Mar Biol
DOI 10.1007/s00227-012-2053-z

ORIGINAL PAPER

Effects of seawater temperature and pH on the boring rates of the sponge *Cliona celata* in scallop shells

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Received: 6 February 2012 / Accepted: 21 August 2012

Abstract Warmer, more acidic water resulting from greenhouse gas emissions could influence ecosystem processes like bioerosion of calcifying organisms. Based on summer-maxima values (temperature = 26 °C; pH = 8.1) at a collection site in New York (40°56′ N, 72°30′ W), explants of the boring sponge *Cliona celata* Grant, 1826 were grown for 133 days on scallop shells in seawater ranging from current values to one scenario predicted for the year 2100 ($T = 31$ °C; pH = 7.8). High water temperature had little effect on sponge growth, survival, or boring rates. Lower pH slightly reduced sponge survival, while greatly influencing shell boring. At pH = 7.8, sponges bored twice the number of papillar holes and removed two times more shell weight than at pH = 8.1. Greater erosion resulted in weaker scallop shells. This study suggests that lower seawater pH may increase boring rates of *C. celata* in shellfish, with potentially severe implications for wild and farmed shellfish populations.

Communicated by P. Kraufvelin.

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Introduction

Greater output and absorption of greenhouse gasses resulting in warmer, more acidic waters will dramatically impact marine ecosystems, influencing countless organisms (Guinotte and Fabry 2008). Effects from these environmental changes will vary among taxonomic groups, with calcifying organisms like corals and mollusks considered to be most at risk (Hoegh-Guldberg et al. 2007; Guinotte and Fabry 2008). For some ecologically important taxonomic groups, like sponges, the combined effects of increasing temperature and decreasing pH are poorly known. Furthermore, it remains unclear how warmer, more acidic water will alter interspecific interactions and influence ecosystem processes (Przeslawski et al. 2008).

Bioerosion of calcium carbonate substrates, produced by corals and shellfish, by cyanobacteria, sponges, fish, and other organisms (e.g., Glynn 1997), is an important destructive process (e.g., Hutchings 1986; Mallela and Perry 2007). On shellfish reefs, for example, bioeroders can infest >80 % of individuals (Hartman 1958; Pomponi and Meritt 1990; Rosell et al. 1999) and excavate >40 % of a given shell (Pomponi and Meritt 1990). High levels of bioerosion can kill mollusks (Kaehler and McQuaid 1999), while low levels can weaken skeletons leaving individuals more vulnerable to predation or physical damage (Stefaniak et al. 2005).

Boring sponges, primarily *Cliona* species, are some of the most common and destructive bioeroders of mollusks, boring into numerous species of oysters (e.g., Rosell et al. 1999; Daume et al. 2010), scallops (Evans 1969), barnacles (Hoeksema 1983), and gastropods (Stefaniak et al. 2005). Clionaids can bore into and damage commercially important wild and farmed shellfish populations (de Nys and Ison 2008; Daume et al. 2010), causing significant financial

Published online: 14 September 2012

losses each year (Daume et al. 2009). Any environmental stress that reduces the fitness of the calcifying organism may increase the abundances of boring sponges and their rates of erosion (Rützler 2002; Schönberg and Ortiz 2008). Clionaids bore into calcareous substrates using chemical and mechanical means. Etching cells chemically carve out small chips, which are mechanically removed from the sponge via the aquiferous system (Rützler and Rieger 1973; Pomponi 1980). Depending on the sponge species, bioerosion rates are influenced by environmental factors like water flow rates, light intensity, substrate density, nutrient levels, and water temperature (reviewed by Schönberg 2008). Temperate clionaids, for example, may stop boring in winter when water temperature falls below a certain level (e.g., Cobb 1975; Pomponi and Meritt 1990). Water temperature is often positively correlated with sponge growth (e.g., Simpson 1968; Turon et al. 1998; Duckworth and Battershill 2001), including growth of clionaids (e.g., Rützler 2002; Carver et al. 2010). Collectively, these studies suggest that as oceans warm (Meehl et al. 2007), it could influence the rate and impact of clionaids boring into calcifying organisms.

In addition to rising water temperature, increasing amounts of atmospheric CO_2 are absorbed by the oceans, lowering the pH and leading to ocean acidification (Orr et al. 2005). Ocean acidification will reduce calcification rates of calcifying organisms (Anthony et al. 2008), which in shellfish results in thinner shells (Talmage and Gobler 2010). Clionaids may also be affected by ocean acidification, as Emson (1966) found that the sponge *Cliona celata* Grant, 1826 started closing its oscules and reducing pumping rates at seawater pH $\leq$ 7.6. Historical evidence also points to mass extinctions of ancient calcifying sponges during periods of warmer water coupled with ocean acidification (Kiessling and Simpson 2011). In contrast, a recent study found that growth and survival of six coral reef sponges common to the Caribbean region were similar after 1 month in waters ranging in pH from 7.8 to 8.1 (Duckworth et al. 2012). Ocean acidification reducing calcification rates of shellfish may therefore allows clionaids to bore faster in thinner shells, unless the sponge is adversely influenced by lower pH.

Cliona celata is commonly found living on and boring into oysters and scallops (Warburton 1958; Nicol and Reisman 1976) and is considered a pest by shellfish farmers, infesting upwards of 90 % of shells in some areas (Hartman 1958). The World Porifera Database currently shows that *C. celata* has a large distribution range in the Atlantic Ocean and Mediterranean Sea (Van Soest 2011). Recent molecular studies have found, however, that *C. celata* is a species complex in both the Northeast Atlantic and Mediterranean Sea (Xavier et al. 2010) and Southwest Atlantic (de Paula et al. 2012). Morphological characteristics (e.g., spicules) are often not sufficient to separate species (de Paula et al. 2012). *C. celata* was referred to in earlier research that was done near this study's collection site in New York (e.g., Hartman 1958; Nicol and Reisman 1976; Fell et al. 1984), so this will be the species name used here. Previous studies have found that *C. celata* (including sponges assumed as conspecifics) may recruit onto new shells from larvae or via shell-to-shell contact (Carver et al. 2010) and is considered a hardy sponge, tolerant of environmental stressors such as high nutrient loads, low salinity, and large temperature fluctuations (Hartman 1958; Carballo et al. 1996). This study focused on the effects of water temperature and pH on the boring rates of *C. celata* in scallop shells, comparing current summer-maxima conditions to predicted values for 2100 (Orr et al. 2005; Meehl et al. 2007). The maximum summer temperature was used because it represents the highest temperature currently experienced by *C. celata* in the study area, thus nearest its upper thermal physiological limit.

Methods

Animal collection

Approximately 20 *C. celata* individuals were collected from Peconic Bay, New York (40°56′ N, 72°30′ W), with all individuals of gamma (i.e., free-living) morphology, healthy, and free of fouling organisms. Collected sponges were transferred underwater to holding tanks with free-flowing water and cut into ~150 smaller pieces or explants using sharp scalpels. Explants were approximately 8 cm^3 in size, with a mean wet weight ± SE = 5.52 ± 0.19 g, and allowed to heal for 2 weeks before being used. Mean initial wet weight was determined by weighing 40 explants that were exposed to air for 10 min to remove excess water (Duckworth and Battershill 2003); these explants were then discarded.

The Atlantic bay scallop, *Argopecten irradians*, the model shellfish used in this study, is found in sea-grass habitats along the US east coast and the Gulf of Mexico (Fay et al. 1983). Atlantic bay scallops are commercially fished and farmed, and all scallops used in this study were farmed in suspended culture in Peconic Bay. Because precise weight measurements (to 0.1 mg) were needed to determine shell loss from sponge boring activities, only clean shells were used and not live scallops. All shells were numbered using a permanent marker and had a mean surface area and weight ± SE = 1907.1 ± 19.7 mm^2 and 5326.6 ± 834.1 mg, respectively.

Experimental setup

Four treatments differing in water temperature (T) and pH were tested, all based on current summer-maxima values for Peconic Bay, New York, of 26 °C and 8.1 pH units (Turner 1982; Breuer et al. 1999). Treatment 1 ($T = 31$ °C, pH = 7.8) tested one predicted scenario for the year 2100 (Orr et al. 2005; Meehl et al. 2007). Treatments 2 ($T = 31$ °C, pH = 8.1) and 3 ($T = 26$ °C, pH = 7.8) tested the individual effects of warmer water or lower pH. Treatment 4 ($T = 26$ °C, pH = 8.1) was the control. Each treatment had 24 scallop shells with sponge explants secured and 12 scallop shells with no explant (control shells), the latter used to separate the effects of seawater pH and temperature from the potential excavating effects of *C. celata*. Explants were secured to the convex side of scallop shells, one explant per shell, using rubber bands. Once the explant had physically attached to the shell (Fig. 1a), the rubber band was removed. Each treatment had 6 replicate aquaria, each with 4 sponge explants and 2 shell controls. All sponge and shell replicates were placed ≥3 cm apart on plastic mesh raised off the aquarium floor. Sponges were grown on scallop shells in the experimental settings for 133 days.

The experimental aquaria held 5 L of running seawater, which flowed through at a rate of 0.1 L min^{-1}; this was sufficient to keep ammonia levels constant at <0.1 mg L^{-1}, checked using Mardel test strips for saltwater aquaria. Air was bubbled into aquaria to provide sufficient oxygen and to mix the incoming water, so temperature and pH were constant throughout. Water temperature was kept at desired values by placing aquaria in water baths containing 600-W water heaters. The pH was lowered in treatments 1 and 3 by using the acid-drip method, where a Pinpoint® pH controller (American Marine, In.) released hydrochloric acid automatically from large holding tanks situated above the experimental aquaria into the incoming seawater when pH > 7.8. pH was manipulated in an "open system" with salinity at 35 ‰ and no addition of carbonate. Although the acid-drip method used here is a useful and valid technique for manipulating seawater chemistry (Andersson and Mackenzie 2012), the fact that we did not correct for carbonate means that not all water chemistry variables (e.g., pCO_2, total alkalinity) in treatments 1 and 3 will be similar to levels predicted for 2100. This study therefore focuses on the effects of seawater pH (and temperature) on sponge growth, survival, and boring.

Water temperature and pH were recorded daily in all tanks using a pHep 5 pH/temperature tester (Hanna instruments) calibrated frequently using supplied buffers (standardized against National Institute of Standards and Technology reference solutions). The pHep 5 compensates automatically for temperature and is accurate to 0.05 pH.

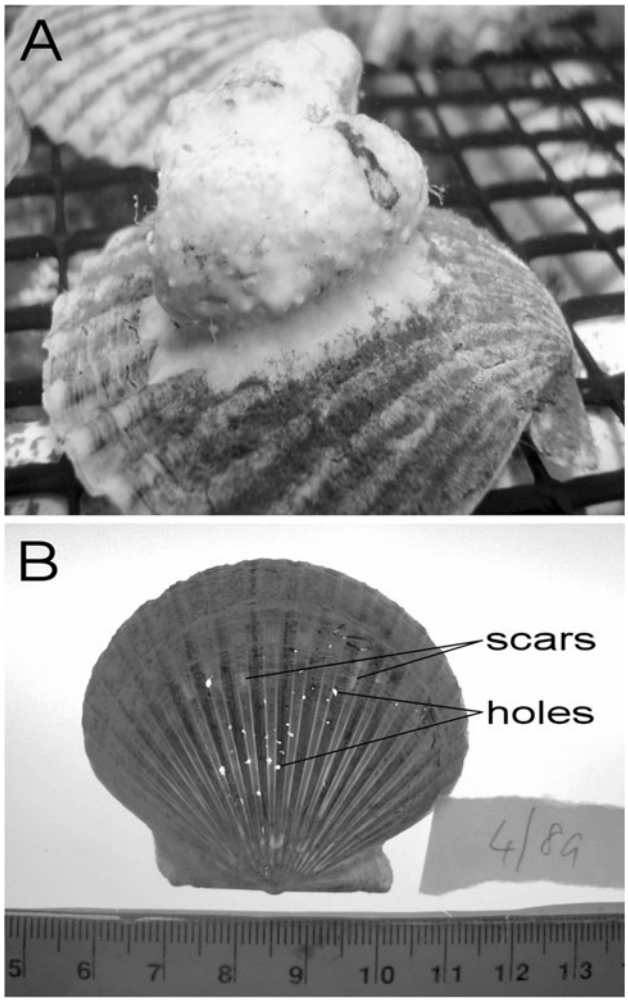

Fig. 1 **a** *Cliona celata* attached to and growing on a scallop shell; **b** Scallop shell on light board showing the papillar holes and boring scars

pH was measured on the total scale and, like temperature, was stable over time in each treatment. This experiment was carried out at the Southampton Marine Station, Stony Brook University, with aquaria replicates randomized within water baths. The water filtration system at the marine station necessitated the addition of supplemental food (Kent Marine MicroVert) to ensure sufficient nutrition and promote sponge growth. Although adding nutrients can alter some water chemistry variables in ocean acidification experiments (Riebesell et al. 2010), the small amount of added food combined with the flow-through water system used here was not expected to cause significant differences between treatments.

Experimental monitoring

Sponge survival and attachment was monitored every week for the first month and then every 2–5 weeks afterward.

At the end of the experiment, all surviving explants were exposed to air for 10 min to remove excess water and then wet-weighed to the nearest 0.01 g. A fine scalpel was used to carefully scrape off any explant that had physically attached to the scallop shell. Before removal, photos of 20 randomly chosen sponges were taken next to a ruler to determine the area attached to each shell or contact area. Changes in scallop shell weight were determined by weighing all shells (minus explants) at the start and end of the experiment, with shells oven-dried at 60 °C before weighing.

Changes in shell weight caused by sponge boring could involve one or more of the following: "papillar holes," where the sponge has bored entirely through the shell (Fig. 1b); "scars" showing initial removal of the shell periostracum (Fig. 1b); and "erosion chambers," which is removal of internal shell material and may connect papillar holes. Shells were photographed next to a ruler on a light board to digitally record papillar hole number and size. Boring scars and erosion chambers were not recorded; however, any loss in shell weight due to excavation is accounted for by weighing shells pre- and post-experiment. Sponge contact area and papillar hole measurements were determined using Image Tool (version 3; image analysis program from University of Texas Health Science Center at San Antonio). Lastly, each shell was subjected to a strength test to determine the force measured in Newton (N) required to fracture it. Using an Instron (Series 5500) load frame, downward force was applied at a constant rate of 2 mm s^{-1}, with the shell convex side up.

Data analysis

Two-way ANOVAs were used to statistically determine whether sponge final weight and shell measurements (e.g., weight loss, strength) were affected by temperature and pH levels, both analyzed as fixed factors. Sponge and shell data were averaged per aquarium to avoid pseudoreplication, so each treatment had 6 replicates; data were log-transformed as needed. Final weights of scallop shells with attached sponges were adjusted proportionally before analysis because final weights of control shells differed between pH (ANOVA, $F_{(1,20)} = 5.85$, $P = 0.025$) and water temperature levels (ANOVA, $F_{(1,20)} = 3.65$, $P = 0.071$); although the result was not significant for temperature, we considered the difference in weight loss between 26 and 31 °C large enough to correct for any potential effect. Linear regressions compared shell strength to other shell measurements. We also tested nonlinear regressions, but their results (not shown here) were similar to the results of linear regressions. Only scallop shells where the sponge survived and attached by the end of the study were included in these statistical analyses. Final sponge survival and attachment (to scallop shells) were examined using a two-way ANOVA on ranks (Zar 1999), because of heterogeneity of variances.

Results

Cliona celata

Final overall wet weights of *C. celata* did not differ significantly between temperature or pH levels, and there was no significant interaction term (Table 1). The final mean weight ± SE = 8.62 ± 0.24 g ($N = 24$), represents an increase of 3.1 g or 56 % of initial weight. On average, sponges that attached to scallop shells grew larger (X ± SE = 8.79 ± 0.25 g) than sponges that did not attach (X ± SE = 6.58 ± 0.84 g).

Final sponge survival varied significantly between pH treatments (Table 1) with all explants surviving at pH = 8.1 and 83 % at pH = 7.8 (i.e., 8 out of 48 sponges died). These eight sponges died between days 32 and 92 of the experiment (Fig. 2). Mortality was recorded in 4 aquaria (2 at each temperature), with 1–3 explants dying per aquaria. Water temperature did not affect survival, nor did it influence how pH changed survival (Table 1).

Final sponge attachment varied significantly between pH treatments, but not between temperature treatments (Table 1). At pH = 8.1, all sponges except one had attached to shells by 32 days (Fig. 2). At pH = 7.8, attachment rates were slower, with 60 % attached by day 32 and 85 % by day 133. Mean contact area ± SE of *C. celata* on scallop shells was 5.1 ± 0.2 cm^2 ($N = 20$).

Scallop shells

The number of papillar holes per shell varied significantly between pH levels (Table 1) with over twice the number of holes at pH = 7.8 (X ± SE = 8.5 ± 1.2) than at pH = 8.1 (X ± SE = 3.9 ± 0.8) (Fig. 3). Water temperature did not significantly affect papillar hole number, nor did it interact with pH (Table 1). None of the 12 control shells in any treatment had any papillar holes.

Papillar hole sizes were similar between temperature and pH levels (Table 1) averaging ± SE = 0.215 ± 0.021 mm^2 (Fig. 3). The smallest measured hole was 0.04 mm^2, while the largest was 2.29 mm^2. The interaction term was not significant (Table 1).

Shell weight loss differed significantly between pH levels, while temperature and the interaction term were not significant (Table 1). After correcting for weight loss of control shells, bored shells lost on average ± SE = 108.9 ± 14.1 mg at pH = 7.8 and 47.86 ± 9.23 mg at pH = 8.1 (Fig. 3). With a mean contact area of 5.1 cm^2, this equates to bioerosion rates of X ± SE = 0.586 ± 0.076 kg m^{-2}

Table 1 Summary of ANOVA's testing effects of water temperature and pH on final sponge and scallop shell measurements

Measurement	Temperature		pH		Temperature*pH	
	F-ratio	*P*	*F*-ratio	*P*	*F*-ratio	*P*
C. celata						
Weight	0.04	0.843	0.00	0.982	0.37	0.550
Survival	0.02	0.891	4.05	0.038	0.02	0.891
Attachment	1.11	0.304	12.74	0.002	0.06	0.81
Scallop shell						
Papillar hole number	0.02	0.892	9.29	0.006	0.09	0.771
Papillar hole size	0.11	0.744	0.61	0.442	3.76	0.067
Weight loss	0.71	0.408	12.48	0.002	0.24	0.632
Strength	1.08	0.310	6.40	0.020	0.57	0.460

F ratios and and interaction. $df = 1, 20$ for all measurements

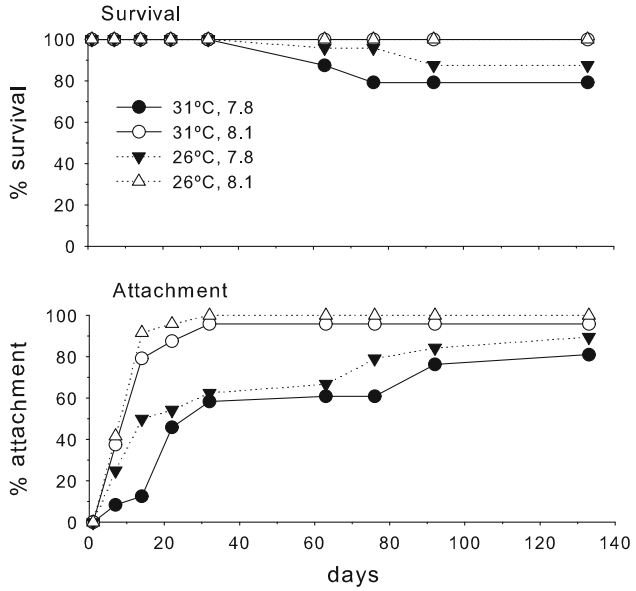

Fig. 2 Mean percent survival and attachment over time for *Cliona celata* in the four treatments. Standard *error bars* not shown for clarity; variation generally <10 %

year^{-1} at pH = 7.8 and 0.258 ± 0.049 kg m^{-2} year^{-1} at pH = 8.1.

Shell strength measured using a compression test varied significantly between pH levels (Table 1), averaging ± SE = 110 ± 13 and 152 ± 11 *N* for shells at pH = 7.8 and 8.1, respectively (Fig. 3). Thus, shells with attached sponges were 28 % weaker on average at pH = 7.8. Neither water temperature nor the interaction term was significant (Table 1). Strength of control shells did not differ significantly between treatments (ANOVA, $P > 0.5$). However, control shells were generally weaker at pH = 7.8 than at pH = 8.1, averaging ± SE = 181 ± 6 and 204 ± 10 N, respectively.

Linear regressions found that shell strength was negatively related to papillar hole number ($r^2 = 0.25$, $F_{1,22} = 7.47$, $P = 0.012$) and shell weight loss ($r^2 = 0.16$, $F_{1,22} = 4.34$, $P = 0.049$), but not papillar hole size ($r^2 = 0.001$, $F_{1,22} = 0.02$, $P = 0.894$) (Fig. 4). The r^2 values were low for all regressions due to high variability in scallop shell measurements.

Discussion

The pH of seawater affected the survival of the sponge *C. celata* and its boring into scallop shells. Almost 20 % of sponges died when grown in seawater with a pH of 7.8, while all sponges survived at pH = 8.1. *C. celata* died after several weeks in culture, suggesting that it was not the shock of being transferred into seawater of pH = 7.8, but the gradual effect of lower pH. Sponge mortality occurred in several aquaria over a period of 30–60 days. These results, when combined with constant environmental conditions during the study, indicate that mortality was not caused by a single event or by experimental error. Low pH may kill or damage marine invertebrates like corals and sea urchins by causing acidosis (Fabry et al. 2008; Przeslawski et al. 2008), involving abnormally high levels of carbonic acid in bodily fluids (e.g., blood) and tissues. Sponges do not have tissues or blood; they are an organized collection of cells through which oxygen diffuses from inhalent water. Therefore, the reason for sponge mortality likely differs from observations made for more developed marine invertebrates. Effects of environmental conditions on sponges can also differ greatly between conspecifics. High sediment loads, for example, can kill explants from one donor sponge, but have little effect on explants from other donor sponges (Maldonado et al. 2008). In this study, explants from donor sponges were first pooled and then randomly placed in different aquaria. It is therefore possible that all 8 explants that died came from 1 or 2 donor sponges that were more susceptible to a seawater pH of 7.8. Most *C. celata* grown at low pH survived, which suggests that ocean acidification will have a limited effect on population numbers overall. However, if some genotypes are more sensitive to pH changes than others, they may be

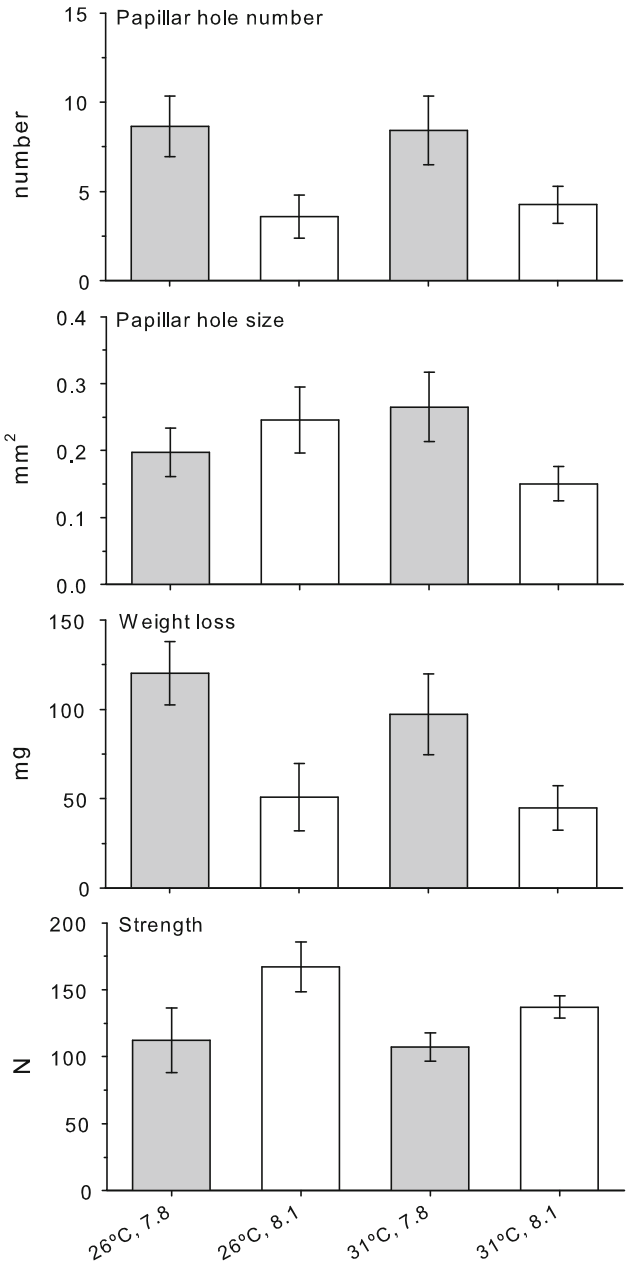

Fig. 3 Final mean values (±SE) of papillar hole number and size, weight loss, and strength of scallop shells in the four treatments

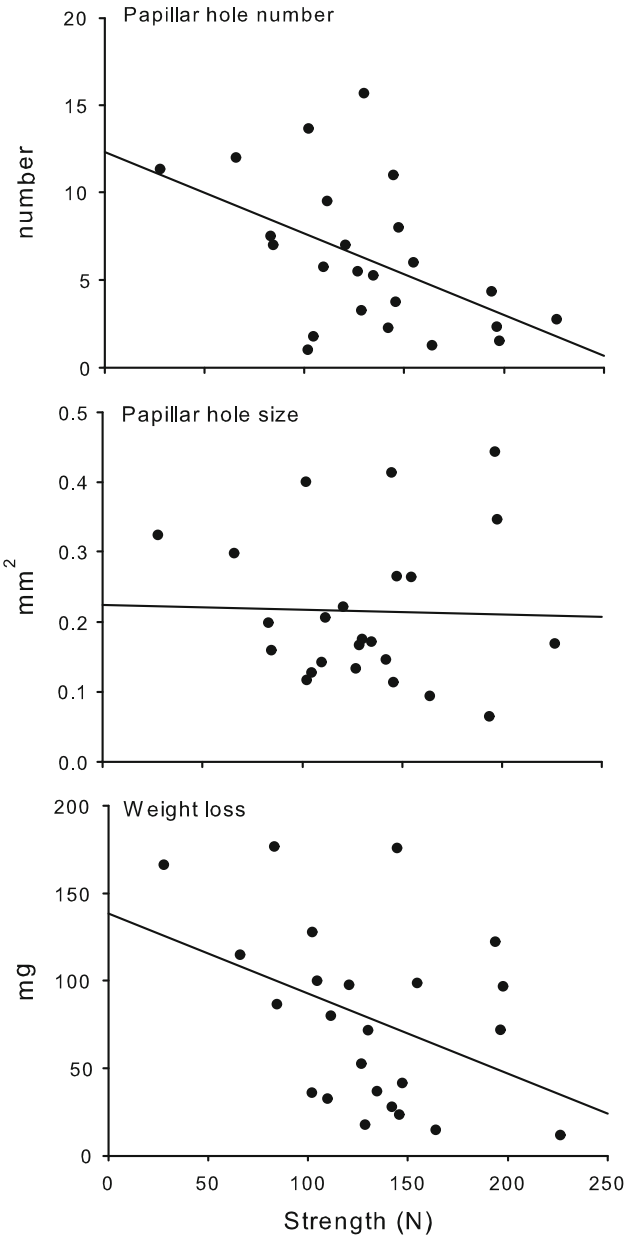

Fig. 4 Linear regressions showing relationship between shell strength to papillar hole number and size, and weight loss

weeded out by global change, altering the genetic structure of the population.

Attachment rates of *C. celata* at pH = 8.1 were comparable to that found by Hartman (1958), where explants attached to oyster shells after 1 month. At pH = 7.8, however, the proportion and rate of sponges attaching to scallop shells were reduced. Attachment rates of clionaids can vary between substrate types (Rosell and Uriz 1992). This study shows that water chemistry can also impact sponge attachment. Sponges attach to a substrate using a collagenous matrix, or basal lamella, secreted by basopinacocytes (Bergquist 1978). Perhaps, low pH interferes with this secretion process.

Final weights of *C. celata* were similar between the two pH levels, indicating the processes that reduced survival and attachment did not affect sponge growth. In a laboratory study, Emson (1966) found that sponges (within the *C. celata* species complex) partially closed oscules when the pH became ≤7.6, with all oscules closed at pH = 6.8. Because closing oscules would reduce pumping rates and thus filtration of suspended food, it is likely that *C. celata* would grow slower at pH values lower than used here. The specific growth rate of *C. celata* in this study was

9 mg day^{-1}, which is similar to other sponge species (Table 2 in Koopmans and Wijffels 2008). While high water temperatures can cause sponges to shrink in size (Pawlik et al. 2007), the threshold of thermal stress is species specific. The maximum temperature used in this study was within 1 °C of reported temperature tolerances for the *C. celata* species complex (Wells et al. 1964; Piscitelli et al. 2011); however, sponges in those studies did not experience 133 days of consistently high temperature, instead experiencing natural cycles of warming and cooling. Factoring in similar survival and attachment rates at 26 and 31 °C, this study suggests that *C. celata* in Peconic Bay will be largely unaffected by rising water temperatures predicted during this century.

Water temperature in this study had little effect on the bioerosion of scallop shells by *C. celata*, with shell strength, weight loss, and papillar hole number and size similar at 26 and 31 °C. Low water temperature during winter can arrest shell boring or infestation for sponges from the *C. celata* species complex, which resumes once water temperature rises above ~19 °C (Cobb 1975; Carver et al. 2010). Thus, water temperature can influence shellfish boring by *C. celata*, but the relationship is not linear, at least not at high levels.

Although high water temperature may have little direct influence on the boring rates of *C. celata*, low pH will. All variables of bioerosion examined in this study, except papillar hole size, were significantly affected by seawater pH. At pH = 7.8, sponges bored twice the number of papillar holes and removed two times more shell weight than at pH = 8.1. Size of papillar holes produced by *C. celata* in this study is comparable to (assumed) conspecifics in natural conditions (Hoeksema 1983). In addition, mean boring rates at pH = 8.1 (3.9 papillar holes after 133 days) are similar to wild *C. celata* (5 papillar holes after 117 days) (Hartman 1958). These results indicate that *C. celata* is largely unaffected by being grown under laboratory conditions, suggesting that sponge boring rates in low-pH treatments are likely to be accurate predictions of boring rates of wild sponges in a future, more acidic ocean. Control shells (with no attached sponge) lost significantly more weight (and were generally weaker) at a pH of 7.8 than at 8.1, probably due to abiotic shell dissolution in lower pH resulting in thinner shells. This likely allowed *C. celata* to bore more easily through shells in seawater of pH = 7.8. Shellfish grown in waters with a pH of 7.8 develop thinner, frailer shells (Talmage and Gobler 2010). Although dead shells were used in this study, the results suggest that boring rates of *C. celata* in shells of live shellfish will be similarly affected.

After 133 days, scallop shells with attached *C. celata* had lost two times more weight at pH = 7.8 than shells at pH = 8.1. This corresponds to mean bioerosion rates of 0.586 and 0.258 kg m^{-2} year^{-1} at pH of 7.8 and 8.1, respectively. These bioerosion rates fall within the range of other clionaids (Tables 4 in Reis and Ledo 2000; Schönberg 2002), though direct comparisons are problematic due to different experimental methods and environmental conditions. The results of this study suggest that pH values predicted for the end of this century may double bioerosion rates of *C. celata*. Considering that sponges took longer to attach to shells at low pH, translating into less boring time, this prediction is likely to be conservative. Greater erosion resulted in weaker scallop shells, with bored shells at pH = 7.8 only three-quarters the strength of shells at pH = 8.1. Loss of shell integrity and strength would increase vulnerability to predation and may have other lethal or sublethal consequences (Kaehler and McQuaid 1999). Although not all water chemistry variables were comparable to predicted levels for 2100, this study suggests that *C. celata* will bore faster into shellfish by the end of this century due largely to lower seawater pH. Higher rates of bioerosion have potentially severe implications for wild and farmed shellfish populations.

Acknowledgments We thank Tom Behling for experimental help and Shirley Pomponi, Brad Furman, Amber Stubler, John Carroll and anonymous reviewers for their helpful comments. This study was partially funded by Blue Ocean Institute.

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