




Population dynamics of the potentially invasive Asian date mussel, *Arcuatula senhousia*, in Arcachon Bay, France

Xavier de Montaudouin^a, Léa Baudot^a, Guillaume Bernard^c, Hugues Blanchet^a, Cécile Masse^b, Marie P.A. Fouet^{a,*} 

^a Université de Bordeaux, CNRS, EPOC, EPHE, UMR 5805, Station Marine d'Arcachon, 33120, Arcachon, France

^b Patrimoine Naturel (PatriNat), OFB, MNHN, CNRS, IRD, 75005, Paris, France

^c IFREMER, LER Arcachon-Anglet, 33120, Arcachon, France

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ABSTRACT

Originated from Asia, *Arcuatula senhousia* has spread globally and is often reported as an invasive species that alters benthic communities and ecosystem functioning. However, very few studies have focused on the population dynamics of this ecosystem-engineering mytilid, partly due to the difficulty in monitoring cohorts of this short-lived, fast-growing species. Through a one-year monthly monitoring of mussel in two distinct locations in Arcachon Bay, France, we observed higher growth performance and P/B ratio at the station closer to the main river mouth, confirming the species preference for brackish, estuarine conditions. Post-recruitment mortality was particularly high, exceeding typical bivalve mortality rates, likely due to the vulnerability of this small species at the sediment surface. Trematode parasites, absent in our samples, were not implicated in mortality. In both locations, the reproductive phenology was similar, with a prolonged spawning season centred in the warmer months. As of 2024, *A. senhousia* remains a colonizing introduced species in Arcachon Bay with relatively low densities. However, vigilance is necessary, as its population dynamics resemble those observed in the few areas where these data are available and where this species has become invasive.

1. Introduction

Non-indigenous species (NIS) are recognized as major threats to marine diversity (Anton et al., 2019). By establishing at new habitats, they can alter community structure and ecosystem functioning (Katsanevakis et al., 2014). Mussels, in particular, tend to form dense aggregations by attaching to the substrate with byssal threads, often functioning as ecosystem engineers (Buschbaum et al., 2009; Jones et al., 1994). The Asian date mussel, *Arcuatula senhousia*, originating from Asia, has spread globally and continues to be recorded in new locations (Encarnação et al., 2024; Yasser et al., 2023). In Western Europe, this invasion has impacted both the Mediterranean Sea (Fortic et al., 2023) and the Atlantic Ocean (Massé et al., 2022). Indeed *A. senhousia* can severely alter the colonized ecosystem by creating reefs which can modify the habitat's architectural structure (Crooks and Khim, 1999) and thus, accumulate fine sediment, disturb biogeochemical and nutrient cycling (Bernard et al., 2020; Takenaka et al., 2018) and create changes in community structure (Crooks, 1998).

In Arcachon Bay, a lagoon in southwestern France, the presence of *A. senhousia* has been documented since 2002 (Bachelet et al., 2009), possibly resulting from a secondary introduction from a Mediterranean lagoon (Hoenselaar and Hoenselaar, 1989). After a 20-year lag time, the abundances of this species have increased considerably since 2018 (Coignard et al., in press). Due to its potential impact on associated communities (Como et al., 2018; Mistri et al., 2004; Munari, 2008) and ecosystem functioning (Bernard et al., 2020), monitoring the population dynamics of this species in the lagoon is essential. Overall, few studies have examined the population dynamics of this species based on year-round surveys (Mistri, 2002; Takenaka et al., 2016); research has largely focused on individual growth and reproductive phenology, often in separate studies (Allen and Williams, 2003; Crooks, 1996; Mastroiuto et al., 2003; Morton, 1974; Sgro et al., 2002; Watson et al., 2021).

In our study, we monitored *A. senhousia* populations in Arcachon Bay over the course of a year, at two stations with contrasting environmental conditions in terms of freshwater influence. The underlying objective

* Corresponding author.

E-mail address: marie.fouet@u-bordeaux.fr (M.P.A. Fouet).

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was to determine the population dynamics, including the Von Bertalanffy Growth Function (L_{∞} and K), mortality constant (Z), production (P), and P/B ratio, as well as reproductive phenology through the condition index and gonad maturity staging. This was done so as to determine if the population dynamics observed for *A. senhousia* in Arcachon Bay support a sustainable population which aligns with patterns seen in invasive populations of this species, at other locations globally.

2. Material and methods

2.1. Study area

Arcachon Bay is a 180 km² lagoon in the southwest of France. The inner lagoon comprises 110 km² of mudflats, which are covered by a large *Zostera noltei* seagrass beds. Arcachon Bay receives freshwater input primarily from the Leyre River and marine water through channels located at the southwest end of the lagoon. These oceanic and freshwater inputs, along with the slow renewal driven by tides, create salinity and temperature gradients within the bay. Water salinity and sediment temperature vary from 4 to 35, and from -2 to 44 °C, respectively (Dang et al., 2008). The sediment composition ranges from mud to muddy sands. *A. senhousia* specimens were collected monthly, during 12 sampling trips, from March 2023 to March 2024 at two stations in Arcachon Bay: Gujan ($44^{\circ}38'58''\text{N}$, $1^{\circ}06'50''\text{W}$) and Arès ($44^{\circ}44'52''\text{N}$, $1^{\circ}07'49''\text{W}$) (Fig. 1), both situated at an approximate tidal level of 2 m. Gujan and Arès belong to two distinct sub-areas, with Gujan being more influenced by continental conditions due to its proximity to the main river input (Fig. 1), compared to Arès (Binias et al., 2014). Both stations are characterized by a sandy-muddy sediment, but Gujan is sandier than Arès (mud content, Gujan: $61\% \pm 23$, Arès: $73\% \pm 14$; D50, Gujan: 76 ± 116 , Arès: 21 ± 13).

2.2. Growth

At each sampling occasion, and each station, six cores (15×15 cm, surface = 225 cm², ~10 cm deep) were collected randomly within mussel patches and sieved through a 1 mm mesh. In the laboratory, mussels were sorted, counted, and their shell heights were measured

with a calliper. Shell height histograms were constructed monthly for each station. From the size histograms, height–frequency data were analyzed using FISAT II software (Gayaniilo et al., 2005). To analyze growth, a Modal class Progression Analysis was performed. Bhattacharya's method was used to identify cohorts by decomposing the polymodal size distribution into its normal distribution components. Cohorts were considered distinct if they had a separation index greater than 2. The temporal series of the average height for each modal group (cohort) was used to estimate the growth parameters of the von Bertalanffy Growth Function (VBGF) using the Appeldoorn method (Gayaniilo et al., 2005).

$$H_t = H_{\infty} \times [1 - e^{(-K \times t)}]$$

where H_{∞} is the asymptotic shell height (mm) and K is the growth coefficient (yr⁻¹).

The negative correlation between H_{∞} and K makes comparisons based on individual parameters unreliable (Pauly and Munro, 1984). Therefore, it is more appropriate to compare the growth performance of bivalve population using the growth performance index Φ' (Valikey, 1990). The estimates H_{∞} and K were used to calculate the growth performance index Φ' (Pauly et Munro, 198) using the equation:

$$\Phi' = 2 \times \log_{10}(H_{\infty}) + \log_{10}(K)$$

2.3. Reproduction

Since first maturity is achieved at a shell height of 14–16 mm (Mistri, 2002), only mussels with a shell height greater than 12 mm were dissected. During dissection, the stage of gonad development was estimated under a stereomicroscope, following a maturation scale ranging from 0 to 3 (Sgro et al., 2002). At stage 0, the gonad is translucent, and the sex cannot be identified. In stage 1, the gonads are translucent to whitish, indicating the early stages of maturation, sex cannot be identified. The gonads of mussels in stage 2 are more mature, and the sex is detectable. In stage 3, the gonads are fully mature, with distinct colours, whitish for males and orange for females.

Additionally, Condition Index (CI , in ‰), which provides information on gametogenesis (indicated by an increase in CI) and spawning

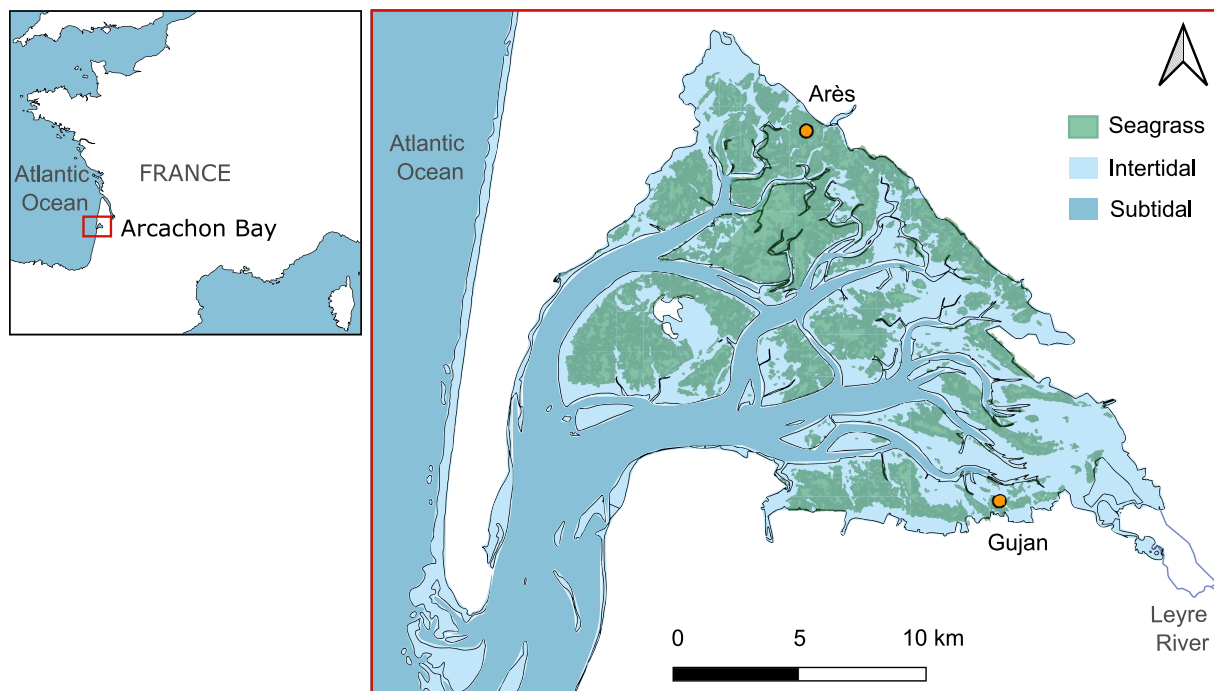


Fig. 1. Localization of Arcachon Bay and the two sampling sites, Arès and Gujan. Seagrass data are providing by Rigouin et al. (2022).

events (indicated by a decrease in CI), was evaluated (Walne and Mann, 1975). Each month, 20 individuals with a shell height greater than 20 mm were sampled from each station, retrieved from the cores. The CI was calculated using the following formula:

$$CI = \frac{[Flesh\ dry\ weight\ (in\ g)]}{[Shell\ dry\ weight\ (in\ g)]} \times 1000$$

2.4. Mortality

The number of individuals in each cohort was insufficient to estimate mortality through the decline in cohort abundance. Therefore, the instantaneous total mortality coefficient (Z) was estimated based on the 1-year population structure monitoring at Arès and Gujan. This approach used the height-converted catch curve method available in the FISAT II software (version 1.2.2, FAO-ICLARM) and the single negative exponential mortality model (Gayaniilo et al., 2005). The height of pooled height-frequency samples were converted into ages using the parameters of the VBGF. Mortality was then calculated through linear regression analysis using the following equations:

$$N_t = N_0 \times e^{-Z \times t}$$

$$dN / dt = -Z \times t$$

where N_0 is the number of individuals at relative age 0, and t represents the age of the mussels.

2.5. Parasitism

Trematode parasites were examined in ten adult individuals retrieved from the cores, with a shell height greater than 20 mm, per station each month. Each mussel was dissected, and the flesh was placed between two glass slides, gently squeezed, and observed under a stereomicroscope.

2.6. Biomass, production and productivity

As with the mortality assessment, the number of individuals in each cohort was insufficient to calculate somatic production by cohort. Therefore, the annual mean biomass, annual somatic production, and the P/B ratio were evaluated from the population size structure monitoring for mussel populations at Arès and Gujan. The VBGF parameters (K and H_∞) used were those previously obtained (see Growth section). To calculate production and biomass, station-specific relationships between shell height and dry flesh weight were estimated. Mussels ranging in size from 6 to 39 mm were selected, and their dry flesh weight (48 h at 60 °C) and shell height were measured, resulting in the following equation:

$$\log_{10}(SFDW) = -5.1739 + 2.77 \times \log_{10}(H)$$

where SFDW is the shell-free dry weight (g), and H is the shell height (mm). The equation was based on 2026 observations, with an R^2 value of 0.91.

The mean annual biomass B (g SFDW. m^{-2}) was calculated using the following equation:

$$B = \sum (N_i \times M_i)$$

where N_i is the mean number of animals per m^2 , and M_i is the mean individual somatic mass in size class i .

Total annual production P (g SFDW. m^{-2} . yr^{-1}) was calculated using the mass-specific growth rate method (Brey, 2001) based on the size-mass relation, the VBGF, and the pooled size-frequency distribution:

$$P = \sum (N_i \times M_i \times G_i)$$

where G_i is the mass-specific growth rate (yr^{-1}), represented by:

$$G_i = b \times K \times (H_\infty - H_i) / H_i$$

In this equation, $b = 2.77$ is the specific constant of the size-mass relation, K and H_∞ , are the VBGF parameters and H_i is the mean height of class i .

The annual P/B ratio of *A. senhousia* populations was evaluated at each station using the annual total production and the annual mean biomass.

3. Results

In total, 1282 individuals were collected over the whole year of sampling in Gujan, and 1753 in Arès. In Gujan, density within mussel patches fluctuated between 200 and 1200 $ind.m^{-2}$, while these values were higher in Arès, and ranged from 320 to 2300 $ind.m^{-2}$. The population structure was similar to what has been observed in other monitoring efforts, showing a unimodal distribution in most cases, with no clear recruitment period but rather sporadic recruitment events, including some unsuccessful ones.

3.1. Growth

Shell growth was faster in Gujan ($\Phi' = 3.27$) than in Arès ($\Phi' = 2.90$) (Table 1). After one year, based on the site-specific Von Bertalanffy growth function, mussels in Gujan could reach a size of 27 mm, while those in Arès only grew up to 18 mm.

3.2. Reproduction

At both stations, the maximum of the mean CI occurred in summer, ranging from 130 to 140 ‰ (June–August), coinciding with the peak of fully mature individuals (Fig. 2). The gradual decrease in CI between July and December–January suggests a relatively long spawning period. After the peak, the minimum CI value was higher in Gujan (90 ‰) compared to Arès (60 ‰). The minimum shell height at which stage 3 maturity was observed was 12 mm in Gujan and 14 mm in Arès (Table 1). The female-to-male sex ratio was 0.54 in Gujan and 0.40 in Arès (Table 1).

3.3. Mortality

The mortality constant (Z) for the youngest cohort (2023) was 10.63

Table 1

Values of the different parameters characterizing the *Arcuatula senhousia* population in Gujan and Arès. CI : condition index, DW : dry weight. H_∞ : asymptotic shell height, K : growth coefficient, Φ' : growth performance index.

	Parameter	Unit	Gujan	Arès
Growth	H_∞	mm	34.21	26.4
	K	yr^{-1}	1.58	1.14
	Φ'		3.27	2.90
Reproduction	CI peak	‰	145, Jul 2023	134, Jul 2023
	CI minimum	‰	88, Jan 2024	64, Dec 2023
	Sex-ratio	F/M	0.54	0.40
	Min. size for maturity	mm	12	14
Mortality	Z cohort 2023	yr^{-1}	10.63	6.28
	Z cohort 2022	yr^{-1}	3.10	1.61
Production	P	g DW. m^{-2} . yr^{-1}	282	67
Biomass	B	g DW. m^{-2} . yr^{-1}	132	240
Productivity	P/B	yr^{-1}	2.14	0.28

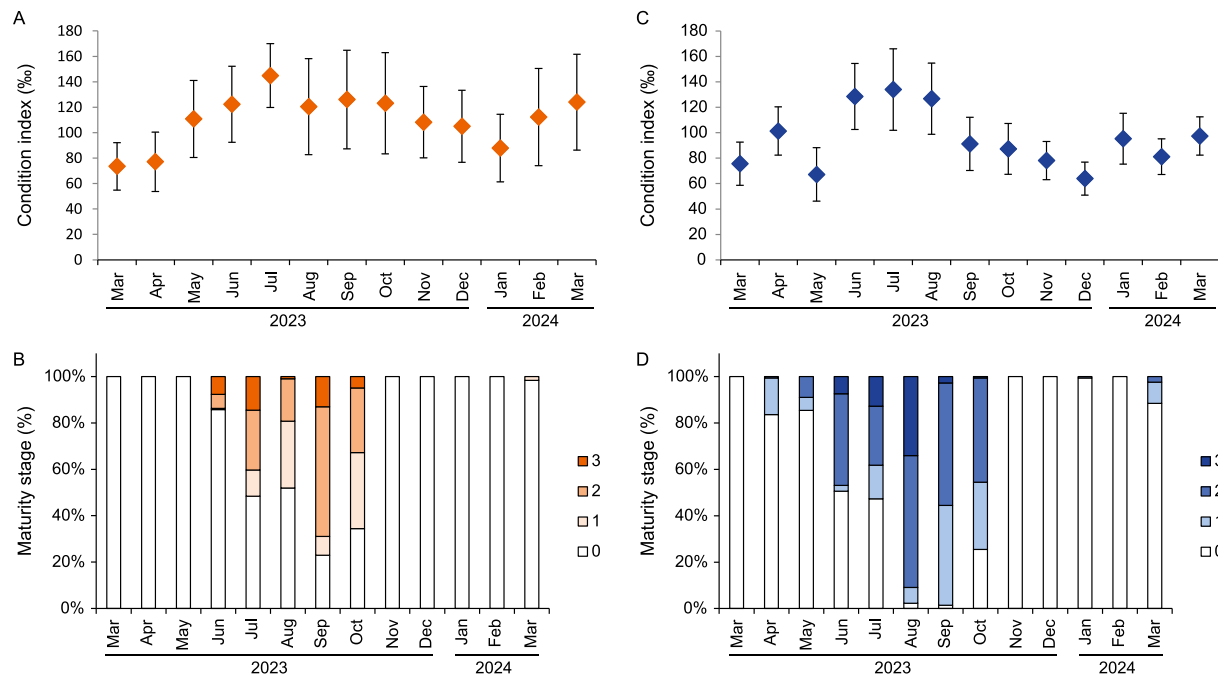


Fig. 2. Mean condition index (\pm standard deviation) of *Arcuatula senhousia* per month, in Gujan (A) and Arès (C), and percentage of individuals per maturity stage in Gujan (B) and Arès (D).

yr^{-1} in Gujan, indicating a 50 % mortality rate within 24 days. In Arès, the Z value is lower at 6.28 yr^{-1} , meaning that 50 % mortality was reached in 40 days (Table 1). For the older cohort (2022), Z values in Gujan and Arès were 3.10 yr^{-1} and 1.61 yr^{-1} , corresponding to 50 % of mortality in 81 and 157 days, respectively.

3.4. Parasitism

No mussels were found to be parasitized by trematodes in either Gujan or Arès.

3.5. Production and P/B ratio

Production (P) in Gujan was four times higher than in Arès, despite the mean yearly biomass (B) being nearly half as much. As a result, the P/B ratio was significantly higher in Gujan (2.14 yr^{-1}) compared to Arès (0.28 yr^{-1}) (Table 1).

4. Discussion

The abundance of mussels within patches at both stations ranged from 200 to 2300 ind.m^{-2} , depending on the month. These densities are relatively low compared to those reported in other ecosystems where the species is considered invasive, whether native as in Lake Nakaumi (Japan) (Yamamuro et al., 2000), or long-established following introduction. For example, densities exceeding 7000 ind.m^{-2} have been recorded in San Diego (USA), where the species was first observed 30 years earlier (Crooks, 1996). In contrast, the lower abundances observed at our two stations are more comparable to those reported in recently invaded sites (within 3 years of initial observation), such as the Tarento Sea (Italy) with fewer than 4000 ind.m^{-2} (Mastrototaro et al., 2003), Southampton (UK) with a maximum of 290 ind.m^{-2} (Watson et al., 2021), and the Shatt Al-Basrah Canal (Iraq) with 102 ind.m^{-2} (Yasser et al., 2023). However, in our case, the estimated introduction occurred approximately 20 years ago, around 2002 (Bachelet et al., 2009). Therefore, the current situation in Arcachon Bay resembles that of Sacca di Goro, where an initially slow population expansion was followed by a rapid population explosion (Mistri et al., 2004). Arcachon Bay may

currently represent an intermediate stage between the lag time and a potential population explosion characteristic of full invasion. However, ecosystems with high species richness, such as Arcachon Bay (Blanchet, 2004), are generally known to resist NIS, due to the limited availability of vacant ecological niches (Chan and Briski, 2017; Marraffini and Geller, 2015). As a result, the lag phase may be prolonged, or effective biotic resistance may eventually develop. In addition, caution is warranted regarding the methodology used to estimate mussel abundance, as it is not always clear in the literature if samples were collected randomly or within mussel patches. In Arcachon Bay, a random sampling in the entire lagoon in 2021 yielded abundance values not exceeding 200 ind.m^{-2} (Coignard et al., In press). Lastly, as extensively described by Coignard et al. (in press), environmental factors, such as consistently high current velocities in subtidal channels or temporary surges during storm events may limit the population growth of *A. senhousia*.

Detecting age classes (cohorts) from monthly shell-size distribution was challenging, as often noted in other studies with similar data (Crooks, 1996; Yamamuro et al., 2000). This difficulty is due to the species' biological traits, being short-lived (1–2 years maximum) (Crooks, 1996) but potentially exhibiting two simultaneous cohorts, a prolonged spawning period (Mastrototaro et al., 2003), and sporadic juvenile recruitment (Crooks, 1996; Yamamuro et al., 2000). Nonetheless, mussel growth was modelled using the VBGF, indicating that after one year, shell height reached 28 mm in Gujan and 18 mm in Arès. These values align with those recorded in other locations, such as San Diego, U.S.A. (17–23 mm) (Crooks, 1996), Tamaki Estuary, New Zealand (20 mm) (Creese et al., 1997), and Ashtamudi Lake, India (25 mm) (George and Nair, 1974a). The higher growth performance index observed in Gujan (3.27) compared to Arès (2.90) may be attributed, for a suspension feeder, to factors such as tidal level (Callaway et al., 2014; de Montaudouin, 1996) as well as food quality and quantity (Bacher et al., 2003; Duarte et al., 2010; Smaal, 1997). The tidal levels at both stations were similar. Stable isotopic analysis on another suspension feeder, potentially competitor (Como et al., 2016), *Ruditapes philippinarum*, provided limited evidence of trophic source differences between Gujan and Arès (Dang et al., 2009). Regarding food quantity, mussel density (Bachelet et al., 2009) and densities of other suspension feeders are also

similar at both stations (Blanchet, 2004; Sanchez et al., 2018), minimizing intraspecific competition. However, Gujan and Arès lie within two distinct sub-systems of the lagoon, which differ in environmental, zooepidemiologic, and planktonic characteristics (Binias et al., 2014; Glé, 2007). Gujan is situated 6 km from primary freshwater input (the Leyre River), closer than Arès (12 km), and is thus more influenced by brackish conditions. These estuarine conditions in Gujan may be advantageous for *A. senhousia* growth and P/B, which shows a preference for brackish over oceanic waters (Hamza et al., 2022; Hosozawa et al., 2020). Finally, the superior mussel growth observed at the Gujan station may be linked to the higher water turnover in this sub-system. An unpublished study (SOGREAH, 2001) reported that approximately two-thirds of the water circulates through the Gujan area, compared to only one-third in the northwestern sub-system where the Arès station is located. Consistently, enhanced growth performance of another suspension feeder, *Crassostrea gigas*, has been documented in the south-eastern sub-system (including Gujan) relative to the northwestern part of the bay, regardless of tidal level (Maurer, 1989). Maurer (1989) attributed these differences to more extreme environmental conditions in areas with lower water turnover, a conclusion that aligns with Binias et al. (2014), who reported a higher frequency of both minimum and maximum temperature events in such areas.

The reproductive phenology was similar at both stations, with a peak of the condition index and maximum maturation observed in summer, followed by an extended spawning period also during the warmer season. This pattern aligns with findings from other studies (Sgro et al., 2002, 2005), although these processes may also begin earlier in spring, as the species can reproduce across a broad temperature range (Ishii et al., 2005; Watson et al., 2021). Size-frequency histograms may be difficult to interpret, with recruitment potentially failing or occurring over prolonged periods (Ishii et al., 2001; Yamamuro et al., 2000). Interestingly, the study revealed an unbalanced sex ratio favoring males, contrary to the female dominance in Solent (UK) (Watson et al., 2021) and the balanced ratio in India (George and Nair, 1974a). However, the minimum size at maturation was consistent with previous findings (Mistri, 2002).

Mortality rates ($6.28\text{--}10.63\text{ yr}^{-1}$) during the early months of benthic life were consistent with typical patterns for bivalves with a benthoplanktonic life cycle (notably high juvenile mortality), although values were comparatively high. Their position at or near the sediment surface likely increases vulnerability, similar to rates seen in the sympatric species *Cerastoderma edule* also living near the sediment surface ($8.26\text{--}10.89\text{ yr}^{-1}$) (Gam et al., 2010), but notably higher than those observed in the deeper-burrowing bivalve *R. philippinarum* ($3.43\text{--}5.83\text{ yr}^{-1}$) (Dang et al., 2010). Principal mortality sources include predation (by birds (Yamamuro et al., 1998) or gastropods (Kushner and Hovel, 2006; Marshall, 2009) and summer anoxia (Como et al., 2018; Mistri, 2002), factors which should be further investigated to understand the mortality rate variations between the two stations. Mussel flesh was also examined for trematode parasites, known to occur in this species' native distribution (George and Nair, 1974b). No trematodes were detected in Arcachon Bay, aligning with the Enemy Release Hypothesis (ERH), which suggests that introduced species are often free of their native parasites (Colautti et al., 2004). This lack or scarcity of infection in *A. senhousia* could contribute to its successful expansion (Miller et al., 2008).

Finally, the P/B ratio calculated for Gujan showed higher values, aligning with the previously discussed superior growth performance. The only available references (Mistri, 2002; Takenaka et al., 2016) reported values between 1.5 and 1.7 yr^{-1} , which are intermediate compared to those found in Arcachon Bay and fall within the typical range for molluscs or filter feeders (1.8 yr^{-1}) (Cusson and Bourget, 2005).

In conclusion, the *A. senhousia* population in Arcachon Bay currently forms patches with densities indicative of recent introductions. Population dynamics parameters (growth, reproduction, mortality, and P/B

ratio) align closely with ecosystem observations where the species has become invasive. This suggests that a similar scenario may develop in Arcachon Bay. However, as a typical *r*-strategy species (short-lived, high mortality rates, rapid growth, and small size), *A. senhousia* could have a localized and short-term impact, as observed in New Zealand, with fluctuations in biomass over time (McDonald and Wells, 2010).

CRediT authorship contribution statement

Xavier de Montaudouin: Writing – original draft, Visualization, Investigation, Formal analysis. **Léa Baudot:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Guillaume Bernard:** Writing – review & editing, Funding acquisition, Conceptualization. **Hugues Blanchet:** Writing – review & editing, Project administration, Funding acquisition. **Cécile Masse:** Writing – review & editing, Project administration, Investigation, Funding acquisition. **Marie P.A. Fouet:** Writing – review & editing, Visualization, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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