Received: 7 June 2022 | Revised: 24 December 2022 | Accepted: 18 January 2023

DOI: 10.1111/maec.12738

RESEARCH ARTICLE

marine ecology WILEY

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

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Funding information
Fondazione di Sardegna and Regione Autonoma della Sardegna

Abstract

The alien Asian date mussel *Arcuatula senhousia* inhabits several coastal environments worldwide. This species can form dense mats where individuals attach through byssus threads, thus altering the structure, functioning and biodiversity of the native communities. We investigated the feeding preference of different predators on this alien species in a Mediterranean coastal lagoon. To do this, a mesocosm experiment was conducted using two crab species (the Mediterranean green crab *Carcinus aestuarii*) and the Say mud crab *Dyspanopeus sayi*, and one gastropod, the banded dye-murex *Hexaplex trunculus* as predators of *A. senhousia* with or without byssus mats. Our data suggest that *C. aestuarii* is a more effective predator against *A. senhousia* than *D. sayi*, and that *H. trunculus* is almost ineffective. A possible implication of this result is the potential use of the native crab *C. aestuarii* for limit the formation of the byssus mats, thus mitigating their potential negative effects on the native communities.

KEYWORDS
alien species, biocontrol, biological invasions, coastal lagoon, Mediterranean Sea, predation

1 | INTRODUCTION

The introduction rate of alien species, including invasive ones, has increased globally during the last decades, to the point that invasive alien species currently represent one of the most important drivers of global biodiversity change (IPBES, 2019; Pyšek et al., 2020). Invasive alien species (IAS), indeed, can modify, directly or indirectly, the structure and composition of native communities and trophic webs (Occhipinti-Ambrogi, 2021), impairing ecosystems' functions and services (Katsanevakis et al., 2014; Pusceddu et al., 2016; Rizzo et al., 2017) and ultimately, causing severe economic issues (Cook et al., 2007).

Spreading of marine IAS can be promoted by natural or anthropogenic disruption of physical barriers (Galil et al., 2015), active transport for commercial purposes (Katsanevakis et al., 2013), passive transport (e.g., ballast waters) (Hulme, 2009) and climate change (Hulme, 2017). In marine ecosystems, due to the limited or absent physical barriers to invasion and the conceivable operational difficulties, IAS eradication after their settlement and expansion tend to be complex, sometimes even almost impossible. Thus, any new and environmentally safe management protocol represents a step forward IAS contention and slowdown of their impacts (Kinsley et al., 2022). For these reasons, prevention and control of IAS spread have become priority tasks for legislators, environmental managers, policy and decision-makers and maritime space planners (Giakoumi et al., 2016).

The Asian date mussel *Arcuatula senhousia* (Benson in Cantor, 1842), native to the Western Pacific (from the Siberian coasts to the Malay Peninsula), has been introduced in numerous localities worldwide, such as New Zealand and Australia (Willan, 1985, 1987), USA (Carlton, 1979; Dexter, 1983; Kincaid, 1947), European Atlantic coasts (Bachelet et al., 2009; Barfeld et al., 2018; Faasse, 2018), West Africa (Lourenço et al., 2018) and the Azov-Black Sea Basin (Kovalev et al., 2017; Micu, 2004). This species entered the Mediterranean Sea as a Lessepsian migrant from the Red Sea in the 1960s, with the first records reported from Israel and Egypt (Barash & Danin, 1971). In 1982, *A. senhousia* was recorded in a French lagoon near Marseille, from which it colonized the surrounding marine area (Hoenselaar & Hoenselaar, 1989). *A. senhousia* was found for the first time in Italy in 1993, along the northern Adriatic coasts (Bucci, 1994; Lazzari & Rinaldi, 1994). Successively, this species was recorded in other areas along the Italian coasts (Brancato & Reitano, 2009; Campani et al., 2004; Margelli et al., 2004; Mastrototaro et al., 2003; Solustri et al., 2003; Ulman et al., 2017).

Arcuatula senhousia was recorded in Sardinia for the first time along the north-eastern coast in the 1990s (Savarino & Turolla, 2000). Sardinian populations of *A. senhousia* have possibly been introduced with cultured mussels *Mytilus galloprovincialis* Lamarck, 1819, which are imported from the northern Adriatic (Mistri et al., 2004). Successively, the species was found in the south (Delongueville & Scaillet, 2006) and west coasts of Sardinia (Gulf of Oristano, Cannas, 2010). In 2010, the species was recorded for the first time in the Santa Gilla lagoon (South Sardinia, Atzori et al., 2013; Cabiddu et al., 2014).

Arcuatula senhousia is a fast-growing organism that could live attached with byssal threads to different hard substrates or semi-buried in the intertidal and shallow subtidal soft sediments of bays, estuaries and lagoons (Como et al., 2018; Crooks, 1996; Mistri, 2002). This species could create large and dense mats, made of individuals and their byssus. These mats can alter the hydrodynamic features on flat bottoms, thus favouring the trapping and deposition of suspended fine particles (Crooks, 1998; Crooks & Khim, 1999). Large mats of *A. senhousia* can indeed suffocate the hosting substrate, isolating the benthos from the overlying water column (Yamamuro et al., 2010). Moreover, *A. senhousia*, being an efficient suspension feeder (Sgrò et al., 2005), can severely reduce the food available for native suspension feeder bivalves, hence possibly promoting interspecific competition for resources (Crooks, 2001). On the other hand, byssal mats created by *A. senhousia* act as novel structures that can enhance habitat heterogeneity, offering shelter for different benthic organisms (Mistri, 2003, 2004a; Mistri et al., 2004; Munari, 2008; Katsanevakis et al., 2014).

To the best of our knowledge, very few studies provided insights on how controlling the growth of the populations of this mussel (Australian Government, 2008). In this regard, the Australian control plan for this species identifies the possible use of several options including manual eradication, chemical treatments, mechanical suffocation and biological controls using genetically modified sterile individuals or natural predators. Any mechanical action aimed at eradicating this species, such as raking or scraping, is extremely time and labour-consuming; moreover, the large mats of this bivalve, if removed either manually or mechanically (e.g. by dredges), are easily fragmented, and the detached individuals can spread to form new populations (Otero et al., 2013). Previous studies suggested that predators, by enhancing the resistance of the recipient native community, could contribute to the prevention of *A. senhousia* invasion at the local scale (Kushner & Hovel, 2006; Marshall, 2009; Reusch, 1998; Yamamuro et al., 2010). For instance, in Southern California (USA), the abundance of *A. senhousia* is locally controlled through a native predator, the muricid snail *Pteropurpura festiva* (Hinds, 1844), which is responsible for a significant mortality in populations of this IAS.

Arcuatula senhousia has invaded the Santa Gilla lagoon (south Sardinia) at an extent that byssus mats are now seasonally provoking constraints to the fishing operation of the bivalve molluscs *Ruditapes decussatus* (Linnaeus, 1758) and *Ruditapes philippinarum* (Adams & Reeve, 1850).This study investigated in mesocosm the feeding rates of three local predators on the invasive alien Asian date mussel, as a knowledge base for the possible use of predators to mitigate the spreading and local impacts of *A. senhousia* in Mediterranean lagoon environments. Our null hypotheses were: (1) prey mortality rates and injury levels would be similar among different predators; (2) predation rates are not affected by the presence of byssus; and (3) different predators do not show a specific food preference for specific prey size classes.

2 | MATERIALS AND METHODS

2.1 | Study area

The Santa Gilla lagoon (southern coast of Sardinia; Tyrrhenian Sea) covers an area of about 1300 ha and is close to the densely populated urban area of Cagliari (ca. 500,000 inhabitants). The Santa Gilla lagoon is one of the most important wetlands in Sardinia, being classified as Special Protection Area (Directive 79/409/EEC), Wetland of International Importance under the Ramsar Convention (DM 03/09/1980) and Special Area of Conservation (ITB040023, Habitats Directive 92/43/EEC). The lagoon opens to the sea through a channel in its southernmost part and receives two freshwater inflows in its northernmost part. The average depth is 1 m (maximum depth 2 m in the artificial channel). The sediments are mainly sandy-silty in the whole lagoon, with a purely muddy area located in the northern part (Degetto et al., 1997; Frontalini et al., 2009). The Santa Gilla lagoon is an important area for artisanal fisheries, commercial harvesting of mollusc bivalves, like *R. decussatus*, *R. philippinarum* and *Cerastoderma glaucum* (Bruguière, 1789) and farming of the mussel *M. galloprovincialis* and oyster *Magallana gigas* (Thunberg, 1793).

2.2 | Experimental design and data analysis

For this study, three species of predators already present in the lagoon were chosen: the muricid gastropod *Hexaplex trunculus* (Linnaeus, 1758), the Mediterranean green crab *Carcinus aestuarii*

Nardo, 1847 and the mud crab *Dyspanopeus sayi* (Smith, 1869), recently recorded in this lagoon (Cabiddu et al., 2020).

To test the potential feeding rates of the three predators for the alien Asian date mussel *Arcuatula senhousia*, a replicated ($n = 3$) experiment with two orthogonal factors was conducted. The first factor (predator) included four fixed levels: the three predator species and a reference with no predators. The second factor (prey) included two fixed levels: presence vs. absence of the byssus mats produced by the alien Asian date mussel. The response variables included the short-term prey mortality rate (i.e. the number of prey individuals that were found dead after 24 h) and the injury rate (i.e. the number of individuals with signs of damage after 24 h).

Specimens of *A. senhousia* were collected in the Santa Gilla lagoon using a shellfish rake (hand-operated dredge) and acclimatized in the laboratory at in situ temperature and salinity for 10 days. Specimens of *H. trunculus*, *D. sayi* and *C. aestuarii* were collected using fishing traps 4 days prior to the experiment start. During those 4 days, the predators were acclimatized in the laboratory at in situ temperature and salinity and maintained in separate tanks without food, to standardize their feeding status.

The experiment was carried out in an ad-hoc built system including 24 15-L PVC tanks. The tanks were arranged in series of three and filled with water derived from a recycling tank, continuously refilled directly from the adjacent S. Gilla lagoon.

At the beginning of the experiment, 100 preys, previously measured (Total Length, TL in mm) with a calliper, were placed in a corner of each tank and one predator at its centre. A non-parametric Kruskal-Wallis's test confirmed the absence of significant differences in the medians size of the preys among all tanks ($p > .05$) (Kruskal & Wallis, 1952). Presence vs. absence of predators' levels was assigned to the different tanks following a random extraction. After 24 h, predators were removed, and the preys, classified as "intact" (without any visible sign of damage), "injured" (shell visibly damaged by predators) or "eaten" (shell fragments).

Differences in the mortality rates of preys with and without byssus were tested, separately for each predator, with non-parametric Mann Whitney paired tests (Mann & Whitney, 1947). Since these differences were not significant, a Kruskal-Wallis's test was also used to assess differences in predating efficacy (in terms of prey mortality rates) among the three predators.

The size-frequency distribution of prey specimens was assessed at the beginning and at the end of the experiment. The two-sample Kolmogorov–Smirnov (K–S) test was used at the beginning of the experiment, to verify the null hypothesis of not significant differences among size distributions of prey offered to the three predators (Smirnov, 1939). The same test was used also to verify the null hypothesis of not significant differences in the prey size distribution (with or without byssus) before and after the exposure to each predator.

3 | RESULTS

During the experiment, temperature, pH, dissolved oxygen and salinity, measured with a multiparametric probe (Hanna Instruments HI9828), ranged 12.0–14.7°C, 8.2–8.4, 6.0–8.5 mg L^{-1}, 26.5–27.4, respectively.

To avoid possible biases associated with the gender or the moulting process, only uninjured male individuals without signs of moulting were retained and subsequently used as predators. Both predator crabs were larger than their respective size at first sexual maturity (Mori et al., 1990; Strieb et al., 1995), with an average carapace width (CW, measured as the distance between the tips of the two most distal marginal teeth) of 20.87 ± 1.11 mm and 36.37 ± 1.75 mm for *D. sayi* and *C. aestuarii*, respectively. The muricid specimens had an average height of 60.03 ± 2.41 mm and unknown sex.

Prey size distribution in control tanks and tanks containing the predators (Table S1) and prey mortality rates during the experiment (Table S2) are reported in Supplementary Material.

In the control tanks (devoid of predators), the mortality rates of mussels with and without byssus were nihil during the entire duration of the experiment. Whichever the predator, the mortality rates did not vary significantly ($p > .05$) between preys with and without byssus (*H. trunculus*: 0.7 ± 0.7% and 4.3 ± 1.9%; *D. sayi*: 21.3 ± 3.8% and 38.7 ± 5.7% and *C. aestuarii*: 64.0 ± 21.0% and 85.7 ± 6.8%) (Figure 1). Overall, prey mortality rates caused by *C. aestuarii* (on

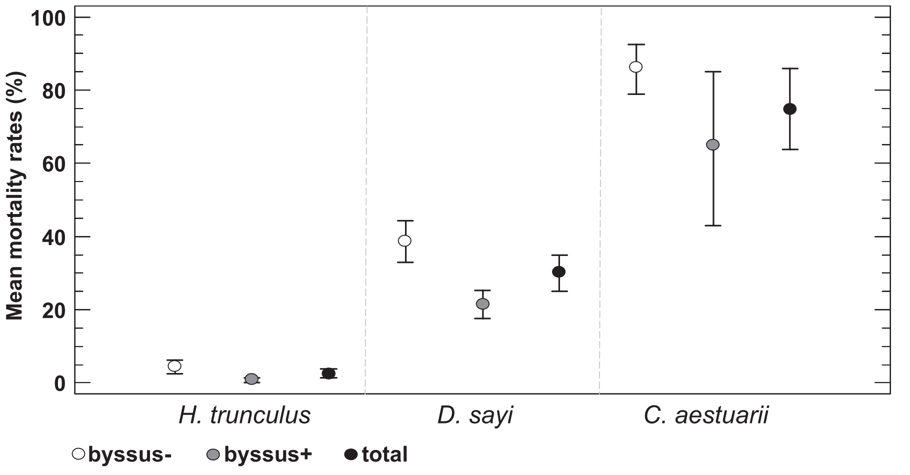

FIGURE 1 Mean mortality rates (± standard error) of *Arcuatula senhousia* without byssus, with byssus and total exposed to *Hexaplex trunculus*, *Dyspanopeus sayi* and *Carcinus aestuarii*.

average 74.8 ±11.0%) were significantly higher than those caused by *D. sayi* (30.0 ±4.9%) and *H. trunculus* (2.5 ±1.2%) (Figure 1). After 24 h of exposure to predators, only minor fractions of uneaten preys (0.3%, 8.5% 0.3% for *H. trunculus*, *D. sayi* and *C. aestuarii*, respectively) showed signs of predators' attack (injured).

Before the exposure to the predators, the size-frequency distributions of *A. senhousia* did not vary significantly between tanks (K-S Test, *p*-value >.05). In control tanks, the size-frequency distributions of *A. senhousia* either without or with byssus did not vary during the experiment (Figure 2a,b). The size-frequency distribution of prey, either in presence or absence of the byssus, did not vary during the experiment carried out with *H. trunculus* (Figure 2c,d). The size-frequency distribution of prey exposed to *D. sayi* did not vary during the experiment conducted with byssus-free individuals, whereas prey with byssus and larger than 9 mm became less frequent after the exposure to the predator (Figure 2e,f). The exposure of prey to *C. aestuarii*, either in the absence or presence of the byssus, determined a significant change of prey size distribution, characterized by the almost complete disappearance of prey with a size >10 mm (Figure 2g,h).

4 | DISCUSSION

The invasive alien Asian data mussel *A. senhousia* often becomes part of the species' diet in the invaded areas (Reusch, 1998). Although a variety of species can eat *A. senhousia* (Crooks, 2002), only few studies compared the effects of different local predators on this invasive alien mussel (Crooks, 2002; Reusch, 1998; Yamamuro et al., 1998). Those studies, moreover, were mostly focused on the interactions between alien and native predators, rather than on their feeding rates or preference for the Asian date mussel. To provide insights on this gap of knowledge, this study was carried out to assess the feeding rates of different predators on the Asian date mussel, with the ultimate aim of providing a first contribution to the knowledge needed to use predation to limit the local spreading and impacts of this IAS in the Santa Gilla lagoon and, possibly, in other Mediterranean lagoons.

At a first glance, our results do not support the (null) hypothesis by which mortality and injury rates of the prey do not vary among the three predator species. *C. aestuarii*, indeed, consumed significantly

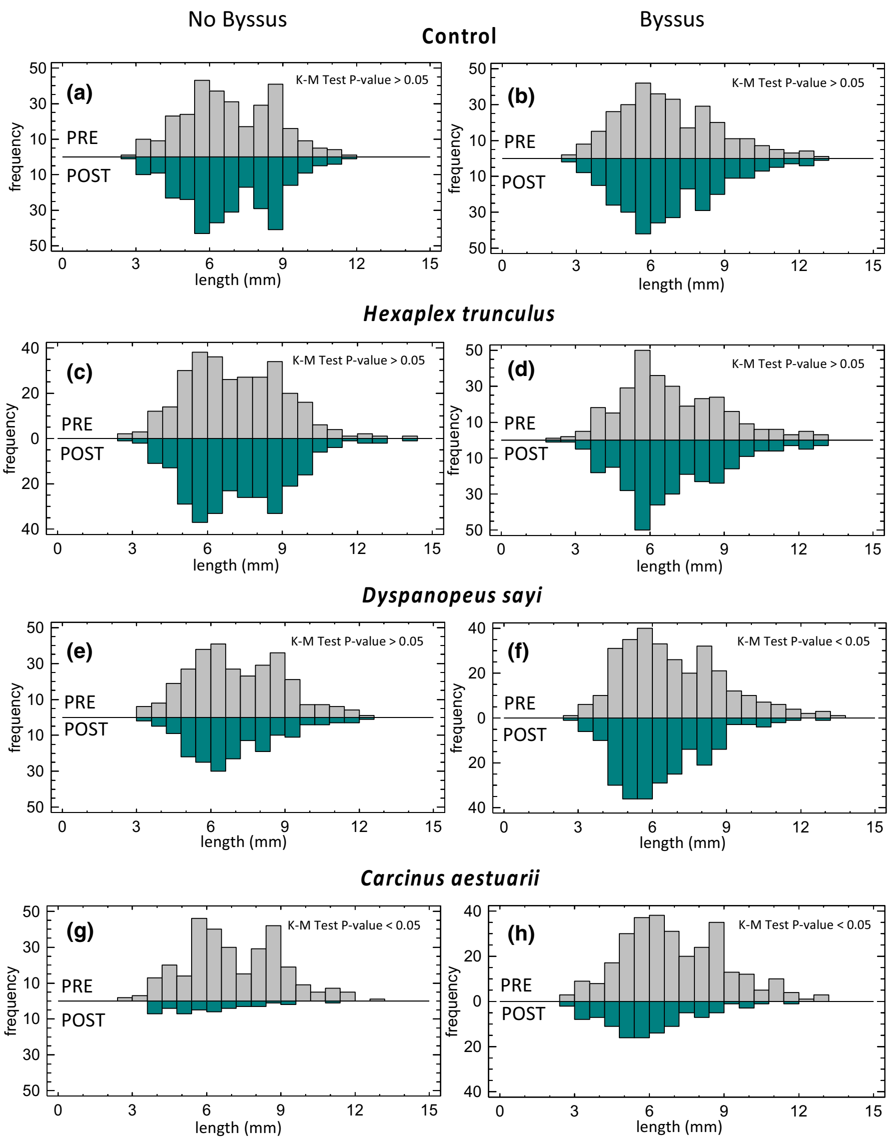

FIGURE 2 Size-frequency distributions of *Arcuatula senhousia* without (left panels) and with (right panels) byssus, at the beginning (pre) and after (post) the experiment in control tanks (devoid of predators; a, b), and in tanks with *Hexaplex trunculus* (c, d), *Dyspanopeus sayi* (e, f) and *Carcinus aestuarii* (g, h).

more prey individuals then *D. sayi* and *H. trunculus*, whereas *D. sayi* damaged mussel shells more than the two other species.

On the one hand, we report here that the muricid *H. trunculus*, even when the unique source of food offered during the experiment was the invasive alien mussel, fed on a relatively low number of prey individuals, suggesting that this species is not an effective predator against *A. senhousia*. This result agrees with previous findings showing that *H. trunculus*, although being an opportunistic and generalist predator (Rilov et al., 2004; Sala, 1997), fed on a relatively low number of bivalve molluscs (Peharda & Morton, 2006). Even adult specimens of *H. trunculus* (50–60 mm shell height) eat only few mussels per day (0.01 juvenile *B. pharaonis* d^{-1} and 0.03 large *M. galloprovincialis* d^{-1}) (Peharda & Morton, 2006; Rilov et al., 2004). Nonetheless, since *H. trunculus*, as other muricids such as *Stramonita haemastoma* (Linnaeus, 1767), has a peculiar group foraging behaviour (Brown & Alexander, 1994; Güler & Lök, 2016, 2019; Peharda & Morton, 2006; Taylor & Morton, 1996), we cannot a priori exclude that the exposure of the prey to multiple individuals of this muricid could exert significant effects on the Asian date mussel populations.

Moreover, we cannot exclude that many other factors, uncontrolled in our experiment, can be invoked to explain the low predation attitude of *H. trunculus* on the invasive Asian date mussel: the size of the offered prey could have been too small, the hunger level of the muricid predator could have been not high enough at the time of the experiment, the duration of the experiment could have been too short to let *H. trunculus* to feed efficiently on the offered prey. Nevertheless, previous studies, although based on different prey species, reported that the attacks by *H. trunculus* on small specimens of the mussel *Brachidontes pharaonic* (Fischer, 1870) (5–10 mm shell length) were completed in <4 h (Rilov et al., 2004). Also, Chatzinikolaou et al. (2019) proved that ca. 45% of 10 days-fasted *H. trunculus* successfully reached the offered food items in <1 h. Considering that the prey individuals used in our experiment had a length <15 mm and the shell of *A. senhousia* is more fragile than that of other mussels, we contend here that the duration of our experiment (24 h) could have not been an interfering factor.

On the other hand, our results suggest that both the crabs *C. aestuarii* and *D. sayi* appear to be effective predators of *A. senhousia* individuals, either offered with or without the byssus, as no significant statistical differences in prey mortality rates with vs. without byssus were observed. Both crabs fed on prey individuals with a size comprised, mostly between 9 and 15 mm TL, that can be classified as medium-small individuals, as the maximum shell length of this species is ca. 35 mm (Crooks, 2002). This result agrees with previous studies showing that predating crabs have a marked preference for small molluscs (Juanes, 1992; Smallegange et al., 2008; Smallegange & van der Meer, 2003; Uzkiaga et al., 2022). For instance, *D. sayi* was found to be more efficient in predating medium-small (15.0–25.0 mm TL) than large (25.1–30.0 mm TL) individuals of *A. senhousia* (Mistri, 2004b). This feeding choice might be partially explained by an energetic trade-off: large shells would in fact require larger energetic costs by the predator, and this would also increase the probability of damage of the predator claws (Juanes, 1992), thus, ultimately, reducing their foraging efficiency (Juanes & Smith, 1995).

Our results revealed also that *C. aestuarii* is some twice more effective in predating *A. senhousia* than *D. sayi*. Considering that *D. say* is an alien species, this result would strongly support the potential use of the native *C. aestuarii* to control *A. senhousia* spreading and impacts, at least in the study area. Our results agree with a previous study showing that a strong predation of *C. aestuarii* on the Asian date mussel might conspicuously contribute to limit the production of the byssus mats and, consequently, to reduce the cost of manual removal (Mistri, 2004c). However, since the biological control of an alien species through its natural predators could be limited by the effects that the same predators can have on other native populations, caution must be paid to assess whether the predator's food choice is preferentially directed towards the alien species more than towards the native ones. Indeed, crabs of the genus *Carcinus* are aggressive feeders due to their voracious predation on other invertebrates (McDonald et al., 2001), with a strong preference for molluscs, especially bivalves (Young & Elliot, 2020). Moreover, native populations of *Carcinus maenas* can have devastating effects on commercial mussel beds (Dare & Edwards, 1976), reduced the density of *Cerastoderma edule* (Jensen & Jensen, 1985; Linnaeus, 1758) and *Macoma balthica* (Linnaeus, 1758; Richards et al., 1999). In this regard, although we did not test the predator's food preference for alien vs. native species, previous studies demonstrated that *C. aestuarii* has a marked preference for *A. senhousia* over the naturalized clam *Ruditapes philippinarum* (Mistri, 2004c). Accordingly, we could conclude that our results support the possible use, through rearing or re-stocking activities of *C. aestuarii* to control *A. senhousia* in the Santa Gilla Lagoon, at least till the alien bivalve will dominate the molluscan fauna.

We notice also that the common crab *C. aestuarii* itself is a species of commercial importance for the local economy. Indeed, it is a common fish food and is also used as a fish bait and feed stock for reared shrimps. Therefore, we contend that a mitigation strategy of *A. senhousia* impacts in the lagoon using new rearing activities of the common crab *C. aestuarii*, especially in the mostly invaded areas of the lagoon, could rise a double advantage: on the one hand, limiting the diffusion and spreading of the alien mussel and, on the other one, stimulating crab aquaculture in the lagoon.

Based on the results of our study, we also think that, among the easy-to-apply measures to control *A. senhousia* spreading in the S. Gilla lagoon, the suspension of crab fisheries in the most invaded areas could limit the development of this invasive alien mussel. Moreover, the implementation of native crabs' abundance with young small-sized individuals during periods in which the juvenile molluscs dominate could limit the formation of the byssus mats, thus mitigating their potential negative effects on the availability of space and oxygen for commercially important clams (Mistri, 2004c). Nevertheless, even assuming as valid the option of enhancing crabs' populations to mitigate the impacts of *A. senhousia* in the lagoon, a special effort should be paid to the choice the sites for, eventually, re-stocking reared crabs.

Finally, we must notice also that this study represents only a first step towards the adoption of a biological control strategy to limit the Asian date mussel impacts in the Santa Gilla lagoon and, possibly, in other invaded lagoons. For instance, based on the results of our experiment, we cannot exclude possible ecological consequences of such an approach as we do not know yet the effects of the interactions between predators in the invaded environment. Moreover, multiple predators may indeed have unexpected effects which cannot be predicted using data from experiments carried out with one predator at time (Chattopadhyay & Baumiller, 2007; Wong et al., 2010).

Although the use of native predators appears a promising option, more studies dealing with the ecological traits of this invasive alien species in lagoon environments, the performance of multiple predators and the associated consequences on the whole benthic communities are still needed to make a prototypal approach an effective nature-based solution.

AUTHOR CONTRIBUTIONS

Conceptualization, S.C., A.P.; data analysis, S.C., A.P.; writing—original draft preparation, S.C.; writing—review and editing, S.C., P.A., F.P., A.P.; funding acquisition, A.P. All authors have read and agreed to the published version of the manuscript.

ACKNOWLEDGEMENTS

The authors acknowledge help and collaboration kindly provided by the Consorzio Ittico Santa Gilla during sampling activities. This research is part of the project "Impact of Invasive Alien Species on Sardinian ecosystems" (CUP: F72F16003100002) funded by Fondazione di Sardegna and Regione Autonoma della Sardegna. Open Access Funding provided by Universita degli Studi di Cagliari within the CRUI-CARE Agreement.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data presented are all available in the Supplementary Material.

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How to cite this article: 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*, *00*, e12738. https://doi.org/10.1111/maec.12738