

Rapid Communication**The arrival of a non-indigenous ecosystem engineer to a heavily invaded and flow-regulated estuary in Europe**João Encarnação¹, Maria Alexandra Teodósio¹ and Pedro Morais^{1,2}¹Centre of Marine Sciences (CCMAR), Universidade do Algarve, Campus de Gambelas, Faro, Portugal²Institute of Environment, Florida International University, Miami, FL, United StatesCorresponding author: João Encarnação (jpencaernacao@ualg.pt)

Citation: Encarnação J, Teodósio MA, Morais P (2024) The arrival of a non-indigenous ecosystem engineer to a heavily invaded and flow-regulated estuary in Europe. *BioInvasions Records* 13(1): 83–95, <https://doi.org/10.3391/bir.2024.13.1.08>

Received: 28 June 2023**Accepted:** 14 September 2023**Published:** 29 November 2023**Handling editor:** Javier Atalah**Thematic editor:** Amy Fowler**Copyright:** © Encarnação et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS**Abstract**

Ecosystem engineering bivalves can shape aquatic ecosystems because their high filtration capacity changes water quality and their shells increase the fractal dimension of benthic ecosystems with consequent abiotic and biotic effects. The Asian date mussel *Arcuatula senhousia* (W. H. Benson, 1842), native to East Asia between the South China Sea and Siberia, is one such bivalve that, despite its small size, can reshape a benthic ecosystem when forming dense, continuous mats. We describe here the first detected population of this non-indigenous species in southern Portugal. The Asian date mussel was found in the middle portion of the Guadiana estuary in 2022. There, river flow has been highly regulated since the construction of the biggest European reservoir in 2002, which may have been the precursor for the establishment of numerous non-indigenous species. We also discuss if this new non-indigenous species indicates an ongoing invasion meltdown process or if it can be framed under the empty niche or niche replacement hypothesis. So far, there is only circumstantial evidence supporting the niche theory hypotheses, but the interaction of several hypotheses promoting the spread and establishment of this species is also likely. Moving forward, better-informed management and conservation efforts should rely on new empirical and experimental evidence to understand the establishment mechanisms of non-indigenous species in the Guadiana estuary.

Key words: invasive species, invasion meltdown, niche theory, Asian mussel, *Arcuatula senhousia*, Guadiana, Portugal

Introduction

The ecosystem impacts of invasive species include changes in nutrient cycling, predation on native species, species extirpation, and habitat alterations (some of which are promoted by ecosystem engineering invaders) (Simberloff et al. 2013). Bivalves are important ecosystem engineers both in native and non-native areas (Carranza et al. 2009; Sousa et al. 2009; Beck et al. 2011), and invasive bivalves may display a wide array of positive effects since they can increase water quality and benthic biodiversity due to, respectively, their filtration capacity (Fahnenstiel et al. 1995; Pranovi et al. 2006; Rosa et al. 2014) or added fractal dimension with their shells (either when the organisms are dead or alive) that provide

refuge, feeding and spawning areas for vertebrates and invertebrates (Burlakova et al. 2012; Novais et al. 2015; Ilarri et al. 2018). However, when they reach high abundances, invasive bivalves disrupt plankton communities and dynamics by triggering a series of cascading effects (Pace et al. 1998; Crooks 2009; Pigneur et al. 2014). For example, the Asian clam *Corbicula fluminea* (O.F. Müller, 1774) produces impacts at different levels, from alteration of habitat structure and competition for space to impacts on organisms at the base of the food chain due to high filtration rates (Sousa et al. 2009; Dias et al. 2014). Financially, the economic impact can be tremendous; the small but highly invasive dreissenid mussels—mainly the zebra mussel *Dreissena polymorpha* (Pallas, 1771) and quagga mussel *Dreissena bugensis* (Andrusov, 1897)—caused over \$51 billion USD in accumulated losses around the world because they clog irrigation and water intake pipes of hydroelectric, nuclear, and thermal power plants (Haubrock et al. 2022).

The Asian date mussel *Arcuatula senhousia* (W.H. Benson, 1842)—originally described as *Modiola senhousia* and known as *Musculista senhousia* until recently—is another small ecosystem engineer that grows up to 28 mm in shell length. This species may form dense, continuous mats of ovoid cocoons anchored on the sediment with a matrix of byssal threads (Morton 1974; Sousa et al. 2009). Native to East Asia between the South China Sea and Siberia (Cheung et al. 1962 in Morton 1974; Kulikova 1978), the species has invaded several coastal ecosystems around the globe, including the Indian Ocean (India, Madagascar, Mauritius, Zanzibar, and the adjacent Persian Gulf) (Barash and Danin 1972; Behera et al. 2019; Yasser et al. 2023), coastal ecosystems scattered along the Eastern Atlantic Ocean (e.g., southern United Kingdom, Bay of Biscay, central Portugal, Guinea-Bissau) (Lourenço et al. 2018; Cabral et al. 2020; Watson et al. 2021; Massé et al. 2022), coastlines along the Mediterranean Sea (e.g., Spain, France, Italy, Croatia, Albania, Turkey, Israel, Tunisia, Algeria) (Hamza et al. 2022) and in the adjacent Black Sea (Zhulidov et al. 2021), off Venezuela on the Western Atlantic Ocean (Martínez-Escarbassiere et al. 2003), Eastern coastal ecosystems of the Pacific Ocean (e.g., Mexico, Colombia) (Crooks 1998; Arellano and Salgado-Barragán 2012; Osorio 2013), and in the southwestern Pacific Ocean (e.g., Australia, New Zealand) (Willan 1987; Creese et al. 1997). The Asian date mussel is an epifaunal bivalve observed in sites with salinities between 5 and 18 (Yamamuro et al. 2010; Hosozawa et al. 2020), but is able to colonize fully marine areas, as observed in the Solent (southern England) (Watson et al. 2021) and French localities along the Bay of Biscay (Massé et al. 2022).

In their native range, the Asian date mussel may reach densities of up to 2500 ind.m⁻² (Morton 1974). However, in invaded areas, it has reached densities of 10,000 ind.m⁻² in Italy (Mistri et al. 2004), 16,000 ind.m⁻² in New Zealand (Creese et al. 1997), and 170,000 ind.m⁻² in Mission Bay (California, United States of America) which is among the highest ever

recorded for marine bivalves (Crooks and Soulé 1999). As an ecosystem engineer, the Asian date mussel also increases habitat complexity, which may result in a increase in species richness and density, particularly of amphipods, gastropods, and polychaetes (Crooks 1998; Crooks and Khim 1999). The water filtration capacity of the species accelerates the transfer of suspended sediment and organic matter from the pelagic compartment into the benthic compartment through the production of faeces and pseudo-faeces. This process alters the nutrient balance of sediment and reduces the redox potential discontinuity layer, which can prevent certain organisms from living below the byssal mats (Morton 1974; Creese et al. 1997; Crooks 1998, 2009).

Our study focuses on the Guadiana estuary (southwest Iberian Peninsula), which has been suffering from ecological impacts for over two decades due to the construction of the biggest water reservoir in Europe—the Alqueva dam—that began operating in February 2002 (Morais 2008). The five most noticeable changes in the Guadiana estuary are the (1) increased salinization of the middle and upper portions of the estuary (Chícharo et al. 2006; Barbosa et al. 2010; Encarnação et al. 2013), (2) change in the phytoplankton community due to a shift from a light-limited ecosystem towards a more nutrient-limited one (Barbosa et al. 2010), (3) decrease in the diversity of zooplankton and increase of annual blooms of invasive jellyfish species (Muha et al. 2012), (4) shift from freshwater-associated fish species in the upper portions of the estuary, such as barbell species, to short-lived fish such as *Atherina* and *Pomatoschistus* species (Chícharo et al. 2006), and (5) appearance of numerous non-indigenous species (Chícharo et al. 2009a; Morais et al. 2009a, 2019; Morais and Teodósio 2016; Cruz et al. 2017; Gonçalves et al. 2017; Seyer et al. 2017; Nuño et al. 2018). The Guadiana estuary is now a hotspot for non-indigenous species, including the Asian clam *Corbicula fluminea*, weakfish *Cynoscion regalis* (Bloch & Schneider, 1801), and Atlantic blue crab *Callinectes sapidus* Rathbun, 1896, just to cite the most prominent (Morais et al. 2009a, 2017, 2019; Morais and Teodósio 2016; Encarnação et al. 2021).

Considering the recent history of biological invasions in the Guadiana estuary, the discovery of the Asian date mussel *Arcuatula senhousia* in October of 2022 is alarming. Therefore, we intend to describe the most recent non-indigenous species detected in the Guadiana estuary and present hypotheses on why so many non-indigenous species have established in this estuary since the construction of the Alqueva dam.

Materials and methods

Study area

The Guadiana River basin is the fourth largest in the Iberian Peninsula and is characterized by a Mediterranean climate (i.e., periods of extended droughts

and infrequent heavy floods) (Morais 2008). River flow is heavily controlled by dams, with the biggest European water reservoir—the Alqueva dam, located in the river mainstem approximately 170 km from the river mouth—regulating the majority of water reaching the estuary (Morais 2008; Morais et al. 2009b) and resulting in pronounced salinity intrusion into the upper estuary (Chícharo et al. 2006; Barbosa et al. 2010; Encarnação et al. 2013). This estuary can be divided into the upper portion of the estuary, with salinity closer to zero but still with tidal influence, middle portion of the estuary, characterized as the mixing zone of brackish water (salinity 0.5–25), and the lower portion of the estuary with salinity above 25 (Chícharo et al. 2009b), although inflow regularization is reshaping such boundaries with the increasing salinization of the estuary.

Sampling methods

Asian date mussels were collected during two sampling campaigns, under the scope of the ATLAZUL project, to evaluate the state of fishing resources and distribution of non-indigenous species in the Guadiana estuary during the spring (April) and fall (October) of 2022. Samples were collected with a bottom beam trawl (mouth opening: 4.2 m wide × 0.5 m tall; total length: 8.0 m) with a variable mesh size, decreasing from 20 mm in the aperture to 10 mm in the cod end. Sampling areas included the lower, middle, and upper portions of the Guadiana estuary.

In 2022, 14 trawls were made in the lower and upper estuary and 15 in the middle estuary. The choice of sampling locations within each estuary section followed previous studies (e.g., Chícharo et al. 2001, 2006; Morais et al. 2009b). Trawls were performed in a boat equipped with an 80 hp engine at a constant speed—between 2 and 5 knots (depending on flow conditions)—during ebb tides and along the same direction of water flow. The number of trawls (minimum of three) and duration varied between sampling locations (shorter distances in sites with boulders or biogenic reefs, longer in areas with muddy or sandy bottoms) and abundance of organisms. Trawl duration varied between 2 and 10 minutes and lasted 7.1 ± 1.8 min on average. Trawl distance varied between 106.1 and 719.19 m, averaging 481.9 ± 131.5 m, while the average sampled area was 2024.1 ± 552.5 m².

After collection, specimens were measured (total shell length and width, ± 0.1 cm), weighed (total fresh weight, ± 0.01 g), and identified in the laboratory. According to descriptions available in the literature, specimens were identified as Asian date mussels *Arcuatula senhousia* (Morton 1974; Hoenselaar and Hoenselaar 1989; Faasse 2018; Lourenço et al. 2018).

Results

Twelve specimens of a previously unknown mussel species for the study area were collected in October 2022 close to Foz de Odeleite in the middle

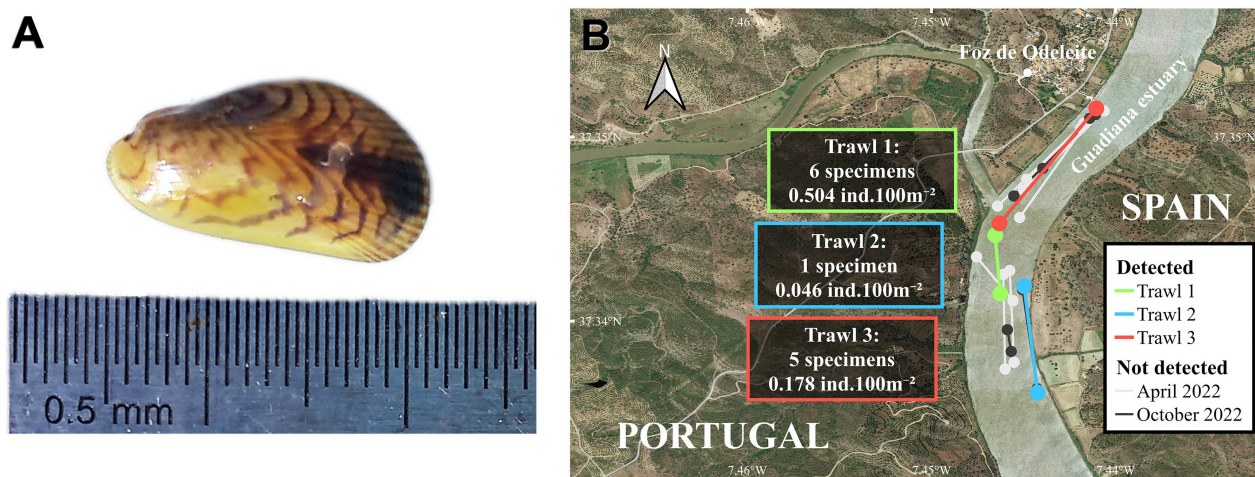


Figure 1. (A) Photo of an Asian date mussel *Arcuatula senhousia* (W. H. Benson, 1842) specimen retrieved from the middle portion of the Guadiana estuary on October 7th, 2022. (B) Location of the bottom beam trawls performed in April and October 2022 in the middle portion of the Guadiana estuary. The number of specimens and density of the Asian date mussels collected are shown for the three trawls in which specimens were collected in October 2022.

Table 1. Morphometric details of the 12 Asian date mussel *Arcuatula senhousia* (W. H. Benson, 1842) specimens collected in the middle portion of the Guadiana estuary on October 7th, 2022.

Specimen	Trawl number	Length (cm)	Width (cm)	Weight (g)	GPS location	Notes
1	1	1.1	0.6	0.05	37.3461 / -7.4450	Broken shell
2	1	1.4	0.8	0.12	37.3461 / -7.4450	Broken shell
3	1	1.2	0.7	0.12	37.3461 / -7.4450	
4	1	0.7	0.5	0.02	37.3461 / -7.4450	
5	1	1.0	0.5	0.05	37.3461 / -7.4450	
6	1	1.5	0.8	0.20	37.3461 / -7.4450	
7	2	1.1	0.7	0.10	37.3433 / -7.4438	
8	3	1.6	0.9	0.30	37.3504 / -7.4432	
9	3	1.5	0.8	0.25	37.3504 / -7.4432	
10	3	1.4	0.8	0.21	37.3504 / -7.4432	
11	3	0.7	0.4	0.03	37.3504 / -7.4432	
12	3	1.4	0.8	0.18	37.3504 / -7.4432	

portion of the Guadiana estuary (Figure 1). Specimens were visually identified as *Arcuatula senhousia* due to the following key morphological features: a thin shell, radiating lines posteriorly and concentric lines in the middle, several riblets at the anterior end, with the periostracum showing a shiny and pale greenish colour and irregular brownish-reddish markings, as well as radiating reddish lines on the posterior area (Faasse 2018; Lourenço et al. 2018).

The Guadiana estuary specimens were collected in three of the seven trawls made in October 2022, representing 7% of the trawls made in 2022 (3 out of 43 trawls). In October 2022, the average water temperature, salinity, and depth in the sites where Asian date mussels were collected were 22.3 ± 0.3 °C, 26.8 ± 1.9 , and 6.6 ± 1.5 m, respectively. On average, the total length and width of Asian date mussels were 12.1 ± 3.0 mm and 6.9 ± 1.6 mm, respectively, and the total weight was 0.14 ± 0.09 g (Table 1). Density in each trawl was 0.046 (trawl 2), 0.178 (trawl 3), and 0.504 ind.100m⁻² (trawl 1).

Discussion

The Asian date mussel and its putative impacts

The constant low-flow conditions set by the Alqueva dam over numerous years, rarely disrupted by heavy rain or floods, has reshaped the ecosystem functioning of the Guadiana estuary, which coincided with the establishment of multiple non-indigenous species. The brackish zone is now a hotspot for non-indigenous species, where they occupy the pelagic and benthic compartments while exploiting different resources (Chícharo et al. 2009a; Morais et al. 2009a, 2019; Encarnação et al. 2013; Morais and Teodósio 2016; Seyer et al. 2017).

The Asian date mussel is the most recent non-indigenous bivalve collected from the Guadiana estuary since 2000. Back then, the Asian clam *Corbicula fluminea* was caught in the upper portion of the estuary, and in 2003 it was already established along the middle and upper portions of the estuary, including several tributaries (Morais et al. 2009a). While the infaunal Asian clam inhabits freshwater and brackish ecosystems (salinities up to 15 but tolerating salinity up to 20) (Ferreira-Rodríguez and Pardo 2016; Bertrand et al. 2017), the Asian date mussel is an epifaunal bivalve commonly observed in environments with salinities between 5 and 18, but can also be found in fully marine zones (Yamamuro et al. 2010; Hosozawa et al. 2020; Watson et al. 2021; Massé et al. 2022). In the Guadiana estuary, we found Asian date mussels in an area with a salinity of 26 in the middle portion of the Guadiana estuary (~ 20 km upstream from the river mouth) during early fall; in this location, salinity can drop to 0 during higher inflow regimes (Morais et al. 2009b). The increased salinity intrusion in the Guadiana estuary, observed since the construction of the Alqueva dam (Chícharo et al. 2006; Morais et al. 2009b; Barbosa et al. 2010; Encarnação et al. 2013), may continue to facilitate the expansion of the Asian date mussel to more upstream locations, considering the salinity ranges previously reported for the species.

The detection of the Asian date mussel in three trawls conducted closely together, out of 43 trawls made along the entirety of the estuary in 2022, suggests that the species was recently introduced and it is not widespread for now. However it is possible that its low density precluded its detection during previous sampling campaigns. In Portugal, the species was found in two estuaries on the western coast—in 2015 in the Sado estuary and 2018 in the Tagus estuary (Cabral et al. 2020). These estuaries are located in the western coast of the country, and the entry to the Guadiana estuary is 370 km of coastline away in the southeastern tip of Portugal. Furthermore, no connecting aquatic corridors or water transfers, which could have transported larvae to the study region, are known between the Tagus/Sado and Guadiana river systems. In Spain, the presence of the Asian date mussel dates back to 2006 in the Bidasoa estuary on the Atlantic border

with France (Bachelet et al. 2009) and in the Mediterranean coast in 2014 in the Ebro delta (Soriano and Salgado 2014) and 2016 in a Barcelona's marina (Ulman et al. 2017). It is also unlikely that the species reached the Guadiana estuary by natural dispersion from any of these locations, so additional primary or secondary introduction events must have occurred. Additional molecular genetics work could be used in the future to shed light on how these populations may be connected to one another and possible vectors that transported, and continue to transport, the species to new locations.

The impact of the Asian date mussel will depend on its invasiveness, but it has the potential to become a serious ecosystem engineer (Crooks 1998, 2009; Crooks and Soulé 1999). Such impacts can be divided into two categories—autogenic and allogenic engineering (Jones et al. 1994). The shells of the Asian date mussel are considered an autogenic engineering by creating three-dimensional habitats for small organisms such as amphipods, gastropods, and polychaetes (Crooks 1998; Crooks and Khim 1999). In the worst-case scenario, the dense mats that Asian date mussels often form could impair the survival of other bivalves, such as the invasive Asian clam in the middle and upper portions of the estuary and native bivalves in the middle and lower portions of the estuary. The most notable native infaunal bivalves in the middle and/or lower portions of the Guadiana estuary are *Scrobicularia plana* (da Costa, 1778), *Ruditapes decussatus* (Linnaeus, 1758), and *Cerastoderma edule* (Linnaeus, 1758) (Conde et al. 2013), besides oyster reefs in the middle portions of the estuary and mussel beds in artificial substrates in the lower portions of the estuary (Morais unpublished data). In New Zealand, dense mats of the Asian date mussel significantly impacted other infaunal suspension-feeding bivalves, such as the endemic pipi *Paphies australis* (Gmelin, 1791), cockle *Austrovenus stutchburyi* (W. Wood, 1828), and black mussel *Xenostrobus pulex* (Lamarck, 1819) (Creese et al. 1997). Allogenic engineering involves the change of the physical state of the ecosystem via, for example, mechanical or chemical means (Jones et al. 1994). At higher densities, the filtration capacity of the Asian date mussel may increase water clarity by removing suspended materials from the water column and transferring them to the benthic compartment (Crooks 2009). This may increase the euphotic zone and enable the growth of macroalgae and seagrass (Strayer et al. 1999; Nielsen et al. 2002; Wall et al. 2008). In the Guadiana estuary, in tandem with the presence of the Asian clam (Morais et al. 2009a) and the saline intrusion into upper areas of the estuary (Chícharo et al. 2006; Barbosa et al. 2010; Encarnação et al. 2013), a reduction in turbidity may result in an alteration of benthic communities, with a higher presence of algae, or even seagrasses that are mainly found in the lower portions of the estuary (Cunha et al. 2013).

The Asian date mussel may also serve as a new food source for other species, including other non-indigenous species. The Atlantic blue crab

C. sapidus was detected for the first time in the Guadiana estuary in 2017 (Morais et al. 2019); since then, its abundance and distribution has increased significantly (Encarnaç o et al. 2021). Bivalves are a common food source for the Atlantic blue crab in the native range, including mussels, oysters, and clams (Laughlin 1982), but also other non-indigenous species, such as *Corbicula* spp. in the Ebro River in Spain (Ventura et al. 2018). Thus, the Asian date mussel, with its small size and relatively fragile shell (Hoenselaar and Hoenselaar 1989; Mass e et al. 2022), may become an additional food source for the Atlantic blue crab in the Guadiana estuary. Maintaining healthy populations of the green crab *Carcinus maenas* (Linnaeus, 1758), a native estuarine omnivore species (Baeta et al. 2006; Young and Elliott 2019), can also contribute to controlling this new invader, as the closely related *Carcinus aestuarii* (Nardo, 1847) is an effective predator of the Asian date mussel in Italy (Mistri et al. 2004; Cabiddu et al. 2023).

The ecosystem engineering capabilities of the Asian date mussel, the high densities it may attain, and their tolerance to a broad range of environmental variables suggest that this species may become a problematic invasive species in the southern Iberian Peninsula. The numerous estuarine ecosystems adjacent to the Guadiana estuary along the Gulf of Cadiz present an opportunity for this species to colonize new habitats and highlight the need to increase transboundary monitoring efforts for the early detection of non-indigenous species.

A hotspot for non-indigenous species – framing hypotheses

We hypothesize that the growing number of non-indigenous species in the middle and upper portions of the Guadiana estuary can be framed either by the invasion meltdown hypothesis (Simberloff and Von Holle 1999) or niche-based hypotheses (Ricciardi et al. 2013). On the one hand, the invasion meltdown hypothesis proposes that a community becomes more and more vulnerable to biological invasions as the number of attempted introductions or established introductions increases (Simberloff and Von Holle 1999). Regarding only the non-indigenous species that our research group has detected in the Guadiana estuary, the numbers have been increasing over the years – *Corbicula fluminea* in 2000 (Morais et al. 2009a); *Blackfordia virginica* Mayer, 1910, *Palaemon macrodactylus* Rathbun, 1902, and *Acartia tonsa* Dana, 1849 in 2008 (Ch ıcharo et al. 2009a; Cruz et al. 2017); *Cordylophora caspia* (Pallas, 1771) in 2015 (Seyer et al. 2017); *Cynoscion regalis* in 2016 (Morais and Teod osio 2016); *Callinectes sapidus* in 2017 (Morais et al. 2019); and *Arcuatula senhousia* in 2022 (this study). On the other hand, the niche-based hypotheses propose that either invasive species use unexplored resources (empty niche hypothesis) or are more competitive than native species to exploit the same limited resource (niche replacement hypothesis) (Ricciardi et al. 2013). Currently, we only have

circumstantial evidence supporting the niche-based hypotheses. For example, the Atlantic blue crab and the Ponto-Caspian hydroid *C. caspia* are likely occupying empty niches in the middle portion of the estuary due to the increased salinization of the estuary (Chícharo et al. 2006; Morais et al. 2009b; Barbosa et al. 2010; Encarnaç o et al. 2013), while the weakfish *C. regalis* is a successful invader because it may outcompete congeners (Cerveira et al. 2021). The Asian date mussel is, to our best knowledge, the only soft sediment epifaunal bivalve in the Guadiana estuary, as other native and invasive bivalves prefer and/or require harder substrate. Therefore, both hypotheses may help explain the presence and putative expansion of the Asian date mussel, which may benefit from a heavily disturbed ecosystem due to anthropogenic impacts and biotic disturbance from previous invasions but also from empty niches that can be promptly colonized.

The differences in a community's competitive ability/resistance towards non-indigenous species are vital in shaping community structure and succession (Belyea and Lancaster 1999; Young et al. 2001). So, the priority effects hypothesis, a broader ecological theory, is also intertwined with the abovementioned hypotheses since the succession of disturbed communities relies heavily on which species were established first (Belyea and Lancaster 1999; Young et al. 2001). Moving forward, empirical and experimental approaches to understand the establishment mechanisms of non-indigenous species in the Guadiana estuary should be conducted; first, to assess if an invasion meltdown is ongoing and, second, to weigh the prevalence of which niche-theory hypothesis prevails according to species traits. Such an approach will better inform management and conservation efforts aiming at tackling non-indigenous species in the Guadiana estuary and other estuaries along the Gulf of Cadiz, hopefully preventing the establishment of new species.

Authors' contribution

All authors contributed to the study conceptualization and design, data analysis and interpretation. Data collection and first draft of the manuscript was performed by JE. All authors commented on previous versions of the manuscript and approved the final version.

Acknowledgements

The authors acknowledge the help in field work provided by mestre Antero Fernandes, V ania Baptista, Agatha N urnberg, Olga Azevedo, and Jessica Cremades. The authors would like to thank the two anonymous reviewers who contributed to improving this manuscript.

Funding declaration

This study and the respective field work were funded by the ATLAZUL project (Poctep/Interreg 0755_ATLAZUL_6_E – Impulso da aliança litoral atl ntica para o crescimento azul). We also acknowledge the Sustainable Horizons SHEs project, a European Union's Horizon Europe project (No. 101071300). Partial financial support was received through Portuguese national funds from Foundation for Science and Technology through projects UIDB/04326/2020, UIDP/04326/2020 and LA/P/0101/2020. JE was supported by Ph.D. scholarships (SFRH/BD/140556/2018; COVID/BD/153280/2023) funded by Foundation for Science and Technology, Portugal.

Ethics and permits

All research pertaining to this article did not require any research ethics permit(s). Sampling campaigns were approved by national entities, namely DGRM (permit 17/2022/DRI) and ICNF (permit 77/2022/CAPT).

References

- Arellano MAO, Salgado-Barragán J (2012) Capítulo III - Mollusca. In: Low-Pfeng AM, Peters-Recagno EM (eds), *Invertebrados Marinos Exóticos en el Pacífico Mexicano*. Geomare, INESEMARNAT, A.C., 235 pp
- Bachelet G, Blanchet H, Cottet M, Dang C, de Montaudouin X, de Moura Queirós A, Gouillieux B, Lavesque N (2009) A round-the-world tour almost completed: First records of the invasive mussel *Musculista senhousia* in the north-east Atlantic (southern Bay of Biscay). *Marine Biodiversity Records* 2: e119, <https://doi.org/10.1017/S1755267209001080>
- Baeta A, Cabral HN, Marques JC, Pardal MA (2006) Feeding ecology of the green crab, *Carcinus maenas* (L., 1758) in a temperate estuary, Portugal. *Crustaceana* 79: 1181–1193, <https://doi.org/10.1163/156854006778859506>
- Barash A, Danin Z (1972) The Indo-Pacific species of Mollusca in the Mediterranean and notes on a collection from the Suez Canal. *Israel Journal of Zoology* 21: 301–374, <https://doi.org/10.1080/00212210.1972.10688367>
- Barbosa AB, Domingues RB, Galvão HM (2010) Environmental forcing of phytoplankton in a Mediterranean Estuary (Guadiana Estuary, South-western Iberia): A decadal study of anthropogenic and climatic influences. *Estuaries and Coasts* 33: 324–341, <https://doi.org/10.1007/s12237-009-9200-x>
- Beck MW, Brumbaugh RD, Airoidi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay MC (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *BioScience* 61: 107–116, <https://doi.org/10.1525/bio.2011.61.2.5>
- Behera DP, Tenjing S, Kosygin L (2019) Occurrence of exotic mussel, *Arcuatula senhousia* (Benson in Cantor, 1842) along southeast coast of India. *Journal of the Marine Biological Association of India* 61: 44–48, <https://doi.org/10.6024/jmbai.2019.61.1.2035-06>
- Belyea LR, Lancaster J (1999) Assembly rules within a contingent ecology. *Oikos* 86: 402–416, <https://doi.org/10.2307/3546646>
- Bertrand C, Devin S, Mouneyrac C, Giambérini L (2017) Eco-physiological responses to salinity changes across the freshwater-marine continuum on two euryhaline bivalves: *Corbicula fluminea* and *Scrobicularia plana*. *Ecological Indicators* 74: 334–342, <https://doi.org/10.1016/j.ecolind.2016.11.029>
- Burlakova LE, Karatayev AY, Karatayev VA (2012) Invasive mussels induce community changes by increasing habitat complexity. *Hydrobiologia* 685: 121–134, <https://doi.org/10.1007/s10750-011-0791-4>
- Cabiddu S, Addis P, Palmas F, Pusceddu A (2023) Differential feeding rates of native and alien predators on the invasive Asian date mussel *Arcuatula senhousia* (Benson in Cantor, 1842) in a Mediterranean coastal lagoon. *Marine Ecology* 44: e12738, <https://doi.org/10.1111/maec.12738>
- Cabral S, Carvalho F, Gaspar M, Ramajal J, Sá E, Santos C, Silva G, Sousa A, Costa JL, Chainho P (2020) Non-indigenous species in soft-sediments: Are some estuaries more invaded than others? *Ecological Indicators* 110: 105640, <https://doi.org/10.1016/j.ecolind.2019.105640>
- Carranza A, Defeo O, Beck M, Castilla JC (2009) Linking fisheries management and conservation in bioengineering species: The case of South American mussels (Mytilidae). *Reviews in Fish Biology and Fisheries* 19: 349–366, <https://doi.org/10.1007/s11160-009-9108-3>
- Cerveira I, Dias E, Baptista V, Teodósio MA, Morais P (2021) Invasive fish keeps native feeding strategy despite high niche overlap with a congener species. *Regional Studies in Marine Science* 47: 101969, <https://doi.org/10.1016/j.rsma.2021.101969>
- Chícharo MA, Chícharo L, Galvão H, Barbosa A, Marques MH, Andrade JP, Esteves E, Miguel C, Gouveia I (2001) Status of the Guadiana estuary (South Portugal) during 1996–1998: An ecohydrological approach. *Aquatic Ecosystem Health & Management* 4: 73–89, <https://doi.org/10.1080/146349801753569298>
- Chícharo MA, Chícharo L, Morais P (2006) Inter-annual differences of ichthyofauna structure of the Guadiana estuary and adjacent coastal area (SE Portugal/SW Spain): Before and after Alqueva dam construction. *Estuarine, Coastal and Shelf Science* 70: 39–51, <https://doi.org/10.1016/j.ecss.2006.05.036>
- Chícharo MA, Leitão T, Range P, Gutierrez C, Morales J, Morais P, Chícharo L (2009a) Alien species in the Guadiana Estuary (SE-Portugal/SW-Spain): *Blackfordia virginica* (Cnidaria, Hydrozoa) and *Palaemon macrodactylus* (Crustacea, Decapoda): Potential impacts and mitigation measures. *Aquatic Invasions* 4: 501–506, <https://doi.org/10.3391/ai.2009.4.3.11>
- Chícharo L, Hamadou RB, Amaral A, Range P, Mateus C, Piló D, Marques R, Morais P, Chícharo MA (2009b) Application and demonstration of the Ecohydrology approach for the

- sustainable functioning of the Guadiana estuary (South Portugal). *Ecohydrology & Hydrobiology* 9: 55–71, <https://doi.org/10.2478/v10104-009-0039-3>
- Conde A, Calvário J, Sprung M, Novais JM, Domínguez J (2013) Converse effect of flooding on intertidal macrobenthic assemblages in the Guadiana estuary. *Journal of the Marine Biological Association of the United Kingdom* 93: 1431–1440, <https://doi.org/10.1017/S0025315413000453>
- Creese R, Hooker S, De Luca S, Wharton Y (1997) Ecology and environmental impact of *Musculista senhousia* (Mollusca: Bivalvia: Mytilidae) in Tamaki Estuary, Auckland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31: 225–236, <https://doi.org/10.1080/00288330.1997.9516760>
- Crooks JA (1998) Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. *Marine Ecology Progress Series* 162: 137–152, <https://doi.org/10.3354/meps162137>
- Crooks JA (2009) The Role of exotic marine ecosystem engineers. In: Rilov G, Crooks JA (eds), *Biological invasions in marine ecosystems*. Ecological studies, vol 204. Springer, Berlin, Heidelberg, pp 287–304, https://doi.org/10.1007/978-3-540-79236-9_16
- Crooks JA, Khim HS (1999) Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology* 240: 53–75, [https://doi.org/10.1016/S0022-0981\(99\)00041-6](https://doi.org/10.1016/S0022-0981(99)00041-6)
- Crooks JA, Soulé ME (1999) Lag times in population explosions of invasive species: Causes and implications. In: Sandlund OT, Schei PJ, Viken A (eds), *Invasive Species and Biodiversity Management*. Kluwer Academic Publishers, The Netherlands, pp 103–125, https://doi.org/10.1007/978-94-011-4523-7_7
- Cruz J, Teodósio MA, Ben-Hamadou R, Chicharo L, Garrido S, Re P, Santos AMP (2017) RNA:DNA ratios as a proxy of egg production rates of *Acartia*. *Estuarine, Coastal and Shelf Science* 187: 96–109, <https://doi.org/10.1016/j.ecss.2016.12.028>
- Cunha AH, Assis JF, Serrão EA (2013) Seagrasses in Portugal: A most endangered marine habitat. *Aquatic Botany* 104: 193–203, <https://doi.org/10.1016/j.aquabot.2011.08.007>
- Dias E, Morais P, Antunes C, Hoffman JC (2014) Linking terrestrial and benthic estuarine ecosystems: Organic matter sources supporting the high secondary production of a non-indigenous bivalve. *Biological Invasions* 16: 2163–2179, <https://doi.org/10.1007/s10530-014-0655-8>
- Encarnaç o J, Leitao T, Morais P, Piló D, Range P, Chicharo L, Chicharo MA (2013) Effects of inter-annual freshwater inflow shifts on the community structure of estuarine decapods. *Cahiers de biologie marine* 54(2): 181–189
- Encarnaç o J, Baptista V, Teodósio MA, Morais P (2021) Low-cost citizen science effectively monitors the rapid expansion of a marine invasive species. *Frontiers in Environmental Science* 9: 752705, <https://doi.org/10.3389/fenvs.2021.752705>
- Faasse M (2018) A record of the Asian mussel *Arcuatula senhousia* (Benson in Cantor, 1842) from NW Europe (the Netherlands). *Spirula* 416: 14–15
- Fahnenstiel GL, Lang GA, Nalepa TF, Johengen TH (1995) Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* 21: 435–448, [https://doi.org/10.1016/S0380-1330\(95\)71057-7](https://doi.org/10.1016/S0380-1330(95)71057-7)
- Ferreira-Rodríguez N, Pardo I (2016) An experimental approach to assess *Corbicula fluminea* (Müller, 1774) resistance to osmotic stress in estuarine habitats. *Estuarine, Coastal and Shelf Science* 176: 110–116, <https://doi.org/10.1016/j.ecss.2016.04.017>
- Gonçalves R, Teodósio MA, Cruz J, Ben-Hamadou R, Correia AD, Chicharo L (2017) Preliminary insight into winter native fish assemblages in Guadiana estuary salt marshes coping with environmental variability and non-indigenous fish introduction. *Fishes* 2: 19, <https://doi.org/10.3390/fishes2040019>
- Hamza H, Beya Mammeria A, Bain A, De Wit R, Klein J (2022) First record of the invasive Asian date mussel *Arcuatula senhousia* (Benson, 1842) in El Mellah Lagoon (Southern coast of Algerian Basin, Western Mediterranean). *BioInvasions Records* 11: 686–699, <https://doi.org/10.3391/bir.2022.11.3.11>
- Haubrock PJ, Cuthbert RN, Ricciardi A, Diagne C, Courchamp F (2022) Economic costs of invasive bivalves in freshwater ecosystems. *Diversity and Distributions* 28: 1010–1021, <https://doi.org/10.1111/ddi.13501>
- Hoenselaar H, Hoenselaar J (1989) *Musculista senhousia* (Benson in Cantor, 1842) in the western Mediterranean (Bivalvia, Mytilidae). *Basteria* 53(4/6): 73–76
- Hosozawa T, Kunii H, Nakamura M, Ojima T, Sugiyama Y, Yamaguchi K (2020) Spatial, temporal and vertical variation of distribution and major habitats in Asian mussel (*Arcuatula senhousia*) in a brackish river along Sea of Japan. *Plankton & Benthos Research* 15: 121–131, <https://doi.org/10.3800/pbr.15.121>
- Ilarri MI, Amorim L, Souza AT, Sousa R (2018) Physical legacy of freshwater bivalves: Effects of habitat complexity on the taxonomical and functional diversity of invertebrates. *Science of the Total Environment* 634: 1398–1405, <https://doi.org/10.1016/j.scitotenv.2018.04.070>
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69: 373–386, <https://doi.org/10.2307/3545850>
- Kulikova VA (1978) Morphology, seasonal population dynamics, and settlement of larvae of the bivalve mollusc *Musculista senhousia* in Busse Lagoon (South Sakhalin). *Soviet Journal of Marine Biology* 4: 69–773

- Laughlin RA (1982) Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bulletin of Marine Science* 32(4): 807–822
- Lourenço PM, Henriques M, Catry I, Granadeiro JP, Catry T (2018) First record of the invasive Asian date mussel *Arcuatula senhousia* (Benson, 1842) (Mollusca: Bivalvia: Mytilidae) in West Africa. *Journal of Natural History* 52: 2567–2571, <https://doi.org/10.1080/00222933.2018.1545058>
- Martínez-Escarbassiere R, García JV, Pereira G, Lasso C, Alcalá OM, Capelo JC (2003) Primer registro del mejillón dátil asiático, *Musculista senhousia* (Benson, 1842) (Bivalvia: Mytilidae) especie introducida en Venezuela. *Memoria de la Fundación La Salle de Ciencias Naturales* 159–160: 309–312
- Massé C, Jourde J, Fichet D, Sauriau P-G, Dartois M, Ghillebaert F, Dancie C (2022) Northern range expansion of the Asian mussel *Arcuatula senhousia* (Benson, 1842) along the French Atlantic coasts. *BioInvasions Records* 11: 700–709, <https://doi.org/10.3391/bir.2022.11.3.12>
- Mistri M, Rossi R, Fano E (2004) The spread of an alien bivalve (*Musculista senhousia*) in the Sacca di Goro Lagoon (Adriatic Sea, Italy). *Journal of Molluscan Studies* 70: 257–261, <https://doi.org/10.1093/mollus/70.3.257>
- Morais P (2008) Review on the major ecosystem impacts caused by damming and watershed development in an Iberian basin (SW-Europe): Focus on the Guadiana estuary. *Annales De Limnologie-International Journal of Limnology* 44: 105–117, <https://doi.org/10.1051/limn:2008012>
- Morais P, Teodósio M (2016) The transatlantic introduction of weakfish *Cynoscion regalis* (Bloch & Schneider, 1801) (Sciaenidae, Pisces) into Europe. *BioInvasions Records* 5: 259–265, <https://doi.org/10.3391/bir.2016.5.4.11>
- Morais P, Teodósio J, Reis J, Chicharo MA, Chicharo L (2009a) The Asian clam *Corbicula fluminea* (Müller, 1774) in the Guadiana River Basin (southwestern Iberian Peninsula): Setting the record strait. *Aquatic Invasions* 4: 681–684, <https://doi.org/10.3391/ai.2009.4.4.14>
- Morais P, Chicharo MA, Chicharo L (2009b) Changes in a temperate estuary during the filling of the biggest European dam. *Science of the Total Environment* 407: 2245–2259, <https://doi.org/10.1016/j.scitotenv.2008.11.037>
- Morais P, Cerveira I, Teodósio MA (2017) An update on the invasion of weakfish *Cynoscion regalis* (Bloch & Schneider, 1801) (Actinopterygii: Sciaenidae) into Europe. *Diversity* 9: 47, <https://doi.org/10.3390/d9040047>
- Morais P, Gaspar M, Garel E, Baptista V, Cruz J, Cerveira I, Leitão F, Teodósio MA (2019) The Atlantic blue crab *Callinectes sapidus* Rathbun, 1896 expands its non-native distribution into the Ria Formosa lagoon and the Guadiana estuary (SW-Iberian Peninsula, Europe). *BioInvasions Records* 8: 123–133, <https://doi.org/10.3391/bir.2019.8.1.14>
- Morton B (1974) Some aspects of the biology, population dynamics, and functional morphology of *Musculista senhousia* Benson (Bivalvia, Mytilidae). *Pacific Science* 28: 19–33
- Muha TP, Chicharo L, Morais P, Pereira R, Ben-Hamadou R, Cruz J, Chicharo MA (2012) The effect of distinct hydrologic conditions on the zooplankton community in an estuary under Mediterranean climate influence. *Ecology & Hydrobiology* 12: 327–335, <https://doi.org/10.2478/v10104-012-0027-x>
- Nielsen SL, Sand-Jensen K, Borum J, Geertz-Hansen O (2002) Depth colonization of eelgrass (*Zostera marina*) and macroalgae as determined by water transparency in Danish coastal waters. *Estuaries* 25: 1025–1032, <https://doi.org/10.1007/BF02691349>
- Novais A, Souza AT, Ilarri M, Pascoal C, Sousa R (2015) Facilitation in the low intertidal: Effects of an invasive species on the structure of an estuarine macrozoobenthic assemblage. *Marine Ecology Progress Series* 522: 157–167, <https://doi.org/10.3354/meps11168>
- Nuño C, Peg M, Mellado-Díaz A, Sánchez-González JR, Toro M (2018) First record of *Synidotea laticauda* Benedict, 1897 (Crustacea: Isopoda) in the Guadiana Estuary (SW Iberian Peninsula). *Limnetica* 37: 173–179, <https://doi.org/10.23818/limn.37.14>
- Osorio MC (2013) Composición de la comunidad malacofauna asociada a sustratos duros en dos ecosistemas (zonas portuarias y zonas estuarinas), del Caribe Colombiano, primer semestre de 2010. B.S. thesis, Universidad de Bogotá Jorge Tadeo Lozano, Bogotá, Colombia, 87 pp
- Pace ML, Findlay SE, Fischer D (1998) Effects of an invasive bivalve on the zooplankton community of the Hudson River. *Freshwater Biology* 39: 103–116, <https://doi.org/10.1046/j.1365-2427.1998.00266.x>
- Pigneur L-M, Falisse E, Roland K, Everbecq E, Deliège J-F, Smitz JS, Van Doninck K, Descy J-P (2014) Impact of invasive Asian clams, *Corbicula* spp., on a large river ecosystem. *Freshwater Biology* 59: 573–583, <https://doi.org/10.1111/fwb.12286>
- Pranovi F, Franceschini G, Casale M, Zucchetta M, Torricelli P, Giovanardi O (2006) An ecological imbalance induced by a non-native species: The Manila clam in the Venice Lagoon. *Biological Invasions* 8: 595–609, <https://doi.org/10.1007/s10530-005-1602-5>
- Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83: 263–282, <https://doi.org/10.1890/13-0183.1>
- Rosa IC, Costa R, Gonçalves F, Pereira JL (2014) Bioremediation of metal-rich effluents: Could the invasive bivalve *Corbicula fluminea* work as a biofilter? *Journal of Environmental Quality* 43: 1536–1545, <https://doi.org/10.2134/jeq2014.02.0069>

- Seyer T, Morais P, Amorim K, Leitão F, Martins F, Teodosio MA (2017) On the presence of the Ponto-Caspian hydrozoan *Cordylophora caspia* (Pallas, 1771) in an Iberian estuary: Highlights on the introduction vectors and invasion routes. *BioInvasions Records* 6: 331–337, <https://doi.org/10.3391/bir.2017.6.4.05>
- Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions* 1: 21–32, <https://doi.org/10.1023/A:1010086329619>
- Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M (2013) Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution* 28: 58–66, <https://doi.org/10.1016/j.tree.2012.07.013>
- Soriano JL, Salgado SQ (2014) Primeras citas de diversos moluscos marinos alóctonos en el Delta del Ebro (Cataluña, España). *Spira* 5: 149–151
- Sousa R, Gutiérrez JL, Aldridge DC (2009) Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions* 11: 2367–2385, <https://doi.org/10.1007/s10530-009-9422-7>
- Strayer DL, Caraco NF, Cole JJ, Findlay S, Pace ML (1999) Transformation of freshwater ecosystems by bivalves: A case study of zebra mussels in the Hudson River. *BioScience* 49: 19–27, <https://doi.org/10.1525/bisi.1999.49.1.19>
- Ulman A, Ferrario J, Occhipinti-Ambrogi A, Arvanitidis C, Bandi A, Bertolino M, Bogi C, Chatzigeorgiou G, Çiçek BA, Deidun A (2017) A massive update of non-indigenous species records in Mediterranean marinas. *PeerJ* 5: e3954, <https://doi.org/10.7717/peerj.3954>
- Ventura MP, Salgado SQ, De Arenas JHN, Cano JV, Mata PR, Soriano JL (2018) Predation of the blue crab *Callinectes sapidus* Rathbun, 1896 on freshwater bivalves (Unionidae & Corbiculidae) in eastern Iberian Peninsula. *Folia Conchyliologica* 47: 3–9
- Wall CC, Peterson BJ, Gobler CJ (2008) Facilitation of seagrass *Zostera marina* productivity by suspension-feeding bivalves. *Marine Ecology Progress Series* 357: 165–174, <https://doi.org/10.3354/meps07289>
- Watson GJ, Dyos J, Barfield P, Stebbing P, Dey KG (2021) Evidence for self-sustaining populations of *Arcuatula senhousia* in the UK and a review of this species' potential impacts within Europe. *Scientific Reports* 11: 1–13, <https://doi.org/10.1038/s41598-021-86876-x>
- Willan RC (1987) The mussel *Musculista senhousia* in Australasia; another aggressive alien highlights the need for quarantine at ports. *Bulletin of Marine Science* 41: 475–489
- Yamamuro M, Hiratsuka Ji, Ishitobi Y (2010) What prevents *Musculista senhousia* from constructing byssal thread mats in estuarine environments? A case study focusing on Lake Shinji and nearby estuarine waters. *Landscape and Ecological Engineering* 6: 23–28, <https://doi.org/10.1007/s11355-009-0074-7>
- Yasser A, Naser M, Abdul-sahib I, Son M, Oliver P (2023) First record of the invasive non-native Asian date mussel *Arcuatula senhousia* (Benson 1842) (Mollusca: Bivalvia: Mytilidae) from Shatt Al-Basrah Canal, Basrah, Iraq. *BioInvasions Records* 12: 265–271, <https://doi.org/10.3391/bir.2023.12.1.22>
- Young AM, Elliott JA (2019) Life history and population dynamics of green crabs (*Carcinus maenas*). *Fishes* 5: 4, <https://doi.org/10.3390/fishes5010004>
- Young TP, Chase JM, Huddleston RT (2001) Community succession and assembly comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration* 19: 5–18, <https://doi.org/10.3368/er.19.1.5>
- Zhulidov A, Kozhara A, Son MO, Morhun H, Velde Gvd, Leuven RS, Santiago-Fandino V, Nalepa T (2021) Additional records of the bivalves *Mytilopsis leucophaeata* (Conrad, 1831) (Dreissenidae) and *Arcuatula senhousia* (Benson, 1842) (Mytilidae) in the Ponto-Caspian region. *BioInvasions Records* 10: 119–135, <https://doi.org/10.3391/bir.2021.10.1.14>