



Combined atmospheric and marine heatwaves exacerbate the impacts of a non-indigenous species, the Asian date mussel *Arcuatula senhousia*, on benthic ecosystem functioning

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ABSTRACT

Climate change is predicted to increase the frequency, severity, and duration of extreme climatic events such as heatwaves. Benthic organisms inhabiting intertidal flats are subjected to both marine and atmospheric heatwaves and can experience extreme temperature variations over relatively short periods of time. Non-indigenous species are generally capable to cope with extreme events more efficiently than native species. The Arcachon bay, a lagoon located along the French Atlantic coast is currently colonised by the invasive mussel, *Arcuatula senhousia*. In this study, we investigated how these two stressors (non-indigenous species colonisation and heatwaves) affect soft-bottom ecosystem functioning. We conducted two seasonal laboratory experiments to investigate the effects of combined marine and atmospheric heatwaves on the biogeochemical dynamics of sediments colonised by *A. senhousia* at different densities. More precisely, we assessed the community scale responses by measuring nutrients (NO_x , NH_4^+ , PO_4^{3-}) and oxygen fluxes across the sediment-water interface. The results highlight that (1) heatwaves affect oxygen and nutrient exchanges across the sediment-water interface, with an increase of oxygen consumption and NH_4^+ , PO_4^{3-} fluxes, (2) the magnitude of these effects can be strongly enhanced by increasing densities of *A. senhousia*, and (3) a marked seasonal-dependence, with more effects during the spring experiment. These results emphasise that the interaction between the seasonality of heatwave occurrence, its intensity and the level of colonisation by non-indigenous ecosystem engineers likely shape their consequences for ecosystem functioning in tidal flats. Our results thus reinforce previous findings suggesting that climate change may profoundly exacerbate the effects of biological invasions.

1. Introduction

Extreme climatic events, such as heatwaves, are expected to increase in frequency, severity and duration due to climate change (Hobday et al., 2016; Oliver et al., 2019). Heatwaves are generally defined as a time period during which temperatures stay abnormal, i.e. above the local climate's 90th percentile, for five days or longer for marine heatwaves (Hobday et al., 2016, 2018) and three days for atmospheric heatwaves (Perkins and Alexander, 2013). In marine ecosystems, consequences of intense and repeated heatwaves have been investigated at many biological scales, ranging from cell (Crespo et al., 2021) to ecosystem (Suryan et al., 2021). As a striking example, long and/or

particularly intense marine heatwaves are known to drastically and durably alter habitat-forming species such as corals, kelps, seaweed or seagrasses, likely prevailing the local subsistence of such crucial habitats and the associated ecosystem functions they display (Filbee-Dexter et al., 2020; Leggat et al., 2019; Román et al., 2020; Serrano et al., 2021). Heatwaves also affect the behaviour, physiology and survival of various groups of organisms, ranging from bacteria, or phytoplankton, to metazoans such as bivalves, fishes or marine mammals (Chauhan et al., 2023; He et al., 2022b; Joint and Smale, 2017; Raymond et al., 2022; Santora et al., 2020; Wade et al., 2019). When exposed to heatwaves, they display higher energy requirements to survive, therefore heatwave hamper their growth, reproduction and survival (Leung et al.,

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2019; Minuti et al., 2021), thereby affecting their ability to cope with the other ever-growing environmental stressors encountered in the Anthropocene, such as chemical pollution, eutrophication or invasive species. Native species are frequently more affected by heatwaves than invasive species, the latter being generally more tolerant to harsh conditions (Gilson et al., 2021; Schneider, 2008; Sorte et al., 2010b). Therefore, as an environmental stressor favouring invasive species, heatwaves can affect ecosystem structure and functioning while destabilising intra and interspecific relationships and niche occupancy (Occhipinti-Ambrogi, 2007).

Within soft sediments, spatial and temporal patterns of ecosystem functioning are underpinned by complex relationships between benthic biodiversity, sediment biogeochemistry and environmental conditions. Important functions displayed in these environments, such as organic matter processing and nutrient cycling, are governed by both abiotic variables (mainly temperature) interacting with microbial communities (Hicks et al., 2018) and the functional traits and densities of key infaunal species (Norkko et al., 2013; Sanders et al., 2024; Schenone and Thrush, 2020) through their biological activities (e.g. bioturbation, respiration, excretion). As temperature deeply controls (1) the physiology and behaviour of benthic organisms (Amorim et al., 2020; Xu et al., 2023a, 2023b) and, (2) biogeochemical reactions kinetics in the sediment (Liikanen et al., 2002), understanding how heatwaves affect the interplay between these two components, involved in the regulation of ecosystem functions, appears fundamental (Kauppi et al., 2023). However, besides the extended increasing knowledge based on experiments assessing the effects of heatwaves on single species or highly simplified systems (Carneiro et al., 2020; Domínguez et al., 2021; Olabarria et al., 2016; Zhou et al., 2022), only a few experiments have been carried out at the community level (Castro et al., 2021; Kauppi et al., 2023; Pansch et al., 2018), despite the crucial importance of also considering changes which may occur in the surrounding benthic community. Moreover, heatwave effects are even more difficult to apprehend in coastal intertidal habitats which are alternatively exposed to marine and atmospheric temperatures during high and low tides, and thereby impacted by both types of heatwaves.

Among the different examples of marine invasive species, the Asian date mussel *Arcautula senhousia* (Benson, 1842) native from Asian east coasts (Hosozawa et al., 2020; Ishii et al., 2001; Takenaka et al., 2016) is known to have successfully colonised several ecosystems across the world (Crooks, 1996; Lourenço et al., 2018; Massé et al., 2022; Mistri, 2002; Watson et al., 2021; Willan, 1985). This species can either live in brackish or euryhaline waters (Kurata and Hiratsuka, 2018; Scirocco, 2018), and is principally found in intertidal mudflats where it lives semi-buried into the sediment (Crooks, 1998; Takenaka et al., 2018). *A. senhousia* is characterised by a rapid growth (Crooks, 1996; Mastrototaro et al., 2004), a long reproductive period (Mistri, 2002; Sgro et al., 2002) and a high dispersal rate during the pelagic larval phase (Shanks, 2009), explaining why it is considered an opportunistic species (Willan, 1987; Yamamuro et al., 2010). Moreover, this species has a very active metabolism leading to high excretion rates compared to other bivalve species (Magni et al., 2000). When reaching high densities (ca. $>1500 \text{ ind.m}^{-2}$), *A. senhousia* populations can profoundly modify the colonised ecosystem by forming dense continuous mats of byssus at the sediment surface in which mussels are embedded (Yamamuro et al., 2010). Establishment of dense mussel populations thus changes the architectural and chemical properties of the habitat (Crooks, 1998). Those changes can induce modifications of faunal communities (Castorani and Hovel, 2015; Crooks and Khim, 1999), food-web (Como et al., 2016), nutrient cycling (Bernard et al., 2020; Takenaka et al., 2018) and geochemical processes (Castorani et al., 2015; Mistri and Munari, 2013).

In its native range, where this species also shows an invasive behaviour, *A. senhousia* is highly tolerant to thermal stress and only negatively affected by high-intensity marine heatwaves (Xu et al., 2023a), pointing out that this adaptive capacity would likely further

promote its ongoing spread in intertidal flats worldwide. Therefore, investigating the effects of marine and atmospheric heatwaves in modulating density-dependent changes in the functioning of ecosystems colonised by *A. senhousia* appears of particular importance. Along the European Atlantic coasts, the presence of *A. senhousia* has been attested in Arcachon Bay (SW France) since 2002 (Bachelet et al., 2009). After a lag time of ca. 20 years, abundances of this species have considerably increased since 2018 (Coignard et al., 2025), raising concerns about the potential consequences of such an invasion process. The present study therefore, aimed at investigating the density-dependent effects of *A. senhousia* on oxygen and nutrient fluxes at the water-sediment interface during heat waves of two different intensities. Given the strong impacts of *A. senhousia* on biogeochemical processes (Bernard et al., 2020; Magni et al., 2000; Mistri and Munari, 2013) as well as its tolerance to high temperature exposition (Xu et al., 2023a; Yamamuro et al., 2010), this study then investigated to which extent naturally occurring heatwaves could exacerbate the impacts of established *A. senhousia* population within mudflats. Mesocosm experiments were carried out to expose intact sediment cores collected in an intertidal mudflat of Arcachon Bay and containing *A. senhousia* at different natural densities to realistic simulated combined marine and atmospheric heatwaves for six days. Community-scale responses were assessed by measuring nutrient and oxygen fluxes across the sediment-water interface.

This experimental work would then allow for a better comprehension of the consequences of *A. senhousia* colonisation for nutrient cycling and benthic-pelagic coupling, and anticipate its impacts on a wider scale in the context of climate change. More generally, it would also contribute to the understanding of the consequences of interactions between two increasingly important stressors associated with global change, namely the spread of non-indigenous invasive species and the occurrence of heatwaves for ecosystem functioning in intertidal environments.

2. Material and methods

2.1. Mesocosm experiments

Two mesocosm experiments were performed in order to assess the effects of combined atmospheric and marine heatwaves on benthic fluxes. Experiments were conducted during two seasons, spring (from the 15th April to the June 9th, 2023) and summer (from the 31st July and the September 15th, 2023) at the experimental facilities of the marine station of Arcachon (44.663598° N, 1.163532° W). For each experiment (season), three batches of 24 intact sediment cores collected in the field and encapsulating natural density gradients of *A. senhousia* were respectively exposed for six days to either (1) “ambient” conditions, (2) a combined (marine + atmospheric) “strong” heatwave, or (3) a combined “extreme” heatwave. “Strong” and “extreme” simulated heatwaves respectively corresponded to heatwaves of category II and IV (respectively two and four times above the 90th percentile of the local climatology) (Hobday et al., 2018). After six days exposure, oxygen and nutrient fluxes across the sediment-water interface were measured in each core.

2.1.1. Field sampling

Samples were collected at low tide in an intertidal flat located in the southern part of Arcachon Bay (Atlantic coast, S-W France, 44.64950° N, 1.06588° W). The site is characterised by a sandy mud sediment (median grain-size: $200 \mu\text{m} \pm 170$, mud content: $45 \% \pm 25$) colonised by a low density patchy *Zostera noltii* meadow as well as visible aggregates of *Arcautula senhousia* most of the time associated with *Gracilaria vermiculophylla* patches. At six occasions (three per season for each heatwave treatment), 24 sediment cores were collected using a PVC cylinder, pushing the entire core in the sediment (height: 30 cm; internal diameter: 9.6 cm) (=72 cores per season in total). A range of different

A. senhousia densities was targeted *a priori*, by collecting: (1) cores in patches without any visible *A. senhousia* individual at the sediment surface, (2) cores capturing visible low density (one or two specimens), and (3) cores visibly including high density of *A. senhousia* (four specimens or more). Back to the lab, the sediment interface level in each core was adjusted by adding foam stoppers from underneath the core so that the interface fitted with the top of the cylinder before being placed into the mesocosm. This allowed for the homogenisation of the sediment interface level amongst the different cores, to avoid tidal pool considering their importance in the response to heat stress (Zhou et al., 2022).

2.1.2. Experimental set-up

Experimental mesocosm consisted in two 500 L tanks, installed side by side and filled with seawater oxygenated with air bubbling (Fig. 1). The water was renewed after each six days experiment. It was placed in a semi-opened room receiving natural light. The first tank received the cores tightly kept upright and randomly placed while the second one served as a buffer tank used to generate an artificial tidal regime (6 h low tide/6 h high tide) by pumping water from one tank to the other. In each tank, water temperature was controlled with an aquarium heater (Eheim Thermocontrol 400W). The first tank containing sediment cores was closed by a transparent plexiglass lid fitted with four ceramic infrared heat radiators (Elstein, Hobby 250W) connected to a temperature controller (Biotherm II, Hobby) allowing for an accurate control of air temperature. Animals contained in the cores were fed daily at high tide with a solution of *Isochrysis galbana* at a concentration of 5000 cells/ml (Albert et al., 2022; Como et al., 2016; Maire et al., 2007).

Marine and atmospheric heatwaves were simulated by adjusting water and air temperatures using the aquarium heaters and the ceramic infrared heat radiators, respectively. On the latter, two sets of

temperatures were programmed, one for the morning and the night (6 p.m.–12 a.m.), added to an increase in temperature during the afternoon low tide (12 a.m.–6 p.m.). A Hobo® temperature sensor was placed at the sediment surface in an additional core to measure temperature variations during the experiment. Recorded temperatures during experiments are shown in Supplementary Fig. 1. In “ambient” condition, no temperature control was applied so that this condition corresponded to the naturally varying aerial and water temperatures. Cores containing animals were acclimated 24h in the mesocosm after collection before slightly increasing the temperature until the target conditions for six days exposure.

2.1.3. Characteristics and intensities of marine and atmospheric heatwaves

The choice of the tested temperatures was based on the definition method of heatwaves proposed by Hobday et al. (2018) and Perkins and Alexander (2013). To do so, we used a real long-term dataset with daily temperatures available from 1987 to 2023 obtained from Arcachon bay seawater temperature monitoring operated by IFREMER. In addition, we used an aerial temperature dataset with the mean and maximum daily temperature from 1987 to 2023 (Météo France, CAP-FERRET monitoring station, id. 33236002). These two datasets are based on measures extracted in the same area as our studied site. Based on this, we calculated the climatology (using 11 days time window for marine heatwaves and 15 days time window for atmospheric heatwaves) and determined the difference between the climatological mean and 90th percentile. Multiples of these differences, following Hobday et al. (2018), describe different categories of heatwaves: moderate ($1-2 \times$, category I), strong ($2-3 \times$, category II), severe ($3-4 \times$, category III), extreme ($>4 \times$, category IV). According to this classification, heatwaves simulated during the experiments corresponded to the strong and extreme levels

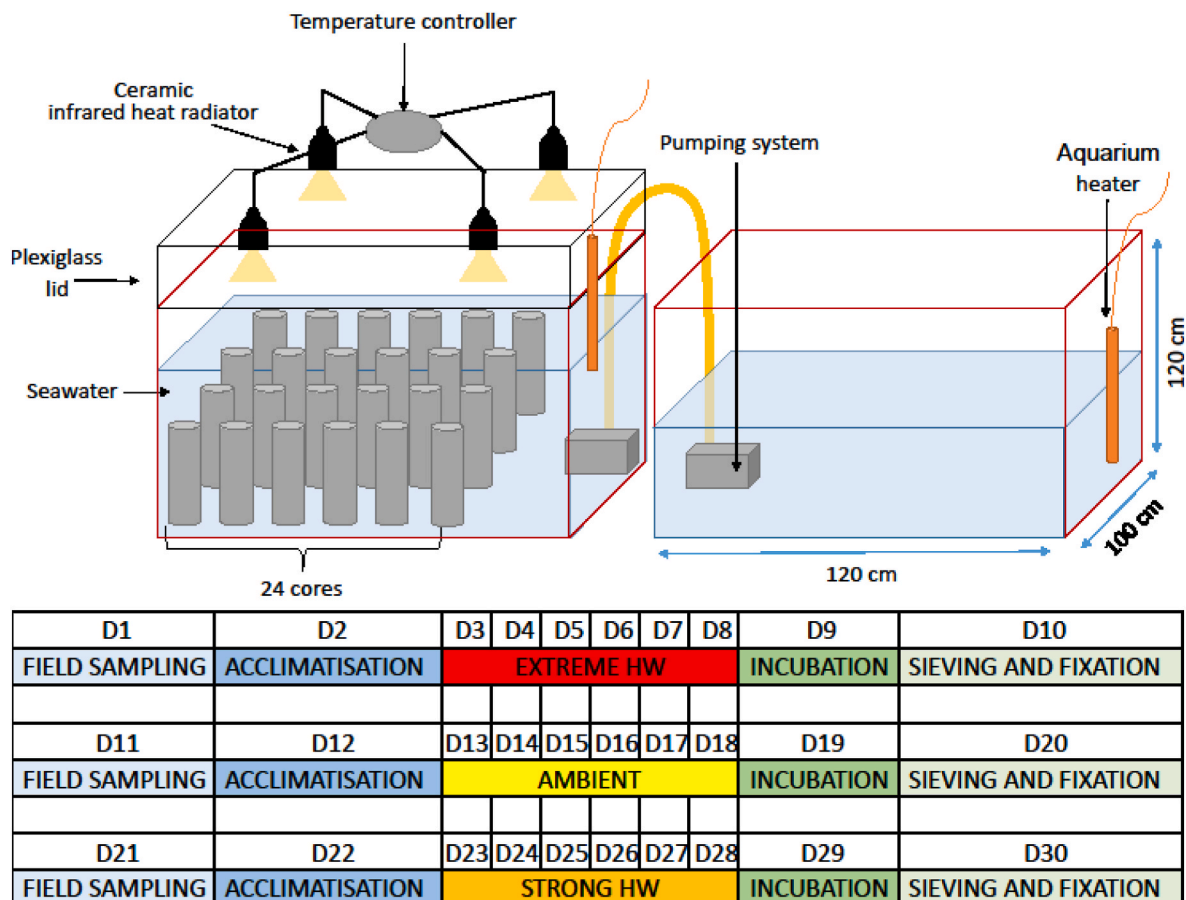


Fig. 1. Schematic diagram of the experimental set-up and the timeline of the experiments.

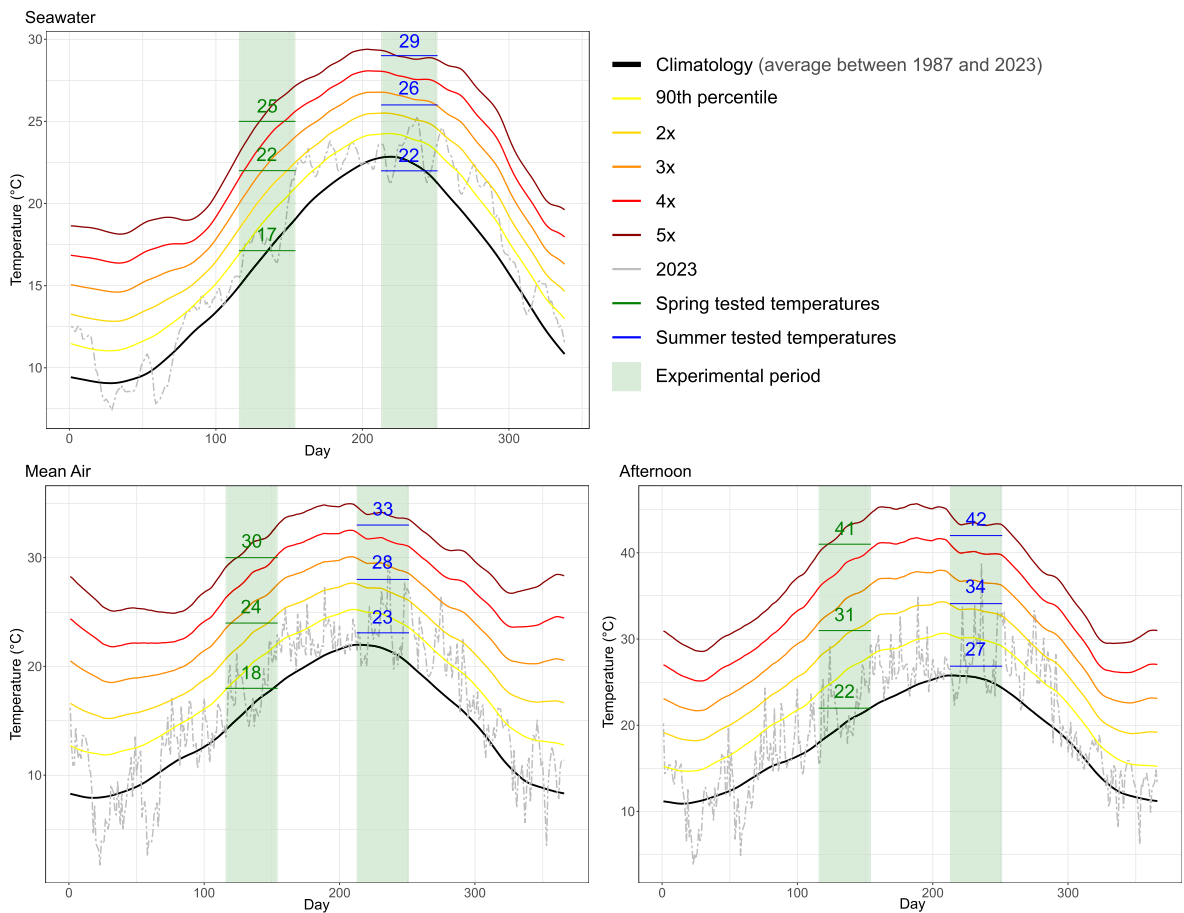


Fig. 2. Categorisation of the different heatwaves based on long-term local climatological data (1987–2023) and targeted temperatures for the spring and summer experiments.

(Fig. 2, Table 1).

2.2. Quantification of nutrient fluxes

At the end of the experiments, following six days of exposure to a heatwave treatment, oxygen (O₂), ammonium (NH₄⁺), nitrates and nitrites (NO₂⁻ and NO₃⁻, grouped under NO_x), and phosphate (PO₄³⁻) fluxes across the sediment-water interface were quantified in each core in darkness (Bernard et al., 2020; Pascal et al., 2016; Richard et al., 2021). Cores were retrieved from the tank and hermetically closed with a PVC 500 mL incubation chamber thereafter gently filled with seawater from the mesocosm. 20 mL of overlying water were immediately sampled for

Table 1
Tested temperatures during ambient condition and stimulated heatwaves.

Experiment	Heatwave intensity treatment	Seawater temperature (°C)	Mean air temperature (°C)	Maximum air temperature (°C)
Spring	Ambient	17	18	22
	Strong (category II)	22	24	31
	Extreme (category IV)	25	30	41
Summer	Ambient	22	23	27
	Strong (category II)	26	28	34
	Extreme (category IV)	29	33	42

the measurement of initial nutrient concentrations. The overlying water was continuously homogenised with a Teflon-coated magnetic stirring bar (~100 rpm). The O₂ concentration was continuously monitored using an oxygen probe (OXROB10, Pyroscience, Aachen, Germany) connected to a Firesting Oxygen Meter (Pyroscience, Aachen, Germany) adjusted in the incubation chambers. The probe was calibrated linearly, from 100 % saturation with air-bubbling seawater to zero oxygen concentration measured in a sodium ascorbate solution. Before the O₂ concentration dropped below 70 % of its initial value (under this value, other anaerobic metabolism could be involved), the incubation was stopped and two replicates of 10 mL of the overlying water were sampled to measure final nutrient concentrations. Samples were immediately frozen pending analysis. All nutrient measurements were performed on a segmented flow analyser (Auto Analyzer III, SEAL, Entraigues Sur La Sorgue, France). The oxygen consumption (mmol·m⁻²·h⁻¹) and nutrient fluxes (μmol·m⁻²·h⁻¹) were determined by calculating the concentration decreases within each experimental unit, using the following equation: Fluxes = (a × V)/(S), where a is the slope of oxygen or nutrient concentrations as a function of time, V is the volume of overlying water, and S is the surface area of the sediment-water interface.

2.3. Macrofauna and macrophytes collection

After measurements of biogeochemical fluxes, sediment cores were gently passed through a 1 mm mesh-sized sieve and residuals were fixed with 4 % formaldehyde. In the laboratory, samples were carefully washed, to collect macrofauna. All specimens were then identified under a stereomicroscope at the lowest taxonomic level possible, counted and

measured. The dry weight of each individual was estimated using specific size-weight allometric relationships established for Arcachon Bay (Blanchet, unpub). In addition, thalli of macroalgae (mainly *Gracilaria vermiculophylla*), as well as roots and leaves of seagrass (*Zostera noltii*) were collected, dried at 60 °C for 48 h and weighed.

2.4. Data processing and statistical analysis

Overall, the initial dataset consisted in 144 samples encompassing core-scale (1) oxygen and nutrient fluxes as well as (2) benthic macrofauna and macrophytes biomasses. It was divided into two distinct

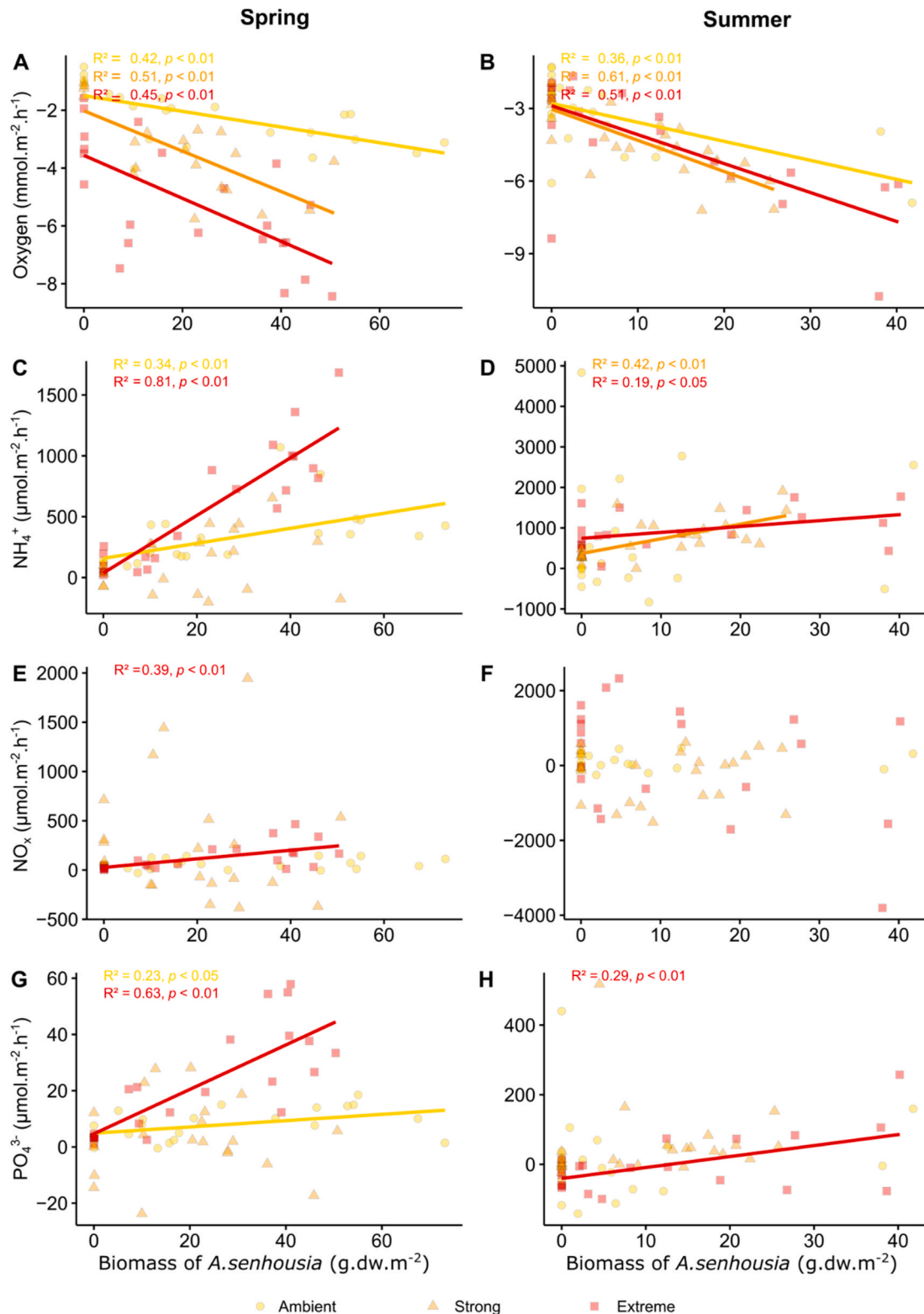


Fig. 3. Relation between fluxes of NO_x, NH₄⁺, PO₄³⁻ and dissolved oxygen with the different biomass of *A. senhousia* for the three tested intensities of heatwave (yellow = ambient, orange = strong and red = extreme) and during the two tested seasons. N = 23, 20, 22, 22, 24, 21 respectively for the six tested conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

seasonal datasets (72 samples each) comprising three heatwave intensity treatments (24 samples each).

First, replicates containing no macrofauna or only a few numbers of *Peringia ulvae*, were considered as outliers, and excluded from the datasets. Samples with very high *A. senhousia* densities were removed from the datasets when they were found in just one treatment to maintain biomass ranges comparable across heatwave intensity treatments for each season. The same approach was carried for the other dominant ecosystem engineer species present within the community, i.e. *Ruditapes philippinarum*. It should be underlined that these dataset adjustments were very limited since in total, only seven and five samples have been removed from the spring and summer datasets, respectively. Then, the final dataset included 132 samples (65 in spring and 67 in summer, 91 % of the initial dataset).

The effects of heatwave intensity on solute fluxes were analysed separately for spring and summer experiments. To do so, univariate permutation analysis of variances (PERMANOVAs, PRIMER v.7 (Anderson, 2008)) were carried out, based on Euclidean distance and using 9999 permutations. In order to include and analyse the effects of *A. senhousia* density gradients that may interact with those of heatwave intensity to affect solute fluxes, *A. senhousia* biomass was added as a covariate (*Ar*) to a design that included a single factor (Heatwave Intensity, HWI) encompassing three modalities (“ambient”, “strong”, “extreme”). Therefore, significant interactions between *Ar* x HWI indicated significant differences in the relationships (slopes) between a given solute flux and *A. senhousia* biomass amongst HWI conditions. Pairwise comparisons were carried out by adding three contrasts (“ambient” vs “strong”, “ambient” vs “extreme”, “strong” vs “extreme”) to HWI.

For each seasonal experiment and HWI condition, the contributions of *A. senhousia* as well as those of the other biodiversity components (macrofauna and macrophytes) in explaining the variability in the solute fluxes were investigated using a distance-based redundancy analysis (dbRDA) performed with the DistLM option in the PERMANOVA + add-on for PRIMER (Anderson, 2008). Forward selection was used to build models using AICc selection criterion. Individual solute fluxes (oxygen and nutrients) were used as response variables and biodiversity components as predictor variables. The number of predictors variables were reduced by grouping polychaete species according to their functional attributes: burrowing polychaetes (including *Glycera* sp., *Hediste diversicolor*, *Nephtys hombergii*, *Marphysa* spp., *Scoloplos armiger*, *Streblospio shrubsolii*, Aricidae, Spionidae), and tube builders (including *Diopatra biscayensis*, Amparetidae, *Melinna palmata*). The set of predictors thus included 11 macrofauna variables (biomasses of: *Abra segmentum*, *Arcuatula senhousia*, Amphipoda, burrowing polychaetes, *Cerastoderma edule*, *Littorina littorea*, *Mytilus edulis*, Oligochaeta, *R. philippinarum*, *Scrobicularia plana*, tube builders) and three macrophyte variables (biomasses of *Gracilaria thalli*, *Z. noltii* leaves, *Z. noltii* roots). Some predictors needed to be transformed (square root or log(*x* + 1)) to equalise variances.

3. Results

3.1. Heatwave-induced effects on nutrient and oxygen fluxes and their modulation across *A. senhousia* density gradients

Overall, heatwave intensity (HWI) significantly affected the magnitude of fluxes, with differences associated with the tested seasons, intensity treatments and fluxes. The direction and magnitude of these effects are described flux per flux below. The biomass of *A. senhousia* also significantly increased the magnitude of benthic fluxes. The relationships between the biomass of *A. senhousia* and fluxes measured in the different tested HWI conditions are presented in Fig. 3. The range of *A. senhousia* biomasses varied from 0 to 73 g.dw.m⁻² during the spring experiment, corresponding to 0 to 12 individuals per core. During the summer experiment, individuals were smaller with a biomass varying

from 0 to 42 g.dw.m⁻², corresponding to 0 to 14 individuals per core. Biomass ranges were not statistically different between HWI conditions at the two seasons (PERMANOVAs, *p* < 0.05) (Supplementary Fig. 2).

3.1.1. Dissolved oxygen fluxes

HWI significantly influenced oxygen fluxes in spring (PERMANOVAs, Pseudo-F = 40.109, *p* < 0.01) but not in summer (Pseudo-F = 1.37, *p* = 0.26). In spring, oxygen fluxes decreased with HWI and were significantly different between the three conditions (PERMANOVAs, *p* < 0.01 for comparisons between “ambient” and “strong”, “ambient” and “extreme”, and between “strong” and “extreme”). Average (±SD) oxygen fluxes in spring were -2.17 ± 0.99 , -3.42 ± 1.45 and -5.18 ± 2.08 μmol m⁻² h⁻¹ for “ambient”, “strong” and “extreme” intensities, respectively. In summer, oxygen consumptions measured in the “ambient” condition were significantly lower than in the “strong” condition (PERMANOVA, *p* < 0.01), but not the “extreme” condition (PERMANOVA, *p* > 0.05, Table 2). Average (±SD) oxygen fluxes in summer were -3.29 ± 1.52 , -4.39 ± 1.46 and -4.35 ± 2.40 μmol m⁻² h⁻¹ for “ambient”, “strong” and “extreme” conditions, respectively.

In both seasons as well as in all heatwave treatments, increasing *A. senhousia* biomass significantly enhanced oxygen consumption (Fig. 3, Table 2). At the two seasons, the slopes of the relationship between *A. senhousia* and oxygen consumption were significantly steeper in “strong” and “extreme” compared to “ambient” conditions (pairwise PERMANOVA, *p* < 0.05), these differences being particularly marked in spring.

3.1.2. Ammonium fluxes (NH₄⁺)

HWI significantly influenced NH₄⁺ fluxes in spring but not in summer (PERMANOVAs, spring: Pseudo-F = 17.99, *p* < 0.01; summer Pseudo-F = 0.197, *p* = 0.84). In spring, fluxes differed significantly between the three conditions (PERMANOVA, *p* < 0.05, Table 2), lowest in “strong” and higher in “extreme”. Average (±SD) NH₄⁺ fluxes in spring were 312.35 ± 249.95 , 134.07 ± 247.05 , and 553.60 ± 489.72 μmol m⁻² h⁻¹ for “ambient”, “strong” and “extreme” conditions respectively. In summer, despite there were no significant differences, average (±SD) NH₄⁺ fluxes increased with the HWI and were 662.60 ± 1375.59 , 751.66 ± 496.75 and 922.07 ± 481.97 μmol m⁻² h⁻¹ for “ambient”, “strong” and “extreme” condition, respectively.

In spring, *A. senhousia* biomass significantly influenced NH₄⁺ fluxes during “ambient” and “extreme” conditions (Fig. 3C). The slope of the relationship between *A. senhousia* and NH₄⁺ fluxes was significantly (Table 2) and remarkably steeper in “extreme” compared to “ambient” condition (pairwise PERMANOVA, *p* < 0.05). In summer, there was a significant influence of *A. senhousia* on NH₄⁺ fluxes under “strong” and “extreme” condition (Fig. 3D). In this case, the slope was slightly steeper in “strong” compared to “extreme” condition.

3.1.3. Nitrous oxide fluxes (NO_x)

For both seasons, NO_x fluxes were not influenced by HWI (PERMANOVAs, spring: Pseudo-F = 2.15, *p* = 0.12; summer: Pseudo-F = 1.46, *p* = 0.24). However, in spring, fluxes increased significantly between “ambient” and “extreme” conditions (PERMANOVA, *p* < 0.05, Table 2). Average (±SD) NO_x fluxes in spring were 60.53 ± 51.03 , 281.86 ± 628.16 , 121.62 ± 131.19 μmol m⁻² h⁻¹ for “ambient”, “strong” and “extreme” conditions respectively. In summer, NO_x fluxes differed significantly between conditions “ambient” and “strong” (PERMANOVA, *p* < 0.05, Table 2). Average (±SD) NO_x fluxes in summer were 101.79 ± 213.02 , -237.68 ± 681.87 , and 196.92 ± 1516.06 μmol m⁻² h⁻¹ for “ambient”, “strong” and “extreme” condition respectively.

For both seasons and the three tested HWI, NO_x fluxes were not influenced by the biomass of *A. senhousia*, except during the “extreme” condition in spring (Fig. 3E).

3.1.4. Phosphate fluxes (PO₄³⁻)

HWI conditions significantly influenced PO₄³⁻ fluxes in spring but not

Table 2

Permanova results between *A. senhousia* biomasses, heatwaves intensities (HWI) and measured benthic fluxes during spring and summer experiments. Bold font indicates significant results ($p < 0.05$).

SPRING					SUMMER				
Flux	Factor	df	Pseudo-F	P(perm)	perms	df	Pseudo-F	P(perm)	perms
O ₂	Ar	1	33.921	0.0001	9847	1	65.599	0.0001	9831
	HWI	2	40.109	0.0001	9937	2	1.3654	0.2629	9950
	Ambient vs Strong	1	26.156	0.0001	9827	1	4.395	0.0419	9812
	Ambient vs Extreme	1	72.331	0.0001	9850	1	0.95031	0.3434	9833
	Strong vs Extreme	1	15.185	0.0002	9836	1	0.35924	0.5734	9844
	Ar × HWI	2	4.4185	0.0171	9943	2	1.0794	0.3194	9939
	Ar × (Ambient vs Strong)	1	6.8362	0.0123	9848	1	2.3338	0.1381	9834
	Ar × (Ambient vs Extreme)	1	6.6463	0.0153	9824	1	1.2518	0.2575	9825
	Ar × (Strong vs Extreme)	1	0.028978	0.8718	9851	1	0.057381	0.8139	9832
	Res	59				61			
	Total	64				66			
	Ar	1	62.175	0.0001	9826	1	4.4485	0.0411	9814
	HWI	2	17.989	0.0001	9951	2	0.197	0.8402	9959
NH ₄ ⁺	Ambient vs Strong	1	4.6338	0.0354	9833	1	0.00005	0.9938	9840
	Ambient vs Extreme	1	19.725	0.0002	9823	1	0.29624	0.6005	9819
	Strong vs Extreme	1	29.826	0.0001	9833	1	1.1782	0.2853	9844
	Ar × HWI	2	16.496	0.0001	9950	2	0.48391	0.5888	9941
	Ar × (Ambient vs Strong)	1	0.18705	0.6705	9835	1	0.61762	0.4336	9833
	Ar × (Ambient vs Extreme)	1	31.122	0.0001	9856	1	0.00748	0.9267	9818
	Ar × (Strong vs Extreme)	1	18.388	0.0003	9829	1	3.4016	0.0706	9823
	Res	59				61			
	Total	64				66			
	Ar	1	0.0033433	0.9577	9863	1	3.2424	0.0739	9803
	HWI	2	2.1518	0.1199	9953	2	1.462	0.238	9938
	Ambient vs Strong	1	2.5804	0.1163	9831	1	4.8084	0.0329	9830
	Ambient vs Extreme	1	7.4735	0.0074	9833	1	0.53631	0.4683	9815
	Strong vs Extreme	1	1.3659	0.2591	9838	1	2.092	0.1503	9833
NO _x	Ar × HWI	2	0.99292	0.375	9953	2	2.3013	0.1102	9950
	Ar × (Ambient vs Strong)	1	0.57102	0.4487	9813	1	0.054371	0.8252	9844
	Ar × (Ambient vs Extreme)	1	10.495	0.0021	9847	1	2.6562	0.1113	9823
	Ar × (Strong vs Extreme)	1	1.2843	0.2646	9856	1	2.0081	0.1649	9853
	Res	59				61			
	Total	64				66			
	Ar	1	17.35	0.0002	9837	1	3.3291	0.0684	9822
	HWI	2	16.603	0.0001	9943	2	1.8892	0.1548	9952
	Ambient vs Strong	1	1.2759	0.2619	9815	1	1.284	0.2916	9831
	Ambient vs Extreme	1	33.561	0.0001	9853	1	0.69199	0.4496	9876
	Strong vs Extreme	1	18.408	0.0002	9834	1	4.5654	0.0196	9901
	Ar × HWI	2	10.911	0.0001	9950	2	0.4284	0.614	9942
	Ar × (Ambient vs Strong)	1	0.48248	0.4907	9839	1	0.0081148	0.9264	9823
	Ar × (Ambient vs Extreme)	1	26.723	0.0001	9839	1	0.6202	0.4076	9813
PO ₄ ³⁻	Ar × (Strong vs Extreme)	1	10.078	0.0036	9814	1	0.7067	0.4244	9838
	Res	59				61			
	Total	64				66			
	Ar	1	17.35	0.0002	9837	1	3.3291	0.0684	9822
	HWI	2	16.603	0.0001	9943	2	1.8892	0.1548	9952
	Ambient vs Strong	1	1.2759	0.2619	9815	1	1.284	0.2916	9831
	Ambient vs Extreme	1	33.561	0.0001	9853	1	0.69199	0.4496	9876
	Strong vs Extreme	1	18.408	0.0002	9834	1	4.5654	0.0196	9901
	Ar × HWI	2	10.911	0.0001	9950	2	0.4284	0.614	9942
	Ar × (Ambient vs Strong)	1	0.48248	0.4907	9839	1	0.0081148	0.9264	9823
	Ar × (Ambient vs Extreme)	1	26.723	0.0001	9839	1	0.6202	0.4076	9813
	Ar × (Strong vs Extreme)	1	10.078	0.0036	9814	1	0.7067	0.4244	9838
	Res	59				61			
	Total	64				66			

in summer (PERMANOVAs, spring: Pseudo-F = 16.6 with $p < 0.01$; summer Pseudo-F = 1.89 with $p = 0.15$). In spring, PO₄³⁻ fluxes were significantly higher in “extreme” compared to both “ambient” and “strong” conditions (PERMANOVAs, $p < 0.01$, Table 2). Conversely, no significant differences were detected between “ambient” and “strong” (PERMANOVA, $p > 0.05$, Table 2). Average (\pm SD) PO₄³⁻ fluxes in spring were 7.68 ± 5.57 , 3.60 ± 14.22 and 21.91 ± 18.62 $\mu\text{mol m}^{-2}\cdot\text{h}^{-1}$ for “ambient”, “strong” and “extreme” conditions respectively. In summer, PO₄³⁻ fluxes only significantly differed between “strong” and “extreme” conditions (PERMANOVA, $p < 0.05$, Table 2). PO₄³⁻ fluxes in summer were 10.15 ± 119.83 $\mu\text{mol m}^{-2}\cdot\text{h}^{-1}$ for “ambient” condition, 54.50 ± 108.96 $\mu\text{mol m}^{-2}\cdot\text{h}^{-1}$ for “strong” and -2.23 ± 83.51 $\mu\text{mol m}^{-2}\cdot\text{h}^{-1}$ for “extreme” condition. In addition, *A. senhousia* biomass significantly influenced PO₄³⁻ fluxes in spring (Table 2), for “ambient” and “extreme” conditions (Fig. 3G). The slope is steeper in “extreme” condition. In summer, *A. senhousia* biomass significantly influenced PO₄³⁻ fluxes only during “extreme” condition (Fig. 3H).

3.2. Contribution of the benthic community to changes in biogeochemical fluxes

In total, 24 benthic macrofauna species/taxa were observed in spring, and 38 in summer. The dominant taxa in terms of biomass were

A. senhousia followed by *R. philippinarum* in spring and *A. senhousia*, followed by *R. philippinarum* and *Scrobicularia plana* in summer. To investigate the importance of other components of benthic biodiversity behind the tested effect of *A. senhousia* biomass, we conducted separate variation partitioning procedures, DistLM (PRIMER PERMANOVA+) with each benthic flux as response variables and macrofauna taxa/groups as well as macrophytes biomasses as potential explanatory variables. The results are presented in Table 3. Identified models explained a substantial part of the variances in benthic fluxes (from 18 to 91 % of the variance explained). In addition, we observed that models explained a larger part of the variability observed in spring than in summer. Overall, in these models, variations in *A. senhousia* biomass were identified as the most important variable explaining the variance in benthic fluxes during both spring and summer experiments. The models also identified the significant contribution of other large species (i.e., *R. philippinarum* and *S. plana*) and the influence of macrophytes (*Z. noltii* leaves and *G. vermiculophylla* thali). Especially, *G. vermiculophylla* significantly contributed to increase NH₄⁺ and NO_x in heatwave conditions (i.e., NH₄⁺ in spring strong and summer extreme HWI and NO_x in spring extreme HWI).

Different patterns of the influence of HWI and *A. senhousia* biomass on benthic fluxes were observed. In some cases, the contribution of *A. senhousia* to the benthic flux increased with increasing HWI. This is

Table 3

Sequential distance-based linear model results between predictors (macrofauna and macrophyte biomasses) and measured benthic fluxes during spring and summer heatwave experiments. Models were identified using the forward selection procedure and AIC selection criterion. Relationship indicates the sense (negative – or positive +) of the correlation between each identified predictor within the model and the considered flux. Bold font indicates significant results ($p < 0.05$).

SPRING								
Flux	HW treatment	Predictor	AICc	Pseudo-F	Part of variance explained	Cum. part of variance explained	P value	Relationship
O ₂	Ambient	<i>A. senhousia</i>	−9.22	15.15	0.419	0.419	0.003	-
		<i>Z. noltii</i> leaves	−19.14	14.57	0.245	0.664	0.018	-
		<i>R. philippinarum</i>	−22.83	6.37	0.084	0.748	0.023	-
		<i>S. plana</i> (log)	−24.70	4.54	0.051	0.799	0.049	-
	Strong	<i>A. senhousia</i>	4.31	18.54	0.507	0.507	0.001	-
		<i>R. philippinarum</i>	−1.37	8.97	0.170	0.678	0.009	-
		<i>S. plana</i> (log)	−1.66	3.02	0.051	0.729	0.095	-
		<i>A. senhousia</i>	22.85	16.03	0.445	0.445	0.001	-
	Extreme	<i>A. senhousia</i> tube builders	274.94	10.90	0.342	0.342	0.003	+
		Bur. Polychaetes (log)	244.77	5.78	0.148	0.489	0.032	+
NH ₄ ⁺	Ambient		243.49	3.85	0.086	0.575	0.083	−
		<i>R. philippinarum</i>	212.98	13.32	0.425	0.425	0.0016	+
		<i>S. plana</i> (log)	208.96	6.90	0.166	0.591	0.0181	−
		<i>G. vermiculophylla</i> thali (log) tube builders	206.18	5.54	0.105	0.696	0.0196	+
	Strong		203.66	5.39	0.080	0.777	0.0331	+
		<i>A. senhousia</i>	239.33	86.55	0.812	0.812	0.0001	+
		<i>R. philippinarum</i>	234.58	7.66	0.060	0.866	0.012	+
		<i>M. edulis</i> tube builders	227.98	9.88	0.047	0.914	0.018	+
	Extreme		227.79	3.00	0.013	0.927	0.113	-
		<i>M. edulis</i>	179.80	4.72	0.184	0.184	0.035	-
NO _x	Ambient	Amphipoda	179.41	2.84	0.101	0.285	0.099	+
		<i>A. senhousia</i>	207.47	12.54	0.385	0.385	0.001	+
		<i>G. vermiculophylla</i> thali (log)	203.52	6.71	0.160	0.546	0.041	+
	Strong	<i>Z. noltii</i> leaves	198.46	7.99	0.140	0.685	0.020	+
		<i>R. philippinarum</i>	196.56	4.63	0.067	0.753	0.045	+
		<i>A. senhousia</i>	76.73	6.13	0.226	0.226	0.024	+
		<i>C. edule</i> (log)	70.76	9.11	0.242	0.468	0.008	-
	Extreme							
		<i>A. senhousia</i>	110.56	33.66	0.627	0.627	0.0001	+
PO ₄ ³⁻	Ambient	<i>G. vermiculophylla</i> thali (log)	108.96	4.10	0.066	0.693	0.066	+
		Bur. Polychaetes (log)	107.31	4.26	0.059	0.752	0.052	−
	Strong							
		<i>A. senhousia</i>	110.56	33.66	0.627	0.627	0.0001	+
		<i>G. vermiculophylla</i> thali (log)	108.96	4.10	0.066	0.693	0.066	+
		Bur. Polychaetes (log)	107.31	4.26	0.059	0.752	0.052	−
	Extreme							
		<i>A. senhousia</i>	110.56	33.66	0.627	0.627	0.0001	+
SUMMER								
O ₂	Ambient	<i>A. senhousia</i>	11.57	11.20	0.359	0.359	0.005	-
		<i>R. philippinarum</i>	1.30	14.18	0.274	0.633	0.002	-
		<i>C. edule</i> (sqr)	−1.77	4.672	0.076	0.708	0.044	-
		<i>A. senhousia</i>	−1.68	34.71	0.612	0.612	0.001	-
	Strong	<i>A. senhousia</i> tube builders	25.56	19.66	0.508	0.508	0.001	-
			10.17	24.69	0.284	0.793	0.01	-
	Extreme	<i>A. senhousia</i>	288.59	15.74	0.417	0.417	0.001	+
		Bur. Polychaetes (log)	283.04	6.38	0.117	0.633	0.02	+
NH ₄ ⁺	Ambient	<i>Z. noltii</i> leaves	286.78	4.26	0.098	0.515	0.072	−
		<i>G. vermiculophylla</i> thali	282.79	2.96	0.049	0.682	0.1	+
		<i>A. senhousia</i> tube builders	258.07	4.41	0.188	0.188	0.047	+
		<i>G. vermiculophylla</i> thali	254.93	4.99	0.176	0.364	0.035	+
	Strong	<i>R. philippinarum</i>	251.24	5.28	0.151	0.515	0.037	+
			245.23	7.44	0.154	0.669	0.014	-
	Extreme							
NO _x	Ambient							
	Strong							
	Extreme							
PO ₄ ³⁻	Ambient							
	Strong							
	Extreme	<i>A. senhousia</i>	182.22	7.86	0.293	0.293	0.008	+
		<i>S. plana</i>	175.57	10.15	0.255	0.548	0.005	-
	<i>C. edule</i> (sqr)	175.34	2.91	0.066	0.614	0.113	+	

the case for NH_4^+ fluxes, during the spring experiment for “ambient” condition, *A. senhousia* explained 34 % of the variability, and this value increased up to 81 % during “extreme” condition. In the same way, during the spring experiment for “ambient” condition, *A. senhousia* explained 23 % of PO_4^{3-} flux variability, and this value increased to reach 63 % during “extreme” condition. Also, during the summer experiment, for oxygen, NH_4^+ and PO_4^{3-} fluxes the contribution of *A. senhousia* was low or not significant while its contribution increased during “strong” and “extreme” conditions.

Another pattern observed was that, more intense the heatwave, more *A. senhousia* alone accounted for most of fluxes variability at the expense

of other species. This was particularly the case for oxygen fluxes. During the spring experiment, although the variance explained by *A. senhousia* did not drastically change across HWI (42, 50, and 45 % during “ambient”, “strong” and “extreme” conditions respectively), the higher the temperature, the lower the contribution of other variables. If under “ambient” and “strong” conditions other species contributed to the variability (*Z. noltii* leaves, *R. philippinarum*, *S. plana*), under “extreme” conditions only *A. senhousia* explained significantly the variability of fluxes. In the same way, during the summer experiment, in “ambient” condition both *A. senhousia* (36 %) and *R. philippinarum* (27 %) explained most of fluxes variations. Under “strong” and “extreme”

conditions *A. senhousia* alone explained more than half of the variability (61 and 51 % respectively). To a lesser degree, this pattern is also observed for PO_4^{3-} fluxes, during the spring experiment, in “ambient” condition *A. senhousia* and *C. edule* contributed to 23 and 24 % of the variance respectively, while in “extreme” condition *A. senhousia* accounted for 63 % of the variability.

4. Discussion

Experimental investigations are required to fully understand the effects of heatwaves, which can often be observed in the field, on ecosystem functioning (Sorte et al., 2010a). However, performing *ex-situ* experiments, using a realistic approach, combining multiple stressors and environmental parameters is challenging (Dolbeth et al., 2021; Smith et al., 2023). Here, the heat wave intensities (HWI) tested scenarios represent a realistic context of heatwave according to the local historical temperature conditions (36-year-old dataset). They then include increases in both atmospheric and water temperature that can alter ecosystem responses. The present experiment is moreover based on incubating sediment cores collected in the field and containing a natural gradient of *A. senhousia* densities (with a range of densities from 0 to 3000 ind.m⁻²) without being manipulated artificially, thus including the associated community changes resulting from the colonisation by this NIS (non-indigenous species). It then addressed the need to properly assess the effects of a NIS by incorporating the environmental complexity. Therefore, our design measures the response of a community to and not of individual species to heatwaves.

Increases in oxygen consumption with rising temperature, and thus during prolonged exposure to heatwave events, have been frequently reported in soft-bottom systems (Kauppi et al., 2023; Nie et al., 2017; Zhou et al., 2022). Interestingly, our results showed that oxygen consumption significantly increased with HWI in spring, by approximately a factor 1.6 in “strong” and 2.4 in “extreme” HWI. This may be explained by increasing temperature triggering respiration rates from: (1) sediment microbial compartment through organic matter aerobic degradation, as well as higher oxygen-mediated geochemical reactions (Glud, 2008), and also (2) the activity of key species (Norkko et al., 2013; Welsh et al., 2015). Conversely, such a regular pattern has not been detected in summer, where oxygen consumption only increased significantly in “strong” HWI compared to “ambient” conditions, but not in “extreme” conditions (Table 2). The reduced oxygen consumption rate observed in “extreme” HWI could partly result from a decrease in microbial-mediated degradation rates of organic matter (Kauppi and Villnäs, 2022).

Several different intertwined biological (e.g. excretion, microphytobenthos and macrophyte uptakes, bioturbation) and biogeochemical (e.g. phosphorus binding, nitrification, denitrification) processes influence nutrient processing within the sediment column, resulting in either upward or downward fluxes at the sediment-water interface. Besides, changes in solute nutrient fluxes during heatwaves have often been observed, driven by metabolic activities of benthic communities that can be stimulated or deprived by heat stress (Crespo et al., 2021; Deldicq et al., 2021; Dolbeth et al., 2021; Kauppi et al., 2023; Kauppi and Villnäs, 2022; Román et al., 2023). In spring, ammonium and phosphate fluxes were significantly affected by heatwave, especially marked by significant increases in both fluxes between “ambient” and “extreme” HWI. However, no significant effects of HWI were detected during the summer experiment. Therefore, while during the spring experiment, increasing temperature could boost the metabolic activity of macrobenthic organisms, in summer, they may have already reached in ambient condition their thermal threshold. It highlights that the seasonal context in which heatwaves occur shapes their effects on ecosystems (Atkinson et al., 2020). Mechanisms underpinning seasonal-dependent ecosystem responses to heatwaves, in term of nutrient processing, could include (1) seasonal variations of the quality and the quantity of sediment organic matter, (2) the specific and

functional compositions of biological micro and macro-benthic communities and (3) the phenology associated with physiological state of one or several key species (Gammal et al., 2025; Lavoie et al., 2016). Accordingly, the marked seasonal variations in hydrological conditions, as well as in seagrass meadows development and associated benthic communities observed in Arcachon Bay (Bernard et al., 2014; Delgard et al., 2016) might interact with those of population size structure and condition index of *A. senhousia* in Arcachon Bay (de Montaudouin et al., 2025) in shaping community metabolism and biogeochemical processes. Thereby, it appears difficult to anticipate the response of colonised habitat to heatwave occurring at other seasons (i.e., winter or autumn) without testing them explicitly.

In both spring and summer “ambient” conditions, oxygen consumption rates and nutrient fluxes were in the same order of magnitude as previously reported within intertidal mudflats of Arcachon Bay (Bernard et al., 2020; Deborde et al., 2008; Delgard et al., 2016). In these habitats, oxygen fluxes are more controlled by densities of benthic macrofauna, and especially of large ecosystem engineer species, through respiration and bioturbation, rather than seasonal temperature changes and organic matter degradation (Delgard et al., 2016; Pascal et al., 2019). These findings align with our results showing that the variability of nutrient and oxygen fluxes was mainly influenced by the presence of NIS, *A. senhousia* and *R. philippinarum*, which explain the major part of the variance between the different cores. This emphasises the major role played by the arrival of *A. senhousia*, taking into account its high respiration rates (Inoue and Yamamuro, 2000) and fast metabolism (Magni et al., 2000).

In spring, significantly steeper slopes of the relationships between oxygen consumption and *A. senhousia* biomass suggest that communities associated with high densities of *A. senhousia* display higher respiration rates in “strong” and “extreme” HWI compared to “ambient” condition (Fig. 3A). Conversely, in summer, oxygen fluxes associated with high densities of *A. senhousia* did not seem to be affected by HWI despite slightly (non-significant) steeper slopes in “strong” and “extreme” HWI compared to “ambient” condition. These results converge with the high tolerance of *A. senhousia* toward heatwaves (Xu et al., 2023a), able to maintain high respiration rates at high water temperatures (30 °C in Inoue and Yamamuro, 2000). In contrast, slightly lower oxygen consumption rates in “extreme” compared to “strong” HWI suggest that, components other than *A. senhousia* (e.g. other macrofauna species, microphytobenthic and microbial communities) are likely negatively affected at this temperature range, resulting in lower respiration rates. Indeed, oxygen consumption rates along with metabolism of the other dominant macrofauna species encountered in the present study, the manila clam *Ruditapes philippinarum*, are known to increase with temperature up to an upper limit identified between 20 and 25 °C above which they decline (Goulletquer et al., 1989; Nie et al., 2017). Such pattern is associated with behavioural mechanisms linked with valve closure (Anacleto et al., 2014), thereby preventing exposure to too severe conditions. This is in good agreement with our results showing that the influence of *R. philippinarum* on oxygen fluxes decreased with HWI in both spring and summer experiments, becoming undetectable above seawater temperature 25 °C (i.e. during “extreme” HWI in spring and both “strong” and “extreme” HWI in summer).

In almost all the tested treatments (except spring “strong” HWI and the summer “ambient” treatments), *A. senhousia* biomass was found as the most important predictor for ammonium and phosphate fluxes (Table 3). This is fully coherent with the high metabolic needs and subsequent excretion rates displayed by this species (Magni et al., 2000). Therefore, this species appears able to dominate and control nutrient processing of intertidal flats through excretion (Bernard et al., 2020; Magni et al., 2014). Consequences of dense *A. senhousia* population development were further exacerbated during spring in “extreme” HWI compared to “ambient” treatment, with significantly steeper slopes of the relationships between both ammonium and phosphate fluxes with *A. senhousia* biomass. Moreover, these effects were noticeably associated

with increases in the explained proportions of variances of fluxes.

Surprisingly, experiments carried out within the spring “strong” HWI and the summer “ambient” conditions did not result in the detection of any significant effects of *A. senhousia* on ammonium nor phosphate fluxes (Table 3). These results could appear somehow controversial given the influence of comparable density gradients of this species, promoting nutrient releases to the water column in all the other tested experimental conditions. They were indeed characterised by lower ammonium and phosphate fluxes on average that resulted from higher numbers of replicates showing influxes of nutrients (negative fluxes directed from the water column to the sediment) (Fig. 3). It suggests that uptake processes of nutrients took place in the sediment that would have been stimulated by increasing *A. senhousia* density and thereby counteracted the otherwise dominant effect of upward fluxes consecutive to excretion. Two non-exclusive, and probably complementary hypotheses could support these results. First, intertidal microphytobenthos can uptake nutrients from the water column in comparable experimental settings (in the dark after an emersion period (Longphui et al., 2009; Thornton et al., 1999)). They would therefore benefit for their growth from increased nutrient release by *A. senhousia* excretion, explaining the observed patterns. Second, sediment microbial communities involved in organic matter remineralisation may be stimulated through habitat alteration caused by *A. senhousia*, which is especially characterised by an enrichment in fine organically rich particles due to biodeposition and the development of byssus cocoons also promoting microbial colonisation and activities (Crooks and Khim, 1999; Moseman et al., 2009; Takenaka et al., 2018). Interestingly, both spring “strong” HWI and summer “ambient” experiments were carried out at similar seawater and mean air temperatures of 22 and 23–24 °C, respectively (Table 1). These temperatures perfectly match with thermal optima (sediment temperature of 20–25 °C) identified in comparable environments for activities and growth of microphytobenthic communities (Blanchard et al., 1997; Savelli et al., 2018), meiofauna (Deldicq et al., 2021) or sediment microbial communities (Joint and Smale, 2017), beyond which they quickly decline. Thereby, in spring, “strong” HWI, while enhancing *A. senhousia* metabolic activities and shifting the system to thermal optima for microbenthos mediated biogeochemical processes, then likely stimulate sediment nutrient influxes and productivity. Conversely, “extreme” HWI occurring at the same season may have inhibited such sediment processes, leading to an exacerbation of the effects of *A. senhousia* enhancing nutrient release to the water column. By contrast, summer “strong” and “extreme” heatwaves, while shifting the system beyond thermal optima inhibiting microbial and microphytobenthic mediated biogeochemical processes, both led to enhanced releases of nutrients to the water column, further enhanced by *A. senhousia* colonisation patterns. Therefore, in intertidal flats colonised by *A. senhousia*, enhanced nutrient releases triggered by heatwaves and combined with the structure created by mussel reefs (Yamamuro et al., 2010) would further favour the development of opportunistic macroalgae (Ohtake et al., 2020) such as the non-native *Gracilaria vermiculophylla* (Bernard et al., 2020; Yamamuro et al., 2010). Moreover, in our experiments *G. vermiculophylla* indeed significantly enhanced natural nitrogen releases to the water column in addition to the effect of *A. senhousia*, despite the fact that these macroalgal biomasses were limited compared to the biomasses recorded in other invaded sites (Cacabelos et al., 2012; Wood and Lipcius, 2022). Such association with another species known to profoundly affect benthic habitats and especially seagrass meadows (Cacabelos et al., 2012; Martínez-Lüscher and Holmer, 2010), therefore, illustrates the facilitation cascading effect recurrent in the case of NIS (Taylor et al., 2015; Thomsen et al., 2013) as another potential consequence of the way global change threatens marine ecosystems. Under combined effect of *A. senhousia* invasion and increasing heatwave occurrence and intensity in the near future, an enhanced development of the invasive algae *G. vermiculophylla* might further negatively affect intertidal *Zostera* meadows already threatened, potentially destabilising the important role of this foundation species in

regulating biogeochemical processes and ecosystem functioning at the longer term (Ward et al., 2022). In the case of another widespread invasive species (i.e., the Japanese oyster *Magalana gigas*), much stronger important ecological impacts have been shown as a result of reef formation. *M. gigas* reefs contain a higher diversity of epifaunal species, but also modify sediment-water fluxes due to the animals metabolisms and high rates of decomposition of biodeposits and associated microbial activity (Herbert et al., 2016).

The high tolerance of *A. senhousia* to heatwave is consistent with responses to thermic stress observed in other mytilid species, such as *Mytilus edulis*, which has a high tolerance to heatwave and metabolic rates only declining above 32–36 °C (King et al., 2024). However, it clearly differs from the co-occurring species *R. philippinarum* which shows a decrease in excretion rates above 20–25 °C (Gouilletquer et al., 1989; Nie et al., 2017). Since species respond differently to increasing temperature (Harvey et al., 2022), future investigations aiming at precisely assessing the relationships between water temperature and metabolic rates (respiration, excretion) of NIS such as *A. senhousia*, as well as the determination of their critical thermal maxima (King et al., 2024) are particularly important to better understand their impact on colonised ecosystem functioning (Bernard et al., 2020; Magni et al., 2006, 2014) within the context of climate warming. However, caution must be made because those CT max could probably also depend on the seasonally-varying physiological state of the organism.

Overall, the results of this study highlight that (1) heatwaves affect oxygen and nutrient exchanges across the sediment-water interface, but also that (2) the magnitude of these effects can be strongly enhanced by increasing densities of the invasive mussel *A. senhousia*. Our study also pointed out (3) the seasonal dependence of these complex relationships. These results emphasise that the interaction between the seasonality of heatwave occurrence, its intensity and the level of colonisation by ecosystem engineering NIS likely shape their consequences for ecosystem functioning. These short-term events can induce consequences of for longer-term nutrient dynamics and benthic-pelagic coupling.

Here, we have only investigated the influence of one short-term heatwave, but multiple scenarios could be considered. Experiments with longer heatwaves may reveal different responses, as well as repeated heatwaves could exacerbate some effects (Kauppi et al., 2023; Pansch et al., 2018). In addition, effects persisting during the recovery period should also be investigated (Ducker et al., 2023; He et al., 2022a). Moreover, since heatwaves often co-occur with other environmental stressors it is crucial to consider potential multiple-stressor interactions (Crain et al., 2008). Future investigations would thus include stressors linked with pollution (Gamain et al., 2018; Polazzo et al., 2022; Zhang et al., 2022), hypoxia (Gruber et al., 2021; Sarà et al., 2021), occurrence of pathogens (Green et al., 2019), etc ... These factors may interact additively, synergistically or antagonistically with heat stress (Smith et al., 2023). Therefore, testing different types of communities, habitat conformations and scenarios appears necessary to assess the resilience of ecosystems to the growing frequency and intensity of both marine and atmospheric heatwaves.

CRedit authorship contribution statement

Marie P.A. Fouet: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Cécile Massé:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Léna Bonnisant:** Writing – review & editing, Methodology, Investigation, Data curation. **Hugues Blanchet:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Olivier Maire:** Writing – review & editing, Conceptualization. **Guillaume Bernard:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Formal analysis, 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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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2025.107560>.

Data availability

Data will be made available on request.

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