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# Infaunal bivalves exhibit resilience to ocean acidification but remain sensitive to food supply

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Soft-sediment habitats are crucial for marine coastal ecosystems, supporting diverse biodiversity both above and below the sediment. Ocean acidification, driven by rising CO<sub>2</sub> and nutrient influx, enhances heterotrophic metabolism, raising CO<sub>2</sub> levels and lowering pH. These alterations complicate the dynamics of tidal flat, emphasizing the need for further research into their impact on biodiversity. Within these ecosystems, deposit- and suspension-feeding bivalves play crucial roles. *Tagelus dombeii*, a bivalve mollusc found in soft sediments, exhibits burrowing behavior linked to food supply and is of significant commercial value in southern Chile. This study assessed the response capacity of *T. dombeii* to key stressors associated with global ocean change, such as ocean acidification and food availability. Our results revealed significant differences in pH levels between the water column and pore water from the sediment in experimental mesocosms. *T. dombeii* was affected by ocean acidification and food availability in terms of its morphological traits (i.e. length, width, height and growth rate), while oxygen consumption was influenced only by the interaction between acidification and food supply. Notably, heart rate remained constant but increased when food supply was low. Our study suggests that *T. dombeii* exhibits partial tolerance to variations in seawater pH and carbonate chemistry, possibly due to its natural exposure to acidic pore water, but it is sensitive to food availability. These plastic physiological responses suggest that *T. dombeii* may be less vulnerable to future global change scenarios, demonstrating potential resilience and ecological success in its natural habitat.

## KEYWORDS

razor clam, mollusc, metabolism, heart rate, tidal flat, mesocosm, sediments, global change

## Introduction

The shallow seas found in coastal areas are highly valued ecosystems, ranking higher than open ocean systems, primarily because of their critical role in storing and cycling essential elements and nutrients (biogeochemical cycling) such as Carbon,  $\text{CaCO}_3$ , nitrogen, and phosphorus (Bendell et al., 2014; Kessouri et al., 2021; Iram et al., 2022). Soft-sediment habitats play a vital role in the functioning of marine coastal areas (Clements and Hunt, 2017). These habitats harbor a significant amount of marine biodiversity both above (epifaunal) and below (infaunal) the sediment surface, including various deposit-feeding and suspension-feeding bivalves (Van Colen et al., 2020). Tidal flats are notable for their infaunal inhabitants, which actively burrow into the mud and act as ecosystem engineers by shaping their surrounding microenvironment (Wetthey and Woodin, 2022; Salas et al., 2022). These infauna organisms encompass a diverse array of species, including molluscs, worms, and crustaceans (Jaramillo et al., 2007; Singer et al., 2023). According to Murray et al. (2019), global tidal flats have experienced a loss of 16% in their extent from 1984 to 2016, amounting to over 20,000  $\text{km}^2$ . These impacts are overlapped with global environmental drivers that are undergoing significant changes, including ocean warming (OW), ocean acidification (OA), and deoxygenation (DO).

The progressive escalating levels of atmospheric  $\text{CO}_2$  driving ocean acidification, combined with the substantial influx of nutrients into coastal regions through upwelling (Torres et al., 2011) or large river systems (Liu et al., 2021) can amplify heterotrophic metabolism. This, in turn, leads to amplified  $\text{CO}_2$  levels in the water column and exacerbates declines in pH (Carlton et al., 2023). These combined factors contribute to the intricate and ever-changing dynamics of tidal flat ecosystems, emphasizing the ongoing need for research and conservation efforts in these unique habitats. Emerging trends in ocean acidification, driven by high emissions in the 21<sup>st</sup> century, are projected to exacerbate atmospheric  $\text{CO}_2$  concentrations, which are expected to surpass 500 parts per million and result in a doubling of ocean heat uptake – levels significantly higher than those observed over the past 420,000 years, a period during which most extant marine organisms evolved (Hoegh-Guldberg et al., 2007; Gleckler et al., 2016).

Shallow-water sediments play crucial roles in the global carbonate cycle as they serve as a significant reservoir of  $\text{CaCO}_3$  (Andersson and Mackenzie, 2004). These sediments can react to the decreasing saturation state of seawater, releasing alkalinity into the overlying water column. The impact of sediment shell hash on the productivity of infaunal bivalves is still unclear and requires further investigation. The saturation state of calcium carbonate ( $\text{CaCO}_3$ ) in seawater is a key driver of shell formation and preservation in marine invertebrates, as it directly influences their ability to deposit calcium carbonate (Barclay et al., 2020). However, this process is also strongly affected by environmental hypercapnia, which reduce carbonate ion availability and thus lower the  $\text{CaCO}_3$  saturation state. As a result, hypercapnia can indirectly impair calcification. Indeed, long-term exposure to high  $p\text{CO}_2$  has been associated with reduced growth and/or calcification rates in several marine taxa, including mussels (Michaelidis et al., 2005; Navarro et al., 2013;

Leung et al., 2022), echinoderms (Asnicar and Marin, 2022), and coral species (Hoegh-Guldberg et al., 2007; Leung et al., 2022; Rathbone et al., 2022). Species with greater tolerance to such conditions often display high metabolic rates, mobility, and activity levels (Medeiros and Souza, 2023). Overall, ocean acidification has been recognized as a significant threat to marine mollusks, including infaunal bivalves (Gazeau et al., 2013; Martel et al., 2022). However, these effects are often described predominantly within the context of water column acidification, overlooking or with comparatively fewer attention on the drastically different pH and carbonate system conditions that infaunal species experience below the sediment-water interface. Consequently, it is often assumed that infaunal organisms are more resilient to ocean acidification (Widdicombe et al., 2011), and several studies support their apparent tolerance to changes in seawater pH and carbonate chemistry (Vlaminck et al., 2023). However, other research has shown that sediment acidification can negatively affect infaunal organisms, particularly marine bivalves (Hu et al., 2014; Clements et al., 2016; Martel et al., 2022; Vlaminck et al., 2023).

Food supply is a factor that could potentially lead to detrimental effects on marine invertebrates, in addition to other global change effects such as ocean acidification (Lawrence et al., 2015; Flombaum and Martiny, 2021; Kwon et al., 2022). Food supply for bivalves depends on marine phytoplankton which contributes roughly 50% of global net primary production (Field, 1998), while for deposit feeders bivalves obtain their food from organic particle settling from water column, biodeposits and/or detritus (Navarro et al., 2008). A recent analysis of a 26-year time series of spatially averaged monthly mean chlorophyll-*a* (Chl-*a*) concentrations in the Southern Pacific Ocean revealed that the largest deviations in Chl-*a* were closely associated with El Niño–Southern Oscillation (ENSO) events, as evidenced by the strong correspondence between Chl-*a* anomalies and the Multivariate ENSO Index (Johnson and Lumpkin, 2024). These fluctuations underscore the central role of ENSO-driven variability in modulating nutrient availability, both through altered oceanographic circulation patterns and the disruption of coastal upwelling systems, which are otherwise critical sources of nutrient input sustaining primary productivity in this region. Furthermore, in the tidal flats, the intensified urbanization of coastal habitats has led to a significant degradation of food-web complexity and ecosystem services due to multiple stressors (Eriksson et al., 2010; Christianen et al., 2017). While the combined effect of both factors (OA and food supply) is not widely discussed in the literature, some studies have examined this effect in mollusks. Studies on the effect on oyster larvae (see Hettinger et al., 2013) have shown that a combination of high  $p\text{CO}_2$  levels and low food supply results in reduced physiological performance. However, this effect occurs independently for each factor and is not additive. It is of vital importance to mention that food supply plays a crucial role in determining an organism's response to stressful situations, with significant implications for shell-forming mollusks (Ramajo et al., 2016a, 2019; Harayashiki et al., 2020). Therefore, we hypothesized that increased food supply would mitigate the negative effects of acidification in infaunal bivalves.

The tidal flats of southern Chile are characterized by the presence of numerous species of bivalve molluscs, many of which are of commercial importance (Clasing et al., 1994; Navarro et al., 2008). Several species of bivalves coexist at the lower intertidal of large tidal flats located in the enclosed or inland coast of the northern area of the North-Patagonic archipelagos on the Chilean coast (ca. 40–42°S): *Tagelus dombeii* (Lamarck), *Tawera gayi*, *Ameghinomya antiqua*, *Semele solida*, *Gari solida*, *Mytilus chilensis*, and *Zemysina inconspicua* (see Stead et al., 2002; Jaramillo et al., 2007). In general, studies have shown that sediments with higher densities of bivalves, particularly those where deep burrowers are most abundant, exhibited greater species richness and higher densities of macroinfauna (Stead et al., 2002; Jaramillo et al., 2007). The majority of eulamellibranch bivalves (i.e. *T. dombeii*) engage in suspension feeding while deposit-feeding behavior has only been observed in the Tellinacea and Lucinacea species (Morse and Zardus, 1997; Lardies et al., 2001; Navarro et al., 2008).

In this study, we investigated the effects of ocean acidification and food supply on the morphological traits and physiological performance of the razor clam *T. dombeii* (Lamarck, 1818), which coexists with the bivalve community in the sandflats of Coihuin, Reloncavi Sound (41°29'S, 72°54'W).

## Material and methods

### Sampling of organisms and mesocosm setup

During spring, 100 juvenile individuals of *Tagelus dombeii* (Lamarck, 1818) (Tellinacea: Solecurtidae) with a mean of 18 mm in length, 7 mm in width, and 3 mm in height, which is below the reported size at sexual maturity (40–50 mm in length; Lépez et al., 1997; Sánchez et al., 2003), were collected from the soft sediments of the Coihuin tidal flat (41°29' S, 72°54' W), located 8 km southeast of Puerto Montt, Los Lagos Region, Chile (see Supplementary material Figures 1). Sea surface temperature follows a seasonal pattern at Coihuin, with the lowest values occurring during the winter months (8°C), increasing towards the summer maximum in January (17°C; Urrutia et al., 2001; Lardies et al., 2001). Near the sampling site, the spectral exponent ( $\beta$ ) of seawater chemical parameters is -1.703 for temperature, -1.584 for salinity and -1.206 for pH indicating high unpredictability dominated by random short-term environmental fluctuations compared with near locations (see Castillo et al., 2024 for details). In contrast, the porewater at a depth of 5 cm in the sediment of the Coihuin tidal flat, during November, has a temperature of 13.19°C, pH of 7.72, and salinity of 30.66 (Lardies et al., unpublished data). The intertidal sediment of Coihuin tidal flat is predominantly sandy (93.81%), and the content of mud (particles < 63  $\mu$ m diameter) is low in Coihuin, with an annual average of 1.83% (Lardies et al., 2001). Observed organic matter content is low (0.68%), and in the biogenic aggregates (i.e. detritus, phytoplankton, and bacteria) that represented an 0.58% (Lardies et al., 2001). The individuals were transported under humid conditions to the

laboratory. No mortalities were recorded during transport. In the laboratory, individuals were acclimated for three days in a “common garden” aquarium containing filtered natural seawater at 12°C (32 ppm salinity, 12D:12N photoperiod), with daily feeding of microalgae, to minimize stress responses associated with transportation. Due to their small size and delicate shells, individuals were not marked to avoid causing harm or shell damage to the animals.

For the mesocosm experiment, random groups of 4 individuals were created and assigned to each 9-liter aquariums for an experimental trial of 67 days. Each aquarium was filled with 6 cm of commercial quartz sand (<https://dondecapo.cl/project/cuarzo-32/>) across the entire bottom and filled to its total capacity with filtered and UV-sterilized natural seawater (see Martel et al., 2022). It is necessary to use inert material to avoid potential effects of sediment altering the chemical properties of the water, such as pH or alkalinity (Brenner et al., 2016). Water and pore water were measured prior to the experiment for all the 16 aquariums to ensure that the system was within the desired environment condition values.

The assigned treatments included levels of acidification and food supply, simulating CO<sub>2</sub> concentration scenarios with a current scenario of 500  $\mu$ atm and a future scenario of 1500  $\mu$ atm (pH = 8.0 and 7.5, respectively; described in Navarro et al., 2013; Vargas et al., 2017). The food source used was microalgae (see below) and was assigned as either optimal or restricted food, relative to the individual's dry weight. As reported by Navarro et al. (2008), the optimal food level corresponds to 4% of individual's dry weight, while the restricted food level corresponds to 1%. Each aquarium was assigned to one of the 4 treatments, that are: 500  $\mu$ atm – 1% food supply, 500  $\mu$ atm – 4% food supply, 1500  $\mu$ atm – 1% food supply and 1500  $\mu$ atm – 4% food supply.

During the experimental period, razor clams were fed daily following this relationship with their dry weight (1% and 4%), using Reef Blizzard-O suspension (Brightwell® Aquatics) diluted in 10 mL of filtered and UV-sterilized seawater. All aquariums were monitored daily for mortality without replacement in case of death, reconsidering the food amount per aquarium. Water in all aquariums was renewed twice per week to maintain appropriate conditions. At the end of the experiment, the morphological and physiological measurement were taken from the individuals that survive and then were sacrificed.

Additionally, one aquarium with identical characteristics was subjected to the CO<sub>2</sub> exposure for each treatment. In each aquarium, three complete shells were placed on the sand surface, while three additional complete shells were buried approximately 3 cm deep in the sand. The buoyant weight, length, width, and height were measured, and at the end of the experiment, the same parameters were measured for each shell. This was done to estimate the rate of dissolution in the empty shells, which were not affected by biological activity. The buoyant weight (from now on referred as growth rate) served as an indicator of calcification (or decalcification; Lagos et al., 2016). During the experiment, additional individuals collected from the same site were used to analyze the relationship between shell length and dry tissue weight, as well as between oxygen uptake and dry tissue weight, using linear regression.

## Seawater $p\text{CO}_2$ levels

The pH treatment levels (8.0 and 7.5) were achieved by adding a mixture of dry air with pure  $\text{CO}_2$  (partial pressure of  $\text{CO}_2$  [ $p\text{CO}_2$ ] = 500 and 1500  $\mu\text{atm}$ , respectively) to each aquarium with seawater in a regular continuous flow using mass flow controllers (Aalborg Instruments & Controls, Inc., Orangeburg, NY, USA; for details see Benítez et al., 2018). The pH of the water (NBS scale) was measured by extracting 60 mL of water from the aquariums with disposable syringes for each aquarium, and then measuring the pH twice with the same water sample. The sediment pH was measured using a 10 mL micropipette (Labnet BioPette Plus), extracting pore water by inserting the micropipette tip around 2–3 cm into the sediment, following the sampling method of Bendell et al. (2014). Water was extracted three times from the same aquarium, transferred to Falcon tubes, and pH was measured twice with each sample. All samples were measured using a pH meter (Mobile 826, Metrohm, Herisau, Switzerland), which was connected to a combined electrode (junction-type). During measurements, temperature was also recorded using a digital thermometer, and seawater salinity was measured using a portable salinometer (Salt6+, Oakton; precision:  $\pm 0.1$  PSU and  $\pm 0.5^\circ\text{C}$ , respectively). Alkalinity samples were collected twice a week, ensuring that all aquaria were sampled in both the water column and pore water during each sampling week. The samples were fixed with a saturated solution of  $\text{HgCl}_2$  and stored in 50 mL Falcon bottles in the laboratory under dark and ambient temperature conditions. At the end of the experiment, alkalinity was analyzed using a multiparameter photometer (Hanna HI83303) in the seawater alkalinity mode. For this, 10 mL of aquarium sample was used as a blank, and then 1 mL of reagent (HI755) was added, based on the colorimetric method. The results were expressed in mg/L and subsequently converted to  $\mu\text{mol/kgSW}$  to assess the carbonate system.

Temperature, salinity, pH, and alkalinity measurements were used to calculate the carbonate system parameters. These included the partial pressure of  $\text{CO}_2$  ( $p\text{CO}_2$ ) and the saturation states ( $\Omega$ ) of calcite and aragonite, which were estimated using the CO2SYS software in Excel (Pierrot et al., 2006) and the dissociation constants from Mehrbach et al. (1973), refitted by Dickson and Millero (1987), for both the water column and the sediment.

## Measurements of biological traits

The measurement of growth rates and morphological changes in individuals during the experiment was obtained by measuring the buoyant weight, length, width, and height of each experimental individual. Buoyant weight corresponds to the weight of the individual in water and is used as a non-invasive estimator of calcification rate, i.e., the growth of individuals (Palmer, 1982). It was measured at the beginning and end of the experiment using an analytical balance ( $\pm 0.1$  mg, AUX 220, Shimadzu, Kyoto, Japan). For measurements of length, width, and height, an electronic caliper Mitutoyo (Sakado, Japan) was used at the beginning and end of the experiment. Empty shells (without soft tissues) from aquariums

under  $\text{CO}_2$  treatments were measured for buoyant weight, without biological activity, using the same analytical balance used for measuring the buoyant weight of individuals, while for length, width, and height were measured using the electronic caliper.

At the end of the 67 days, the metabolic rate and heart rate were measured to obtain the energy expenditure value of the individuals. Metabolic rate measurements were taken before daily feeding, using 0.067 L glass respirometry chambers with a PreSens Mini Oxy-4 respirometer (PreSens GmbH, Regensburg, Germany). To measure oxygen consumption ( $\text{mgO}_2 \text{ L}^{-1} \text{ h}^{-1}$ ), dissolved oxygen in the chambers was quantified every 15 seconds for approximately 1 hour. Finally, the obtained measurement was standardized per gram of weight to obtain the specific metabolic rate of each individual (see Lardies et al., 2021). Background measurements (chambers without animals) were made at the same experimental conditions to quantify microbial oxygen consumption to be subtracted from each experimental measurement. No reduction over 3% of oxygen consumption was recorded (see Osoreo et al., 2017). Previously, the sensors were calibrated in anoxic water, using a  $\text{Na}_2\text{SO}_3$  solution for 0% oxygen and water saturation with air bubbles for 100% oxygen. The obtained measurement was standardized per gram of weight. Heart rate measurements were taken following the methodology of Gaitán-Espitia et al. (2014) and Rodríguez-Romero et al. (2022) using as a proxy of cardiac activity at constant temperature of  $12^\circ\text{C}$  for all measurements. Individuals were immobilized with adhesive tape on a plate. One measurement per individual was taken in batches of 4 individuals, each in an individual chamber installed in the temperature-controlled bath ( $\pm 0.5^\circ\text{C}$ , LWB-122D, LAB TECH). The protocol included 5 minutes of initial acclimation and 15 minutes of measurement. An AMP 03 heartbeat amplifier (Newshift Lda<sup>®</sup>) was used, connected to an oscilloscope. Measurements were taken for all the individuals, and the results were expressed in beats per minute.

## Statistical analysis

To avoid pseudo-replication errors, variables for each individual were averaged by aquaria. First, homogeneity and normality tests were performed for the data, including Levene and Kolmogorov-Smirnov tests, respectively. To assess the difference in pH levels of both water and sediment water (pore water), a repeated ANOVA measure was performed, considering the variable place (source of water) as a within-subjects factor (within the same aquaria) and sampling time was treated as between-subjects factor.

A Two-Way ANOVA was conducted to assess the effect of  $\text{CO}_2$  levels, food availability, and the interaction between both factors on morphological traits (length, height, width and growth rates), dissolution rates, oxygen uptake, and heart rate. This determined whether the factors separately or their interaction had significant effects on the individuals. Tukey's HSD was used as a *posteriori* test when the main factors indicated significant differences between levels of the corresponding factor (Underwood, 1997). Additionally, the effect size of the treatments on both physiological and morphological variables was calculated using the log response

ratio (lnRR), defined as  $\ln RR = \text{treatment/control}$ . This approach allowed for a direct comparison of treatment effects relative to the controls. Bootstrapping was used to estimate the 95% confidence intervals of the lnRR values. All the analyses were conducted in R statistical environment (R Core Team, 2024).

## Results

All environmental variables remained stable in all of the treatments throughout the experimental period, with low variations in pH, salinity, and temperature (see Table 1). Based on the analysis of characterization of the population, the relationship between length and dry tissue weight of the individuals showed an  $R^2$  value of 0.91, while the relationship between oxygen uptake and dry tissue weight showed an  $R^2$  of 0.57 (see Supplementary Figures S2A, B).

A significant difference in pH levels was observed between the water column and the pore water ( $P < 0.01$ , repeated measures ANOVA, see Supplementary Table S1, Figure S3), but no differences were found based on the sampling time. On average, the pH of the water column was  $7.81 \pm 0.017$  SE, while the pH of the pore water was  $7.54 \pm 0.018$  SE (see Supplementary Figures S3, S4). Particularly, a difference in pH was observed between the overlying water and the sediment, which ranged between 0.28 and 0.57 units under  $\text{CO}_2$  levels of 500  $\mu\text{atm}$  and between 0.16 and 0.34 units under  $\text{CO}_2$  levels of 1500  $\mu\text{atm}$ .

Mortality was assessed after the experimental trial. Under the 500  $\mu\text{atm}$   $\text{CO}_2$  treatment, individuals exposed to a 4% food supply exhibited a mortality rate of 38.5%, whereas those maintained at a lower food level (1%) showed reduced mortality (14.3%). In contrast, at 1500  $\mu\text{atm}$   $\text{CO}_2$ , mortality remained at 25.0% under

the 4% food condition but increased markedly to 54.0% under the 1% food supply, highlighting an interactive effect between food availability and  $\text{CO}_2$  levels on survival.

## Morphological traits

The interaction between  $p\text{CO}_2$  and food supply affected the individuals' morphological characteristics (i.e. length, width, height, growth rate) (Figure 1; Table 2). High food supply in low pH conditions increased total width, with a marginally significant effect in the interaction of the treatments (Figure 1B; Two-Way ANOVA;  $F_{1,10} = 4.90$ ,  $P = 0.051$ ), while for low food supply in low pH conditions there was a decreased in total height, with a marginally significant effect in the interaction of the treatments (Figure 1C; Two-Way ANOVA;  $F_{1,10} = 4.52$ ,  $P = 0.059$ ). Furthermore, pH conditions and food supply affected the total increase length, and growth rate, but this effect was not significant (but see size effect, Supplementary Figure S6). Moreover, shell dissolution recorded for empty shells (see Figure 2A) was higher exposed to the water column and the interaction between the treatments  $p\text{CO}_2$  and location in the sediment resulted in a significant effect (Two-Way ANOVA;  $F_{1,4} = 7.81$ ,  $P = 0.049$ ). Although shell carbonate content tended to be higher in organisms from both  $\text{CO}_2$  treatments under 4% food supply, the difference was not statistically significant, being higher in the  $p\text{CO}_2$  treatment (see size effect, Supplementary Figure S7 and Figure 2C).

## Physiological traits

The food supply and  $p\text{CO}_2$  treatment impacted the physiological variables of the razor clams (Table 2). A non significant effect was

TABLE 1 Mean values ( $\pm$  SE) of carbonate system parameters for each experimental treatment, including  $p\text{CO}_2$  levels (500 and 1500  $\mu\text{atm}$ ) and food supply (1 and 4% of tissue dry weight), among the two sampling sites within the aquaria (water and pore water).

| Treatments                            | Place      | Temperature (°C) | Salinity (psu)   | pH (25°C)        | $A_T$          | $p\text{CO}_2$ | $\Omega_{ca}$   | $\Omega_{ar}$   |
|---------------------------------------|------------|------------------|------------------|------------------|----------------|----------------|-----------------|-----------------|
| 500 $\mu\text{atm}$ – 1% Food supply  | Water      | 12.02 $\pm$ 0.13 | 31.91 $\pm$ 0.36 | 8.03 $\pm$ 0.02  | 2051 $\pm$ 96  | 425 $\pm$ 58   | 2.86 $\pm$ 0.47 | 1.82 $\pm$ 0.30 |
|                                       | Pore water |                  |                  | 7.69 $\pm$ 0.03  | 2087 $\pm$ 118 | 1288 $\pm$ 291 | 1.57 $\pm$ 0.52 | 1.00 $\pm$ 0.33 |
| 500 $\mu\text{atm}$ – 4% Food supply  | Water      | 12.28 $\pm$ 0.11 | 31.63 $\pm$ 0.46 | 7.97 $\pm$ 0.02  | 2135 $\pm$ 49  | 542 $\pm$ 67   | 2.47 $\pm$ 0.24 | 1.57 $\pm$ 0.15 |
|                                       | Pore water |                  |                  | 7.55 $\pm$ 0.03  | 2323 $\pm$ 58  | 1514 $\pm$ 218 | 1.25 $\pm$ 0.15 | 0.79 $\pm$ 0.09 |
| 1500 $\mu\text{atm}$ – 1% Food supply | Water      | 12.44 $\pm$ 0.13 | 31.46 $\pm$ 0.42 | 7.63 $\pm$ 0.01  | 2035 $\pm$ 100 | 942 $\pm$ 94   | 1.39 $\pm$ 0.09 | 0.88 $\pm$ 0.06 |
|                                       | Pore water |                  |                  | 7.25 $\pm$ 0.086 | 2472 $\pm$ 380 | 2451 $\pm$ 375 | 0.86 $\pm$ 0.16 | 0.55 $\pm$ 0.10 |
| 1500 $\mu\text{atm}$ – 4% Food supply | Water      | 12.44 $\pm$ 0.05 | 31.95 $\pm$ 0.34 | 7.61 $\pm$ 0.01  | 2097 $\pm$ 29  | 1023 $\pm$ 77  | 1.36 $\pm$ 0.06 | 0.86 $\pm$ 0.03 |
|                                       | Pore water |                  |                  | 7.36 $\pm$ 0.02  | 2226 $\pm$ 58  | 2332 $\pm$ 168 | 0.72 $\pm$ 0.04 | 0.46 $\pm$ 0.03 |

The pH is reported on NBS scale,  $A_T$  refers to total alkalinity expressed in  $\mu\text{mol kg}^{-1}$ , and  $\Omega_{ca}$  and  $\Omega_{ar}$  represent the calcite and aragonite saturation states in seawater.

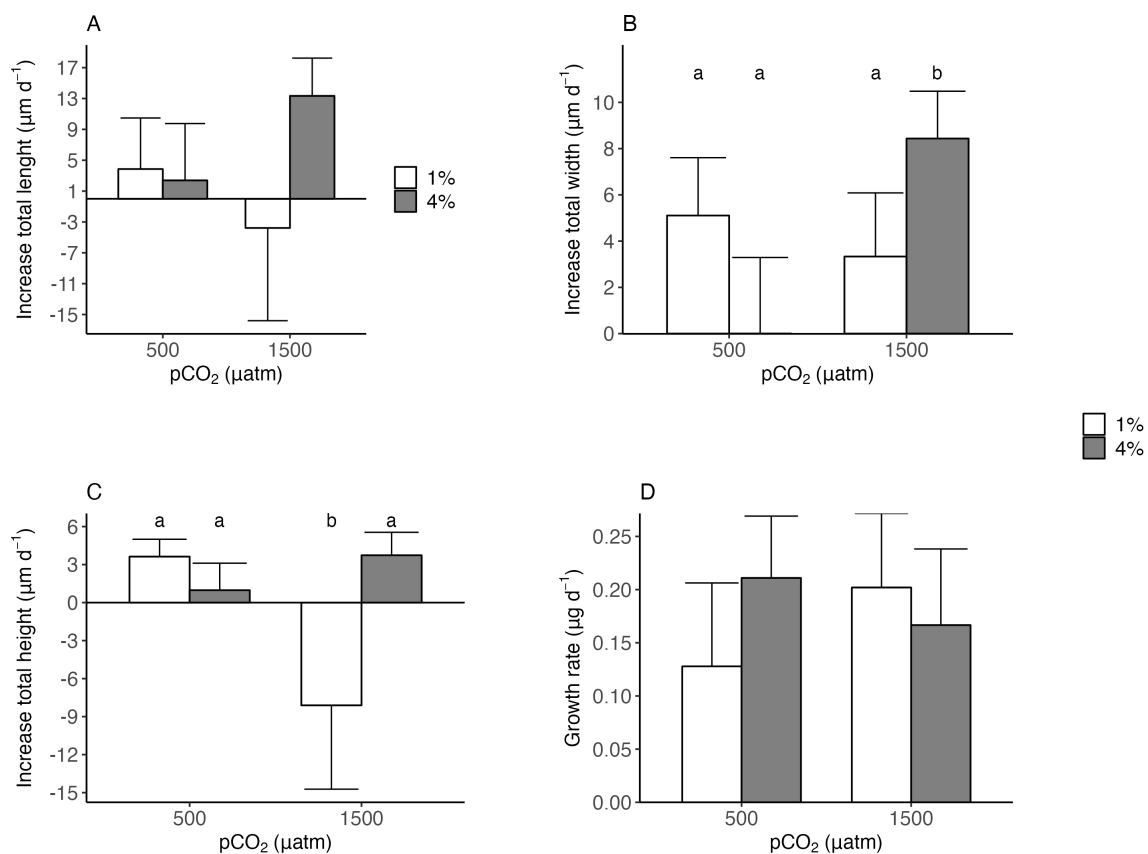


FIGURE 1

*Tagelus dombeii*: morphological changes with increase of total length (A), increase of total width (B), increase of total height (C), and growth rate (D) in each experimental condition. The treatments were conditions of pH (500  $\mu\text{atm}$  and 1500  $\mu\text{atm}$ ) and food supply (1% and 4% dry weight). The letters in lowercase indicate and mark the significance.

observed on the oxygen uptake rate, which decreased when the organisms were exposed to low pH (Two-Way ANOVA;  $F_{1,10} = 4.47$ ,  $P = 0.06$ ), and the interaction between  $\text{CO}_2$  and food supply (Two-Way ANOVA;  $F_{1,10} = 4.556$ ,  $P = 0.058$ ; Figure 3; but see size effect Supplementary Figure S8.). The interaction between the treatments food supply and  $p\text{CO}_2$  did not influence heart rate (Figure 4). However, the individuals tended to increase their heart rate in conditions of low food supply (see Figure 4).

## Discussion

The ongoing rise in  $\text{CO}_2$  emissions is accelerating both climate change and ocean acidification, significantly impacting various marine invertebrates (Shi and Li, 2024). However, the magnitude and direction of these effects vary according to the specific characteristics of each species (Goethel et al., 2017; Vargas et al., 2017; Harvey et al., 2013). In this context, infaunal bivalves could show greater resilience to these disturbances, attributable, among other factors, to their exposure to pore water, which has an intrinsically lower pH compared to the water column. Our results indicate that *T. dombeii* possesses adaptive mechanisms that allow it to cope with environmental stress, such as ocean acidification, but

not for limited food supply. These mechanisms include morphological modifications and physiological trade-offs that optimize its ability to survive under unfavorable conditions.

The characteristics of pore water are strongly influenced by the dynamics of the overlying water (Zhang et al., 2013; Precht et al., 2004). Various processes, such as the decomposition of organic matter, the sedimentation of materials of terrestrial origin, and the biological activity of both microorganisms and infaunal organisms, can generate a decrease in the pH of sediments (Hohaia et al., 2014) in addition to other processes that can contribute to pH reduction in sediments, such as sulfide oxidation or metal presence (see Bonner et al., 1990). This localized acidification of the benthic environment could have significant implications for key processes in bivalves, such as settlement, recruitment, and survival (Meseck et al., 2018; Clements and Hunt, 2018; Cummings et al., 2009). The pH of pore water tends to be more acidic than that of surface water, a condition attributed to the processes previously described (Hu et al., 2014; Cummings et al., 2009). The observed pH gradient between the overlying water and the sediment highlights the potential for differential buffering capacities at the sediment–water interface. These results are consistent with those reported by McGarrigle and Hunt (2024), who, in controlled experiments, documented that the pH of the water under constant acidification

TABLE 2 Summary of Two-way ANOVA for the effects of pH conditions, food supply, and interaction among both, upon morphological physiological variables (large, width, height, and growth rate).

| Dependent Variable      | Source of variation           | d.f | MS (Mean) | F        | P            |
|-------------------------|-------------------------------|-----|-----------|----------|--------------|
| Increase total large    | CO <sub>2</sub>               | 1   | 5.5530    | 0.069    | 0.797        |
|                         | Food supply                   | 1   | 320.74    | 4.024    | 0.072        |
|                         | CO <sub>2</sub> x Food supply | 1   | 35.255    | 0.442    | 0.521        |
|                         | Residuals                     | 10  | 79.692    |          |              |
| Increase total width    | CO <sub>2</sub>               | 1   | 15.727    | 1.072    | 0.324        |
|                         | Food supply                   | 1   | 6.8348    | 0.465    | 0.510        |
|                         | CO <sub>2</sub> x Food supply | 1   | 71.876    | 4.900    | 0.051        |
|                         | Residuals                     | 10  | 14.668    |          |              |
| Increase total height   | CO <sub>2</sub>               | 1   | 34.530    | 1.306    | 0.279        |
|                         | Food supply                   | 1   | 49.247    | 1.862    | 0.202        |
|                         | CO <sub>2</sub> x Food supply | 1   | 119.72    | 4.528    | 0.059        |
|                         | Residuals                     | 10  | 26.439    |          |              |
| Growth rate             | CO <sub>2</sub>               | 1   | 0.0001    | 0.001    | 0.992        |
|                         | Food supply                   | 1   | 0.0072    | 0.697    | 0.423        |
|                         | CO <sub>2</sub> x Food supply | 1   | 0.0259    | 2.508    | 0.144        |
|                         | Residuals                     | 10  | 0.0103    |          |              |
| Shell dissolution rate  | CO <sub>2</sub>               | 1   | 0.0353213 | 1.809489 | 0.250        |
|                         | Location                      | 1   | 0.0263002 | 1.347344 | 0.310        |
|                         | CO <sub>2</sub> x Location    | 1   | 0.1525338 | 7.814213 | <b>0.049</b> |
|                         | Residuals                     | 4   | 0.0195200 |          |              |
| Shell carbonate content | CO <sub>2</sub>               | 1   | 0.0037139 | 4.219588 | 0.070        |
|                         | Food supply                   | 1   | 0.0034304 | 3.897520 | 0.079        |
|                         | CO <sub>2</sub> x Food supply | 1   | 0.0014170 | 1.609966 | 0.236        |
|                         | Residuals                     | 9   | 0.0008802 |          |              |
| Oxygen uptake           | CO <sub>2</sub>               | 1   | 15.637    | 4.479    | 0.060        |
|                         | Food supply                   | 1   | 6.7483    | 1.932    | 0.194        |
|                         | CO <sub>2</sub> x Food supply | 1   | 15.908    | 4.556    | 0.058        |
|                         | Residuals                     | 10  | 3.4911    |          |              |
| Heart rate              | CO <sub>2</sub>               | 1   | 166.70    | 0.545    | 0.477        |
|                         | Food supply                   | 1   | 601.58    | 1.969    | 0.191        |
|                         | CO <sub>2</sub> x Food supply | 1   | 324.15    | 1.061    | 0.327        |

The significant P-values are highlighted in bold.

conditions was  $7.73 \pm 0.13$ , while that of the sediment was  $7.29 \pm 0.19$ , evidencing an average difference of 0.44 units. Such micro-scale heterogeneity is ecologically significant, as it may influence the exposure of benthic organisms to acidified conditions and thus mediate their physiological responses. Although ocean acidification has been a central research topic in recent decades, the carbonate system in sediments has yet to be fully explored. Our results reveal, in addition to a difference in pH between the water column and

pore water, variations in the carbonate systems of both environments. The sediments exhibited more acidic conditions, with higher partial pressure of CO<sub>2</sub> ( $p\text{CO}_2$ ), accompanied by a decrease in the saturation states of calcite and aragonite. Under these undersaturated conditions ( $\Omega_{\text{ca}} < 1$  and  $\Omega_{\text{ar}} < 1$ ; see Table 1), such as the pore water, the shell's mineral phase is likely to undergo dissolution, leading to higher energy demands for maintaining its structure and function. In our case, the findings indicate a higher

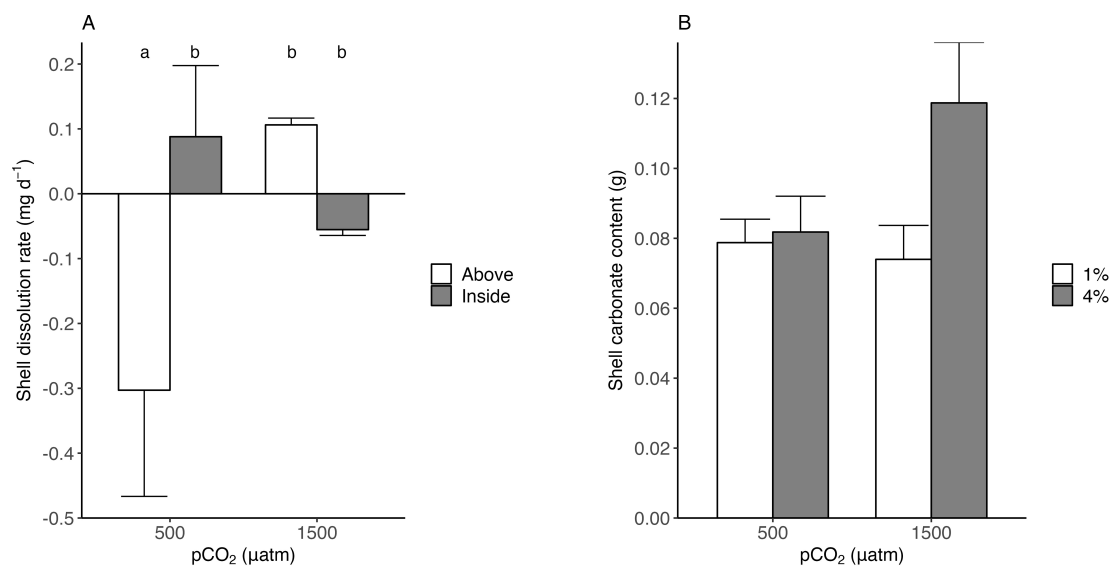


FIGURE 2

Shell dissolution rate (A), measured above and below the sediment, and shell carbonate content (B) in empty shells of *Tagelus dombeii* after 67 days of exposure to experimental conditions. The treatments in panel B correspond to pH levels (500 μatm and 1500 μatm) combined with food supply (1% and 4% dry weight). The letters in lowercase indicate and mark the significance.

carbonate content in individuals exposed to acidified conditions with 4% food supply, despite the low saturation states of calcite ( $\Omega_{ca} = 0.72$ ) and aragonite ( $\Omega_{ar} = 0.46$ ). This suggests an increased investment in shell production under ocean acidification, potentially as a compensatory response when food availability is optimal. Such a response may help maintain shell integrity despite the thermodynamically unfavorable conditions for calcification. However, sustained low aragonite/calcite saturation states in sediments may have long-term consequences for bivalve shell integrity and calcification capacity. While significant short-term effects were detected, chronic exposure to undersaturated conditions could progressively impair shell formation.

The outcomes revealed variable morphological effects, highlighting a significant impact on the increase in total height

and width, attributed to the interaction between both treatments. However, measurements related to the growth rate in terms of increase in total length, calcification (change in growth rate), and shell carbonate content did not show significant differences. These findings coincide with those reported by Liang et al. (2022), who observed that individuals of the infaunal bivalve *Sinonovacula constricta* subjected to controlled pH conditions (pH = 8.1) and projected future scenarios (pH = 7.7) did not show significant changes in their growth performance. The fact that the treatments have generated mostly non-significant morphological effects suggests that this species could possess some resistance to acidification. Previous studies have indicated that infaunal organisms, which are regularly exposed to acidified conditions in their natural habitats, such as in our case, where individuals

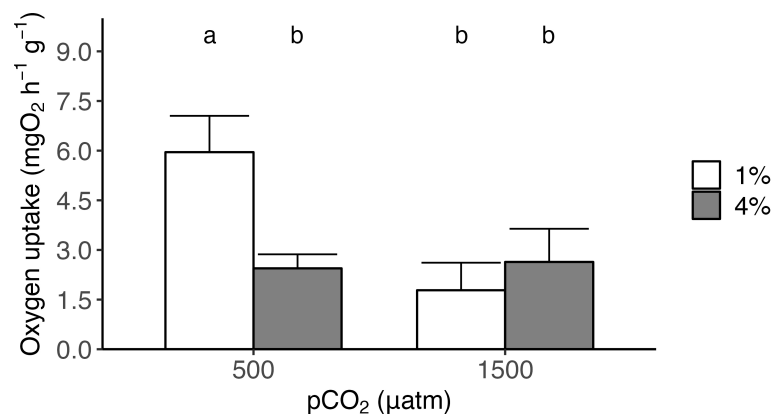


FIGURE 3

*Tagelus dombeii*: metabolic rate as oxygen uptake (mgO<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup>) for razor clams in each experimental condition. The treatments were conditions of pH (500 μatm and 1500 μatm) and food supply (1% and 4% dry weight). The letters in lowercase indicate and mark the significance.

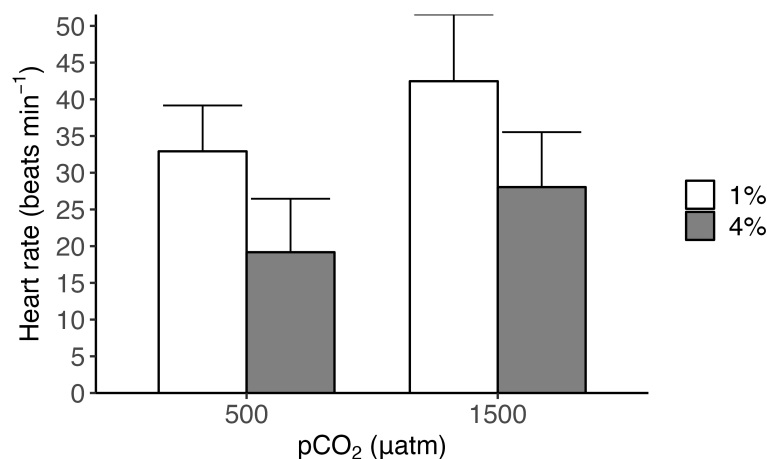


FIGURE 4

*Tagelus dombeii*: heart rate as beats min<sup>-1</sup> for razor clams in each experimental condition in a mesocosm for 67 days. The treatments for B were conditions of pH (500 µatm and 1500 µatm) and food supply (1% and 4% dry weight).

originate from an environment with a pH of 7.7, may exhibit greater tolerance and experience fewer morphological effects under acidification scenarios (Liang et al., 2022; Hu et al., 2014). On the other hand, McGarrigle and Hunt (2024) propose that, during periods of stress, such as exposure to constant elevated levels of CO<sub>2</sub>, organisms tend to prioritize survival overgrowth, strategically redistributing the available energy. Additionally, it has been suggested that calcifying organisms could overcome the energetic limitations associated with ocean acidification as long as they have sufficient amounts of food (Clements and Darrow, 2018). In this context, food supply could play a key role in physiologically compensating for the stress induced by acidification conditions (Goethel et al., 2017; Ramajo et al., 2016a). Furthermore, individuals of *T. dombeii* show a dual feeding behavior, using both suspension feeding and deposit feeding strategies (Lardies et al., 2001). This species can alternate between these strategies according to the conditions, obtaining food from both the water column (suspension) and the sediment surface (detritus; Navarro et al., 2008). Additionally, individuals tend to employ suspension feeding when they are at greater depths in the sediment, while they opt for deposit feeding when they are closer to the surface (Lardies et al., 2001; Navarro et al., 2008) thus increasing the likelihood of sustaining feeding activity and coping with adverse conditions, such as environmental stressors like OA and limited food supply.

The results indicate a significant decrease in oxygen consumption under acidification conditions, suggesting metabolic depression in organisms exposed to these conditions. Metabolic depression is a strategy adopted by organisms to extend short-term survival in adverse environments (Ramajo et al., 2016b; Hu et al., 2014). Although this metabolic depression may represent an acute response to environmental stressors, its persistence and long-term consequences remain uncertain. Prolonged exposure to low pH

conditions could either lead to physiological acclimation or, conversely, to cumulative energetic deficits that compromise growth, reproduction, or survival. Further studies with longer exposure periods are needed to determine whether this response is transient or maintained over time, and whether it translates into reduced fitness or population-level impacts.

Previous studies have documented this response in various species, including the infaunal brittlestar (Hu et al., 2014), scallops (Ramajo et al., 2016b), and infaunal clams (Martel et al., 2022). Food supply has been shown to enhance resilience to ocean acidification (Ramajo et al., 2016a), as organisms with access to adequate food exhibit higher growth, metabolism, calcification, and ingestion rates compared to those with limited food supply, both under control conditions and acidification scenarios (Navarro et al., 2016). In line with these findings, our study shows that organisms exposed to high food availability and low pH exhibit greater survival than those under low food availability and low pH conditions (see Supplementary Figure S5). However, food availability alone does not always guarantee effective intake and assimilation. Under acidified conditions, metabolic depression can impair feeding and nutrient processing, thereby limiting the benefits of increased food supply. This decoupling between external resource availability and internal energy acquisition has been observed in other bivalves and may compromise energy allocation to growth and reproduction (Ramajo et al., 2016b; Clements and Darrow, 2018).

Heart rate (HR) in mollusks is a fundamental physiological indicator that reflects their health status and their ability to adapt to different environmental conditions (Davis et al., 2023; Fernández et al., 2024). This parameter responds to a variety of stress factors, showing notable plasticity in populations inhabiting variable environments. In the present study, *Tagelus dombeii* showed a higher (but not significant) heart rate with lower food supply, would

indicate an increase in stress experienced by the organism (Davis et al., 2023). Under extreme conditions, the relationship between HR and metabolic rate may decouple (Marshall and McQuaid, 2020); mollusks can maintain a constant HR while decreasing their metabolic rate, adopting alternative strategies to ensure their survival (Marshall and McQuaid, 2020). Consistent with these findings, our results show that *T. dombeii* exhibited a reduced oxygen consumption rate under low pH conditions, while heart rate increased when food supply was limited. This suggests a decoupling between HR and metabolic rate, likely reflecting an adaptive response to the combined stressors of ocean acidification and food supply. Likewise, ocean acidification can induce metabolic depression, evidenced by a reduction in metabolism, which constitutes an energy-saving strategy against the stress associated with low pH, regardless of changes in heart rate (Martel et al., 2022).

Our results indicate an effect of the interaction between pH and food supply on oxygen consumption but not on food supply. This finding could be explained by the ability of *T. dombeii* to employ both types of feeding, which allows it to obtain nutrients from two different sources, thus improving its efficiency in food acquisition (Navarro et al., 2008). Although this study did not quantify the time spent on each type of feeding, we suggest that these organisms could alternate between suspension feeding and deposit feeding to minimize the ingestion of low-pH water under acidification conditions (see Vlaminck et al., 2023). This feeding flexibility allows infaunal filter-feeding bivalves to mitigate the effects of acidification, maintaining acid-base balance and avoiding physiological alterations (see Vlaminck et al., 2023), which reinforces the resilience and robustness of these organisms, in line with the results obtained in *M. calcarrea* (Goethel et al., 2017).

The variability in responses to adverse conditions of marine invertebrates depends on the habitat of origin, the scales of environmental variability, and the simultaneous presence of other stress factors (Lefevre, 2016; Castillo et al., 2024; Gaitán-Espitia et al., 2017). These elements influence the physiological responses of organisms to cope with unfavorable conditions. In this study, the razor clams analyzed come from Coihuin, a site near the Reloncaví fjord, which is characterized by high variability in  $p\text{CO}_2$  and food supply (Vergara-Jara et al., 2019; Lardies et al., 2001; Castillo et al., 2024). This suggests that infaunal organisms in the tidal flat would show greater signs of phenotypic plasticity, given the wide environmental variability of this quasi-estuarine system (see Osorio et al., 2017; Castillo et al., 2024).

Global change, particularly ocean acidification, poses significant threats to marine species and fisheries, including *T. dombeii*. The species metabolic depression in response to acidification could reduce its harvestable biomass, thereby affecting the maximum sustainable yield and threatening economic stability in affected regions. The previous plus pressure of artisanal fisheries on *T. dombeii*, with an annual harvest of 2,203 Mt (100 Mt from the Los Lagos Region), face potential losses. For example, between 1996 and 2007, the selectivity for *T. dombeii* dropped from a mean size of 76 mm to 54 mm (legal commercial size 65 mm), indicating a shift toward smaller harvestable individuals in the Bio-Bio region (Hernández et al., 2011). This trend could lead to significant economic losses,

underlining the need for adaptive fisheries management that accounts for both climate stressors and ecological dynamics.

*Tagelus dombeii* demonstrates partial resilience to ocean acidification due to its natural exposure to acidic pore water and flexible feeding strategies. This adaptability allows it to optimize nutrient acquisition and maintain physiological balance under stressful conditions. However, its survival and performance are compromised under low food supply, highlighting the importance of trophic conditions. These findings highlight the complexity of infaunal marine invertebrate responses to global change, emphasizing the need to consider multiple stressors in future projections and fisheries.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

## Author contributions

MA: Formal Analysis, Investigation, Writing – original draft, Writing – review & editing, Data curation, Methodology, Visualization. NL: Data curation, Formal Analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing, Software. PC: Conceptualization, Data curation, Investigation, Methodology, Writing – original draft. ML: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2025.1568035/full#supplementary-material>

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