



# Thermal regulation of benthic fluxes in temperate estuaries

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**Abstract.** The effects of short-term heatwave extremes on biogeochemical cycling and fluxes in a temperate estuary of a semi-dry climate were studied using an experimental setup of temperature-controlled benthic incubations. The results demonstrated a strong thermal effect, notably under extreme warming events, for shifts in exchanges across the sediment-water interface. Extreme heatwave conditions (+5 °C of the seasonal mean) boosted acidification, hypoxia, and ammonification, due to accelerated remineralization rates, resulting in strong effluxes of NH<sub>4</sub>, Si(OH)<sub>4</sub>, and PO<sub>4</sub> to the overlying water. These excessive nutrient loads may increase eutrophication risk via runoff or tidal action, specifically in adjacent oligotrophic coastal waters. CO<sub>2</sub> production rates reached ~4000 µatm under extreme hypoxia and acidification, 2.3-fold higher than the ambient rate, with a maximal flux of ~27.0 mmol m<sup>-2</sup> d<sup>-1</sup>. Hence, our experiments show that marine heatwaves amplify CO<sub>2</sub> emissions while reducing the CO<sub>2</sub> buffering capacity of temperate estuaries. It emphasizes temperate estuaries as highly sensitive ecosystems to climate change.

## 1 Introduction

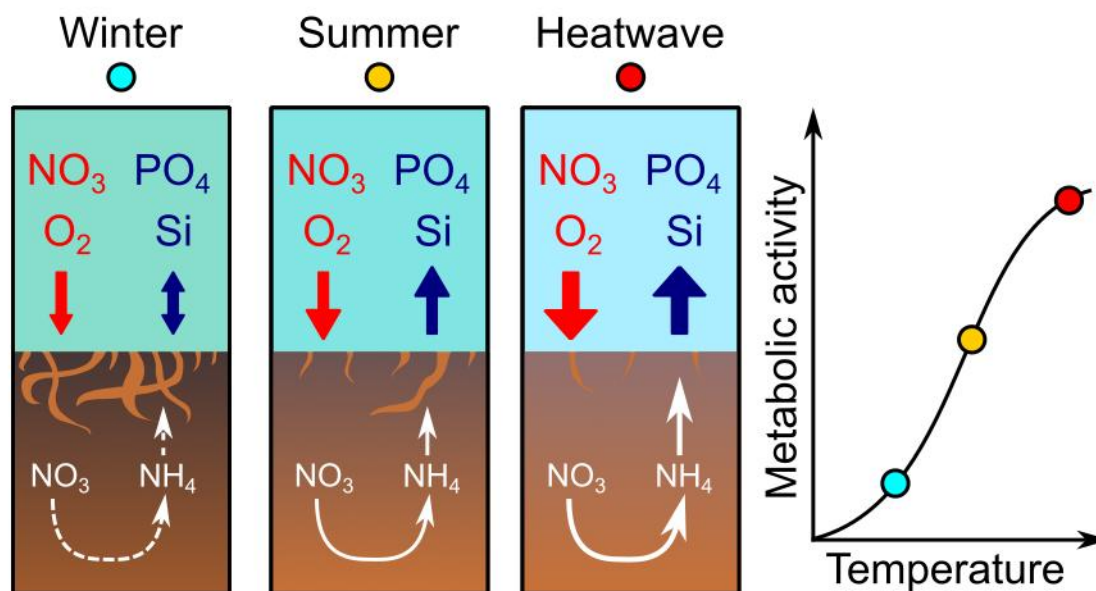
Estuaries play an important role in buffering carbon and nutrients as they transition from land to sea (Borges and Abril, 2011). This makes them a major carbon reservoir and a CO<sub>2</sub> source to the atmosphere, notably in the mid to high latitudes (Laruelle et al., 2010). Yet their shallow depths make them remarkably sensitive to temperature changes, both in the long term with climate change (Prum et al., 2024; Scanes et al., 2020) and in the short term, with extreme events such as heatwaves (Nardi et al., 2025; Tassone et al., 2022). These warming trends and anomalies have a significant, and yet far from fully understood, impact on both nutrient and carbon fluxes from these estuaries, which may, in turn, also affect their adjacent coastal marine ecosystem.

The fundamental hypothesis is that with increasing temperatures, microbial metabolic rates increase (Price and Sowers, 2004), thereby accelerating the remineralization of organic matter (Fig. 1). Moreover, for nutrient-regulating reactions, such as denitrification or ammonia oxidation, temperature exerts a significant effect (Canion et al., 2014). Recent experimental observations, carried out in the mid-to-high latitudes estuaries, have demonstrated the expected metabolic effect as well as the potential impact of warming during heatwaves on carbon fluxes (Douglas et al., 2025; Palmas et al., 2025) and on nutrient fluxes (Fouet et al., 2025; Göbeler et al., 2025).



Yet, these experiments did not account for the microbial likely adaptation to the warmer conditions prevailing in the tropical and sub-tropical regions and other related modifications to the fundamentals of these systems. The Mediterranean Sea, notably the Southeastern Mediterranean Sea (SEMS), already hosts such communities, adapted to higher temperatures and large thermal variabilities (Christaki et al., 2011; Givati, 2020; Marasco et al., 2023), and is experiencing an increase in marine heatwaves (Ibrahim et al., 2021). Additionally, microbes in the SEMS are also adapted to utilize low-abundance, highly refractory organic matter, which characterizes this region (Alkalay et al., 2020; Tselepides et al., 2000). Therefore, this region's extreme environmental conditions establish a framework that could be considered a good model of future anthropogenically modified scenarios to study the impact of heatwaves on coastal ecosystems

This work aims to test the short-term thermal effects of extreme heatwaves on benthic fluxes in an estuary setting in the SEMS region. Following the above hypothesis that metabolic rates would increase with temperature, incubation experiments were carried out in both summer and winter using estuary sediments to evaluate the direction and intensity of fluxes of both nutrients and inorganic carbon.



45 **Figure 1: A conceptual model illustrating the expected research hypothesis with increased nutrient release and oxygen consumption as microbial activity increases with temperature. .**



## 2 Methods

Our experiments were designed to explore the effects of short-term heatwave extremes on biogeochemical cycling in a temperate estuary under semi-dry climate conditions, relative to ambient background conditions. The “ambient-low” (16°C), “ambient-high” (24°C), and “extreme” (35°C) selected temperatures in our experiments realistically represent the mean winter and annual average in the study region (Ibrahim et al., 2021; Ozer et al., 2022), and projected extreme heatwave temperatures based on air temperature at sea level (Wedler et al., 2023). This study's experimental results show a significant thermal effect on the flux magnitude of most solutes, with differences observed across the tested seasons and thermal treatments.

Two experiments were carried out in the scope of this study, one in summer 2025 and one in winter 2026. Sediment samples consisting of dark sandy silt were collected in the Naaman estuary (32.90901°N, 35.08201°E). Within two hours, in the lab, ~100ml of sediment was transferred to 500ml wide-neck bottles, which were prewashed with HCl, then with filtered seawater. The sediment in each bottle was topped to full (no headspace) with filtered fresh coastal seawater. Sets of six (duplicates in summer experiments, triplicates in winter experiments) were placed in water baths. The first set of samples was placed in an ambient bath in a room chilled to 16°C (internal room temperatures oscillated by  $\pm 2^\circ\text{C}$ ); the second set was placed in a covered bath heated to 24°C, while a third set was placed in a covered bath heated to 35°C. These three temperatures represent winter, spring-summer, and heatwave conditions. All baths were tested with a thermometer for consistent temperatures and maintained at the target temperatures with a thermostat-regulated heating element at the bottom of the bath. The experiments were run in a closed internal room with no direct sunlight. The bottles were left for 12h in the baths to equilibrate before measurements began for a total experimental run of 84h for the summer experiment and 90h for the winter experiment. Given the low light availability in estuary waters, these approximate the conditions that would be dominated by heterotrophic activity. Direction and magnitude of oxygen fluxes during dark incubation were shown to be reasonable proxies for the activity and metabolism of heterotrophic microbes (Seidel et al., 2023). For the scope of this work, it should be noted that such heterotrophic processes are more sensitive to thermal shifts than autotrophic metabolism (Göbeler et al., 2025).

Throughout the experiment, a subset of bottles was removed from the baths. Using a syringe, water was removed from the bottles without disturbing the sediment. The bottles were sampled first from the 24°C treatment, then the 35°C treatment, and the 16°C in a room set to 21°C to allow the measurements to occur as close to conditions as possible. Water samples were immediately filtered and subsampled for the different analyses. Two subsamples were used immediately to measure pH and O<sub>2</sub> using a Radiometer, PHM240, and an optical sensor WTW(R), respectively. Nutrient subsamples were collected in sterile 15ml centrifuge tubes and frozen. Samples for pH on a total scale at 25°C and alkalinity were collected in 120 ml dark glass bottles with overflow to minimize atmospheric exposure.



The pH was measured immediately after sampling using a CONTROS HydroFIA pH spectrophotometric system; alkalinity samples (only for winter experiment) were chilled and measured by potentiometric titration using a Methrom 848 Titrino plus system, by the Gran method (Sass and Ben-Yaakov, 1977). For the winter experiment, Total Alkalinity ( $A_T$ ),  $\text{pH}_{\text{Total}}$  at 80 25 °C, and density (for salinity verification) were measured.  $\text{PCO}_2$  was calculated from the measured carbonate properties using CO2Sys 2.1 (Lewis and Wallace, 1998).

Dissolved inorganic nutrients ( $\text{NO}_x$ ,  $\text{NH}_4$ ,  $\text{PO}_4$ , and  $\text{Si}(\text{OH})_4$ ) were determined using a Seal auto-analyzer system, utilizing a colorimetric detection described in prior publications (Sisma-Ventura et al., 2022). The reproducibility of the analyses was 85 determined using certified reference materials (CRM): MOOS 3 and Salt 1 ( $\text{NO}_x$ ,  $\text{NH}_4$ ,  $\text{PO}_4$ , and  $\text{Si}(\text{OH})_4$ ), VKI 4.1 ( $\text{NH}_4$ ), and VKI 4.2 ( $\text{PO}_4$  and  $\text{Si}(\text{OH})_4$ ). Results were accepted when measured CRM's were within  $\pm 5\%$  of the expected values. The limit of detection (LOD) was estimated as three times the standard deviation of 10 measurements relative to the blank (here, low nutrient seawater collected from the offshore surface SEMs). LODs were 9 nM for  $\text{PO}_4$ , 30 nM for  $\text{Si}(\text{OH})_4$ , 50 nM for ( $\text{NO}_x$ ) and 90 nM for  $\text{NH}_4$ . These values are replicable and verified by quality control on nutrient measurements using 90 internal and certified reference standards, as well as participation in international laboratory performance exercises (QUASIMEME).

Statistical analysis was carried out using PAST (Hammer et al., 2001) with verification of some results and plotting done in R Software (Peterson and Carl, 2007; R Core Team, 2024; Wickham et al., 2023). Carbon system parameters were calculated from pH and alkalinity using CO2SYS (Humphreys et al., 2020). All raw values are included in the supplement 95 with specific supplement tables referenced through the text.

### 3 Results and Discussion

#### 3.1 Thermal effect on oxygen and solute fluxes

##### 3.1.1 Thermal regulation of oxygen consumption and acidification

Dissolved oxygen (DO) consumption rates, tracing respiration, were higher in our summer incubations compared to the 100 winter experiment, and higher in the “extreme” and “ambient-high” conditions compared to the “ambient-low” conditions (Fig. 2a and 3a). Average ( $\pm$ SD) oxygen concentration change rate in the summer experiment for ambient-low, ambient-high, and extreme treatments were  $-2.99 \pm 1.51$ ,  $-4.66 \pm 0.77$ , and  $-3.67 \pm 0.81$   $\text{mmol m}^{-2} \text{d}^{-1}$ , respectively. These were higher than in the winter experiment, where the oxygen concentration change rate averaged  $-1.36 \pm 0.4$ ,  $-2.35 \pm 0.82$ , and  $-2.23 \pm 0.39$   $\text{mmol m}^{-2} \text{d}^{-1}$ , respectively (Fig. 4; Table S1). These observations are in line with the expectation that higher respiration 105 rates in temperate estuaries would be thermally controlled under ambient conditions (Apple et al., 2006).

Similar patterns of oxygen consumption were also observed under elevated temperature experiments at higher latitudes. Incubations of intertidal flat sediments (Arcachon Bay, Atlantic coast, S-W France), where in summer experiments, oxygen consumptions measured in the “extreme heatwave” condition (25-29 °C) were significantly higher than “ambient”



condition (17-22 °C), yet not significantly different from their “strong heatwave” conditions (22-26 °C; Fouet et al., 2025).  
110 Likewise, an experimental heatwave setup, using *in situ* chambers over the sandy bay seafloor of the Finnish Archipelago,  
showed higher oxygen consumption in most chambers under heatwave conditions (Göbeler et al., 2025). A moderate  
heatwave boosted oxygen consumption in an experimental heatwave setup on muddy sediments in the Northern Baltic Sea  
estuary. In this setup, however, a strong summer heatwave suppressed oxygen consumption rates (Kauppi and Villnäs,  
2022). Likewise, oxygen consumption rates in our experimental setup were significantly higher in extreme conditions than in  
115 the ambient-low conditions ( $p > 0.05$  in both summer and winter experiments), but not significantly different from “ambient-  
high” conditions (Table S2).

Oxygen consumption during aerobic remineralization is considered a primary driver of bottom acidification and  
hypoxia in estuaries, therefore yielding a strong correlation with pH (Wallace et al., 2014). Our acidification rates were the  
highest in the extreme heatwave conditions (varying between  $-3.1 \times 10^{-3}$  and  $-5.5 \times 10^{-3}$  pH units  $\text{h}^{-1}$  in winter and summer,  
120 respectively) and the lowest in the ambient-low conditions (varying between  $-0.7 \times 10^{-3}$  and  $-1.4 \times 10^{-3}$  pH units  $\text{h}^{-1}$ ; Fig. 2 and  
3) (slope comparison test;  $p < 0.01$  in both seasons; Table S2). The extreme heatwave rates were higher, but not statistically  
significantly different from ambient-high conditions (Table S2). The  $\text{pH}_T$  exhibited strong linear correlation with DO as a  
function of temperature ( $R^2 = 0.87$ ; 0.92, in summer and winter, respectively; Fig. 5), indicating that temperature is the  
primary factor over aerobic remineralization in our estuary system. Indeed, extreme heatwave conditions in our experimental  
125 setup enforced acidification and hypoxia, as observed *in situ* in other temperate estuary systems under annual variability  
(Wallace et al., 2014).

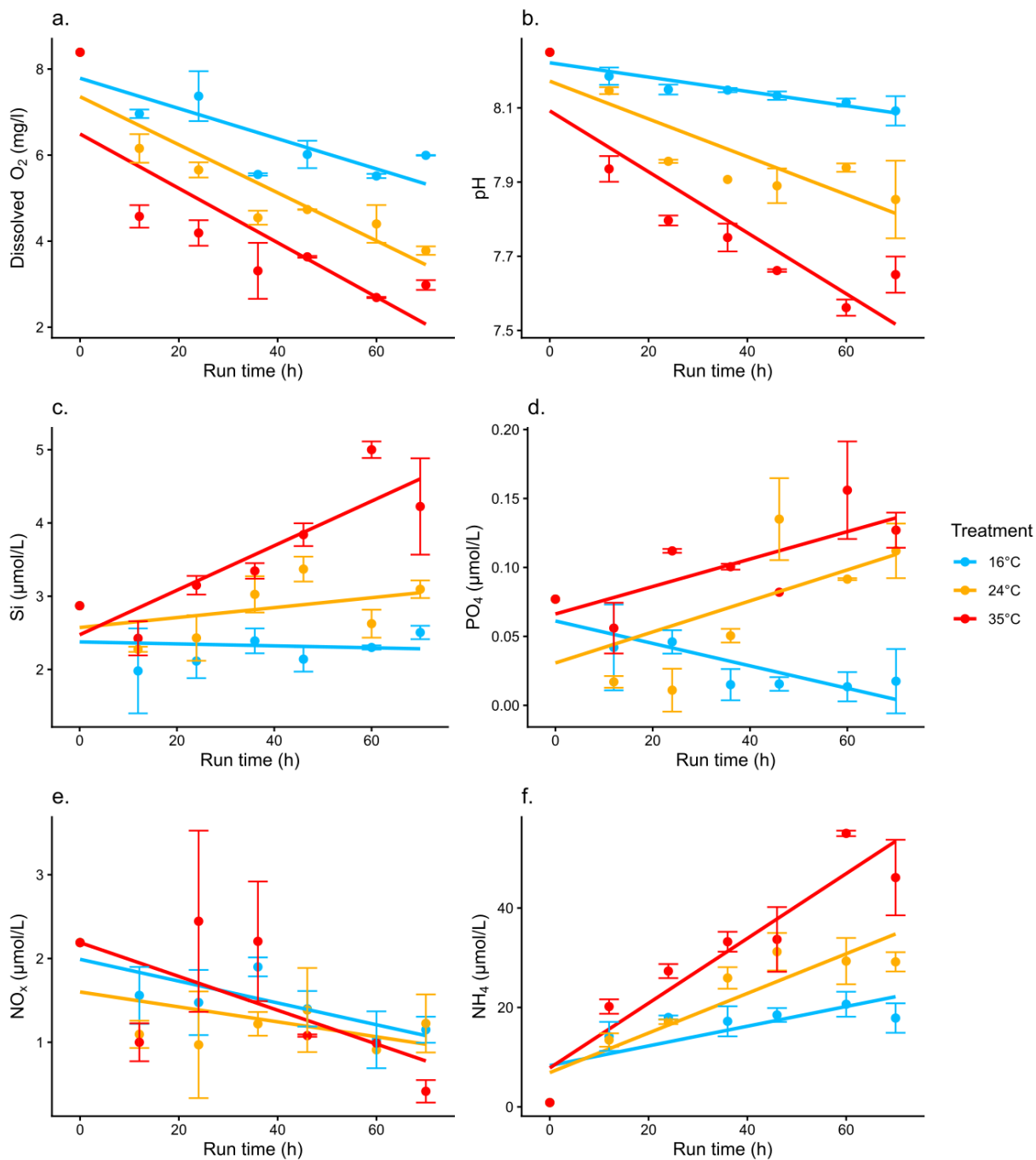
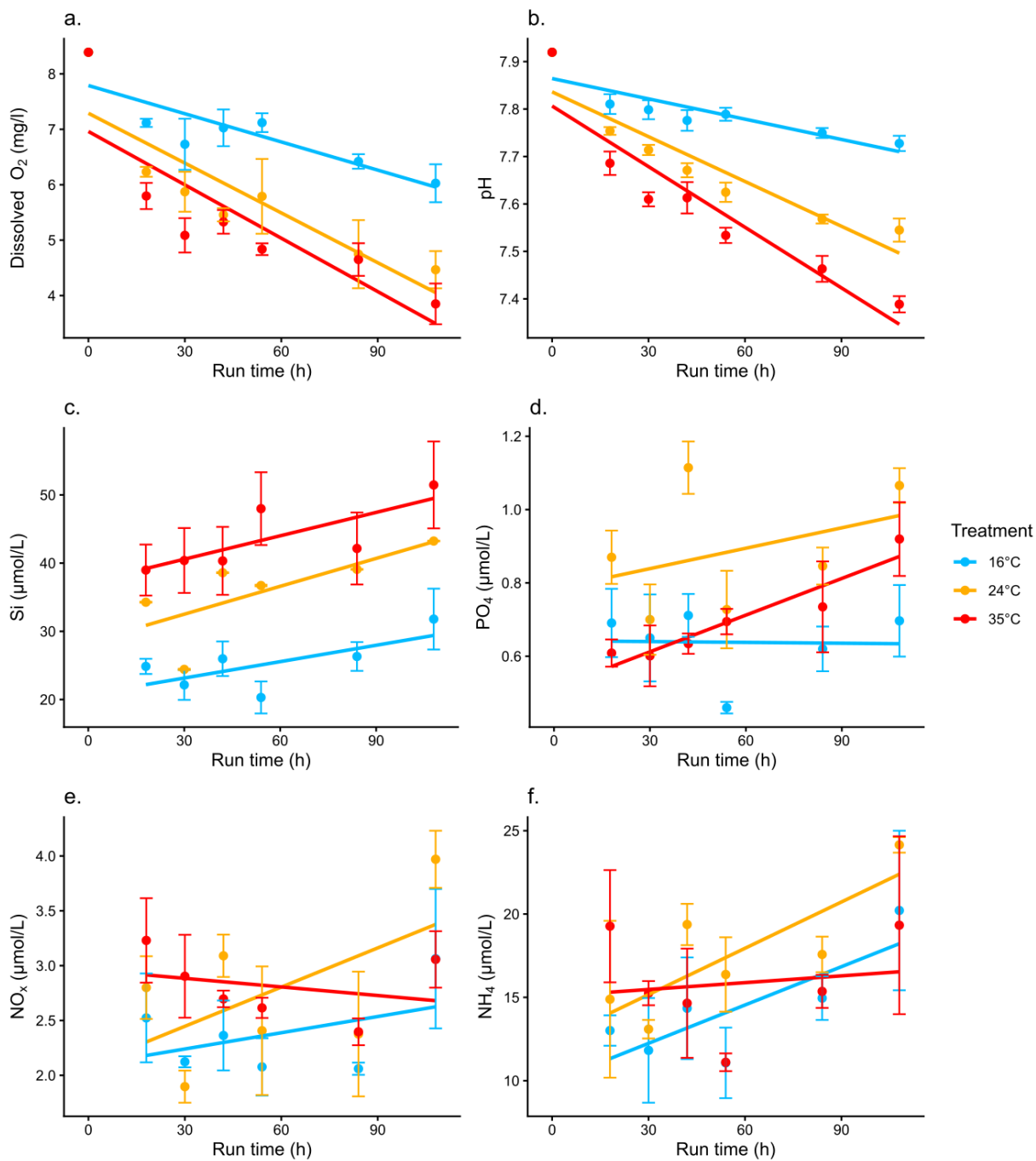


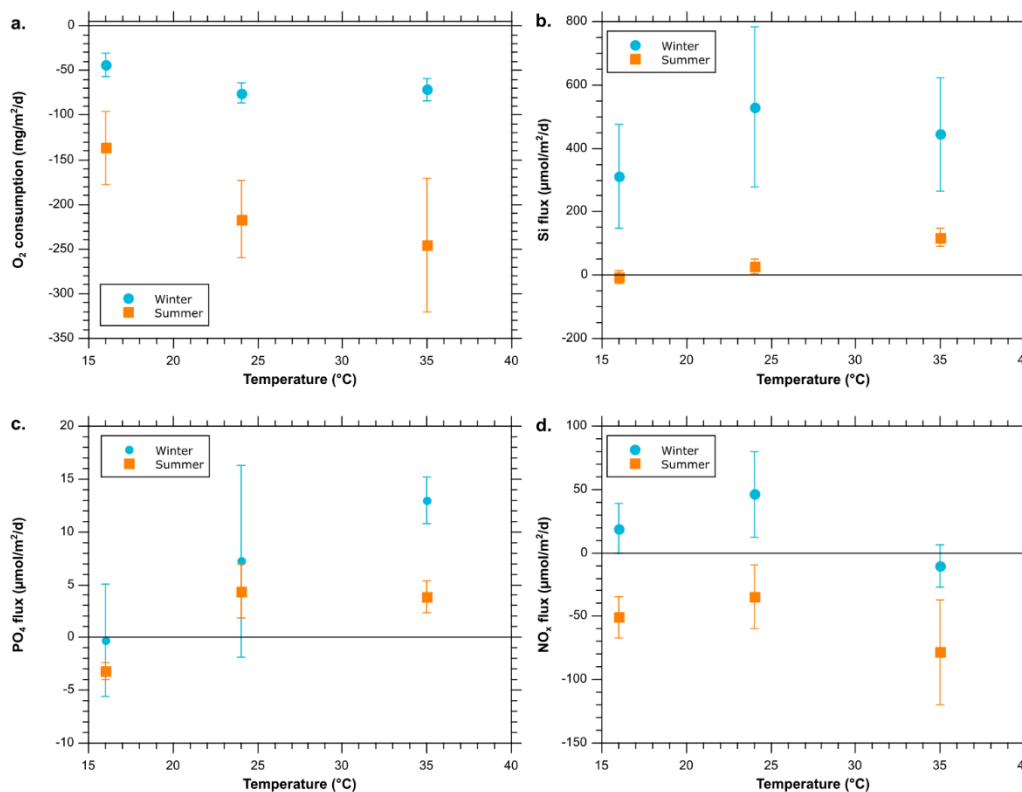
Figure 2: Results of summer experiment showing change in time for a. dissolved O<sub>2</sub>; b. pH, c. Si; d. PO<sub>4</sub>; e. NO<sub>x</sub> and f. NH<sub>4</sub>.



130 Figure 3: Results of winter experiments showing change in time for a. dissolved O<sub>2</sub>; b. pH, c. Si; d. PO<sub>4</sub>; e. NO<sub>x</sub> and f. NH<sub>4</sub>.

### 3.1.2 Thermal regulation of nutrients and CO<sub>2</sub> fluxes

135 Faster metabolic turnover under warming has been observed in microbial communities and can lead to more rapid cycling of  
 organic matter and nutrients (Apple et al., 2006; Middelburg et al., 1993; Segschneider and Bendtsen, 2013). Here, while all  
 nutrients exhibit an increase in flux with temperature, the effects varied between individual nutrients. The initial setting up  
 phase of the system and temperature changes generate a perturbation in the first 24h of the experiments. This is evident by  
 the absence of a common intercept point for most of the nutrients, notably in the winter experiment (Fig. 3c-f). This initial  
 pulse is not captured in detail in this work, as it represents a different mechanism related to the immediate response to the  
 140 perturbation rather than the intermediate-term response investigated here, for which the post-initial-perturbation mode is the  
 baseline.



**Figure 4:** Calculated net fluxes through the experiment for a. O<sub>2</sub>; b. Si; c. PO<sub>4</sub> and d. NO<sub>x</sub>. Note that this is a linearization, whereas during the experiments both release and consumption may occur, notably for NO<sub>x</sub> (Figs. 2e and 3e).

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Both NH<sub>4</sub> and Si(OH)<sub>4</sub> exhibit a very strong thermal effect in both experiments while other nutrients, such as NO<sub>3</sub> + NO<sub>2</sub> (NO<sub>x</sub>) and PO<sub>4</sub>, showed moderate flux shifts (Fig. 4). Summer NH<sub>4</sub> effluxes increased as a function of temperature, from a



rate of  $0.77 \pm 0.30 \text{ mmol m}^{-2} \text{ d}^{-1}$  in the ambient-low condition to a rate of  $1.55 \pm 0.32 \text{ mmol m}^{-2} \text{ d}^{-1}$  and  $2.53 \pm 0.42 \text{ mmol m}^{-2} \text{ d}^{-1}$  in the ambient-high and extreme conditions, respectively (Table S1). Winter  $\text{NH}_4$  effluxes also increased as a function of  
150 temperature, from a rate of  $0.297 \pm 0.217 \text{ mmol m}^{-2} \text{ d}^{-1}$  in the ambient-low condition to a rate of  $0.359 \pm 0.114 \text{ mmol m}^{-2} \text{ d}^{-1}$  and  $\text{mmol m}^{-2} \text{ d}^{-1}$  in the ambient-high conditions, respectively. In the extreme conditions,  $\text{NH}_4$  was firstly removed at a rate of  $-0.812 \pm 0.148 \text{ mmol m}^{-2} \text{ d}^{-1}$ , followed by a net release at a rate of  $0.59 \pm 0.026 \text{ mmol m}^{-2} \text{ d}^{-1}$ .

Significant differences were observed between the  $\text{NH}_4$  effluxes of extreme and ambient-high from ambient-low conditions in summer (slope comparison test;  $p < 0.01$  and  $p = 0.034$ , respectively) but not significantly different in winter (Table S2).  
155 Extreme  $\text{NH}_4$  concentrations (mean =  $35.92$  and median =  $33.45 \text{ }\mu\text{M}$ ) were on average 1.47 fold higher (t-test,  $p < 0.05$ ) than the ambient-high concentration (mean =  $24.35$  and median =  $27.55 \text{ }\mu\text{M}$ ), yet their fluxes were not significantly different (slope comparison test,  $p < 0.05$ ). The strong negative covariance between  $\text{NH}_4$  release and oxygen consumption in our experiments (polynomial fit,  $R^2 > 0.9$ ; Fig. 5), as well as the acidification trend (polynomial fit,  $R^2 = 0.88$ ), was observed only in summer. Both of which support  $\text{NH}_4^+$  release from organic matter oxidation via anaerobic respiration (Devol and  
160 Abraham, 1993).

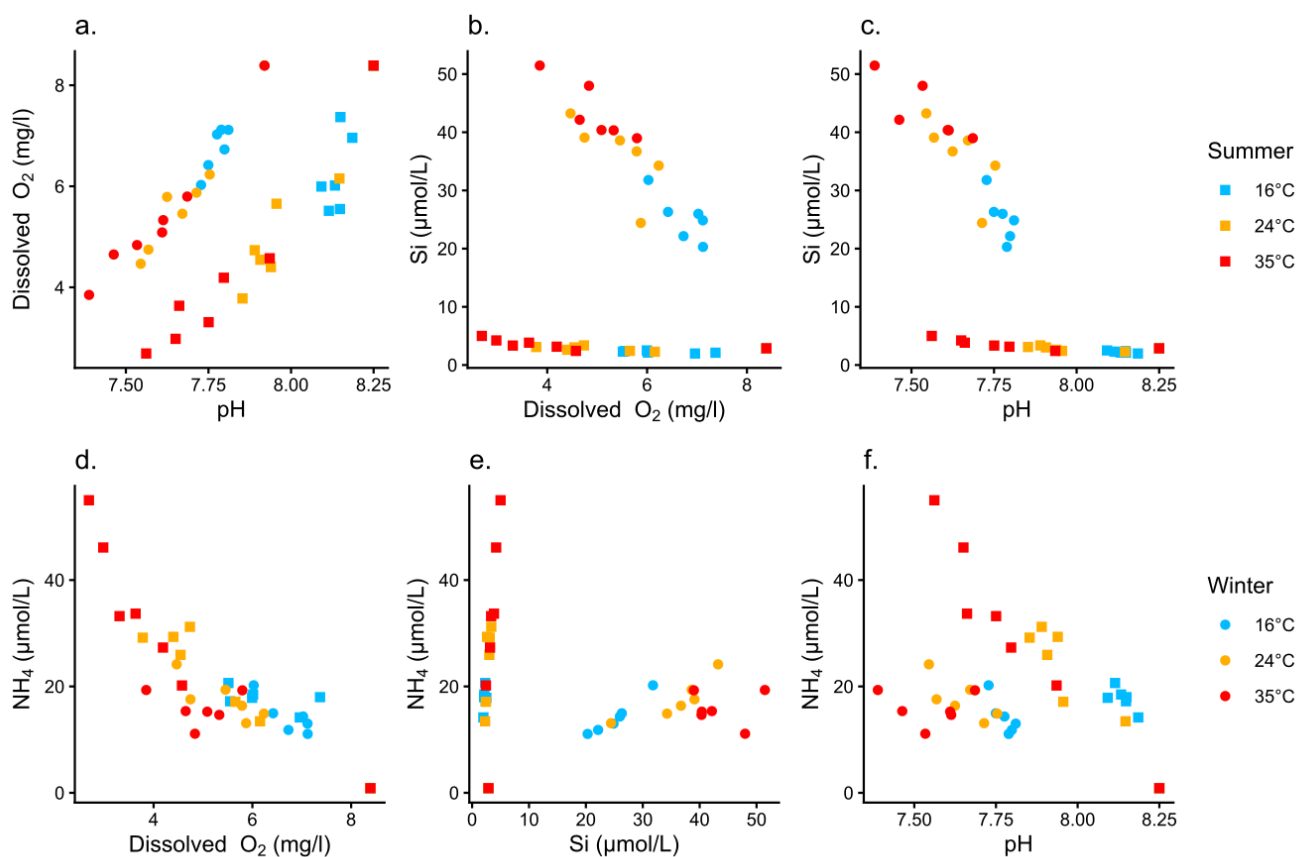
Unlike the effluxes of  $\text{NH}_4$ ,  $\text{NO}_x$  fluxes were variable in their magnitude and direction. In summer experiments,  $\text{NO}_x$  intake rate to the sediment was observed under extreme ( $-73.7 \pm 58.3 \text{ }\mu\text{mol m}^{-2} \text{ d}^{-1}$ ) and ambient-low ( $-37.1 \pm 20.3 \text{ }\mu\text{mol m}^{-2} \text{ d}^{-1}$ ) conditions. In comparison, the ambient-high conditions resulted in efflux to the overlying water ( $5.4 \pm 15.3 \text{ }\mu\text{mol m}^{-2} \text{ d}^{-1}$ ). In the winter experiment, while both ambient-low and ambient-high conditions resulted in a net release of  $\text{NO}_x$  to the  
165 overlying water ( $19.04 \pm 19.82$  and  $46.64 \pm 34.98 \text{ }\mu\text{mol m}^{-2} \text{ d}^{-1}$ , respectively), the extreme conditions yielded a net intake to the sediments ( $-10.1 \pm 16.7 \text{ }\mu\text{mol m}^{-2} \text{ d}^{-1}$ ). This  $\text{NO}_x$  intake by the sediments under extreme heatwave conditions supports anaerobic organic matter oxidation via denitrification (Devol and Abraham, 1993), Fig. 4). Hence, the model of nitrogen cycling in our experimental setup supports strong  $\text{NH}_4$  production during organic matter decomposition. The  $\text{NH}_4$  flux being 26-fold higher than the  $\text{NO}_x$  flux excludes denitrification being a major source of  $\text{NH}_4$  and necessitates an external source of  
170 nitrogen being degraded, such as amino acids. This decomposition could be by anaerobic oxidation of organic matter under an extreme heatwave, which had superimposed further oxidation to  $\text{NO}_3$  via denitrification (Devol and Abraham, 1993). The observed pattern (Figs. 2e, 3e-f) indicates both consumption and release of  $\text{NO}_x$  and ammonia through the experiment in both winter and summer. These may indicate a change in the microbial community function through the course of the experiment, notably in the extreme heatwave conditions.

Anaerobic oxidation of organic matter under extreme heatwaves can also explain the  $\text{Si}(\text{OH})_4$  fluxes in our  
175 experiments. In the summer experiment,  $\text{Si}(\text{OH})_4$  effluxes from the sediments to the overlying water were highest at the extreme heatwave conditions ( $144.9 \pm 33.8 \text{ }\mu\text{mol m}^{-2} \text{ d}^{-1}$ ), while the ambient-low conditions were lowest ( $28.1 \pm 10.13 \text{ }\mu\text{mol m}^{-2} \text{ d}^{-1}$  Fig. 4; Table S1). A nearly significant difference ( $p = 0.06$ ) was also observed between the extreme and the ambient-high  $\text{Si}(\text{OH})_4$  effluxes ( $46.5 \pm 29.94 \text{ }\mu\text{mol m}^{-2} \text{ d}^{-1}$ , Table S1). Much higher concentrations of  $\text{Si}(\text{OH})_4$  were measured during  
180 the winter setup (Figs. 2 and 3). Specifically, winter  $\text{Si}(\text{OH})_4$  concentrations (mean =  $34.95 \pm 9.16 \text{ }\mu\text{M}$ ) were, on average, 12-



185 summer.

fold higher than summer concentrations (mean =  $2.81 \pm 0.79 \mu\text{M}$ ). Summer  $\text{Si}(\text{OH})_4$  fluxes further support thermal regulation of silica fluxes, yet at much lower magnitudes (Fig. 2; Table 2).  $\text{Si}(\text{OH})_4$  fluxes were tightly related to  $\text{NH}_4$  fluxes ( $r > 0.5$ ), indicating the recycling of biogenic silica is also important in summer (Fig. 5). This suggests strong recycling of biogenic silica, most likely due to diatom blooms in the spring (thus, absent in winter) that progressively decay in the



**Figure 5:** Cross plots of dissolved O<sub>2</sub>, pH, dissolved Si, and dissolved NH<sub>4</sub>; blue for the 16°C treatment, yellow for the 24°C treatment, and red for the 35°C treatment. Circles are used for the winter experiment and squares for the summer experiment. a. pH vs. O<sub>2</sub>; b. O<sub>2</sub> vs. Si; c. pH vs. Si; d. O<sub>2</sub> vs. NH<sub>4</sub>; e. Si vs. NH<sub>4</sub>; f. pH vs. NH<sub>4</sub>.

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PO<sub>4</sub> effluxes from the sediment to the water were observed in both seasons under extreme ( $12.96 \pm 2.19$  and  $4.59 \pm 2.09 \mu\text{mol m}^{-2} \text{d}^{-1}$ , in winter and summer, respectively) and ambient-high ( $7.22 \pm 9.05$  and  $7.49 \pm 2.6 \mu\text{mol m}^{-2} \text{d}^{-1}$ ) conditions compared to the ambient-low conditions influx to the sediment ( $-0.29 \pm 5.34$  and  $-2.09 \pm 0.81 \mu\text{mol m}^{-2} \text{d}^{-1}$ ). This agrees well with other observed nutrient fluxes, particularly ammonium, phosphate, and silicate, under heatwave conditions,

195 both here and across different heatwave experimental settings (Fouet et al., 2025; Kauppi and Villnäs, 2022). It is indicative



of both increased diffusion rates and higher metabolic activity of organisms at higher temperatures, as well as increased degradation processes (Kauppi and Villnäs, 2022). Our results support that extreme heatwaves can accelerate the decomposition of bloom depositories in the sediments or downstream transported organic matter and enhance nutrient fluxes to the overlying water.

200 This massive perturbation from extreme heatwaves will be accompanied by strong CO<sub>2</sub> degassing into the atmosphere (Wallace et al., 2014). This stands in somewhat contrast to open marine systems, in which net CO<sub>2</sub> degassing decreases due to marine heatwaves (Mignot et al., 2022). Indeed, the global estuaries' CO<sub>2</sub> emission to the atmosphere is a significant component in the global carbon cycle (Borges and Abril, 2011). As expected, *p*CO<sub>2</sub> concentrations showed a strong thermal regulation, with a production rate of 21.9 ± 1.69, 9.47 ± 0.76, and 1.97 ± 0.23 μatm h<sup>-1</sup> in the extreme, ambient-high, and ambient-low conditions, respectively (*p* < 0.01). In the extreme heatwave conditions, *p*CO<sub>2</sub> levels reached 4000 μatm. Thus, extreme heatwaves are expected to release massive amounts of CO<sub>2</sub> to the atmosphere. Comparable and even higher *p*CO<sub>2</sub> values were measured in different estuary systems (Borges and Abril, 2011). *p*CO<sub>2</sub> at 25°C was calculated to distinguish the thermal effect on partial pressure, and the effect of anaerobic respiration under extreme heatwaves (Fig. 6). The thermal effect on partial pressure explains about 25.0% of the *p*CO<sub>2</sub> efflux; the rest is attributed to anaerobic respiration.

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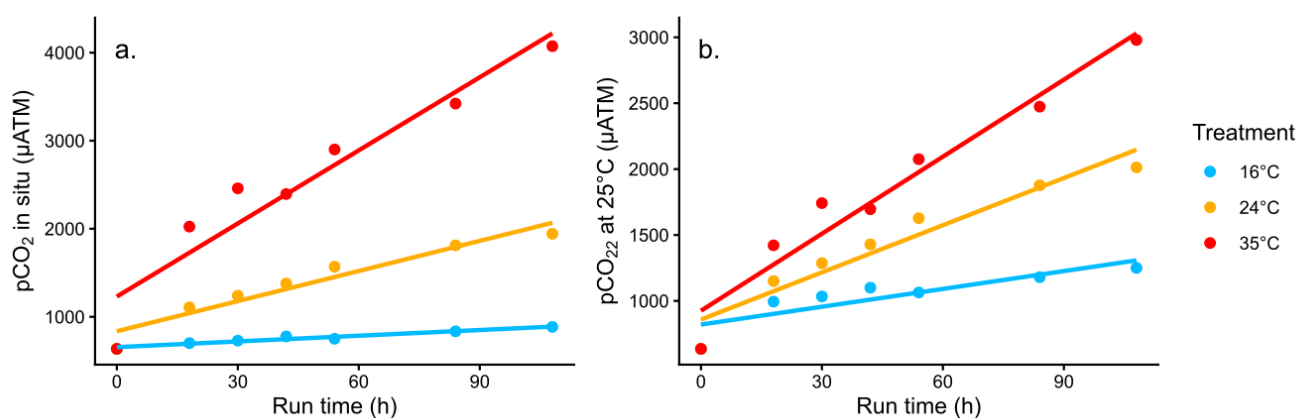


Figure 6: pCO<sub>2</sub> change with time for the winter experiment for (a.) in situ temperatures and (b.) corrected to 25°C.

### 215 3.2 Thermal effect on estuary biogeochemical cycles in a fast-warming region

Despite their relatively small footprint (Laruelle et al., 2025), estuaries are a major global sink for carbon (Borges and Abril, 2011; Deb and Mandal, 2021; Pusceddu et al., 2003). As shallow confined water bodies, they are also highly sensitive



systems to temperature anomalies (Ahmed et al., 2025; Des et al., 2025). Estuaries in the Mediterranean region are typically shallow, inherently stratified, with a limited buffer capacity to withstand the effects of increasing air temperatures (De Vicente, 2021; Vidussi et al., 2011). Traits that make them particularly vulnerable to climate change-induced heatwaves (Palmas et al., 2025). Since temperature strongly affects the rates of biochemical reaction, strong temperature anomalies, such as heatwaves, could alter the direction and magnitude of benthic fluxes, particularly in sensitive water bodies, such as estuaries and lagoons (Fouet et al., 2025; Göbeler et al., 2025; Kauppi and Villnäs, 2022; Palmas et al., 2025; Pansch et al., 2018). Indeed, our experimental results demonstrate a strong thermal effect, notably in extreme warming, for shifts in exchanges across the sediment-water interface. The setup used here focused in particular on the sediment, which presents one side of the interaction, with prior experiments also demonstrating effects in the water (Douglas et al., 2025; Palmas et al., 2025). The net effect of marine heatwaves profoundly altered the biogeochemistry of temperate estuaries. Despite the wide ambient temperature range of  $\sim 15$  °C (reaching over 30°C in summer height) at the current study site, a clear effect of the extreme can still be observed. Extreme heatwave conditions in our experimental setup boosted acidification, hypoxia, and ammonification, due to accelerated remineralization rates. Well in line with expectations (Apple et al., 2006; Hopkinson and Smith, 2005), notably for anaerobic reactions, but possibly also aerobic ones. Local estuaries in this region have varied oxygen levels, depending on their depths and organic matter load (Bar-Zeev and Rahav, 2015; Suari et al., 2019). Oxygen level in the course of the experiments here also allows for aerobic remineralization, notably of dissolved organic matter, which is high in local estuaries in summer and promotes high bacterial activity (Bar-Zeev and Rahav, 2015). Fungi, highly abundant in the local river mouth (Rubin-Blum et al., 2022), may also contribute to remineralization.

Our experimental results show that increased remineralization of winter depositories, including diatoms, under extreme heatwave conditions may accelerate the effluxes of  $\text{NH}_4$ ,  $\text{Si}(\text{OH})_4$ , and  $\text{PO}_4$  to the overlying water. These excessive nutrient loads may trigger eutrophication in adjacent oligotrophic coastal waters via runoff or tidal action (Karydis and Kitsiou, 2012; Padedda et al., 2019). Extreme heatwave conditions in our experimental setup also enhanced denitrification rates and  $\text{NO}_x$  removal by the sediments. This is despite the fact adjacent estuary in the Qishon has been reported to host heterotrophic nitrogen fixation (Geisler et al., 2020). Moreover,  $\text{NH}_4$  production, mostly due to organic matter oxidation, resulted in a 26-fold higher flux over that of  $\text{NO}_x$ , suggesting there is no tight recycling of nitrogen in the system. Strong covariance between oxygen consumption (or acidification) and the effluxes of  $\text{NH}_4$  and  $\text{Si}(\text{OH})_4$  further supports enhanced organic matter recycling, under extreme heatwaves, while emphasizing diatom bloom deposits as a major source of nutrients and carbon in the current study (Roberts, 2006).

More profoundly, increased anaerobic remineralization of depository organic matter in estuaries under extreme heatwaves can potentially affect the storage of blue carbon (Palmas et al., 2025) by increasing estuaries' contribution of  $\text{CO}_2$  emissions to the atmosphere (Borges and Abril, 2011; Douglas et al., 2025). Here, the effect of increase in  $\text{pCO}_2$  can be shown to be significant between the treatment even when correcting for the thermal effect on solubility (Fig. 6). Anticipated global warming will increase the frequency, intensity, and duration of marine heatwaves (Palmas et al., 2025), therefore



severely impairing the ability of coastal water bodies to store organic carbon (Douglas et al., 2025). Indeed, CO<sub>2</sub> production in our experimental heatwave conditions reached ~4000 μatm under extreme hypoxia and acidification, 2.3-fold higher than the ambient rate. This translates into a maximal daily flux of 27.13 mmol m<sup>-2</sup> d<sup>-1</sup> for an average wind speed of ~ 4.0 m s<sup>-1</sup> and atmospheric CO<sub>2</sub> of 420 ppm. For comparison, the maximum estuary daily flux was 11.708 mmol m<sup>-2</sup> d<sup>-1</sup> for ambient-high  
255 conditions. The CO<sub>2</sub> flux of adjacent coastal water is 6.2 mmol m<sup>-2</sup> d<sup>-1</sup> during the warm season (Sisma-Ventura et al., 2017). Hence, our experiments show that marine heat waves amplify CO<sub>2</sub> emissions to the atmosphere while reducing the CO<sub>2</sub> buffering capacity of temperate estuaries. Nevertheless, further studies are needed to better understand changes in biogeochemical cycling in coastal systems, including estuaries under global warming and marine heat waves. Specifically, studies that focus on the fate of greenhouse gases and carbon storage in fast-warming regions are urgently needed, as well as  
260 those looking at the downstream effects as the modified waters from the estuary continue into coastal waters.

#### 4 Conclusions

Temperature asserts a significant impact on remineralization in estuary sediments. This effect is expected to be enhanced with climate change and peak during heatwaves. The effects of this remineralization affect both nutrient budgets and carbon budgets in temperate estuaries (Fig. 1). This calls for further consideration of these effects on the estuary habitat, as well as its adjacent coastal environments.  
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#### Code and data availability

All code and data relevant for this study are included in the supplement.

#### Author contributions

270 OMB and GSV jointly carried out the conceptualization, methodology development, sample acquisition, experimental operation, formal analysis, and writing. Visualization and code writing were carried out by OMB.

#### Competing interests

The authors declare that they have no conflict of interest.



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