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# Effects of ocean acidification on the interaction between calcifying oysters (*Ostrea chilensis*) and bioeroding sponges (*Cliona* sp.)

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Ocean acidification can negatively affect a broad range of physiological processes in marine shelled molluscs. Marine bioeroding organisms could, in contrast, benefit from ocean acidification due to reduced energetic costs of bioerosion. Ocean acidification could thus exacerbate negative effects (e.g. reduced growth) of ocean acidification and shell borers on oysters. The aim of this study was to assess the impact of ocean acidification on the oyster *Ostrea chilensis*, the boring sponge *Cliona* sp., and their host-parasite relationship. We exposed three sets of organisms 1) *O. chilensis*, 2) *Cliona* sp., and 3) *O. chilensis* infested with *Cliona* sp. to pH<sub>T</sub> 8.03, 7.83, and 7.63. Reduced pH had no significant effect on calcification, respiration and clearance rate of uninfested *O. chilensis*. Low pH significantly reduced calcification leading to net dissolution of oyster shells at pH<sub>T</sub> 7.63 in sponge infested oysters. Net dissolution was likely caused by increased bioerosion by *Cliona* sp. at pH<sub>T</sub> 7.63. Additionally, declining pH and sponge infestation had a significant negative antagonistic effect (less negative than predicted additively) on clearance rate. This interaction suggests that sponge infested oysters increase clearance rates to cope with higher energy demand of increased shell repair resulting from higher boring activity of *Cliona* sp. at low seawater pH. *O. chilensis* body condition was unaffected by sponge infestation, pH, and the interaction of the two. The reduction in calcification rate suggests sponge infestation and ocean acidification together would exacerbate direct (reduced growth) and indirect (e.g., increased predation) negative effects on oyster health and survival. Our results indicate that ocean acidification by the end of the century could have severe consequences for marine molluscs with boring organisms.

## KEYWORDS

ocean acidification, host-parasite interaction, boring sponge, flat oyster, *Cliona* sp., *Ostrea chilensis*, shellfish shells, global change

# 1 Introduction

Anthropogenic carbon dioxide (CO<sub>2</sub>) emissions are increasing CO<sub>2</sub> concentrations in the atmosphere, leading to an increase in the amount of CO<sub>2</sub> being absorbed by the world's surface seawater. The subsequent reduction in seawater pH due to the resulting increase in H<sup>+</sup> concentrations is called ocean acidification (Caldeira and Wickett, 2003). The rapid and ongoing decrease in seawater pH and alteration of seawater carbonate chemistry is threatening marine life on a global scale (Raven et al., 2005; Kroeker et al., 2013). Marine calcifiers such as corals, coralline algae and shellfish are particularly susceptible to this impact because lower seawater pH reduces their calcification rates (Feely et al., 2009; Hofmann et al., 2010). The direct negative effects of ocean acidification are well described in marine shelled molluscs and include effects on survival, development, growth, and shell morphology (Ries et al., 2009; Gazeau et al., 2013; Kroeker et al., 2013).

However, ocean acidification could also indirectly affect marine shelled molluscs by increasing bioerosion rates. Bioerosion is the erosion of substrates such as shells and sediments by bioeroding organisms (Bromley and Hanken, 1981; Holmes et al., 2000). Bioeroding sponges, such as *Cliona* sp., erode calcium carbonate through chemical and mechanical mechanisms (Warburton, 1958; Rützler and Rieger, 1973). Sponge bioerosion rates are positively affected by low seawater pH (Duckworth and Peterson, 2013; Fang et al., 2013, 2014; Wisshak et al., 2013, 2014; Stubler and Peterson, 2016) and could increase under ocean acidification. However, there might be a threshold of pH reduction that could have negative impacts on sponge health and therefore reduce bioerosion rates (Duckworth and Peterson, 2013; Enochs et al., 2015; Morris et al., 2022). Low seawater pH creates a more favourable chemical gradient, thus lowering energetic costs of bioerosion by sponges (Fang et al., 2013, 2014; Schönberg et al., 2017). Bioeroding sponges are common macroborers in the shells of molluscs (Bergquist, 1961, 1968; Probert et al., 1979; Pritchard et al., 1984). They can heavily damage mollusc shells and are regarded as a pest in the oyster aquaculture and fisheries industries (Alagarwami and Chellam, 1976; Thomas, 1979; Rützler, 2002a, b; Carver et al., 2010).

Oysters have a high socio-economical value (Grabowski et al., 2012; Lemasson et al., 2017) and are undergoing extensive restoration in many parts of the world (Duarte et al., 2020; Howie and Bishop, 2021; Smith and Pruett, 2024) due to significant loss (~80%) of wild oyster populations over the past 140 years (Beck et al., 2011; Zu Ermgassen et al., 2012; Gillies et al., 2018). Ocean acidification and increasing bioerosion could threaten these restoration efforts and healthy oyster populations worldwide. Negative effects of ocean acidification on oysters affect all life stages (Lemasson et al., 2017). In adult oysters, reduced pH negatively impacts shell calcification, making shells softer and more fragile (Beniash et al., 2010; Dickinson et al., 2012), as well as reducing calcification rates (Gazeau et al., 2007; Ries et al., 2009; Beniash et al., 2010; Waldbusser et al., 2011b) and increasing shell dissolution (Ries et al., 2009; Waldbusser et al., 2011a). Further, low pH can significantly impact respiration (Beniash et al., 2010) and feeding rates of oysters (Lemasson et al., 2018) and reduce oyster body condition (hereafter condition) (Lannig et al., 2010). The impacts of ocean acidification on oyster physiology

could create shifts in species interactions by increasing oyster susceptibility to biological stressors such as bioerosion from sponges (Sanford et al., 2014).

Increased bioerosion rates under ocean acidification could be detrimental for hosts of sponges, further exacerbating the direct negative impacts of ocean acidification they already experience. Oysters might experience higher energetic expenditure under lower seawater pH due to higher costs of shell deposition and maintenance, which could lead to metabolic depression of other processes (Lannig et al., 2010). Additionally, oyster energy budgets could be negatively affected due to active reduction of respiration and feeding/clearance rates under ocean acidification. Respiration and feeding rates can be reduced as a means to protect soft-tissues from unfavourable conditions such as low pH (Rastrick et al., 2018). Consequently, the ability to maintain or increase energy assimilation likely determines resilience to ocean acidification (Lemasson et al., 2018). For sponge-infested oysters, energy expenditure under ocean acidification may be further increased by the high energetic costs of shell repair (Dame, 1976; Carroll et al., 2015). The negative impacts of sponge boring on oyster growth and condition (Carroll et al., 2015; Watts et al., 2018; Hanley et al., 2019; Dieudonne and Carroll, 2022) could thus be exacerbated under ocean acidification because of higher borer activity.

The wild oyster population of the native flat oyster *Ostrea chilensis* in the Foveaux Strait (FS), New Zealand, is heavily colonised by the boring sponge *Cliona* sp. (Böök, 2024). The oysters are important to commercial, recreational, and indigenous fishers (Michael, 2010). *Cliona* sp. is a native sponge that is widespread along New Zealand coastal water and infestation in the FS oyster fishery can affect as many as 100% of oysters (*O. chilensis*) in certain areas (Böök, 2024). *Cliona* sp. has long been considered a “parasite” in *O. chilensis* from the FS that might contribute to poor quality and mortality of oysters (Stead, 1971a, b; Michael et al., 2015, 2019, 2021; Michael, 2018). More recent studies however did not find biological and disease processes of *O. chilensis* to be strongly impacted by *Cliona* sp. (Böök et al., 2023; Böök, 2024). With the anthropogenically driven fast changes in oceanic pH, it is crucial to understand how future conditions might affect the relationship between oysters and bioeroding sponges.

The aim of this study was to assess the impact of ocean acidification on the oyster *O. chilensis*, the boring sponge *Cliona* sp., and their interaction. We hypothesised that 1) reduced pH would decrease calcification rate and condition of oysters and increase both clearance rates and respiration rates due to higher energetic costs of calcification; 2) that ocean acidification would increase the bioerosion rate, clearance rate, and respiration rate of *Cliona* sp.; and 3) that sponge infestation would increase calcification, clearance rate, and respiration rates and reduce condition of oysters due to additional energy needed for shell repair and possible negative effects of sponge boring on oyster soft-tissues. To test these hypotheses, we exposed oysters with and without sponge infestation and sponges infesting dead oyster shells to three projected and present-day pH levels (roughly 8.03, 7.83, 7.63, see Supplementary Table 1 for details) and used standard physiological methods such as growth measurements (buoyant weight), closed-chamber respirometry, clearance rates and an

oyster condition index to assess the effect of these treatments on the organisms.

## 2 Materials and methods

### 2.1 Organism collection and acclimation

Samples were collected in the FS oyster fishery area (46°S 40.2, 168°E 10.8) in May 2021 by the Bluff Oyster Management Company (BOMC) from single dredge tows using commercial fishing vessels. The samples were collected under the NIWA project code (SIL20302), using the NIWA special permit (665). Sixty-four living oysters without sponge infestation (uninfested oysters), 64 oysters with sponge infestation (infested oysters, visually assessed) and 64 dead shells with sponge infestation (sponges) were collected. The sponges on infested oysters and dead shells were all in the alpha stage (boring stage), meaning that sponge infestation was clearly visible as sponge papillae (boreholes) protruding from the shell surface (see [Supplementary Figure 1](#)). The living oysters were of minimum legal size (>58 mm shell length). Samples were transported alive in polystyrene boxes to Wellington (New Zealand) within 24 hours of collection. At the experimental facility, samples were carefully cleaned of epibionts (as much as possible) and dirt, and labelled with Hallprint Shellfish Tags (Hallprint Inc., Hindmarsh Valley, South Australia, Australia) before distributing them into the experimental tanks. Though sponges were out of water during transport and handling, the sponge tissue remained moist and visibly undamaged before and during the experiment. The organisms were slowly acclimatised to experimental conditions by decreasing the pH by 0.1 units per day ([Doo et al., 2020](#)) (from 8.03) until the target pH for the respective treatments was reached. This was followed by an acclimation phase of one week. Subsequently the experiment ran for 119 days from 20<sup>th</sup> May 2021 (T0) to 14<sup>th</sup> September 2021 (T2).

### 2.2 Experimental setup and treatments

The experiment was designed to include three different treatments of differing mean seawater  $\text{pH}_T$  ([Supplementary Table 1](#)). A control treatment was chosen to represent the mean present-day  $\text{pH}_T$  of the coastal waters around New Zealand (8.03 or ambient; see [Supplementary Table 1](#) for mean  $\text{pH}_T$ ). The other two treatments (7.83, 7.63; see [Supplementary Table 1](#) for mean  $\text{pH}_T$ ) represent two ocean acidification scenarios, which were informed by expected future pH levels for different relative concentration pathways (RCPs, RCP 4.5 2100, RCP 8.5 2100) outlined by the Intergovernmental Panel on Climate Change (IPCC) ([Gattuso et al., 2015](#)). Calcite saturation states corresponding to the treatments are  $3.24 \pm 0.03$  SE,  $2.41 \pm 0.07$  SE and  $1.61 \pm 0.03$  SE respectively. pH predictions under different RCP scenarios are very similar across most of the surface oceans and therefore should accurately reflect local conditions (see [Law et al., 2018b, a](#)). The  $\text{pH}_T$  levels 8.03 and 7.63 were replicated 18 times (six tanks each for uninfested oysters, infested oysters and sponges on dead shells), and  $\text{pH}_T$  level 7.83 12

times (four tanks each for uninfested oysters, infested oysters and sponges on dead shells; [Supplementary Figure 2](#)). The uneven replication was due to spatial restrictions in the experimental facilities, and it was considered better to have more replicates in the two farthest treatment levels to each other as modern statistical models can deal with unbalanced designs easily (see [Boyd et al., 2018](#)). The 48 experimental tanks (~4 L each; 17.5 cm W x 23 cm L x 12 cm H) were arranged in groups of six into 60 L water baths (56 cm W x 76 cm L x 18.5 cm H). Eight water baths in total were used to hold all experimental tanks and each water bath contained three experimental tanks from two treatments ([Supplementary Figure 2](#)). Each tank contained four specimens of either uninfested oysters, sponge-infested oysters, or sponge-infested dead shells. Additionally, twenty-seven tanks contained a dead control shell without any sponge infestation, to monitor for additional biotic and abiotic influences on shell weight (e.g., passive dissolution, leftover borers and calcifying epibionts). The location of tanks per treatment within the water bath was mostly alternated sequentially between the eight water baths, for equal distribution of the experimental tanks over the whole setup. However, this was not entirely possible because of the differences in replicate numbers. The experimental setup was spread out over two shelf levels because of spatial restrictions in the experimental facility.

### 2.3 Seawater supply

The raw seawater used for the experiment was sourced from a rocky reef kelp forest ecosystem in front of the laboratory facilities (Victoria University of Wellington Coastal Ecology Laboratory) and pumped directly into the setup. The seawater was fed through aquarium chillers to reduce temperature variability and chilled water was collected in two intermediate tanks (one per shelf level with ~60 L each; 56 cm W x 76 cm L x 18.5 cm H). From here, water was pumped into the header tanks (~20 L each; 30 cm W x 25 cm L x 38 cm H) using submersible pumps (Jeboa DC-650, 200 L h<sup>-1</sup>). There was a total of eight header tanks, and one header tank supplied each of six experimental tanks (3 per water bath) with 150 mL seawater per min. Each header tank contained one pump (Jeboa DC-650, 650 L h<sup>-1</sup>) to ensure water mixing. The organisms were fed with Shellfish Diet 1800 (Reed Mariculture Inc., Campbell, CA, USA) at least 5 times a week. The Shellfish Diet 1800 contains algal cells of 4–20  $\mu\text{m}$  diameter. The raw seawater alone should be suitable for sponge feeding because *Cliona* sp. is found on the Wellington Cook Strait coastline in front of the laboratory (personal obs. I. M. Böök, [Berman, 2011](#)). Nevertheless, feed was added to all tanks to ensure nutrition for oysters and to keep conditions the same across all tanks. Prior to feeding, the seawater supply was turned off to avoid flushing the feed out while the smaller jet pumps placed in each experimental tank ensured mixing and kept the feed in suspension (Hailea BT100, 150 L h<sup>-1</sup>). During feeding, previously diluted Shellfish Diet was poured into each experimental tank and organisms were left for 1–2 hours to feed. Each organism was supplied with the equivalent of approximately 1 mL of undiluted Shellfish Diet per feeding (~3% algae dry weight per oyster dry meat weight, as per manufacturers recommendations).

## 2.4 Seawater pH maintenance and seawater carbonate chemistry

Over the course of the day, pH levels fluctuated around the mean  $\pm 0.1$  units during certain times due to natural variability from the nearby kelp forest in the incoming raw seawater. pH was lowest during the day (8 am to 4 pm) and highest during the night (8 pm to 4 am); the rest of the time the pH was approximately equivalent to the target mean pH (see [Supplementary Figure 3](#) for daily pH variability). Due to the natural variation in pH in the subtidal kelp forest in front of the laboratory, pH fluctuations were difficult to remove, especially when incoming water had a very low pH. Therefore, we opted to allow for some pH variation, while keeping the mean pH stable over the course of one day. The pH levels for the respective treatments (see [Supplementary Table 1](#)) were regulated inside the header tanks with an aquarium control system (AquaController, Neptune systems, USA). pH electrodes connected to the control system were placed inside the header tanks. The control system reduced or increased pH automatically by bubbling CO<sub>2</sub> or air into the header tanks through connected solenoid valves. The variability of seawater pH and total alkalinity (A<sub>T</sub>) inside the experimental tanks were monitored in each header tank and in randomly selected experimental tanks of each water bath at regular intervals (for results see [Appendix Supplementary Table 1](#)). The pH was measured at least once per week with a pH meter (HQ40D equipped with IntelliCal PHC101 probe, Hach Company, Loveland, USA), which was calibrated on the total scale (pH<sub>T</sub>) using Tris/HCl buffers (after [Dickson et al., 2007](#)). From now on we refer to pH<sub>T</sub> used as pH throughout unless otherwise stated. Water samples for titrations of A<sub>T</sub> were taken every two weeks and A<sub>T</sub> was calculated with a modified Gran function ([Dickson et al., 2007](#)). Titrations (AS-ALK2, Apollo SciTech, USA) of certified reference material (CRM, Batch 190 provided by A.G. Dickson lab, University of California, San Diego, USA) yielded A<sub>T</sub> values which deviated on average  $3.76 \pm 1.39 \mu\text{mol kg}^{-1}$  from the reference material. Seawater carbonate chemistry was calculated with the “seacarb” package in R ([Gattuso et al., 2021](#)) and the Microsoft Excel programme Co2sys v2.1 ([Pierrot et al., 2006](#)) (see [Supplementary Table 1](#)). In the Co2sys programme we used constants K1 and K2 (carbonic acid constants) ([Mehrbach et al., 1973](#); refitted: [Dickson and Millero, 1987](#)), K<sub>H2SO4</sub> (sulfate constant) ([Dickson, 1990](#)) and B<sub>T</sub> (total boron concentration) ([Lee et al., 2010](#)).

## 2.5 Temperature control

Temperature was controlled by aquarium chillers and by submersible 300 W titanium heaters (Weipro MX1021) which were placed in each water bath and connected to a controller (AquaController, Neptune systems, USA). Temperature probes connected to the control system were placed in each water bath: Temperature control was improved by pumps (Jeboa DC-650, 650 L h<sup>-1</sup>) placed in each water bath which guaranteed mixing of water. Additionally, each experimental tank contained one smaller jet pump to create horizontal water motion for improved pH and temperature control. Temperature was measured at least once per

week (for results see [Appendix Supplementary Table 1](#)) with an external probe (Kangaroo Traceable Thermometer, Fisherbrand, Fisher Scientific, Toronto, Canada). The temperature in the experimental setup ( $\sim 14.4^\circ\text{C}$ ) reflects average summer temperatures (2011–2021) in FS (167°E 37.5, 46°S 52.5; 168°E 37.5, 46°S 37.5) inferred from satellite derived data (NOAA OI SST V2 High Resolution Dataset data provided by the NOAA PSL, Boulder, Colorado, USA, from their website at <https://psl.noaa.gov>).

## 2.6 Mean net calcification/bioerosion

All individuals were weighed using the buoyant weight technique ([Jokiel et al., 1978](#)) once the acclimation period was completed (20<sup>th</sup> May 2021, T0) after one month (T1) and at the end of the experiment (T2). To measure buoyant weight a tray (wire mesh) was connected to the hook on the underside of a scale (Pioneer Precision Balance PX2202, Ohaus, New Jersey, USA) with fishing line. A container with seawater was placed below the scale and the tray was completely submersed in the water. Individuals were placed on the tray and the weight was recorded.

Buoyant weight (BW) was corrected using the following formula:

$$BW_{corr} = \frac{BW}{(1 - \frac{D_s}{D_c})} \quad (1)$$

where D<sub>s</sub> is the density of seawater, and D<sub>c</sub> is the density of calcite (2.71 kg L<sup>-1</sup>). The density of seawater was calculated using temperature and salinity measurements taken during the buoyant weight sampling. For most organisms the difference between T0 and T2 was used to determine weight changes, however for individuals that died before T2 (4 uninfested and 4 infested oysters) the difference between T0 and T1 was used. Weight changes between timepoints were corrected for the average proportional weight change per original weight (T0) of control shells across treatments ( $-0.0080 \pm 0.0009$  SE). Finally, weight changes were converted into dry weight of CaCO<sub>3</sub> and used to calculate net calcification/bioerosion (mg CaCO<sub>3</sub> g<sup>-1</sup> day<sup>-1</sup>) respectively. The buoyant weight technique has been used to measure sponge bioerosion in previous studies (e.g., [Wisshak et al., 2012](#); [McNally, 2022](#)).

## 2.7 Incubations to assess respiration and short-term calcification/chemical bioerosion

Closed-chamber respirometry was used to measure respiration rates and collected water samples were used to determine short-term calcification/bioerosion rates through changes in calcium concentration (see 2.9). For the incubations, five different individuals from each group (uninfested oysters, infested oysters, sponges) from each treatment were selected blindly (i.e., randomly) for analysis. Specimens were placed in clear plastic beakers (Ø11.43 cm, 16.43 cm high) together with a stirrer bar that was separated from the organism. Containers were closed underwater inside the header tanks with an airtight lid and enclosure of air bubbles were avoided. Closed containers (Volume: 1000 mL) were then placed inside a water-filled



tank on a submersible stirring plate (2mag MIXdrive6, 2mag AG, Munich, Germany), which was placed in a temperature control room. Incubations were run for 6 hours in order to get measurable results for sponge bioerosion (after Webb et al., 2017). Oxygen content did not drop below 6.5 mg L<sup>-1</sup> in any of the incubations, therefore the organisms should have not been negatively affected by low oxygen. Water samples and measurement of dissolved oxygen (HQ40D equipped with IntelliCal LDO101 probe oxymeter, Hach Company, Loveland, USA) were taken in the header tanks at the starting point (T<sub>0</sub>) and inside the incubation containers at the end point (T<sub>end</sub>). Empty shells without sponge served as a control and were placed into identical containers on the stirrer plate during incubations. Mean changes in O<sub>2</sub> (-0.1 mg L<sup>-1</sup>, within measurement error) in the control chambers were deducted from change caused by the organisms. Respiration rate was calculated per organism dry weight or ash-free dry weight (sponges) as mg O<sub>2</sub> g<sup>-1</sup> DW h<sup>-1</sup> (see 2.10 and 2.11). Respiration rates of infested oysters were corrected for sponge respiration. The average respiration rate of sponges per dry weight from the sponge incubations was multiplied with the tissue dry weight of sponges from the sponge infested oysters in order to calculate sponge respiration in sponge infested oysters. The resulting value was subtracted from the uncorrected respiration rate of sponge infested oysters. The incubations were run between days 28 and 43 of the experimental phase.

## 2.8 Clearance rate

A second set of incubations was conducted to measure clearance rate (volume of water cleared of suspended particles per unit of time). For these incubations, five different individuals from each group (uninfested oysters, infested oysters, sponges) from the ambient and pH 7.63 treatment were selected blindly (i.e., randomly) for analysis. Specimens were placed in clear plastic containers (1000 mL) which were filled in the header tanks and Shellfish Diet 1800 was added to each container to give an initial concentration of ~100,000 cells mL<sup>-1</sup>. A stirrer bar that was separated from the organism was added and containers were then placed on a submersible stirring plate (2mag MIXdrive6, 2mag AG, Munich, Germany) to ensure that the algae remained in suspension. This plate was placed in a water-filled tank in a temperature-controlled room. Incubations were run for 1 hour. Water samples were taken at the starting point (T<sub>0</sub>), at half time (T<sub>1</sub>) and at the end of the incubation (T<sub>2</sub>). Changes in particle concentration were measured with a Coulter counter (Coulter Z series; Beckman Coulter, Buckinghamshire, UK). Three different particle size ranges were measured: >5–60 μm, >2.5–60 μm and 2.5–5 μm. Control chambers with control shells (empty shells without sponge) were also placed on the stirrer plate during incubations. Mean changes in particle concentrations in the control chambers were deducted from clearance rate of the organisms. The timeframe (T<sub>0</sub>–T<sub>1</sub> or T<sub>1</sub>–T<sub>2</sub>) which had the highest change in particle concentration was chosen to calculate clearance rate of the organisms. Clearance rates of organism groups were calculated after Coughlan (1969):

$$\text{Clearance rate} = \frac{V}{t} \ln \left( \frac{C_0}{C_t} C_f \right) \quad (2)$$

where V is the volume of the incubation chamber, t is the time elapsed between C<sub>0</sub> and C<sub>t</sub> (30min), C<sub>0</sub> is the particle concentration used as the start point (T<sub>0</sub> or T<sub>1</sub>), C<sub>t</sub> is the particle concentration used as the end point (T<sub>1</sub> or T<sub>2</sub>) and C<sub>f</sub> is a correction factor for particle sedimentation in the control chambers. C<sub>f</sub> is calculated by dividing the end concentration measured for the control by the initial concentration in control chambers (C<sub>tc</sub>/C<sub>0c</sub>). Finally, clearance rate was standardised per gram dry weight or ash-free dry weight (see 2.10 and 2.11). The incubations were run between days 106 and 117 of the experimental phase.

## 2.9 Determination of calcium concentrations

Changes in calcium ion (Ca<sup>2+</sup>) concentration were determined by titration. Seawater samples (see 2.7) were titrated for Ca<sup>2+</sup> with EGTA (ethyleneglycol-bis (2-aminoethylether)-N, N, N', N', tetraacetic acid) and the selective metal indicator GHA (glyoxal-bis (2hydroxy-anil)) (Tsunogai et al., 1968). For this work, the EGTA titrant was standardised using a 'secondary' seawater standard, for which the [Ca<sup>2+</sup>] had been previously determined in an 'initial' standardisation using a different batch of EGTA titrant. The 'secondary' standard used were seawater Certified Reference Materials (CRMs) provided by the Scripps Institution of Oceanography, which had been filtered and poisoned with mercuric chloride (Dickson et al., 2007). The 'initial' EGTA titrant was standardised using standard [Ca<sup>2+</sup>] solutions prepared by dissolving a known mass of pure CaCO<sub>3</sub> in deionised water using a minimal amount of hydrochloric acid. In the determination of the 'secondary' seawater standard [Ca<sup>2+</sup>], a multiplicative factor of 0.9946 was applied to the final titre to correct for the interference of strontium and magnesium ions (Tsunogai et al., 1968). As the matrix effects had thus been accounted for, no correction was applied to the standardisation of EGTA using the secondary seawater standards. Approximately 10 g of each seawater sample was accurately weighed (4 decimal points) into a 100 ml conical flask. Sufficient EGTA (~10 mM) was added to the flask to complex at least 99% of the total calcium. 2 ml of 0.05% GHA in n-propanol and 4 ml borate buffer solution (10 g Na<sub>2</sub>B<sub>4</sub>O<sub>7</sub>·10H<sub>2</sub>O and 30 g NaOH in 500 ml of water) were added. After stirring for 3 minutes to allow colour development, 8 ml of n-butanol was added. The titration with EGTA was continued until the red colour had completely disappeared from the organic layer. If the initial addition of EGTA was not >99% of the final titre value, the result was discarded, and the analysis repeated. Changes in [Ca<sup>2+</sup>] were corrected for mean change of the control samples. Subsequently, change in [Ca<sup>2+</sup>] was corrected for water volume and incubation time to obtain net bioerosion/calcification rates. Calcification/bioerosion rates were determined as 1 mole change in Ca<sup>2+</sup> representing 1 mole change in CaCO<sub>3</sub>. Finally, calcification and chemical bioerosion rates were standardised per gram dry weight or ash-free dry weight (sponges) in mmol CaCO<sub>3</sub> per g<sup>-1</sup> DW h<sup>-1</sup> (see 2.10 and 2.11). Only samples for the ambient treatment

(8.03) and the lowest pH treatment (7.63) were processed because of time constraints for the sample processing.

## 2.10 Oyster condition index (CI) and meat dry weight

At the end of the experiment (after 26 days of treatment), oysters were shucked completely and their meat and valves were dried in a drying oven. Meat dry weight (70°C, 72 h) and shell dry weight (70°C for 24 h) were used together to calculate the following condition index (Lawrence and Scott, 1982; Rainer and Mann, 1992):

$$\text{Condition index (CI)} = \frac{\text{MDW}}{\text{SW}} \times 100 \quad (3)$$

MDW = meat dry weight, SW = shell dry weight.

CI is a commonly used oyster condition index (see Rainer and Mann, 1992; Abbe and Albright, 2003) and compares investment into calcification (shell repair, shell growth) and investment into somatic and gametic growth. The index reflects energy reserves by comparing tissue weight, which is sensitive to short-term changes to shell weight, which is relatively stable over time and does not decrease except during shell erosion (Rainer and Mann, 1992). In sponge-infested oysters CI could be slightly positively inflated due to reduced shell weight which would likely be more impactful than the fact that shell dry weight included sponge dry weight for sponge-infested shells. The meat dry weight was used to standardise metabolic rates of oysters. For six uninfested oysters and six infested oysters that died during the experimental period only shell dry weight could be measured. Meat dry weight for these individuals was estimated by using a conversion factor based on the meat dry weights and shell dry weights of all other uninfested and infested oysters (n = 116).

## 2.11 Sponge ash-free dry weight

Sponge tissue ash-free dry weight from sponges and infested oysters at the end of the experiment was calculated by weighing dried shells (70°C for 24 h) with sponge and control shells and then combusting them at 500°C for 4 h. Control shells lost on average  $2.16 \pm 0.28\%$  of their weight during combustion. Shell weights for infested oysters and sponge shells were corrected for the weight loss of the control to correct for potential weight loss due to attached epibionts. Sponge ash-free dry weight was determined as the difference between the corrected shell weight and the combusted shell weight (see Carroll et al., 2015).

While this method was used for all 64 infested oysters it was not possible to determine sponge dry weight for all sponge samples (n = 64) because some sponges from the 8.03 and 7.63 treatment (n = 39) were used in a following experiment and could not be sacrificed. Therefore, a relationship between sponge wet weight and sponge ash-free dry weight was established for the remaining 25 sponge samples. Sponge wet weight was calculated by subtracting density corrected buoyant weight (T2) of the sponge shells from shell wet weight (semi-dry, in air) of the sponge shells (T2). The average percentage weight loss that controls shells lost from wet weight to buoyant weight was used to

adjust sponge wet weight. The resulting conversion factor (sponge ash-free dry weight/sponge wet weight) was used to estimate sponge ash-free dry weight for the remaining 39 sponge samples.

## 2.12 Statistics

Linear mixed effect models were used to test the effects of pH and sponge infestation on the different measured physiological rates and parameters. pH was used as a continuous predictor and fixed effect, while water bath and header tank were used as random effects. Differences between calcification rates of uninfested and infested oysters were compared separately for each pH treatment using linear mixed effect models with Category (uninfested/infested) as a fixed factor while including the above-mentioned random effects. Additionally, the effects of pH and sponge infestation and their interaction on oysters were tested by adding pH (continuous) and sponge infestation (yes/no) as fixed factors to the model. Conditional coefficients of determination ( $R^2$ ) values were taken from the full model. For all data sets the assumptions of normality and equality of variance were evaluated through graphical analyses of residuals. All tests and analyses were conducted using R (R Core Team, 2022) implemented in RStudio (RStudio Team, 2020, Version 1.4.1717). We used the R software packages “lme4”, “sjPlot”, “MuMin”, “lmerTest” in addition to packages implemented in base R. We used alpha = 0.05 as a significance level for all analyses but regarded alpha < 0.1 as a noteworthy trend. All the calculated uncertainties are given as standard errors.

## 3 Results

### 3.1 Net calcification/bioerosion

Net calcification in oysters without sponge infestation was not significantly affected by pH (Figure 1A, Supplementary Table 2). However, net calcification and net bioerosion respectively were significantly impacted by pH in sponge-infested oysters (Figure 1B, Supplementary Table 2) and sponges (Figure 1C and Supplementary Table 2). The net calcification rate increased with increasing pH from  $-0.19 \pm 0.35$  to  $1.34 \pm 0.27$  mg  $\text{CaCO}_3$   $\text{g}^{-1}$  DW  $\text{day}^{-1}$  in sponge-infested oysters. In sponges, the net bioerosion rate decreased significantly with increasing pH from  $-6.46 \pm 2.54$  to  $2.36 \pm 1.03$  mg  $\text{CaCO}_3$   $\text{g}^{-1}$  DW  $\text{day}^{-1}$ .

There was no significant difference between calcification of uninfested oysters and infested oysters when separately compared between treatments (Supplementary Table 3) and pH did not significantly affect the calcification rates of uninfested oysters and sponge-infested oysters grouped together (Interactive model, Supplementary Table 4). There was a tendency for a negative effect of sponge infestation on calcification (Interactive model, model significance p = 0.06, Supplementary Table 4). The interaction between decreasing pH and sponge infestation also had a strong tendency to negatively affect calcification rates (model significance p = 0.06, Supplementary Table 4). From pH 8.03 to pH 7.83 the interactive effect was positively antagonistic (less positive than

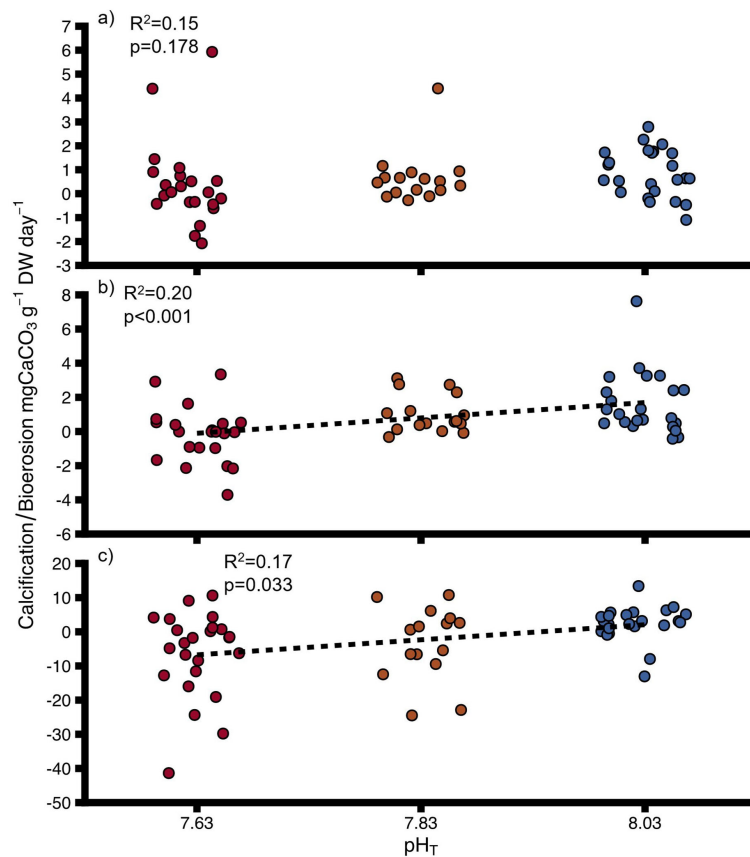


FIGURE 1

Net calcification (positive values)/net bioerosion rates (negative values) for (A) uninfested oysters, (B) infested oysters, (C) sponges at different pH. DW, dry weight for oysters and ash-free dry weight for sponges. Negative values indicate bioerosion activity, positive values indicate calcification activity. Points show individual values. Colours indicate pH treatment (blue = 8.03, orange = 7.83, red = 7.63). Dashed lines indicate significant trends. Proportions of variation ( $R^2$ ) and p-values were obtained from full linear mixed effect models.

predicted additively) and from pH 8.03 to pH 7.63 the interaction was negatively synergistic (more negative than predicted additively).

### 3.2 Respiration

Respiration rate was not significantly impacted by pH in uninfested oysters (Figure 2A, Supplementary Table 5), sponge-infested oysters (Figure 2B, Supplementary Table 5) and sponges (Figure 2C, Supplementary Table 5). pH levels did not significantly impact oyster respiration when uninfested and infested oysters were grouped together (Interactive model, Supplementary Table 6). Sponge infestation did not have any effect on respiration rates of oysters (Interactive model, Supplementary Table 6). Additionally, there was no statistical interactive effect of pH and sponge infestation on respiration rates (Supplementary Table 6).

### 3.3 Clearance rate

Clearance rate of uninfested oysters, infested oysters and sponges was not significantly impacted by pH (Figure 3 and Supplementary Table 7). Oyster clearance rate of particles  $>2.5 \mu\text{m}$  varied from  $0.51 \pm$

$0.21 \text{L g}^{-1} \text{h}^{-1}$  at pH 8.03 to  $0.03 \pm 0.05 \text{L g}^{-1} \text{h}^{-1}$  at pH 7.63 and clearance rate of particles  $2.5\text{--}5 \mu\text{m}$  varied from  $0.50 \pm 0.21 \text{L g}^{-1} \text{h}^{-1}$  (pH 8.03) to  $0.04 \pm 0.05 \text{L g}^{-1} \text{h}^{-1}$  (pH 7.63). For the sponges, no positive clearance rate was determined after correction for particle sedimentation in the control chambers. Therefore, we did not correct clearance rates of sponge-infested oysters for possible sponge clearance rate. Decreasing pH had a significant negative effect on clearance rates of all particle sizes of uninfested oysters and sponge-infested oysters grouped together (Interactive model, Supplementary Table 8, Figure 4) and sponge infestation had a significant positive effect on clearance rates (Interactive model, Supplementary Table 8). The interaction of pH and sponge infestation had a significant positive effect on clearance rates of all particle sizes (Supplementary Table 8). The interactive effect was negative antagonistic (less negative than predicted additively).

### 3.4 Short-term calcification/chemical bioerosion

Uninfested and sponge-infested oysters seemingly did not calcify (or not enough to be detectable) over the course of the incubations as no net decrease in calcium concentration between start and end of the

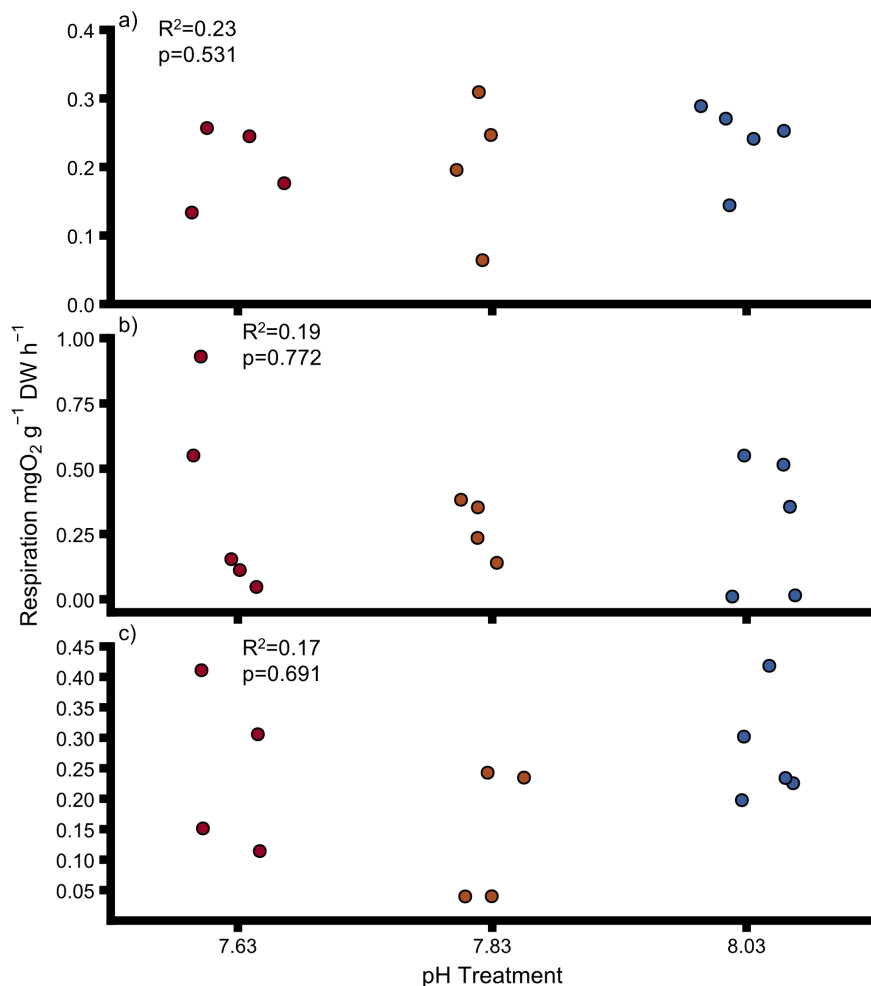


FIGURE 2

Respiration rates for (A) uninfested oysters, (B) infested oysters, (C) sponges at different pH. Points show individual values. Colours indicate pH treatment (blue = 8.03, orange = 7.83, red = 7.63). DW, dry weight for oysters and ash-free dry weight for sponges. Dashed lines indicate significant trends. Proportions of variation ( $R^2$ ) and p-values were obtained from full linear mixed effect models.

incubations was detected. The dissolution rate (increase in calcium) of uninfested oysters and sponge-infested oysters was not significantly impacted by pH (Figures 5A, B, Supplementary Table 9) and neither was the chemical bioerosion rate of sponges (Figure 5C, Supplementary Table 9). Decreasing pH had no significant effect on calcification/net dissolution of uninfested oysters and sponge-infested oysters grouped together, and sponge infestation had no effect on calcification/net dissolution when treatments were disregarded (Interactive model, Supplementary Table 10). There was no statistical interactive effect of pH and sponge infestation on calcification/net dissolution rates (Supplementary Table 10). Overall, some of the calculated differences between T0 and Tend of the incubations were not discernible within the uncertainty of the measurement.

### 3.5 Oyster condition

Oyster condition was not significantly impacted by pH in uninfested oysters (Figure 6A, Supplementary Table 11) and

sponge-infested oysters (Figure 6B, Supplementary Table 11). pH did not significantly impact condition when uninfested and infested oysters were grouped together, and sponge infestation did not have a significant effect when pH treatments were disregarded (Interactive model, Supplementary Table 12). There was also no significant interactive effect of pH and sponge infestation on oyster condition (Supplementary Table 12).

## 4 Discussion

Our results showed that pH had no measurable effect on calcification, respiration, clearance rate and condition of uninfested oysters indicating that *O. chilensis* might be largely unaffected by ocean acidification, opposing our initial hypotheses. Reduced pH caused a significant reduction in calcification in sponge infested oysters. However, respiration, clearance rate and condition were not measurably affected by pH, also opposing our initial hypotheses. The reduction in calcification rates of sponge infested oysters is likely related to the observed positive effect of pH on



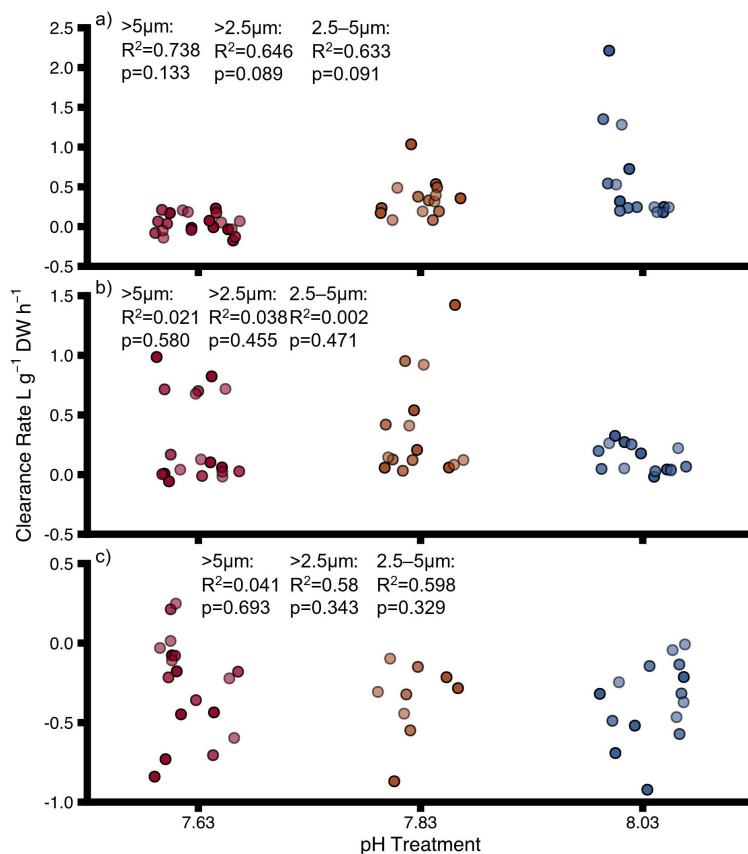


FIGURE 3

Clearance rates for (A) uninfested oysters, (B) infested oysters, (C) sponges at different pH for different particle size ranges. DW, dry weight for oysters and ash-free dry weight for sponges. Points show individual values. Colours indicate pH treatment (blue = 8.03, orange = 7.83, red = 7.63). The transparency of the colours reflects the particle size range: dark colours = >5–60 µm, medium colours = >2.5–60 µm, light colours = 2.5–5 µm. Proportions of variation (R<sup>2</sup>) and p-values were obtained from full linear mixed effect models.

bioerosion rate of *Cliona* sp. as initially hypothesised. Respiration rate and clearance rate of *Cliona* sp. was not measurably affected by reduced pH, which could indicate that *Cliona* sp. will not be strongly affected by future ocean acidification. Without measurable impacts of pH on *Cliona* sp., gross bioerosion is likely to increase under ocean acidification. Therefore, oysters and other marine shelled molluscs infested with *Cliona* sp. will likely be especially vulnerable to future decreases in seawater pH.

#### 4.1 Effect of pH and sponge infestation on oyster physiology

The net calcification rate of infested oysters significantly decreased with declining pH and turned into net dissolution at pH 7.63. The observed net dissolution of infested oysters suggests that at low pH, sponge bioerosion outpaces calcification, which is supported by the strong trend ( $p = 0.06$ ) for sponge infestation to decrease calcification. Similarly, in an earlier study, *Cliona* sp. infestation significantly reduced calcification of *Crassostrea virginica* (McNally, 2022). Sponge infestation may not have a significant negative effect ( $p$

= 0.06) on calcification in our study because shell repair, triggered when the boring organism breaks through to the inner valve surface of the oyster (Thomas, 1979; Hoeksema, 1983; Handley, 1998), counteracted bioerosion by the sponge. In comparison large (old) adult oysters naturally have low calcification rates (Kraeuter et al., 2007; Burchell et al., 2013). Together, low calcification rates of uninfested oysters and increased shell repair in infested oyster could explain the lack of significant difference between calcification of uninfested and infested oysters when compared per treatment. While we visually assessed the level of sponge infestation to be high in infested oysters, it is unclear whether the sponge broke through to the inner surface to trigger a response in all samples.

Increased shell repair would increase the energy demand in infested oysters (Palmer, 1992; Handley, 1998). An increased energy demand of sponge-infested oysters could explain why sponge infestation had a significant positive effect on clearance rate (Interactive model). In *C. virginica*, clearance rates were unaffected by sponge infestation while condition and growth were significantly reduced (Carroll et al., 2021). In contrast, respiration and condition were unaffected by sponge infestation and pH in our study. Therefore, the increase in clearance rate (increased energy

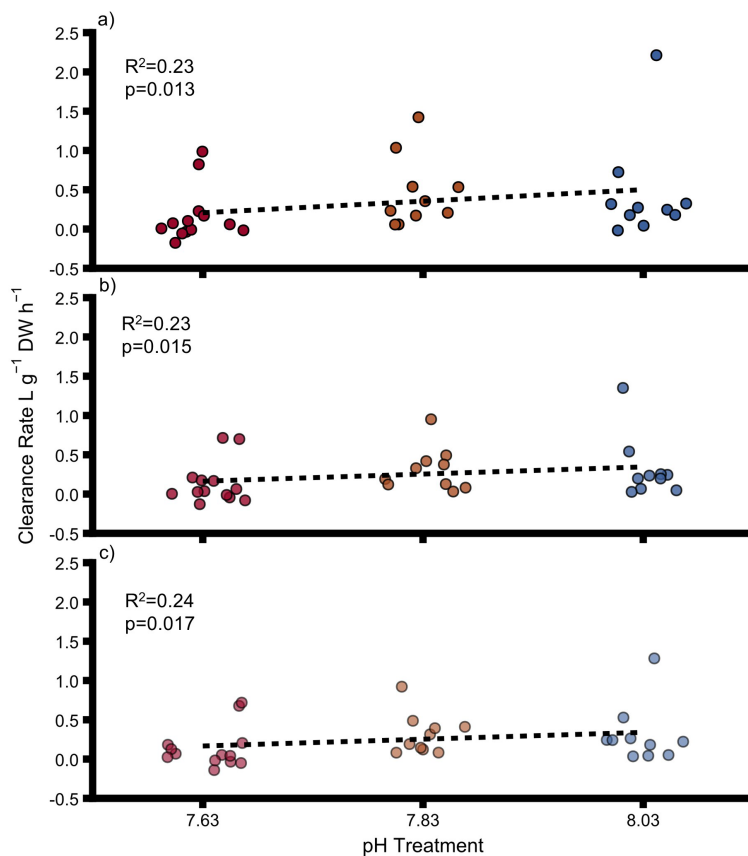


FIGURE 4

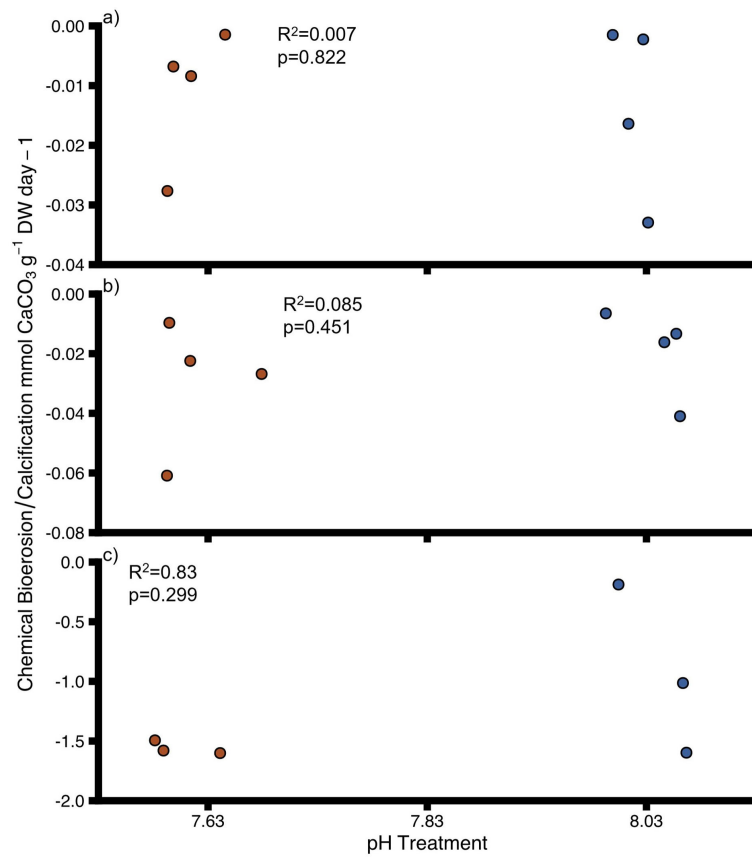
Clearance rates for uninfested and infested oysters at particle size ranges of (A) >5–60  $\mu\text{m}$  (B) >2.5–60  $\mu\text{m}$  and (C) 2.5–5  $\mu\text{m}$ . DW = dry weight for oysters and ash-free dry weight for sponges. Points show individual values. Colours indicate pH treatment (blue = 8.03, orange = 7.83, red = 7.63). The transparency of the colours reflects the particle size range: dark colours = >5–60  $\mu\text{m}$ , medium colours = >2.5–60  $\mu\text{m}$ , light colours = 2.5–5  $\mu\text{m}$ . Proportions of variation ( $R^2$ ) and p-values were obtained from full linear mixed effect models.

assimilation) might represent a coping mechanism for sponge-infested oysters which allows the maintenance of other metabolic processes (see Lannig et al., 2010), while meeting energetic demands of shell repair.

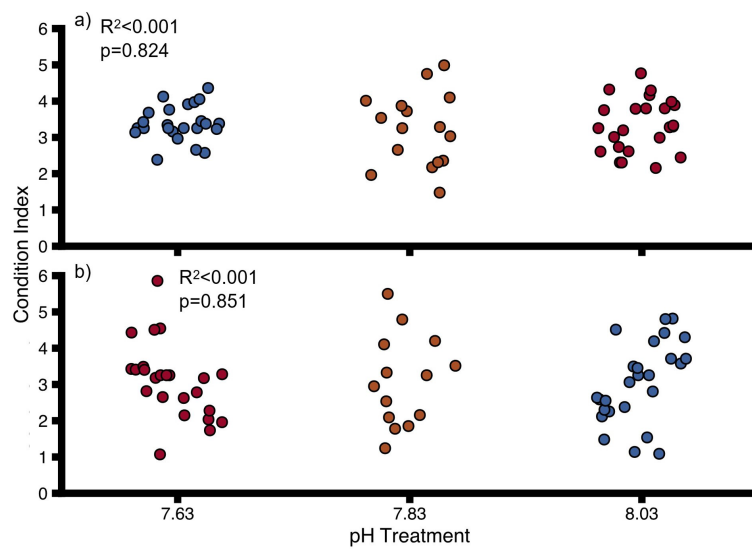
Surprisingly, net calcification of uninfested oysters was not significantly impacted by pH, even though reduced pH significantly affected net calcification in other oyster species. One explanation for the differing results could be the smaller range of ocean acidification/pH treatments ( $p\text{CO}_2$  from 475.0–1151.7  $\mu\text{atm}$  or  $p\text{CO}_2$  482.6–1170.3 ppm) used in our study compared to in others (*Magallana gigas*,  $p\text{CO}_2$  421–2351 ppm: Gazeau et al., 2007; *C. virginica*,  $p\text{CO}_2$  280–2856 ppm: Ries et al., 2009; *C. virginica*,  $p\text{CO}_2$  380–3500  $\mu\text{atm}$ : Beniash et al., 2010; Dickinson et al., 2012). For example, there was a tendency ( $p < 0.10$ ) for calcification of *C. virginica* to decline from pH 7.8 to ~7.0, but a tipping point was identified below pH 6.98, after which net calcification drastically decreased with pH ( $p < 0.01$ ) (Lutier et al., 2022). Therefore, there is a possibility that the pH reduction used in our study was not strong enough to significantly affect calcification of *O. chilensis*. *O. chilensis* calcification may thus remain unaffected by seawater pH values predicted for the end of the century. Nevertheless, the calcification rate of uninfested oysters at pH 7.63 was ~half of the calcification

rate at pH 8.03 indicating that the variability between individual samples within treatments might have hindered the detection of a significant effect.

Individual variability likely also hindered the detection of a significant effect of pH on average clearance rate of uninfested oysters which was reduced by 82–96% between the highest and lowest pH treatment. Reduction of clearance rate can be a mechanism to reduce contact of adverse seawater pH with internal tissues (Rastrick et al., 2018), but reduced clearance rate could also lead to a decline in the energy available for calcification. The interactive model showed that pH had a negative effect on clearance rate of uninfested and infested oysters combined. The lack of an impact on condition could indicate that oysters reduced calcification as a trade-off for reduced clearance rates instead of reducing other metabolic processes, such as somatic growth. Similarly, *M. gigas* reduced clearance rates by ~40% from 400 ppm to 750 ppm, while condition and standard metabolic rate were unaffected (Lemasson et al., 2018). The CI of sponge infested oysters in our study could have been slightly positively inflated due to reduced shell weight and thus could have been affected by differential bioerosion rates in treatments. Nevertheless, sponge infestation and pH also had no impact on the condition of *C.*



**FIGURE 5**  
 Chemical bioerosion (negative values) and calcification (positive values) for (A) uninfested oysters, (B) infested oysters and (C) sponges at different pH. DW = dry weight for oysters and ash-free dry weight for sponges. Points show individual values. Colours indicate pH treatment (blue = 8.03, red = 7.63). Proportions of variation (R<sup>2</sup>) and p-values were obtained from full linear mixed effect model.



**FIGURE 6**  
 Condition Index for (A) uninfested oysters, (B) infested oysters at different pH. Points show individual values. Colours indicate pH treatment (blue = 8.03, orange = 7.83, red = 7.63). Proportions of variation (R<sup>2</sup>) and p-values were obtained from full linear mixed effect models.

*virginica* (McNally, 2022) and condition was also not affected by pH in uninfested oysters in this study.

## 4.2 Interactive effect of pH and sponge infestation on oysters

pH and sponge infestation had a near but not significant interactive effect ( $p = 0.06$ ) on oyster calcification in this study. By contrast, in other oysters (such as *C. virginica*) such interactive effects of pH and sponge infestation have not been found (McNally, 2022). Here, any interaction seems to be occurring across a non-linear antagonistic gradient that slowly reverses as pH declines. pH and sponge infestation first seem to have a slightly positive effect, due to higher calcification rates of sponge-infested oysters at pH 8.03 and pH 7.83 compared to uninfested oysters. However, the average net dissolution of infested oysters at pH 7.63 suggests that at this pH, both factors were interacting to have a more negative effect than the simple addition of both effects (negative synergistic, definitions following Piggott et al., 2015). Simultaneously, the interaction of sponge infestation with decreasing pH had a significant negative antagonistic (i.e., less negative than negative effects of both added together) effect on clearance rate of oysters. Infested oysters might be able to reduce negative effects of sponge infestation on calcification by increasing clearance rates, shown by positive calcification rate and increased clearance rate at pH 7.83. Further, the slight reduction in average clearance rate of sponge-infested oysters at pH 7.63 could reflect the increased need to avoid internal tissue exposure to low pH seawater (Rastrick et al., 2018). The inability to further increase clearance rate could lead to the observed net dissolution, likely influenced by increased boring activity of *Cliona* sp.

## 4.3 The effect of pH and sponge infestation on short-term calcification/chemical bioerosion

Oysters had net loss of calcium carbonate over the course of six hours during the incubations, but no significant effect of pH was detected. The mean net dissolution calculated for infested oysters was slightly lower (not significantly) than that of uninfested oysters for both treatments. However, no interactive effect of pH and sponge infestation was detected. The results suggest that boring sponges were more active during the incubations than oysters. It is possible that sponges were less affected by stress caused from being removed from treatment tanks and being placed in incubation chambers. The low number of replicates overall (control:  $n = 4$ , sponges:  $n = 6$ , infested oysters  $n = 8$ , uninfested oysters  $n = 8$ ) might have impaired our ability to detect significant trends due to lack of power. The low number of replicates here was due to logistic constraints. In contrast to our results, chemical sponge bioerosion has been shown to increase significantly with ocean acidification in bioeroding sponges from tropical reefs (Fang et al., 2013; Wisshak et al., 2013; Webb et al., 2017; Watts et al., 2018) and temperate waters (Wisshak et al., 2014).

## 4.4 Effect of pH on physiology of *Cliona* sp.

Net bioerosion rate of *Cliona* sp. in the shells of dead oysters increased significantly with decreasing pH. This contrasts with the lack of impact of pH detected on chemical bioerosion. Accordingly, reduced pH caused an increase in net bioerosion in *C. orientalis* from the Great Barrier Reef (Fang et al., 2013; Wisshak et al., 2014; Webb et al., 2017) and *C. celata* in cold-temperate waters (New York, USA, Duckworth and Peterson, 2013; Heligoland, Germany, Wisshak et al., 2014). In two Caribbean sponges (*P. lampa*, *Cliona varians*) bioerosion rates increased non-linearly with reduced pH (Enochs et al., 2015; Morris et al., 2023). In this study, the fact that sponge-infested shells in the ambient treatment gained weight on average is non-sensical and probably caused by the subtraction of the average percentage weight change of the control shells, which was done to correct for passive dissolution (and possible weight change due to leftover epibionts/borers) to obtain net bioerosion rates. This indicates that sponges in the control treatment did not erode the shells to an extent that an effect beyond passive dissolution was detectable (see uncorrected rates, Supplementary Table 13). Nevertheless, significantly increased net bioerosion activity at pH 7.83 and 7.63 indicates that sponge erosion will benefit from ocean acidification.

There was no significant effect of pH on sponge respiration. The effects of low seawater pH on sponge respiration have been variable. For example, in an experiment with two temperate sponges, the low seawater pH treatment (7.62) significantly increased the respiration rate of *Tethia bergquistae* compared to the control ( $\sim 8.05$ ), but did not affect respiration in *Crella incrustans* (Bates and Bell, 2018). Contrastingly, OA significantly depressed the respiration rate of the Great Barrier Reef sponge *Stylissa flabelliformis* (Bennett et al., 2017). The bioerosion rate of temperate *C. celata* (New York, USA) increased significantly with pH but so did mortality rate (Duckworth and Peterson, 2013). Chemical bioerosion rates of the sponge *Pione lampa* followed a parabolic curve and were depressed again at a  $p\text{CO}_2$  of  $\sim 1000$   $\mu\text{atm}$  (Enochs et al., 2015). In our study the survival of sponges was unaffected by pH (no mortality) and no negative effects of pH on sponge on health were observed. Alpha stage (boring) sponges used here and in other studies with seemingly pH tolerant sponges (Wisshak et al., 2014), are completely hidden inside the oyster shell except for their papillae. Reduced contact with seawater could also explain the higher tolerance to reduced pH compared with gamma stage (massive) sponges (e.g., Duckworth and Peterson, 2013). Another reason for the lack of negative impact of pH on respiration and sponge health observed here could be the slight diurnal pH variation in treatments. Diurnal pH variation might alleviate negative effects of low seawater pH on bioeroding sponges and can increase bioerosion rates compared to static treatments (Morris et al., 2022). Similar to respiration, there was no effect of pH on clearance rate of sponges, but the average clearance rate was also negative for all treatments. This suggests that sponges did not feed, even in the smaller particle range (2.5–5  $\mu\text{m}$ ) that should have been suitable for sponge feeding. Sponges can show high food selectivity, so it is possible that *Cliona* sp. was selectively feeding on particles outside of our measured range that were available from the raw seawater (Varamgianni-Mamatsi et al., 2021; Harris, 2022).

## 5 Conclusion

Our results show that sponge infestation can interact with further ocean acidification and increase bioerosion activity of sponges and therefore exacerbate the effects of sponge infestation and pH on oysters. The net dissolution rates of infested oysters at pH 7.63 suggest that oysters will not be able to calcify fast enough to work against the significantly increased bioerosion activity of the sponge at this pH. Therefore, even in cases where sponge infestation seems to have limited effects on their hosts as suggested for *O. chilensis* from FS (Böök et al., 2023), sponge infestation could increasingly affect host organisms by the end of this century. Oysters seemed to be able to mitigate some of the effects of increased sponge erosion by increasing clearance rates at reduced pH (significant positive antagonistic effect of sponge infestation and pH on clearance rate), which could also explain condition and respiration being unaffected by sponge erosion and pH. Adult oysters that might have naturally reduced shell growth compared to juvenile oysters could be severely impacted by sponge erosion that outpaces their shell repair and shell growth. Weakening of shells occurs in many bivalves at low seawater pH. Increasing bioerosion in addition to already weakened shells could lead to higher mortality in adult oysters due to increased predation and simply through crumbling of their shells. While this study provides insight into interaction between bioeroders and host-organisms in a less alkaline ocean, CO<sub>2</sub> emissions are also causing our oceans to warm up due to the greenhouse effect and increase the frequency and intensity of marine heatwaves. It is important that future studies investigate the effect of ocean warming and marine heatwaves together with ocean acidification on the interaction of bioeroding sponges and *O. chilensis*. This study highlights that calcifying organisms that are colonised by bioeroding organisms could be especially vulnerable to changes in seawater pH and also indicates that bioerosion might increase under predicted future ocean acidification scenarios. It is therefore crucial to further increase our knowledge on interactions of bioeroding organisms and calcifying organisms in a fast-changing environment.

## Data availability statement

The raw data supporting the conclusions of this article is available at Dryad (DOI: 10.5061/dryad.4qrf6qkj).

## Ethics statement

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

## Author contributions

IB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. EK: Conceptualization, Investigation, Methodology, Visualization, Writing – review & editing. NP: Conceptualization, Methodology, Resources, Supervision, Writing –

review & editing. KM: Conceptualization, Methodology, Resources, Supervision, Writing – review & editing. JB: Conceptualization, Methodology, Resources, Supervision, Writing – review & editing. WD: Investigation, Methodology, Resources, Writing – review & editing. CC: Conceptualization, Investigation, Methodology, Resources, Supervision, 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 Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1444863/full#supplementary-material>



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