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Effect of acidified seawater and high temperature on the survival and behaviour of supralittoral and sublittoral amphipods (Crustacea)

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Abstract

Amphipods are one of the most diverse groups of marine crustaceans. The impacts of changing environmental parameters on such organisms are unclear. The study aimed to determine the effect of low pH and high temperatures on the survival and behaviour of two amphipods from contrasting environments; namely *Platorchestia cf platensis* (supralittoral) and *Cymadusa filosa* (sublittoral). Amphipods were collected from the field, exposed to artificially acidified seawater (pH 7.0, 6.0, 5.0), and to temperatures of 30 - 39°C. *C. filosa* could not build tubes, and *P. platensis* did not display its normal jumping behaviour but remained burrowed in the sediment at low pH and high temperatures. *P. platensis* was tolerant to 33°C but not to 36°C and 39°C. High temperatures (30°C, 33°C, 36°C) are lethal to *C. filosa* (100% mortality recorded within 10 days). *P. platensis* was able to tolerate pH variations with at least 50% survival at the end of 4 weeks. *C. filosa* do not survive more than 20 days at the lowest pH treatment (7.0). There was no significant difference between survival rates of the males, females and juveniles of both species (p>0.05) at the various temperatures and pH. Size and gender had little effect on the tolerance of the individual amphipod species. *P. platensis* was found to be more tolerant to changes compared to *C. filosa*. The current study provides insights into the species-specific nature of responses, survival and behaviour of organisms due to climate change related environmental parameters.

Keywords: Amphipods, survival, behaviour, low pH, high temperature

Introduction

When climatic conditions change, organisms respond primarily by displaying physiological and behavioural adaptations (Somero, 2012; Guerra et al., 2014). Over the last decade, the global average surface temperature has increased by approximately 0.6° C and is projected to increase at a rapid rate (Houghton et al., 2001). Increasing temperature is thought to have an adverse stimulatory effect on metabolism until lethal levels are reached (Byrne, 2011). Richard et al. (2015) report that when an organism is exposed to high temperature, there are two particular processes that influence their survival potential; firstly tolerance, and secondly plasticity. Plasticity ensures long term survival as it dictates counter measures for the normal functioning of biological processes to achieve acclimation. However, tolerance only helps in short term survival. Studies on the impacts of temperature

on amphipods include that of Tsoi et al. (2005), Bedulina et al. (2010), Guerra et al. (2014), Shyamasundari (1973), Moore and Francis (1986), Timofeyev et al. (2009), Madeira et al. (2015), Foucreau et al. (2014), and Magozzi and Colosi (2015).

Oceanic absorption of carbon dioxide changes the seawater chemistry causing a decrease in pH. If the use of fossil fuels and–greenhouse gases emissions continue at the current rate, the pH is expected to decrease by 0.3–0.4 units per year untill the end of this century, and by 0.67 units by 2300 (Caldeira and Wickett, 2003). The detrimental effects of elevated pH on crustaceans have been described by Fabry et al. (2008), Hernroth et al. (2012), Long et al. (2013), Hauton et al. (2009), and Egilsdottir et al. (2009). Two adverse consequences on marine biota are expected; namely changes in the internal acid/base

balance of marine organisms, and a reduction in calcification rate by calcifying organisms (Hauton *et al.*, 2009; Logan, 2010).

In this paper, we aimed to describe the effects of high temperature and acidic pH on the survival of two amphipods from contrasting environments namely; *Cymadusa filosa* (sublittoral) and *Platorchestia cf platensis* (supralittoral). The objectives were to observe the survival and behaviour of the amphipods at different temperatures ranging from 30 °C to 39 °C and at different pH ranging from 5.0 to 7.0.

Materials and methods

Stock collection and maintenance

The species P. platensis and C. filosa were chosen because they are easily collected and sorted. P. platensis were collected from Vieux Grand Port (20°22'37.5"S; 57°43'08.3"E) during the months of September and October 2014. They were quickly transported to the laboratory in plastic bags and kept at room temperature together with a stock of algae (Sargassum sp.). C. filosa were collected from Pointe aux Sables (20°9'56"S 57°27'3"E) during the months of October and November 2014 from a depth of approximately 50 cm. They were kept in two continuously aerated aquaria stocked with Ulva sp. placed in a well-lit area. The aquaria were cleaned weekly by changing approximately 25 % of the water and removing excess detritus from the bottom. Males of both species are characterised by having enlarged gnathopod 2. Males of C. filosa have dense plumose setae whereas females have slender setae on their antennae. These characteristics were used to distinguish males from females using either a magnifying glass or a stereomicroscope. Amphipods approximately less than 5 mm and which were not displaying any adult characteristics were classified as juveniles. Organisms were allowed to acclimatize for one week before any experiment was conducted. The physical parameters during the acclimation period were room temperature and a pH of 7.8 ± 0.3 for both species. A salinity of 29 psu for P. platensis and 33 - 36 psu for C. filosa was recorded during this period. No mortality was observed during the acclimation period.

Experimental set up

P. platensis were kept in beakers (1000 ml) filled with moist sediment and small pieces of algae. Seawater was added to the beakers every week, or as and when needed to maintain humidity, and algae (Sargassum sp.) were added when required. C. filosa species were

kept in small triple vented Petri dishes (to allow free passage of air) containing 14 cm³ of seawater collected from Pointe-aux-Sables. A single individual amphipod was kept in each Petri dish. A small piece of thallus (*Ulva* sp.) was added as food together with some detritus found at the base of the stock aquarium. Approximately 50 % of seawater was changed every 2 - 3 days. The algae in the Petri dishes were replaced every day, or as required. All Petri dishes were kept in a well-lit area in the laboratory.

Effects of increased temperature

10 males, 10 females and 10 juveniles of each species with the experimental setup described above were left at room temperature as a control. Experimental trials were performed in incubators. The physical parameters used for the thermal treatments for *P. platensis* were 33 ± 0.5 °C, 36 ± 0.5 °C and 39 ± 0.5 °C. Salinity was maintained at 29 psu and pH at 7.8. The physical parameters for *C. filosa* consisted of temperatures of 30 ± 0.5 °C, 33 ± 0.5 °C and 36 ± 0.5 °C. Salinity varied from 33-36 psu and pH was maintained at 7.8 ± 0.3 . For each set of temperatures, 10 males, 10 females and 10 juveniles of each species were used. The amphipods were placed in preheated Petri dished or beakers for each specific temperature used.

Effects of acidic pH

10 males, 10 females and 10 juveniles of each species with the same experimental setup were left at room temperature as a control. pH of seawater was adjusted by bubbling carbon dioxide up to a pH of 5.0 (Long et al., 2013). The resulting seawater was then added to seawater from the site to obtain the desired pH. For both species, pH of 5.0, 6.0 and 7.0 were used and maintained at room temperature. In the case of *P. platensis*, the salinity was maintained at 29 psu and pH at 7.8. Salinity varied from 33 - 36 psu and pH varied from 7.5 - 8.1 for the *C. filosa*. For each set of pH treatments, 10 males, 10 females and 10 juveniles of each species were used.

Length of the amphipods were measured upon the completion of the experiments.

Statistical analyses

All statistical analysis were done using IBM SPSS statistics version 21. Normality and equal variance of the data were tested by the Shapiro-Wilk test and Levene's test respectively (Zhang *et al.*, 2015). Statistical significance was tested at *p*-value <0.05. Non-parametric Kruskal-Wallis ANOVA (assumptions for normality

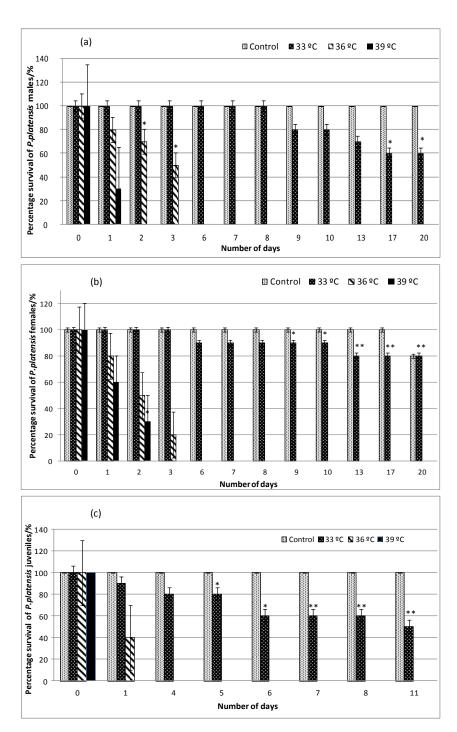


Figure 1. Percentage survival (\pm S.E) of *Platorchestia of platensis* (a) males, (b) females and (c) juveniles at different temperatures (n=10 at each temperature and n=5 at control). * and ** indicate significant difference at p < 0.05 and p < 0.01 respectively, between the control and the heat shock treatments at each time point.

or homocedasticity of data were not met) was performed to find out if the differences between the mean survival rate of the control and that of the treatments are statistically different (Madeira *et al.*, 2015). Moreover, Kruskal-Wallis tests were performed to determine if there was any significant differences between the mean survival rate of males, females

and juveniles of both *P. platensis* and *C. filosa*. A regression analysis was done to investigate the relationship between *C. filosa* body length (measured after the experiment) and the respective tube length built by the latter in the control, and the different treatments. The Pearson correlation was used to determine the significance of that relationship (Appadoo and Myers, 2003).

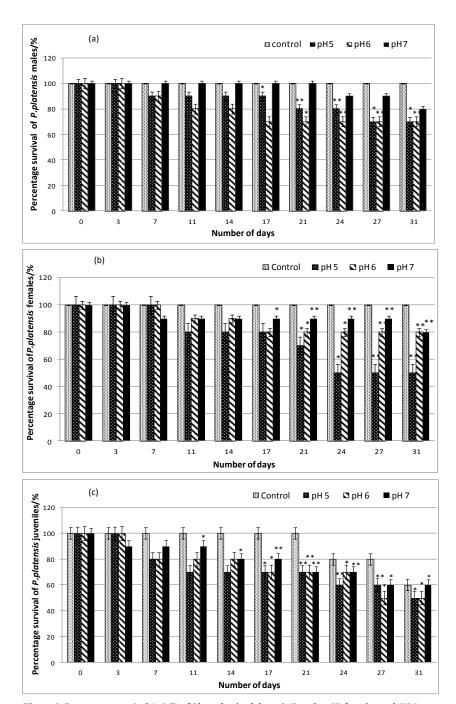


Figure 2. Percentage survival (\pm S.E) of *Platorchestia of platensis* (i) males, (ii) females and (iii) juveniles at different temperatures (n=10 at each pH and n=5 at control). * and ** illustrate significant difference at p< 0.05 and p< 0.01 respectively between control and the pH treatments at each time point.

Results

Survival of *Platorchestia cf platensis* at different temperatures

At 36 °C and 39 °C, the amphipods (males, females and juveniles) did not survive more than 3 days (Fig. 1). At 33 °C, 60 % of males, 80 % of females and 50 % of the juveniles were alive at the end of the experiment. The mean survival rate at 33 °C, 36 °C and 39 °C was significantly different compared to the control (p<0.05).

Moreover, there was no difference between mean survival rates of the male, female and juvenile *P. platensis* (33 °C: df=2, n=32, p=0.057; 36 °C: df=2, n=13, p=0.893; 39 °C: df=2, n=9, p=0.990)

Survival of Platorchestia cf platensis at different pH

It was observed that there was a high survival rate in all 3 treatments (at least 50 % of the males, females and juveniles of this species were alive at the end of

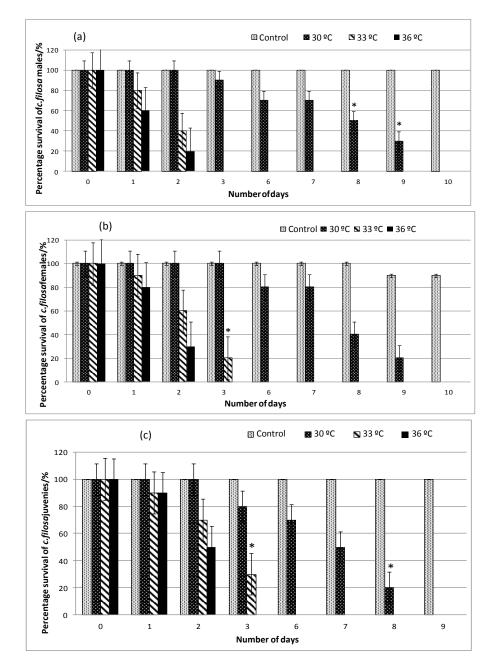


Figure 3. Percentage survival (\pm S.E) of *Cymadusa filosa* (a) males, (b) females and (c) juveniles at different temperatures (n=10 at each temperature and control). *p < 0.05 indicate significant difference between the control and the treatment groups at each time point.

4 weeks (Fig. 2). Mean survival rate (of males, females and juveniles)—was significantly different at all pH treatments (p<0.05) compared to the control, but no difference was found between the treatments (p>0.05). No difference was observed between the survival of the males, females and juveniles of *P. platensis* (pH 7.0: df=2, n=30, p=0.060; pH 6.0: df=2, n=30, p=0.087; pH 5.0: df=2, n=30, p=0.193).

Survival of *Cymadusa filosa* at different temperatures

At temperatures of 33 °C and 36 °C, high mortality rates were observed within 6 days (Fig. 3) for males,

females and juveniles. At a temperature of 30 °C, they survived for approximately 8 to 9 days. The mean survival rates recorded for the three treatments are significantly different from the control for males and juveniles (p<0.05). There was no difference between the survival rates of *C. filosa* males, females and juveniles (30 °C: df=2, n=26, p=0.945; 33 °C: df=2, n=14, p=0.988; 36 °C: df=2, n=12, p=0.924).

Survival of Cymadusa filosa at different pH

The males and females survived for approximately 3 weeks at pH 7 and pH 6, respectively, and for 2 weeks at

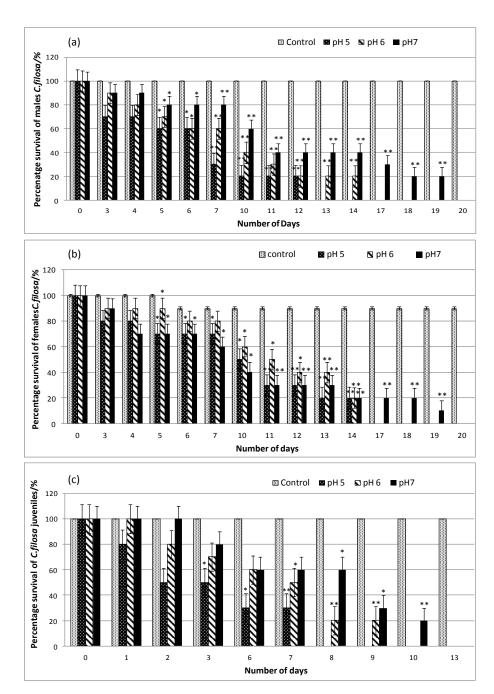


Figure 4. Percentage survival (\pm S.E) of *Cymadusa filosa* (a) males, (b) females and (c) juveniles at different pH (n=10 at each pH and n=5 at control). *p < 0.05 and **p < 0.01 indicate significant difference respectively between the control and the acidification groups at each time point.

pH 5 (Fig. 4). High mortality rates were observed for the juveniles. Statistically, there was no difference between the survival rates of the males, females and juveniles of this species (pH 7.0: df=2, n=40, p=0.393; pH 6.0: df=2, n=33, p=0.645; pH 5.0: df=2, n=29, p=0.798).

Behaviour of Platorchestia cf platensis

Under normal conditions, *Platorchestia of platensis* were all well burrowed in the sediment. When the beaker was disturbed (moved or shaken) during the

observations, the latter would actively jump for some minutes before burrowing back into the sediment. They were very "jumpy and energetic" (Simpson, 2011).

Generally, *P. platensis* (males, females and juveniles) were all well burrowed in the sediment during the observations in both acidic and thermal treatments. *P. platensis* were lethargic (less energetic and jumpy) at temperatures 36°C and 39°C compared to those at

temperature 33°C, and the control. The same behaviour was displayed in the hypercapnic treatments.

Behaviour of Cymadusa filosa

Tubes were made with detritus and amphipod silk, while in some cases, the algae were used as part of the construction materials for the tubes. These materials were glued together with amphipod silk. In some cases, multiple tubes were built (an average of the tube lengths were used for statistical purposes). A high positive linear relationship between tube length and body length of *C. filosa* (males n=9, r=0.825, r^2 =0.861, p=0.006; females n=8, r=0.956, r^2 =0.978, p=0.000; and juveniles n=9, r=0.941, r^2 =0.885, p=0.010) was obtained in the control (Table 1).

The amphipods did not build tubes at pH 5. In the hypercapnic treatments, there was no relation between the body length and the tube length of *C. filosa* (Table I) males (pH 7.0: n=5, r=0.485, r²=0.235, p=0.408; pH 6.0: n=5, r=0.179, r²=0.032, p=0.773), and females (pH 7.0: n=4, r=0.169, r²=0.028, p=0.831; pH 6.0: n=5, r=0.539, r²=0.290, p=0.349). No tubes were built at pH 5 and pH 6 by the juveniles. Only 1 juvenile was seen to build tubes at pH 7. The tube appeared at day 6. At day 8, 2 tubes were built by the same amphipod.

In the treatments, tubes were observed only at 30° C and the percentage of individuals that built tubes at this temperature was very low compared to the control. There was no relationship between the body length and tube length (Table 1) for males (n=5, r=0.253, r²=0.064, p=0.681), females (n=4, p=0.910), and juveniles (n=3, r=0.777, r²=0.603, p=0.433). It was

observed that those individuals that did not build tubes died prior to those that built tubes.

Discussion

Survival of amphipods at different temperatures

It is well known that rising temperature is one of the abiotic factors that affects survival of amphipods (Moore and Francis, 1986). The survival rate of the amphipods decreased with increasing temperatures. In this study there were no significant differences between the mean survival rates of males, females and juveniles of the same species. Similar observations have been reported in many studies (Shyamasundari, 1973; Edwards and Irving, 1943; Foucreau et al., 2014). Shyamasundari (1973) observed that size and sex of amphipods Corophium triaenonyx did not have an effect on the tolerance of the amphipod to different temperatures. Male and females crab (Emerita talpoida) have the same response to increased temperature (Edwards and Irving, 1943). Hence, it can be inferred that the physiological responses in these organisms do not differ between genders, or between juveniles and adults.

C. filosa do not tolerate high temperatures. It was observed that most of the C. filosa individuals that did not built tubes died prior to those that built tubes. A similar result was obtained in the study by Shyamasundari (1973) where the amphipod Corophium triaenonyx that were within their tubes were found to be more tolerant to changes in physical parameters.

P. platensis, on the other hand, showed tolerance to a temperature of 33°C. However, survival rate decreases significantly with higher temperatures. A study by

Table 1. Relationship between body length and tube length of <i>Cymadusa filos</i>	Table 1. Relationship	oetween body	v length and tub	e length of C	wmadusa filoso
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Category	Regression Model	n	F	Р
Males (Control)	y= 0.961 + 0.709x	9	14.972	0.006
Females (Control)	y = 0.889 + 0.739x	8	261.94	0.000
Juveniles (Control)	y = -2.372 + 0.923x	9	46.05	0.010
Males (pH 7.0)	y= 11.334 + 0.419x	5	0.922	0.408
Males (pH 6.0)	y = 6.112 + 0.319x	5	0.1	0.773
Females (pH 7.0)	y = 0.173 + 0.834x	4	0.59	0.831
Females (pH 6.0)	y = -3.246 + 0.947x	5	1.227	0.349
Males (30 °C)	y= 25.944 - 0.885x	5	0.205	0.681
Females (30 °C)	y = 0.934 + 0.05x	4	0.910	0.016
Juveniles (30 °C)	y = -3.504 + 1.138x	3	1.525	0.433

Moore and Francis (1986) with the amphipod Orchestia gammarellus (also family Talitridae) shows similar results. It is believed that this tolerance to thermal stress is due to the evolutionary adaptability of talitrid amphipods to non-marine conditions (Moore and Francis, 1986). The peroxidase enzyme is crucial for the resistance to oxidative stress caused by high temperatures (Timofeyev et al., 2009). These authors also concluded that in the freshwater amphipod *E. cyaneus*, this enzyme showed a "clear tendency to reduced activities with exposure time" which explains its early death compared to G. lacustris which expressed peroxidase activity for a longer period. Thermotolerance in amphipod species is also regulated by heat shock proteins which provide a certain degree of protection to the functioning of cells against fluctuations in temperature (Shatilina et al., 2011).

Survival of Cymadusa filosa v/s Platorchestia cf platensis

In the present investigation, it was observed that C. filosa was more sensitive and has higher mortality rates compared to P. platensis. A similar result was obtained in the study by Bedulina et al. (2010) which found that *Gammarus oceanicus* (a sublittoral species) is less resistant to higher temperatures than the supralittoral species Orchestia gammarellus. It was argued that these differences may be due to the adaptations of these species to the various thermal conditions arising from their different natural habitats. Nevertheless, effects of "phylogenetic history, body size and other species-specific traits" also play a key role (Bedulina et al., 2010). Madeira et al. (2015) reports that organisms living in the higher intertidal zone had higher basal levels of HSP70. Consequently, higher basal biomarker levels can be attributed to effective buffering of thermal stress effects. Moreover, Magozzi and Calosi (2015) showed that shrimps (such as *P. elegans*) residing in variable environments have higher upper thermal limits which make them more tolerant to increasing temperatures at the cost of higher metabolism, as opposed to shrimps thriving in stable environments (such as P. serratus). They also attribute these differences to species evolutionary ecology, and not phylogenetic relations.

Survival of amphipods at different pH

The current investigation demonstrated that *C. filosa* is lethally affected when exposed to acidified seawater. Multiple studies on crustaceans show similar results (Long *et al.*, 2013; Zhang *et al.*, 2015; Miles *et al.*, 2007). A recent study by Long *et al.* (2013) reports that

mortality rate of the crabs *Paralithodes camtschaticus* and *Chionoecetes bairdi* decreases with decreasing pH. The sea urchin *P. miliaris* also has low survival rates (Miles *et al.*, 2007) at a pH of 6.16. This can be explained by the disruption of the acid-base balance responsible for sustaining protein conformation and ultimately enzymatic activity and metabolism, or a reduction in calcification rate caused by increase in hydrogen ions in seawater (Hauton *et al.*, 2009). Furthermore, reduction in survival rate in calcareous marine organisms can be explained by "physiological compensation of maintaining normal processes such as growth, shell formation and metamorphosis in low pH marine environment" (Wood *et al.*, 2008; Zheng *et al.*, 2010).

On the other hand, *P. platensis* had low mortality rates when exposed to low pH values. Comparable results were obtained when such studies were undertaken with other crustaceans. Hendriks *et al.* (2015) stated that some calcifying organisms can biologically control their internal environment of carbonate deposition. They do so by producing sharp pH gradients in their diffusive boundary layer which controls the pH in extracellular fluid, or by controlling the deposition in a regulated, intracellular environment.

Survival of Cymadusa filosa v/s Platorchestia cf platensis

Different species have different responses to fluctuations in environmental parameters even within the same taxon (Zheng et al., 2015). The majority of crustaceans are water-breathers (including C. filosa) and therefore in close contact with their exterior environment via their gills (Taylor and Taylor, 1992, cited in Whiteley, 2011). Environmentally induced acidosis disrupts normal excretion of carbon dioxide through the gills which causes the concentration of the latter to increase in haemolymph. This in turn disrupts the acid-base equilibria of body fluids required for protein function (Whiteley, 2011). pH disbalance in the haemolymph is important to maintain oxygen supply. Hypercapnia therefore can decrease the oxygen affinity of the respiratory pigment and hence reduce oxygen delivery to the tissues (Taylor and Whiteley, 1989, cited Whiteley, 2011). Such disruptions can therefore severely impact survival of crustaceans in hypercapnic conditions.

P. platensis, on the contrary, had high survival rates at the different pH used. Being a supratidal species, P. platensis lives in beach wracks. They are not fully in

contact with seawater, as opposed to *C. filosa*. Moreover, they are also air-breathers (Griffiths *et al.*, 2011). It can therefore be inferred that elevated seawater pH does not have the same negative effects as described by Whiteley *et al.* (2011) on water-breathing crustaceans. In addition, impacts on the survivorship may take a longer time than the experimental duration.

Behaviour of Platorchestia cf platensis

Impacts of environmental parameters on the visible behaviour of talitrid amphipods is not well documented. The organisms were all in burrows during the observations which is thought to help them combat heat stress and desiccation (Karlbrink, 1969). Moreover, it is known that *P. platensis* can actually tolerate up to 30 % water loss (Poulin and Latham, 2002). It is known that high temperatures induce physiological responses such as production of antioxidant enzymes and heat shock proteins (Timofeyev *et al.*, 2009). Energy resources of *P. platensis* could have been utilised for this purpose rather than displaying the active jumping behaviour.

The observed change in behaviour at different pH may be attributed to the acid - base disequilibrium induced by low pH. Energy resources might have been dedicated to essential reactions to maintain life (Whiteley, 2011). However, this effect might be limited given the high survival rate of *P. platensis* in all the pH treatments.

Behaviour of Cymadusa filosa

Observations on the tube building behaviour and the relationship with body length (control experiment) concur with observations made in other studies such as on *Cymadusa filosa* (Appadoo and Myers, 2003), *Ampithoe laxipodus* (Appadoo and Volbert, 2011), *Lembos websteri* and *Corophium bonnellii* (Shillaker and Moore, 1978).

No relationship between body length and tube length was observed at temperatures of 30°C, as the survival rate was very low at this temperature. The organisms may have died before completing their tubes. Moreover, vital energy might have been diverted to the production of enzymes and proteins to counter the negative effects of elevated temperature (Timofeyev et al., 2009). In a previous study, Whiteley (2011) puts forward that exposure to hypercapnia has adverse effects on the growth and reproduction of crustaceans by diverting their vital energy towards the continuation of essential compensatory responses.

The inability to build tubes makes these tube-building amphipods vulnerable to predators and also to the fluctuating environmental parameters.

One of the limitations of this study was that salinity used is that closest to the stock culture, and varies for each species. Salinity amplitude for *C. filosa* during the experiments may have been high and may have confounded the results.

Conclusion

Chronic exposure to acidified seawater and elevated temperatures are detrimental to the studied amphipod species. This study demonstrated that P. platensis (a supralittoral species) is resistant to extreme pH values and to small increases in temperature. On the other hand, C. filosa (sublittoral species) cannot tolerate increases in temperature. Moreover, C. filosa is very sensitive to low pH. Survival rates of males, females and juveniles of the studied species do not significantly differ from each other. It can thus be inferred that gender and size does not affect the fitness of the organisms. The data from the experiments confirm the hypothesis that supralittoral species are robust (mainly because of the high variability in their natural environment and hence better adaptation mechanisms) and will survive better in the predicted climate change scenarios, as opposed to the sublittoral species which thrives in an environment where variations are minimal (compared to supralittoral environment). Behaviour was affected in all of the organisms when they were subjected to changes in temperature and pH. P. platensis could not display its normal active jumping behaviour but remained burrowed in the sediment when subjected to changes in physical parameters. C. filosa could not build tubes at high temperatures and low pH. The current study provides insights on the species-specific nature of impacts of climate change-related environmental parameters on marine organisms. It shows that it is not only survival but individual behaviours that are also affected. Such sublethal effects will definitely have consequences on the fitness of these individuals and needs further attention and research.

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