Research Article

Author for correspondence:
Manon Broadribb,
E-mail: manon.broadribbpayne@vuw.ac.nz

Rapid acclimation in sponges: seasonal variation in the organic content of two intertidal sponge species

Manon Broadribb[1] , James J. Bell[1,2] and Alberto Rovellini[1]

[1]School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington, New Zealand and [2]Institute of Biological, Environmental & Rural Sciences (IBERS), Aberystwyth University, Gogerddan, Aberystwyth, Ceredigion, SY23 3EE, UK

Abstract

The ability to acclimate quickly to changing environmental conditions is important for sessile organisms that cannot move to areas with more favourable conditions. Sponges are known to exhibit considerable phenotypic plasticity in response to environmental variability. However, most studies examining differences in sponge morphology have looked at spatial variation in morphological characteristics by comparing sponges at sites with differing environmental conditions. Here we explored the potential of two intertidal sponge species (*Halichondria panicea* and *Hymeniacidon perlevis*) to show seasonal acclimation to changing environmental conditions at two sites on the Welsh coast, UK. Both species had a higher proportion of inorganic tissue content in winter months, which correlated with higher levels of wave action and lower temperature, representing either an increase in spicule size/number or a loss of organic material. We also detected rapid decreases in organic content in some months, which corresponded with previously reported reproductive timings for the two species, and likely represent gamete release events. While the increased inorganic content in winter months may be a secondary consequence of reduced food and the sponges having to rely on organic reserves to meet metabolic demand, the higher level of inorganic material in winter likely makes sponges stiffer and stronger, and better able to deal with higher levels of wave action during winter months.

Introduction

Determining the capacity of organisms to acclimate to changing conditions is key to understanding how they might respond to future environmental change (Foo & Byrne, 2016). Acclimation to specific environmental conditions often occurs through developmental plasticity, which optimizes a phenotype–environment match during the early stages of an organism's development (Dewitt *et al.*, 1998; Agrawal, 2001). However, environmental conditions can change, and an ability to respond rapidly to temporal environmental variability is also essential for survival, especially for sessile organisms unable to move to more favourable conditions (Bradshaw, 1965; Barua & Heckathorn, 2004). Therefore, sessile organisms have evolved strategies to maximize their ability to feed (Arkema, 2009), compete with other species (Chadwick & Morrow, 2010) and reproduce (Sarà, 1984).

Marine sponges (Phylum: Porifera) are sessile suspension feeders that are an important component of the benthic fauna throughout temperate, tropical and polar habitats, fulfilling a wide range of ecological roles (Diaz & Rutzler, 2001; Bell, 2008). Importantly, sponges exhibit high levels of morphological variation, often due to differences in local environmental conditions, which is thought to facilitate their survival in a range of different environments (Gaino *et al.*, 1995). Sponges have been shown to exhibit plasticity in many ways, from their gross morphology (e.g. Lopez-Legentil *et al.*, 2010) to their metabolic physiology (e.g. Morley *et al.*, 2016), and it is important to know which, if any, environmental cues explain this variation. For example, wave action exposure (Palumbi, 1986), light intensity (Becerro *et al.*, 1994; Uriz *et al.*, 1995), temperature (Schönberg & Barthel, 1997; Mercurio *et al.*, 2000; Subagio *et al.*, 2017), sedimentation level (Manconi & Pronzato, 1991; McDonald *et al.*, 2002) and other environmental factors (Hadi *et al.*, 2015) have all been correlated with various sponge features including morphology, spicule number and levels of spongin. These factors are so closely tied it has even been recently suggested that sponge functional morphologies could be used to inform about the specific environmental conditions in which they are living (Schönberg, 2021). These differences in morphology can be extreme, and individuals within the same species have been found to vary greatly depending on their local environmental conditions (e.g. Bell *et al.*, 2002). However, most studies examining variability in sponge morphology have focused on spatial variation (e.g. Bell & Barnes, 2000; Bell *et al.*, 2002; Farnham & Bell, 2018; Meyer *et al.*, 2019) and there is a paucity of studies looking at temporal changes in sponge morphology.

Sponge species found in the class Demospongiae typically have skeletons made of silica in the form of spicules (Müller *et al.*, 2007), which provide important structural support. The proportion of spicules (inorganic material) *vs* live tissue (organic material) is thought to influence the

structural strength and toughness of the sponge. Palumbi (1984) showed that the strength and stiffness of sponges were influenced by their environment, with sponges living in higher wave energy environments having greater inorganic content than those living in lower wave energy environments. As well as this, levels of inorganic material, including changes in spicule size and number, have been shown to be directly influenced by temperature (Mercurio *et al.*, 2000; Subagio *et al.*, 2017). The proportion of inorganic content tends to be greater at colder temperatures, though not necessarily due to increases in spicule size and number and potentially due to a decrease in organic material (Schönberg & Barthel, 1997). It is not only local environmental conditions that can influence the organic *vs* inorganic content of sponges. Gametogenesis may result in an increase in organic material within a sponge as reproductive elements develop, while gametic or larval release would cause a sudden drop in the ratio between organic/inorganic material. The reproductive timing of sponges is also known to be influenced by environmental conditions (e.g. Witte *et al.*, 1994; Xue *et al.*, 2009; Bautista-Guerrero *et al.*, 2010; Zarrouk *et al.*, 2013), potentially making it difficult to distinguish between reproductive and environmentally associated changes in organic content. Sponge organic content can change with food availability, as in low food environments sponges may need to use organic storage compounds to meet metabolic demand; this would increase the proportion of inorganic material in the sponge.

In this study we explored the seasonal morphological acclimation ability of two sponge species. We measured temporal variability in the organic and inorganic content of two species of demosponges found on the west Wales coast, *Halichondria panicea* (Pallas, 1766) and *Hymeniacidon perlevis* (Montagu, 1818). We hypothesized that inorganic material would be higher in the winter months due to an increase in wave action (after Palumbi, 1984), and decrease in temperature (Schönberg & Barthel, 1997; Mercurio *et al.*, 2000; Subagio *et al.*, 2017), and that as reproductive timings of *H. perlevis* and *H. panicea* have been shown to depend on environmental conditions, including temperature (Witte *et al.*, 1994 and Xue *et al.*, 2009, respectively), a sudden drop in organic content is likely to occur at some point in the year consistent with their previously described reproductive timings.

Materials and methods

This study was conducted at two rocky shore sites on the west coast of Wales, north of Aberystwyth. The first site was located at the south end of Clarach beach (52.43211 −4.08016) and the second site was located ~6 km north of the first site (52.47976 −4.05238) at the south end of Borth beach. Both sites are moderately exposed intertidal rocky areas with typical north-east Atlantic zonation patterns (Lewis, 1964). The area consists of reef platforms (90–100% bedrock), with many small gulleys and rockpools that support abundant sponge populations on the very low shore. The sponges *Halichondria panicea* and *Hymeniacidon perlevis* are abundant on the lower shore, although *H. perlevis* generally extends further up the shore than *H. panicea*.

Hymeniacidon perlevis, family Halichondriidae (Montagu 1818), is typically orange to red and varies from encrusting to massive in shape (Gaino *et al.*, 2010). It occurs in the littoral zone of the UK coastline all year round (Stone, 1970a). *Hymeniacidon perlevis* is viviparous (Stone, 1970b) with ova being fertilized in the sponge, where they develop into larvae that are eventually released (Xue *et al.*, 2009). The reproductive season of *H. perlevis* occurs from April to August in temperate seas (spring/summer in the northern hemisphere) (Topsent, 1911; Levi, 1956; Wapstra & van Soest, 1987; Gaino *et al.*, 2010), although the exact timing depends on various environmental conditions (Xue *et al.*, 2009). This species also reproduces by fragmentation (Stone, 1970b), potentially when conditions

for larval settlement are not suitable. *Halichondria panicea*, family Halichondriidae (Pallas, 1766) is another intertidal sponge, varying from encrusting to massive in shape (Vethaak *et al.*, 1982) and is widely found in the shallow coastal waters of temperate regions (Witte *et al.*, 1994). Like *H. perlevis*, *H. panicea* is viviparous (Amano, 1986), with larval release occurring from May to October in temperate seas (spring/summer in the northern hemisphere) (Barthel, 1986; Witte *et al.*, 1994; Gerasimova & Ereskovsky, 2007).

Thirty samples were collected of each species every month from both sites between July 2004 and February 2005, and March 2004 and February 2005 for *H. perlevis* and *H. panicea*, respectively. Each sponge sampled was at least 1 m apart from each other to reduce the potential for sampling clones. While some identical genotypes (patches) may have been sampled in different months, this is only likely to account for a small number of the total samples collected since the total population sizes across the shores were in the 1000s. Approximately 5 cm^2 of each sponge was collected, and in no cases were complete sponges collected. Samples were preserved in 90% ethanol, which was then poured off before the samples were washed in fresh water and dabbed dry before drying. Any internal and external contaminants (e.g. shell material) were removed from the samples before being transferred to a pre-weighed crucible (crucibles were labelled and then washed, rinsed in distilled H_2O and dried at 60°C for 2 h, before being weighed). Crucibles containing samples were then transferred to an oven and dried at 60°C for at least 4 h. Crucibles containing samples were then weighed together, before subtracting the weight of the crucible to obtain dry weight. Crucibles containing samples were then placed in a furnace and combusted at 400°C for 6 h. These were left in a desiccator at room temperature to cool, then weighed again before subtracting the weight of the crucible to obtain ash weight. Ash weight gave the inorganic (spicule) content of the sample, and this was removed from the sample dry weight to give the ash free dry weight, or organic content of the sample. These were then used to calculate percentage organic and inorganic content for each sample.

Wave height data and sea surface temperature data were taken from the Irish Data Buoy Network (2004) from weather buoy M5 in the Irish Sea off the coast of Pembrokeshire. Mean daily wave height and mean daily sea surface temperature for the sampling months were averaged to give mean monthly wave height and mean sea surface temperature from March 2004 to February 2005.

Normality of the inorganic weight was visually assessed using quantile-quantile plots. Then, two-way analysis of variance tests (ANOVAs) were performed, including interaction effects, to determine the effect of month and site on mean percentage organic and inorganic content of *H. perlevis* and *H. panicea* and to determine whether inorganic content changed over time. Non-significant interaction effects were removed from the model. If the results of the ANOVA were significant ($P < 0.05$), a Tukey's post-hoc test was performed to disentangle differences among groups. We tested for collinearity of temperature and height with an ANOVA. They appeared to only exhibit a weak negative correlation ($R^2 = 0.54$) so both temperature and wave height were analysed in the final model. To determine the effects of wave height and temperature on the percentage of inorganic content of *H. perlevis* and *H. panicea*, a multiple linear regression model was fitted for each species. Models had inorganic content as the outcome variable, and wave height, temperature, and the interaction between these two as predictors. Non-significant effects were removed from the models sequentially. Interaction effects, if present, were then analysed to find estimated marginal means at different wave heights/temperatures. As environmental data were taken from the same weather buoy for both sites, differences were not analysed. All data were analysed using the software R Studio (RStudio Team, 2016).
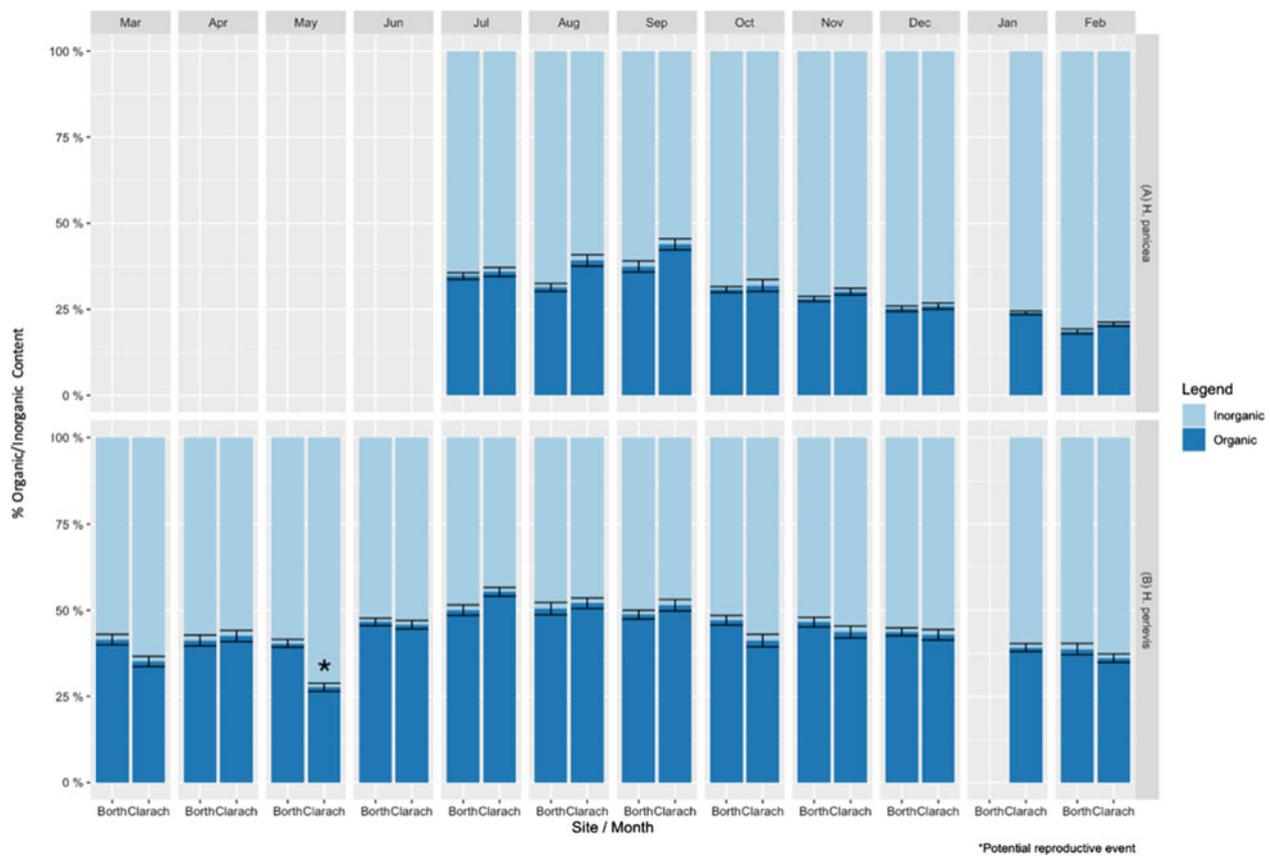
Fig. 1. Mean percentage organic and inorganic content ± standard error of (A) *Halichondria panicea* and (B) *Hymeniacidon perlevis* at Borth and Clarach for each month surveyed. * marks potential reproductive event.

Results

Halichondria panicea

Mean inorganic content of *H. panicea* differed significantly between sites (ANOVA, $F(1, 433) = 11.782$, $P < 0.01$) and months (ANOVA, $F(7, 433) = 70.973$, $P < 0.05$). Interaction effects were also found to be significant (ANOVA, $F(6, 433) = 3.072$, $P < 0.01$), so they were included in the final model. Post hoc comparisons using the Tukey Honestly Significant Difference (HSD) test indicated that the mean inorganic content of *H. panicea* was significantly higher at Borth compared with Clarach in August and September ($P < 0.01$) (Figure 1A).

Post hoc comparisons using the Tukey HSD test indicated that at Clarach *H. panicea* had significantly lower inorganic content during September than during all other months ($P < 0.05$). Levels of inorganic content then generally increased from September to February, where *H. panicea* had significantly higher mean inorganic content than all other months except December and January ($P < 0.05$). At Borth, September had significantly lower mean inorganic content than all months except July ($P < 0.05$). Inorganic content then generally increased until February, when it was higher than all other months ($P < 0.05$) (Figure 1A).

Hymeniacidon perlevis

Mean inorganic content of *H. perlevis* differed significantly between sites (ANOVA, $F(1, 660) = 13.881$, $P < 0.01$) and months (ANOVA, $F(11, 660) = 31.486$, $P < 0.01$). Interaction effects between site and month were also significant (ANOVA, $F(10, 660) = 6.086$, $P < 0.01$) so they were included in the final model. Post hoc comparisons using the Tukey HSD test indicated that mean inorganic content of *H. perlevis* was significantly higher at Clarach than Borth in

May ($P < 0.01$). No other months had significantly different inorganic content between sites ($P > 0.05$) (Figure 1B).

Post hoc comparisons using the Tukey HSD test indicated that at Clarach the highest mean inorganic content of *H. perlevis* was in May, significantly higher than during any other month ($P < 0.05$). The second highest level of inorganic content was found in March ($P < 0.05$), which then decreased through to July, which had the lowest inorganic content, significantly lower than all months except August and September ($P < 0.05$). Inorganic content then increased again through to February. There was also a sudden increase in the level of inorganic content from April to May at Clarach, which did not follow the general month to month trend, potentially due to a sudden drop in organic content levels which may indicate a reproductive event (e.g. spawning, Figure 1B).

Post hoc comparisons using the Tukey HSD test indicated that at Borth *H. perlevis* had the highest inorganic content during February, significantly higher than all months except December and March ($P < 0.05$). Inorganic content then generally fell until July and August, which had significantly lower levels than all months except May, June and September ($P < 0.05$). No other differences between months were found to be significant ($P > 0.05$) (Figure 1B).

Wave height and temperature

Temperature had a significant effect on inorganic content ($P < 0.01$) ($F(1446) = 354$, $R^2 = 0.44$) of *H. panicea*. Specifically, for every 1 unit increase in temperature, the inorganic content of *H. panicea* decreased by 2.35% (Figure 2). Interaction effects between temperature and wave height were not significant. Temperature and wave height also had a significant correlation with the inorganic content of *H. perlevis* ($P < 0.01$), and their
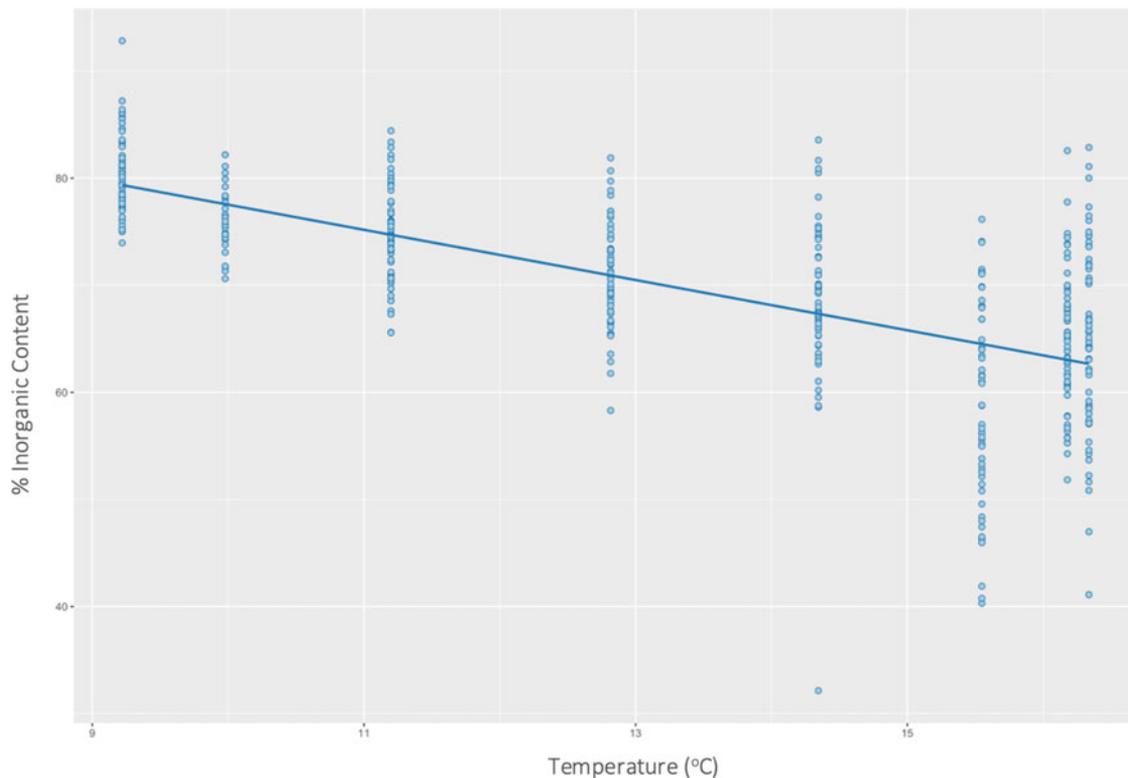
Fig. 2. Effects of temperature on the inorganic content of *Halichondria panicea* at both sites combined.

interaction effect was also significant ($P < 0.01$), so was kept in the final model, which explained 24% of the variation in inorganic content ($F(3679) = 74.14$, $R^2 = 0.24$). Further analysis of interaction effects found that at mean wave height (2.4 m) and low temperatures (mean – 1 SD = 10.1°C), inorganic content would be 61.9% (95% CI: 60.8–63.0%). However, at mean wave height (2.4 m) and high temperatures (mean + 1 SD = 15.3°C), inorganic content would be 51.8% (95% CI: 50.3–53.3%). These differences show the effects of wave height on *H. panicea* to be strongest at low temperatures (Figure 3).

Discussion

The ability of organisms to make changes to their morphology over short time scales allows them to react to seasonal changes in environmental conditions and increase their chances of survival. Palumbi (1984) previously described spatial variation in the relationship between wave action and stiffness/strength in the sponge *H. panicea* by transplanting sponges from high to low energy environments and vice versa. We aimed to explore whether our two sponge species can exhibit temporal variation in organic and inorganic content within the same environment. We found that both *H. perlevis* and *H. panicea* displayed seasonal plasticity in their organic/inorganic content. Both exhibited short-term changes that were correlated with local environmental conditions. This suggests that these two species can acclimate over short time frames to gradual changes in environmental conditions.

As predicted, proportions of inorganic content were generally higher in the winter months. They lowered in the summer months, showing a positive relationship with wave height data and a negative relationship with temperature. *Halichondria panicea* showed less variation in inorganic content between sites than *H. perlevis*, indicating that *H. panicea* is less responsive to, or at least less influenced by localized environmental change with

respect to inorganic content (most likely indicative of spicule size and number) or organic tissue content. There is a possibility that inorganic content does not directly correlate with spicule size or number, as many sponges have been found to incorporate foreign material into their tissues to strengthen their skeletons (Cerrano *et al.*, 2007). However, no evidence suggests that this is a strategy used by the two sponge species considered in our study.

We also observed a rapid drop in the organic content of *H. perlevis* from April to May at Clarach, which did not follow the general month to month trend and could be indicative of a reproductive event (see Figure 1B). At Clarach organic content generally increased from March to July, but declined in May, which could have resulted from a gamete or larval release and is consistent with previously reported reproductive timings of this species (Gaino *et al.*, 2010). However, this only occurred at one site, suggesting that local environmental conditions could have been more favourable for reproduction at Clarach than at Borth. Nonetheless, the proximity of these two sites makes it difficult to disentangle what conditions could be influencing the timing of this potential reproductive event. It would be important to collect local environmental data for the specific sampling sites over time for future studies. A reproductive event occurring during lower wave action and higher temperature may indicate that these are optimum conditions for reproduction due to higher food availability and higher larval settlement potential. As this potential reproductive event happened in May for *H. perlevis*, and we did not begin sampling of *H. panicea* until July, it is possible we would have seen a similar pattern in *H. panicea* if this species responds to the same reproductive cues as *H. perlevis*. To ascertain whether this is the case *H. panicea* sampling would have to be carried out during the earlier months of the year.

Temperature differences accounted for more variation in the inorganic content of *H. panicea* than wave height, which contrasts with *H. perlevis*, which was influenced by both wave height and
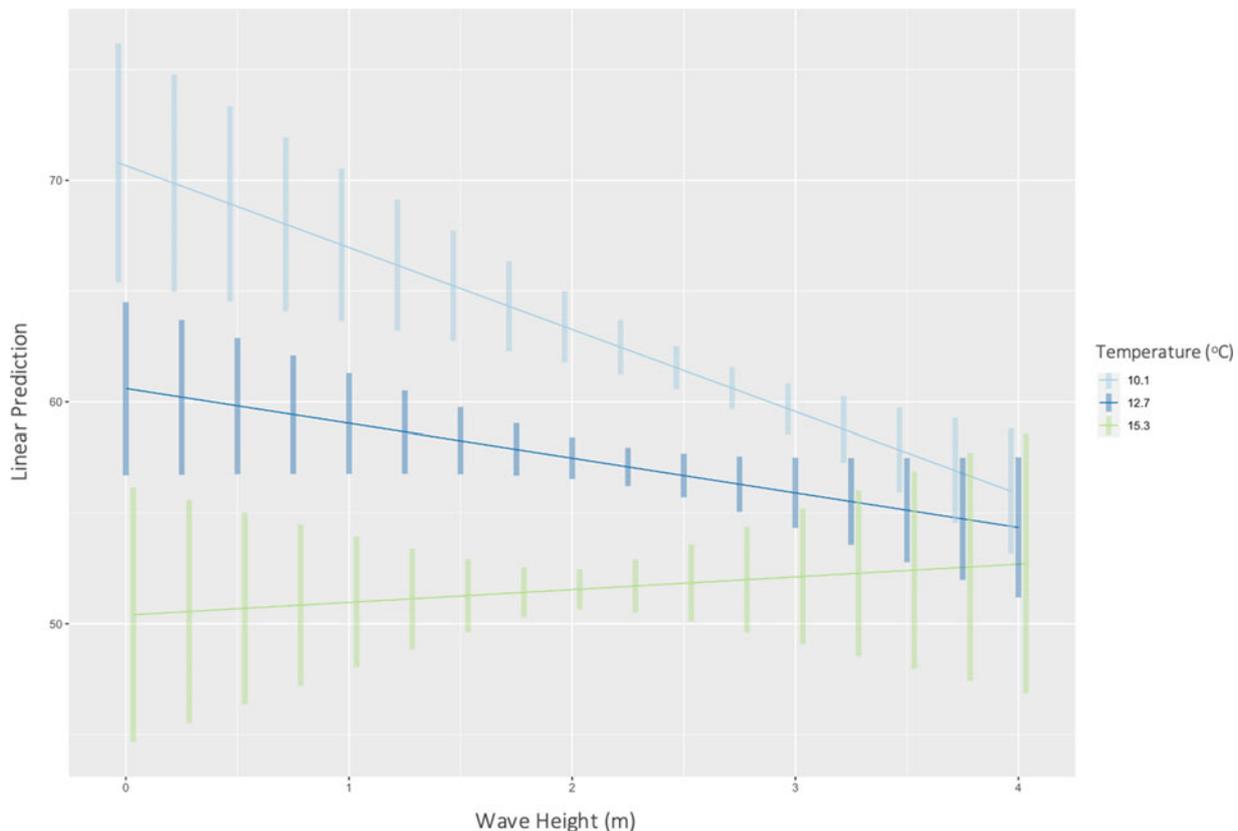
Fig. 3. Predicted correlations (with CIs) between wave height and inorganic content of *H. perlevis* at mean (12.7°C), mean − 1 SD (10.1°C), and mean + 1 SD (15.3°C) temperatures at both sites.

temperature. It is possible that as *H. panicea* was only sampled from July to February we are not seeing the real influence of wave height, as it could have a stronger correlation with inorganic content in the months that were not sampled. To explore the influences of wave height and temperature further, *H. panicea* needs to be surveyed throughout the whole year. As expected, the inorganic content of *H. perlevis* was influenced by both wave height and temperature, and these two predictors interacted with one another. Wave height and inorganic content became less negatively correlated as temperature increased, to the point where they were weakly positively correlated at high temperatures. Based on previous studies (Palumbi, 1984; Schönberg & Barthel, 1997, 2000; Mercurio *et al.*, 2000) we predicted wave action to have the strongest effects on inorganic content, and this is the highest in winter and spring when temperatures are lowest, in keeping with our results. It is important to note that an increase in the proportion of inorganic content does not necessarily indicate an increase in size and number of spicules, but could indicate a drop in organic content levels (Schönberg & Barthel, 1997).

It is possible that changes in organic and inorganic content could be due to factors other than morphological acclimation or reproductive timing, for example as a response to predation (Knowlton & Highsmith, 2000, 2005) or disease (Webster, 2007). However, there is no evidence that sponge predation changes seasonally at this site, and we found no specific reports of natural sponge disease on either species (and no disease was evident when samples were collected). Increased temperature and decreased flow rate have been shown to increase bacterial populations on *H. panicea* in induced laboratory conditions (Hummel *et al.*, 1988). However if this were the cause of a decrease in organic content this would likely happen in the summer months.

In addition, seasonal changes in food availability may also explain the changes in sponge organic/inorganic tissue content. The patterns reported may be a consequence of other processes rather than morphological acclimation. Since less food is likely to be available during the winter months (Duckworth & Battershill, 2001; Lüskow *et al.*, 2019), sponges may have to consume internal resources to meet metabolic demand, thus reducing organic content. As the temperature is likely to correlate with food availability, it is again challenging to disentangle these potential drivers. There is also the potential that nutrient fluxes and food availability in the water column could influence spicule growth rate and therefore influence inorganic content (Maldonado *et al.*, 2012), but no data on nutrient fluxes for the region are currently available so we were unable to test this. Regardless, we believe based on our results coupled with previous studies (Palumbi, 1984, 1986; Bell & Barnes, 2000; Schönberg, 2021) that the increased inorganic content during winter months is a response to the need for protection from the damaging effects of wave action. In addition, it is possible that since temperature has been shown to influence reproductive timing (Witte *et al.*, 1994; Xue *et al.*, 2009), and wave action has been shown to influence the stiffness of sponges (Palumbi, 1984), we see both effects co-occurring. Further experiments will be needed to enable these effects to be disentangled conclusively.

References

Agrawal AA (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* **294**, 321–326.

Amano S (1986) Larval release in response to a light signal by the intertidal sponge *Halichondria panicea*. *Biology Bulletin* **17**, 371–378.

Arkema KK (2009) Flow-mediated feeding in the field: consequences for the performance and abundance of a sessile marine invertebrate. *Marine Ecology Progress Series* **388**, 207–220.

Barthel D (1986) On the ecophysiology of the sponge *Halichondria panicea* in Kiel bight. I. Substrate specificity, growth and reproduction. *Marine Ecology Progress Series* **2**, 291–298.

Barua D and Heckathorn SA (2004) Acclimation of the temperature set-points of the heat-shock response. *Journal of Thermal Biology* **29**, 185–193.

Bautista-Guerrero E, Carballo JL and Maldonado M (2010) Reproductive cycle of the coral-excavating sponge *Thoosa mismalolli* (Clionaidae) from Mexican pacific coral reefs. *Invertebrate Biology* **129**, 285–296.

Becerro MA, Uriz MJ and Turon X (1994) Trends in space occupation by the encrusting sponge *Crambe crambe*: variation in shape as a function of size and environment. *Marine Biology* **121**, 301–307.

Bell JJ (2008) The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science* **79**, 341–353.

Bell JJ and Barnes DKA (2000) A sponge diversity centre within a marine island. *Hydrobiologia* **440**, 55–64.

Bell JJ, Barnes D and Turner J (2002) The importance of micro and macro morphological variation in the adaptation of a sublittoral demosponge to current extremes. *Marine Biology* **140**, 75–81.

Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**, 115–155.

Cerrano C, Calcinai B, Di Camillo C, Valisano L and Bavestrello G (2007) How and why do sponges incorporate foreign material? Strategies in Porifera. In Custódi MR, Lôbo-Hajdu G, Hajdu E and Muricy G (eds), *Porifera Research: Biodiversity, Innovation and Sustainability*. Rio de Janeiro: Museu Nacional, pp. 239–246.

Chadwick NE and Morrow KM (2010) Competition among sessile organisms on coral reefs. In Dubinsky Z and Stambler N (eds), *Coral Reefs: An Ecosystem in Transition*. Dordrecht: Springer, pp. 347–371.

Dewitt TJ, Sih A and Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* **13**, 77–81.

Diaz MC and Rutzler K (2001) Sponges: an essential component of Caribbean coral reefs. *Bulletin of Marine Science* **69**, 535–546.

Duckworth AR and Battershill CN (2001) Population dynamics and chemical ecology of New Zealand Demospongiae *Latrunculia* sp. nov. and *Polymastia croceus* (Poecilosclerida: Latrunculiidae: Polymastiidae). *New Zealand Journal of Marine and Freshwater Research* **35**, 935–949.

Farnham E and Bell J (2018) Spatial variation in a shallow-water sponge-dominated reef in Timor-Leste (East Timor). *Pacific Science* **72**, 233–244.

Foo SA and Byrne M (2016) Acclimatization and adaptive capacity of marine species in a changing ocean. *Advances in Marine Biology* **74**, 69–116.

Gaino E, Manconi R and Pronzato R (1995) Organizational plasticity as a successful conservative tactic in sponges. *Animal Biology* **4**, 31–43.

Gaino E, Frine C and Giuseppe C (2010) Reproduction of the intertidal sponge *Hymeniacidon perlevis* (Montagu) along a bathymetric gradient. *Open Marine Biology Journal* **4**, 47–56.

Gerasimova EI and Ereskovsky AV (2007) Reproduction of two species of *Halichondria* (Demospongiae: Halichondriidae) in the White Sea. In Custódi MR, Lôbo-Hajdu G, Hajdu E and Muricy G (eds), *Porifera Research: Biodiversity, Innovation and Sustainability*. Rio de Janeiro: Museu Nacional, pp. 327–333.

Hadi TH, Hadiyanto H, Budianto A and Niu W (2015) The morphological and species diversity of sponges in coral reef ecosystem in the Lembeh Strait, Bitung. *Marine Research in Indonesia* **40**, 61–72.

Hummel H, Sepers ABJ, de Wolf L and Melissen FW (1988) Bacterial growth of the marine sponge *Halichondria panicea* induced by reduced water flow rate. *Marine Ecology Progress Series* **42**, 195–198.

Irish Data Buoy Network Wave Height Data for Weather Buoy M5 (2004) Available at http://vis.marine.ie/dashboards/#/dashboards/weather?buoy=M5&measurement=WaveHeight (Accessed 11 December 2020).

Knowlton AL and Highsmith RC (2000) Convergence in the space–time continuum: a predator–prey interaction. *Marine Ecology Progress Series* **197**, 285–291.

Knowlton AL and Highsmith RC (2005) Nudibranch–sponge feeding dynamics: benefits of symbiont-containing sponge to *Archidoris monter-eyensis* (Cooper, 1862) and recovery of nudibranch feeding scars by *Halichondria panicea* (Pallas, 1766). *Journal of Experimental Marine Biology and Ecology* **327**, 36–46.

Levi C (1956) Etude des Halisarca de Roseoff. Embryologie et systematique des Demosponges. *Archives de Zoologie Expérimentale et Générale* **93**, 1–181.

Lewis JR (1964) *The Ecology of Rocky Shores*. London: The English Universities Press.

Lopez-Legentil S, Erwin PM, Henkel TP, Loh TL and Pawlik JR (2010) Phenotypic plasticity in the Caribbean sponge *Callyspongia vaginalis* (Porifera: Haplosclerida). *Scientia Marina* **74**, 445–453.

Lüskow F, Riisgård HU, Solovyeva V and Brewer J (2019) Seasonal changes in bacteria and phytoplankton biomass control the condition index of the demosponge *Halichondria panicea* in temperate Danish waters. *Marine Ecology Progress Series* **608**, 119–132.

Maldonado M, Ribes M and van Duyl FC (2012) Nutrient fluxes through sponges: biology, budgets, and ecological implications. *Advances in Marine Biology* **62**, 113–182.

Manconi R and Pronzato R (1991) Life cycle of *Spongilla lacustris* (Porifera, Spongillidae): a cue for environment-dependent phenotype. *Hydrobiologia* **220**, 155–160.

McDonald JI, Hooper JNA and McGuinness KA (2002) Environmentally influenced variability in the morphology of *Cinachyrella australiensis* (Carter, 1886) (Porifera: Spirophorida: Tetillidae). *Marine and Freshwater Research* **53**, 79–84.

Mercurio M, Corriero G, Scalera Liaci L and Gaino E (2000) Silica content and spicule size variations in *Pellina semitubulosa* (Porifera: Demospongiae). *Marine Biology* **137**, 87–92.

Meyer HK, Roberts EM, Rapp HT and Davies AJ (2019) Spatial patterns of Arctic sponge ground fauna and demersal fish are detectable in autonomous underwater vehicle (AUV) imagery. *Deep Sea Research Part I: Oceanographic Research Papers* **153**, 103137.

Morley SA, Berman J, Barnes DKA, de Juan CC, Downey RV and Peck LS (2016) Extreme phenotypic plasticity in metabolic physiology of Antarctic demosponges. *Frontiers in Ecology and Evolution* **3**, 157.

Müller WEG, Li J, Schröder HC, Qiao L and Wang X (2007) The unique skeleton of siliceous sponges (Porifera; Hexactinellida and Demospongiae) that evolved first from the Urmetazoa during the Proterozoic: a review. *Biogeosciences Discussions* **4**, 385–416.

Palumbi SR (1984) Tactics of acclimation: morphological changes of sponges in an unpredictable environment. *Science* **225**, 1478–1480.

Palumbi SR (1986) How body plans limit acclimation: responses of a demosponge to wave force. *Ecology* **67**, 208–214.

RStudio Team (2016) *RStudio: Integrated Development for R*. Boston, MA: RStudio. Available at http://www.rstudio.com/.

Sarà M (1984) Reproductive strategies in sessile macrofauna. *Bollettino di Zoologia* **51**, 243–248.

Schönberg CHL (2021) No taxonomy needed: sponge functional morphologies inform about environmental conditions. *Ecological Indicators* **129**, 107806.

Schönberg CHL and Barthel D (1997) Inorganic skeleton of the demosponge *Halichondria panicea*. Seasonality in spicule production in the Baltic Sea. *Marine Biology* **130**, 133–140.

Stone AR (1970*a*) Seasonal variation in the gross biochemical composition of *Hymeniacidon perleve* (Montagu). *Journal of Experimental Marine Biology and Ecology* **5**, 265–271.

Stone AR (1970*b*) Growth and reproduction of *Hymeniacidon perleve* (Montagu) (Porifera) in Langstone Harbour, Hampshire. *Journal of Zoology* **161**, 443–459.

Subagio IB, Setiawan E, Hariyanto S and Irawan B (2017) Spicule size variation in *Xestospongia testudinaria* Lamarck, 1815 at Probolinggo-Situbondo coastal. *AIP Conference Proceedings* **1854**, 020034. https://doi.org/10.1063/1.4985425.

Topsent E (1911) Sur les affinites des Halichondria et la classification des Halichondrines d'apres leurs formes larvaires. *Archives de Zoologie Expérimentale et Générale* **7**, 1–15.

Uriz MJ, Turon X, Becerro MA, Galera J and Lozano J (1995) Patterns of resource allocation to somatic, defensive, and reproductive functions in the Mediterranean encrusting sponge *Crambe crambe* (Demospongiae, Poecilosclerida). *Marine Ecology Progress Series* **124**, 159–170.

Vethaak AD, Cronie RJA and Van Soest RWM (1982) Ecology and distribution of two sympatric, closely related sponge species, *Halichondria panicea* (Pallas, 1766) and *H. bowerbanki* (Burton, 1930) (Porifera, Demospongiae), with remarks on their speciation. *Contributions to Zoology* **52**, 82–102.

Wapstra M and van Soest RWM (1987) Sexual reproduction, larval morphology and behaviour in demosponges from the southwest of the Netherlands. In Vacelet J and Boury-Esnault N (eds), *Taxonomy of*

Porifera. NATO ASI Series (Series G: Ecological Sciences), vol. **13**. Berlin: Springer, pp. 281–307.

Webster NS (2007) Sponge disease: a global threat? *Environmental Microbiology* **9**, 1363–1375.

Witte U, Barthel D and Tendal O (1994) The reproductive cycle of the sponge *Halichondria panicea* Pallas (1766) and its relationship to temperature and salinity. *Journal of Experimental Marine Biology and Ecology* **183**, 41–52.

Xue L, Zhang X and Zhang W (2009) Larval release and settlement of the marine sponge *Hymeniacidon perlevis* (Porifera, Demospongiae) under controlled laboratory conditions. *Aquaculture* **290**, 132–139.

Zarrouk S, Ereskovsky AV, Mustapha KB, Abed AE and Pérez T (2013) Sexual reproduction of *Hippospongia communis* (Lamarck, 1814) (Dictyoceratida, Demospongiae): comparison of two populations living under contrasting environmental conditions. *Marine Ecology* **34**, 432–442.