increment; (d) when salinity variations were repeated the same behavioural responses were observed, however their magnitude was higher on the 1st salinity variation cycle when compared to the 2nd cycle. A clear relationship between changes in salinity and behaviour was observed, with cockles actively burrowing in the sediment column when water salinity is within the optimal performance range for this species [16] and emerging when salinity drop below a low salinity threshold (<10). Although this pattern was consistent throughout the experiment, the observed lower magnitude on the 2nd cycle of salinity variation may indicate an altered physiological condition of specimens subjected to experimental conditions for too long [16,29,41,42].

Salinity is one of the factors determining the biological features and spatial distribution of species on estuarine habitats [16,29,30]. In the Mondego estuary, increased mortality of the common cockle *C. edule* and the peppery furrow shell *Scrobicularia plana* was observed during flooding events, impacting the population structure and dynamics of these bivalves [8,43,44]. Low salinities also modified their behaviour (e.g., affecting burrowing/emergence behaviour, feeding activity, movement and valves opening/closure), impairing their overall activity [16]. Conversely, these species showed the best performance within a narrow optimal salinity range (20–25 for *C. edule*; 20–30 for *S. plana*) [16], and *C. edule* population occupy preferentially downstream intertidal and subtidal sandflats [16,39].

C. edule is better suited to higher salinity areas [7,16] and is impaired by abrupt salinity declines [16], especially during long and intense flooding episodes [8,24,43]. Under these circumstances, organisms respond initially with behavioural changes, which in the event of prolonged exposure result in mortality [16]. On previous experimental studies [16] the absence of burrowing behaviour under low salinity conditions was considered a protection mechanism related to valve closure, retraction of sensitive body parts and an overall inactivity to avoid osmotic stress [16,29,34,36,45]. In an in situ personal observation during low tide, numerous cockles were found at the sediment surface in the Mondego south arm intertidal sandflat during a period of high freshwater inflow. This suggests that buried organisms actively emerged to the sediment surface during adverse conditions, putting themselves at risk.

The pattern observed in this study seems to indicate a behavioural strategy to endure severe salinity declines. During riverine flooding events, increased freshwater inflow leads to reduced salinity and improved hydrodynamics, promoting sediment erosion and bedload transport of materials, with associated impacts on the populations of *C. edule* [8,43,45,46]. In these conditions, cockles can be involuntarily or passively mobilized by currents or when the sediments they live in become eroded [47–50]. With the observed behaviour, cockles emerge at the sediment surface when salinity drops (<10), becoming more likely to be dragged to further downstream areas, where salinities are higher (Figure 5). As such, it can be viewed as an avoidance mechanism allowing organisms to avoid impacts associated with severe salinity declines. Dispersion of adult cockles has been previously observed in a field experiment study, with individuals being dragged “upslope” by the tide over distances up to 200 m [51].

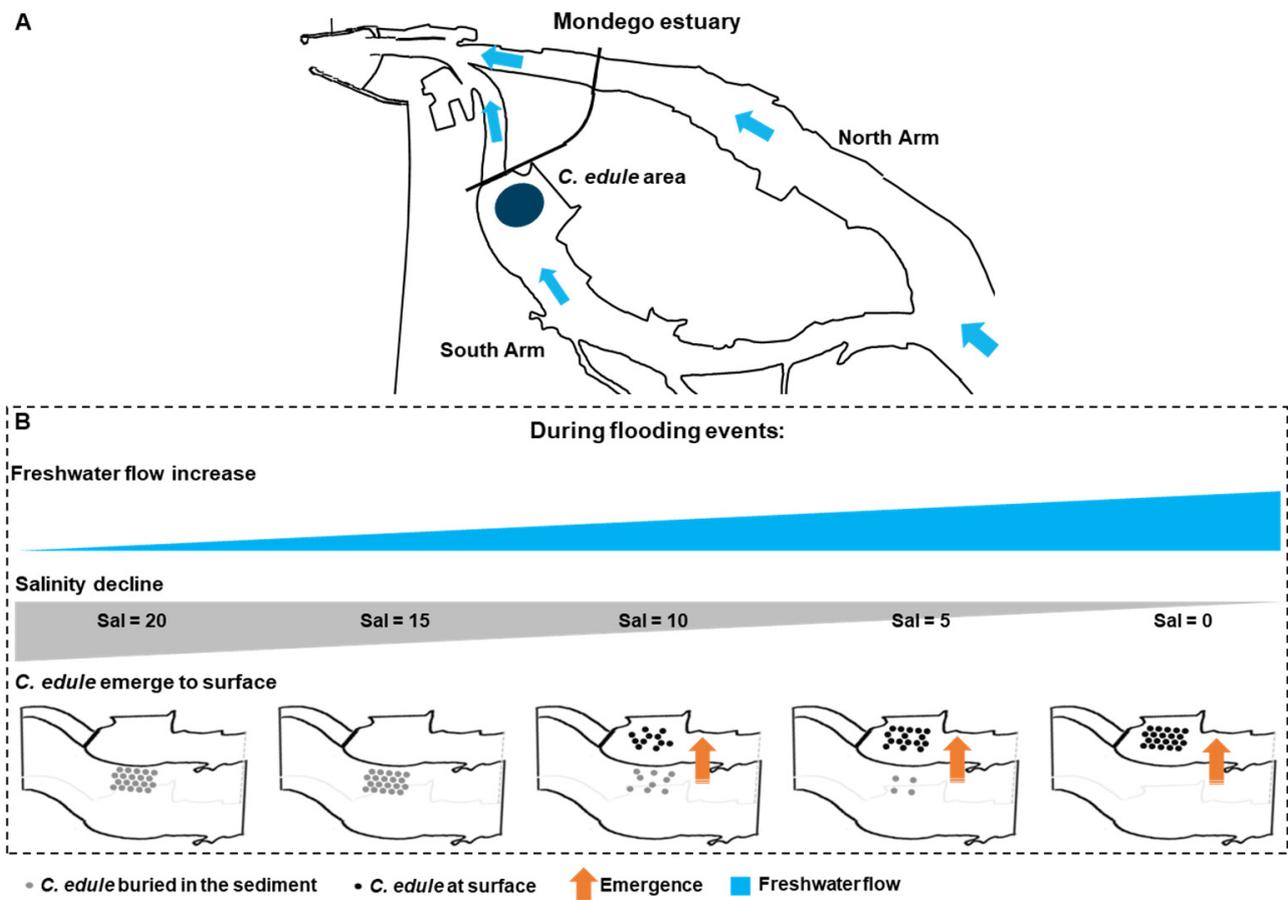


Figure 5. Illustration of *C. edule* response to flooding events on the Mondego estuary—unburrowing from the sediment and consequently being dragged further downstream. (A) Location of *C. edule* intertidal area (blue shaded) and water flow (sky blue arrows) in the system. (B) *C. edule* response behaviour facing water flow and salinity levels variations.

Avoidance can be: (i) active—ability to detect environmental stressors and to move (by swimming, flying, walking) towards less stressed environments or to change the behaviour (e.g., unburrowing) [52–55]; (ii) passive or drift—consists in the passive displacement of aquatic organisms in running waters [56]. Macroinvertebrates dispersion to downstream areas by means of drift has been widely documented [57–60] and many factors, such as predation, population density, current/discharge, photoperiod, water chemistry, life-cycle stage, genetic, food availability and quality, and contamination seem to induce their displacement [57,58,61].

How exactly *C. edule* can detect salinity changes, and the mechanism underlying the observed behavior, are unclear and outside the scope of this work, although we suspect it could be triggered in a physiologically similar way to what was observed by Peteiro et al. [62] when investigating drifting capability and physiological response to salinity stress. Regardless the mechanism, by adopting this behavioural strategy organisms increase their chance to find suitable conditions downstream for their survival, although at the expense of longer exposure to pelagic predators and the risk of being transported too far.

The idea that living adult *C. edule* can be transported by improved hydrodynamic conditions (e.g., storms), facilitated by its bulbous-shaped shells, is not entirely new and has long been documented [63–65]. Cadée [65] recently highlighted that adult cockles of *C. edule* could be eroded from a tidal flat on Texel (Wadden Sea) by storm events and be naturally transported by rolling over to a nearby beach, proving this can indeed occur in the field. As well, Anta et al. [50] reported the bedload transport of large amounts of *C. edule* in the Ulla River estuary (Galicia, Spain) after severe storm events. Evidence of escaping to reduce the exposure to stressors has also been reported and pointed out as beneficial in previous bivalve studies in order to avoid mass mortality episodes and recruitment failures [62].

5. Conclusions

Overall, our laboratory experiment highlighted a vertical migratory behaviour of cockles in the sediment column with changes in the water salinity. At low salinity, cockles were observed emerging at the sediment surface, while at high salinity they burrow in the sediment. This migration pattern could be a behavioural strategy for cockles' survival when facing flood events, consisting of avoidance of the stressful and impairing low salinity conditions allowing themselves to be dragged to higher salinity areas downstream where environmental conditions are favourable. This strategy may increase *C. edule's* survival probabilities under extreme scenarios, such as riverine flooding events on estuarine areas, representing an advantage on the coastal environmental change scenarios. Nevertheless, the sustainability of this behaviour and physiological consequences must be further investigated.

Findings of the present study constitute a first step to bring new insights regarding the effects of climate change stressors (floods) on adult bivalves' behaviour and to highlight the relevance of in situ monitoring to investigate the impacts of environmental change on key species. Future studies should consider and expand knowledge on species specific behavioural responses when planning and implementing management solutions for current and future bivalve fisheries and conservation/restoration projects worldwide.

Author Contributions: T.V. and P.A. conceptualized and designed the research. T.V. and H.V. performed field, laboratory work, and analysed data. T.V., H.V. and J.C. wrote the original draft of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This work was financed by national funds through FCT-Foundation for Science and Technology, I.P., within the scope of the projects UIDB/04292/2020–MARE-Marine and Environmental Sciences Centre, and of the Regional Operational Programme CENTRO 2020 within the scope of the project CENTRO-01-0145-FEDER-000006. This work was also funded by: FCT through a Post-Doc Grant attributed to Tiago Verdelhos (SFRH/BPD/66838/2009); FCT and University of Coimbra through the Decree-law 57/2016 contracts of Tiago Verdelhos and Helena Verissimo, subsidised by

the European Social Fund and Portuguese Ministry of Science, Technology and Higher Education (MCTES) through the Human Potential Operational Programme (POPH); MAR2020 through the project ReSEt-Restauro de Sapais Estuarinos com Vista à Sustentabilidade.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study can be replicated from it.

Acknowledgments: The authors would like to thank all the colleagues who collaborated in the field and laboratory work, and to José Paulo Sousa and Rui Ribeiro for the useful statistical contribution.

Conflicts of Interest: The authors declare no conflict 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.

References

1. IPCC *Special Report on the Ocean and Cryosphere in a Changing Climate*; Pörtner, H.-O.; Roberts, D.C.; Masson-Delmotte, V.; Zhai, P.; Tignor, M.; Poloczanska, E.; Mintenbeck, K.; Alegria, A.; Nicolai, M.; Okem, A.; et al. (Eds.) Intergovernmental Panel on Climate Change: Geneva, Switzerland, 2019; in press.
2. Díaz, S.; Settele, J.; Brondízio, E.; Ngo, H.; Guèze, M.; Agard, J.; Arneth, A.; Balvanera, P.; Brauman, K.; Butchart, S.; et al. *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*; The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services: Bonn, Germany, 2019.
3. Lotze, H.K.; Tittensor, D.P.; Bryndum-Buchholz, A.; Eddy, T.D.; Cheung, W.W.L.; Galbraith, E.D.; Barange, M.; Barrier, N.; Bianchi, D.; Blanchard, J.L.; et al. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 12907–12912. [[CrossRef](#)]
4. Smale, D.A.; Wernberg, T.; Oliver, E.C.J.; Thomsen, M.; Harvey, B.P.; Straub, S.C.; Burrows, M.T.; Alexander, L.V.; Benthuyssen, J.A.; Donat, M.G.; et al. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Chang.* **2019**, *9*, 306–312. [[CrossRef](#)]
5. Norkko, A.; Villnäs, A.; Norkko, J.; Valanko, S.; Pilditch, C.A. Size matters: Implications of the loss of large individuals for ecosystem function. *Sci. Rep.* **2013**, *3*, 1–7. [[CrossRef](#)]
6. Beukema, J.J.; Dekker, R.; Philippart, C.J.M. Long-term variability in bivalve recruitment, mortality, and growth and their contribution to fluctuations in food stocks of shellfish-eating birds. *Mar. Ecol. Prog. Ser.* **2010**, *414*, 117–130. [[CrossRef](#)]
7. Malham, S.K.; Hutchinsom, T.H.; Longshaw, M. A review of the biology of European cockles (*Cerastoderma* spp.). *J. Mar. Biol. Assoc. UK* **2012**, *92*, 1563–1577. [[CrossRef](#)]
8. Verdelhos, T.; Cardoso, P.G.; Dolbeth, M.; Pardal, M.A. Recovery trends of *Scrobicularia plana* populations after restoration measures, affected by extreme climate events. *Mar. Environ. Res.* **2014**, *98*, 39–48. [[CrossRef](#)] [[PubMed](#)]
9. Olivier, A.V.D.S.; Jones, L.; Le Vay, L.; Christie, M.; Wilson, J.; Malham, S.K. A global review of the ecosystem services provided by bivalve aquaculture. *Rev. Aquac.* **2020**, *12*, 3–25. [[CrossRef](#)]
10. Newell, R. Ecosystem influences natural and cultivated populations of suspension-feeding bivalve mollusks: A review. *J. Shellfish Res.* **2004**, *23*, 51–61.
11. Norkko, J.; Shumway, S.E. Bivalves as bioturbators and bioirrigators. In *Shellfish Aquaculture and the Environment*; John Wiley & Sons, Inc.: Hoboken, NJ, USA, 2011; pp. 297–317.
12. Karlson, A.M.L.; Pilditch, C.A.; Probert, P.K.; Leduc, D.; Savage, C. Large Infaunal Bivalves Determine Community Uptake of Macroalgal Detritus and Food Web Pathways. *Ecosystems* **2021**, *24*, 384–402. [[CrossRef](#)]
13. Longshaw, M.; Malham, S. A review of the infectious agents, parasites, pathogens and commensals of European cockles (*C. edule* and *C. glaucum*). *J. Mar. Biol. Assoc. UK* **2013**, *93*, 227–247. [[CrossRef](#)]
14. Maia, F.; Barroso, C.M.; Gaspar, M.B. Biology of the common cockle *Cerastoderma edule* (Linnaeus, 1758) in Ria de Aveiro (NW Portugal): Implications for fisheries management. *J. Sea Res.* **2020**, *171*, 102024. [[CrossRef](#)]
15. Genelt-Yanovskiy, E.; Poloskin, A.; Granovitch, A.; Nazarova, S.; Strelkov, P. Population structure and growth rates at biogeographic extremes: A case study of the common cockle, *Cerastoderma edule* (L.) in the Barents Sea. *Mar. Pollut. Bull.* **2010**, *61*, 247–253. [[CrossRef](#)]
16. Verdelhos, T.; Marques, J.C.; Anastácio, P. The impact of estuarine salinity changes on the bivalves *Scrobicularia plana* and *Cerastoderma edule*, illustrated by behavioural and mortality responses on a laboratory assay. *Ecol. Indic.* **2015**, *52*, 96–104. [[CrossRef](#)]
17. Verdelhos, T.; Marques, J.C.; Anastácio, P. Behavioural and mortality responses of the bivalves *Scrobicularia plana* and *Cerastoderma edule* to temperature, as indicator of climate change's potential impacts. *Ecol. Indic.* **2015**, *58*, 95–103. [[CrossRef](#)]
18. Dabouineau, L.; Ponsoero, A. *Synthesis on Biology of the Common European Cockle Cerastoderma edule*, 2nd ed.; Réserve Naturelle Nationale Baie de St-Brieuc, Université Catholique de l'Ouest: Angers, France, 2009; p. 23.

19. Burdon, D.; Callaway, R.; Elliott, M.; Smith, T.; Wither, A. Mass mortalities in bivalve populations: A review of the edible cockle *Cerastoderma edule* (L.). *Estuar. Coast. Shelf Sci.* **2014**, *150*, 271–280. [[CrossRef](#)]
20. Kang, C.K.; Sauriau, P.G.; Richard, P.; Blanchard, G.F. Food sources of the infaunal suspension-feeding bivalve *Cerastoderma edule* in a muddy sandflat of Marennes-Oléron Bay, as determined by analyses of carbon and nitrogen stable isotopes. *Mar. Ecol. Prog. Ser.* **1999**, *187*, 147–158. [[CrossRef](#)]
21. Sauriau, P.G.; Kang, C.K. Stable isotope evidence of benthic microalgae-based growth and secondary production in the suspension feeder *Cerastoderma edule* (Mollusca, Bivalvia) in the Marennes-Oléron Bay. *Hydrobiologia* **2000**, *440*, 317–329. [[CrossRef](#)]
22. Rossi, F.; Herman, P.M.J.; Middelburg, J.J. Interspecific and intraspecific variation of δC and δN in deposit- and suspension-feeding bivalves (*Macoma balthica* and *Cerastoderma edule*): Evidence of ontogenetic changes in feeding mode of *Macoma balthica*. *Limnol. Oceanogr.* **2004**, *49*, 408–414. [[CrossRef](#)]
23. Christianen, M.J.A.; Middelburg, J.J.; Holthuijsen, S.J.; Jouta, J.; Compton, T.J.; van der Heide, T.; Piersma, T.; Sinninghe Damsté, J.S.; van der Veer, H.W.; Schouten, S.; et al. Benthic primary producers are key to sustain the Wadden Sea food web: Stable carbon isotope analysis at landscape scale. *Ecology* **2017**, *98*, 1498–1512. [[CrossRef](#)]
24. Parada, J.M.; Molares, J.; Otero, X. Multispecies Mortality patterns of commercial bivalves in relation to estuarine salinity fluctuation. *Estuaries Coasts* **2012**, *35*, 132–142. [[CrossRef](#)]
25. The Food and Agriculture Organization. *The State of World Fisheries and Aquaculture 2018: Meeting the Sustainable Developing Goals*; The Food and Agriculture Organization: Rome, Italy, 2018; Licence: CC BY-NC-SA 3.0 IGO.
26. Carss, D.N.; Brito, A.C.; Chainho, P.; Ciutat, A.; Montaudouin, X.; Fernández-Otero, R.M.; Incera Filgueira, M.; Garbutt, A.; Goedknecht, M.A.M.; Lynch, S.A.; et al. Ecosystem services provided by a non-cultured shellfish species: The common cockle *Cerastoderma edule*. *Mar. Environ. Res.* **2020**, *158*, 104931. [[CrossRef](#)]
27. Moyle, P.B.; Lund, J.R.; Bennett, W.A.; Fleenor, W.E. Habitat variability and complexity in the upper San Francisco estuary. *San Franc. Estuary Watershed Sci.* **2010**, *8*, 1–24. [[CrossRef](#)]
28. Bassett, A.; Barborne, E.; Elliott, M.; Li, B.; Jorgensen, S.E.; Lucena-Moya, P.; Pardo, I.; Mouillot, D. A unifying approach to understanding transitional waters: Fundamental properties emerging from ecotone ecosystems. *Estuar. Coast. Shelf Sci.* **2013**, *132*, 5–16. [[CrossRef](#)]
29. Gosling, E. *Bivalve Molluscs Biology, Ecology, and Culture*; Blackwell Publishing: Oxford, UK, 2004.
30. Telesh, I.V.; Khlebovich, V.V. Principal processes within the estuarine salinity gradient: A review. *Mar. Pollut. Bull.* **2010**, *61*, 149–155. [[CrossRef](#)] [[PubMed](#)]
31. Doney, S.C.; Ruckelshaus, M.; Duffy, J.E.; Barry, J.P.; Chan, F.; English, C.A.; Galindo, H.M.; Grebmeier, J.M.; Hollowed, A.B.; Knowlton, N.; et al. Climate Change Impacts on Marine Ecosystems. *Annu. Rev. Mar. Sci.* **2012**, *4*, 11–37. [[CrossRef](#)] [[PubMed](#)]
32. Fuji, T. Climate change, sea-level rise and implications for coastal and estuarine shoreline management with particular reference to the Ecology of intertidal benthic macrofauna in NW Europe. *Biology* **2012**, *1*, 597–616. [[CrossRef](#)]
33. Wetz, M.S.; Yoskowitz, D.W. An 'extreme' future for estuaries? Effects of extreme climatic events on estuarine water quality and ecology. *Mar. Pollut. Bull.* **2013**, *69*, 7–18. [[CrossRef](#)]
34. Akberali, H.B. Behaviour of *Scrobicularia plana* (da Costa) in water of various salinities. *J. Exp. Mar. Biol. Ecol.* **1978**, *33*, 237–249. [[CrossRef](#)]
35. Akberali, H.B.; Davenport, J. The detection of salinity changes by the marine bivalve molluscs *Scrobicularia plana* (da Costa) and *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* **1982**, *58*, 59–72. [[CrossRef](#)]
36. Chandran, V.R. Intracellular Osmoregulation in the Estuarine Mollusc *Villorita cyprinoides* var. *Cochinensis* (Mollusca:Bivalvia) Hanley. Ph.D. Thesis, Cochin University, Cochin, India, 2002.
37. Parada, J.M.; Molares, J. Natural mortality of the cockle *Cerastoderma edule* (L.) from the Ria of Arousa (NW Spain) intertidal zone. *Rev. Biol. Mar. Oceanogr.* **2008**, *43*, 501–511. [[CrossRef](#)]
38. Neto, J.M.; Teixeira, H.; Patrício, J.; Baeta, A.; Veríssimo, H.; Pinto, R.; Marques, J.C. The response of estuarine macrobenthic communities to natural and human-induced changes: Dynamics and ecological quality. *Estuaries Coasts* **2010**, *33*, 1327–1339. [[CrossRef](#)]
39. Crespo, D.; Verdelhos, T.; Dolbeth, M.; Pardal, M.A. Effects of the over harvesting on an edible cockle (*Cerastoderma edule* Linnaeus, 1758) population on a Southern european estuary. *Fresenius Environ. Bull.* **2010**, *19*, 2801–2811.
40. Underwood, A.T.; Chapman, M.G.; Crowe, T.P. Identifying and understanding ecological preferences for habitat or prey. *J. Exp. Mar. Biol. Ecol.* **2004**, *300*, 161–187. [[CrossRef](#)]
41. Evans, D.H. *Osmotic and Ionic Regulation: Cells and Animals*; CRC Press: Boca Raton, FL, USA, 2009.
42. Carregosa, V.; Figueira, E.; Gil, A.M.; Pereira, S.; Pinto, J.; Soares, A.M.V.M.; Freitas, R. Tolerance of *Venerupis philippinarum* to salinity: Osmotic and metabolic aspects. *Comp. Biochem. Physiol. A* **2014**, *171*, 36–43. [[CrossRef](#)]
43. Cardoso, P.G.; Raffaelli, D.; Lillebø, A.I.; Verdelhos, T.; Pardal, M.A. The impact of extreme flooding events and anthropogenic stressors on the microbenthic communities' dynamics. *Estuar. Coast. Shelf Sci.* **2008**, *76*, 553–565. [[CrossRef](#)]
44. Anastácio, P.M.; Verdelhos, T.; Marques, J.C.; Pardal, M.A. A validated population-dynamics model for *Scrobicularia plana* (Mollusca, Bivalvia) in a south-western European estuary. *Mar. Freshw. Res.* **2009**, *60*, 404–416. [[CrossRef](#)]
45. Dolbeth, M.; Cardoso, P.G.; Grilo, T.F.; Bordalo, M.D.; Raffaelli, D.; Pardal, M.A. Long-term changes in the production of estuarine macrobenthos affected by multiple stressors. *Estuar. Coast. Shelf. Sci.* **2011**, *92*, 10–18. [[CrossRef](#)]

46. Grilo, T.F.; Cardoso, P.G.; Dolbeth, M.; Bordalo, M.A.; Pardal, M.A. Effects of extreme climate events on the macrobenthic communities' structure and functioning of a temperate estuary. *Mar. Pollut. Bull.* **2011**, *62*, 303–311. [[CrossRef](#)] [[PubMed](#)]
47. Huxham, M.; Richards, M. Can postlarval bivalves select sediment type during settlement? A field test with *Macoma balthica* (L.) and *Cerastoderma edule* (L.). *J. Exp. Mar. Biol. Ecol.* **2003**, *288*, 279–293. [[CrossRef](#)]
48. Hunt, H.L.; Maltais, M.-J.; Fugate, D.C.; Chant, R.J. Spatial and temporal variability in juvenile bivalve dispersal: Effects of sediment transport and flow regime. *Mar. Ecol. Prog. Ser.* **2007**, *352*, 145–159. [[CrossRef](#)]
49. Peña, E.; Anta, J.; Puertas, J.; Teijeiro, T. Estimation of Drag Coefficient and Settling Velocity of the Cockle *Cerastoderma edule* Using Particle Image Velocimetry (PIV). *J. Coast. Res.* **2008**, *24*, 150–158. [[CrossRef](#)]
50. Anta, J.; Peña, E.; Puertas, J.; Cea, L. A bedload transport equation for the *Cerastoderma edule* cockle. *J. Mar. Syst.* **2013**, *111*, 189–195. [[CrossRef](#)]
51. Coffen-Smout, S.S.; Rees, E.I.S. Burrowing behaviour and dispersion of cockles *Cerastoderma edule* L. following simulated fishing disturbance. *Fish. Res.* **1999**, *40*, 65–72. [[CrossRef](#)]
52. Roper, D.S.; Hickey, C.W. Behavioural responses of the marine bivalve *Macomona liliana* exposed to copper- and chlordane-dosed sediments. *Mar. Biol.* **1994**, *118*, 673–680. [[CrossRef](#)]
53. Hellou, J. Behavioural ecotoxicology, an “early warning” signal to assess environmental quality. *Environ. Sci. Pollut. Res. Int.* **2011**, *18*, 1–11. [[CrossRef](#)]
54. Ward, D.J.; Simpson, S.L.; Jolley, D.F. Avoidance of contaminated sediments by an amphipod (*Melita plumulosa*), A harpacticoid copepod (*Nitocra spinipes*), and a snail (*Phallomedusa solida*). *Environ. Toxicol. Chem.* **2013**, *32*, 644–652. [[CrossRef](#)]
55. Araújo, C.V.M.; Moreira-Santos, M.; Ribeiro, R. Active and passive spatial avoidance by aquatic organisms from environmental stressors: A complementary perspective and a critical review. *Environ. Int.* **2016**, *92*, 405–415. [[CrossRef](#)]
56. Allan, J.D. Macroinvertebrate drift in a Rocky Mountain stream. *Hydrobiologia* **1988**, *144*, 261–268. [[CrossRef](#)]
57. Brittain, J.E.; Eikeland, T.J. Invertebrate drift—A review. *Hydrobiologia* **1988**, *166*, 77–93. [[CrossRef](#)]
58. Humphries, S.; Ruxton, G.D. Estimation of intergenerational drift dispersal distances and mortality risk for aquatic macroinvertebrates. *Limnol. Oceanogr.* **2003**, *48*, 2117–2124. [[CrossRef](#)]
59. Svendsen, C.R.; Quinn, T.; Kolbe, D. *Review of Macroinvertebrate Drift in Lotic Ecosystems*; Final Report, Manuscript 92; Ildlife Research Program, Environmental and Safety Division: Seattle, WA, USA, 2004.
60. Flecker, A.S. Fish predation and the evolution of invertebrate drift periodicity: Evidence from neotropical streams. *Ecology* **1992**, *73*, 438–448. [[CrossRef](#)]
61. Linke, O. Die Biota des Jadebusenwattes. *Helgoländer Wiss. Meeresunters.* **1939**, *1*, 201–348. [[CrossRef](#)]
62. Peteiro, L.G.; Woodin, S.; Wethey, D.; Costas-Costas, D.; Martínez-Casal, A.; Olabarria, C.; Vázquez, E. Responses to salinity stress in bivalves: Evidence of ontogenetic changes in energetic physiology on *Cerastoderma edule*. *Sci. Rep.* **2018**, *8*, 1–9. [[CrossRef](#)] [[PubMed](#)]
63. Kristensen, I. Difference in density and growth in a cockle population in the Dutch Wadden Sea. *Arch. Neerl. Zool.* **1957**, *12*, 351–453. [[CrossRef](#)]
64. Schäfer, W. *Fossilien, Bilder und Gedanken zur Paläontologischen Wissenschaft*; Waldemar Kramer: Frankfurt am Main, Germany, 1980; 244p.
65. Cadée, G.C. Rolling Cockles: Shell Abrasion and Repair in a Living Bivalve *Cerastoderma edule* L. *Ichnos* **2016**, *23*, 180–188. [[CrossRef](#)]