



Assassins and apples: the environmental constraints of two snails that threaten Australian aquatic systems

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ABSTRACT

Context. Alien freshwater snails pose a substantial risk to Australian native aquatic biota. **Aims.** This study aims to determine the thermal and salinity ranges of two introduced species within Australia, *Pomacea* sp. and *Anentome* sp., to facilitate predictions of their potential geographic range should they become widely established. **Methods.** Laboratory tests were conducted to assess behavioural responses of snails to altered temperature or salinity after different acclimation regimes. **Key results.** After acclimation at 25°C, *Pomacea* sp. had a median activity range of 13.5–38°C and *Anentome* sp. of 12–38.5°C. Higher acclimation temperatures produced observable effects, whereas lower acclimation temperatures did not. Salinity tolerances differed, with *Pomacea* sp. remaining active at up to 8 parts per thousand (ppt) (after acclimation at 25°C), with acclimation at 20°C resulting in a lower salinity tolerance. By contrast, *Anentome* sp. snails were active at up to 5 ppt after low salinity acclimation, demonstrating enhanced salinity tolerance compared with non-salinity acclimations. **Conclusions.** These results showed that both snails are capable of surviving temperatures and salinities that would allow invasion into subtropical and warm-temperate Australian aquatic systems. **Implications.** Free from the constraints of natural predators, competitors, and parasites, these snails should be of great concern to biosecurity agencies in Australia.

Keywords: *Anentome*, apple snail, assassin snail, biosecurity, invasive snail, *Pomacea*, salinity tolerance, thermal tolerance.

Introduction

Invasive species represent a serious risk to receiving ecosystems around the world. The introduction of alien species can lead to competition, predation, and extirpation of native species, reduced production of economically important crops and animals, and increased spread of diseases and alien parasites (Arthington and Blühorn 1995; Cowie 2002). Thus, it is important to understand the preferred habitats, physiological tolerances, and the capacity for range increases in already established invasive species. The ornamental aquarium trade in Australia has been responsible for the introduction of many invasive aquatic species (Morrisey *et al.* 2011; Ebner *et al.* 2020). Several of these threaten damage to native freshwater ecosystems or affect economically important endemic species (Morrisey *et al.* 2011). The keeping of exotic species has become a widespread and highly profitable international industry worth over A\$100 million globally (Peres *et al.* 2018). Increased use of online sources by hobbyists has led to increased demand for exotic species and has facilitated the inter-continental trade and smuggling of species (Mazza *et al.* 2015; Peres *et al.* 2018), many of which are restricted or prohibited for trade in Australia (Ebner *et al.* 2020). Not all imported species have established wild populations and most remain within the confines of home aquaria across Australia. However, multiple incursion events since the 1970s have been attributed to deliberate ornamental fish dumping, with the exotic species then establishing breeding populations in Australian waterways (Lintermans 2004; Holmes *et al.* 2020). In addition, the

inadvertent release of potentially invasive ornamental species can also result from the disposal of tank water contaminated with eggs or larvae (Mills et al. 1993; Ebner et al. 2020). Such introductions result in the modification of native ecosystems (Rahel 2002) and the decline of native populations, leading to extinctions of native fauna in extreme circumstances (Mack et al. 2000). Biosecurity agencies, therefore, need to understand the physiological and ecological characteristics of potentially invasive species to develop policies to prioritise threats, mitigate the risk of release, and develop prevention and preparedness plans for a future potential outbreak (Ebner et al. 2020).

As important components of aquatic ecosystems, freshwater invertebrates contribute to ecosystem functions such as regulation of primary production, nutrient cycling, and decomposition (Feminella and Hawkins 1995; Graça 2001; Vanni 2002). Freshwater snails fulfil a number of these roles and are found across a wide range of natural and modified habitats (Ponder et al. 2016). Australia has more than 400 described native species of freshwater snails, with many more yet to be described formally; however, the number of invasive snails established in Australia is increasing (Ponder et al. 2016; Ebner et al. 2020), primarily in urban waterways (Ponder et al. 2016). The threats posed by these species include the displacement of native species, competition for food and habitat, and the potential introduction of new exotic parasites and diseases (Arthington and Blüthorn 1995; Ponder et al. 2016; Ebner et al. 2020).

The ‘golden mystery’ or ‘apple’ snails, *Pomacea* Perry, are herbivorous aquatic snails mostly native to inland South America (Simone 2006) that have become widespread internationally because of their popularity with aquarists for controlling algal growth (Cowie 2002; Hayes et al. 2008). These snails primarily feed on detritus and algae, but they can adapt their diet to include most vegetation (Aditya and Raut 2001). They are also amphibious, possessing both a gill and a lung, and are dioecious with high fecundity, laying eggs above the waterline at night (Cowie 2002; Coelho et al. 2012; Watanabe et al. 2015). Releases from aquaria have allowed the establishment of populations of *Pomacea* species across the Americas (Howells et al. 2006), India (Aditya and Raut 2001) and Australia (Walker 2005; Ebner et al. 2020). *Pomacea* specimens from Australia have previously been identified as *Pomacea diffusa* (Hayes et al. 2008); however, because the occurrence of additional species due to multiple independent incursions from the ornamental trade is possible, we refer to the specimens in our study as *Pomacea* sp. The primary concern in the Australian context is that this invasive species is a rapidly reproducing and competes for resources with native herbivorous species (Aditya and Raut 2001).

The ‘assassin snail’ is one of the few freshwater nassariids and is closely related to marine dog whelks (Galindo et al. 2016). Usually referred to as *Anentome helena* (von dem Busch), recent evidence suggests that individuals in the

aquarium trade fall under one of four closely related species that are difficult to distinguish morphologically, with speciation linked to isolation resulting from paleo-drainage of water systems (Strong et al. 2017). As such, in this study assassin snails are referred to as *Anentome* sp. Originating in Java, *Anentome* species occur throughout much of South-East Asia (van Benthem Jutting 1959; Ng et al. 2016), inhabiting freshwater streams, lakes and reservoirs, with both solid and soft substrates (Ng et al. 2016). In the wild they are carnivorous, primarily feeding on worms, carrion, and other gastropods (Monks 2016). Assassin snails are a popular aquarium species in Asia, Europe, North America (Bogan and Hanneman 2013) and, more recently, Australia, being valued in aquarium settings (Ng et al. 2016) because of their ability to control populations of other nuisance invertebrates (Bogan and Hanneman 2013). Assassin snails are dioecious, with females laying from one to four eggs each per clutch, each coated in a transparent case (Coelho et al. 2013). Only recently have the *Anentome* species been considered invasive, with a population that has become established in a reservoir in Singapore, a country outside its native range (Ng et al. 2016). Assassin snails have not yet been reported as established in Australian waterways but have recently been smuggled into the country and are being sold through the online, non-commercial aquarium trade (Ebner et al. 2020). These species represent a major risk to Australian freshwater environments owing to their predatory nature, because there are no native freshwater carnivorous snails in the country (Ponder et al. 2016).

Temperature is a critical variable in determining the potential range over which an invasive species might establish (Prosser and Heath 1991). Snails exposed to temperature extremes will experience a potentially reversible state of immobility, referred to as a coma, dying after prolonged exposure (Hamby 1975, Gaitán-Espitia et al. 2013). There exist only anecdotal reports of the thermal range of *Pomacea* species, arising from their popularity as aquarium species. Aquarium forums report a ‘comfortable range’ between 20 and 29°C (Woods 2018). A formal investigation into thermal capacity has yet to be conducted for any *Anentome* species, although they have been reported to have a thermal optimum between 18 and 27°C (Yakovenko et al. 2018) and the report of the first known invasive population in Singapore was found in environmental temperatures up to 31.6°C (Ng et al. 2016).

Salinity also affects the physiology and dispersal capability of aquatic organisms. Adult *Pomacea* sp. can survive at salinities of 3.3 parts per thousand (ppt) over a 2-week period (Jordan and Deaton 1999). At this salinity, they are hyperosmotic, becoming osmotic conformers as salinity increases (Jordan and Deaton 1999). No published studies on the salinity tolerance of any *Anentome* species are available.

Here, we assess the behavioural responses of Australian *Anentome* sp. and *Pomacea* sp. to changes in temperature and salinity, and whether acclimation influenced these

responses. We tested the hypotheses that these snails would demonstrate thermal ranges that reflected that of their native tropical environments, that these species would demonstrate the ability to withstand low levels of salinity and that acclimation would enable them to withstand a wider range of thermal and saline conditions. This information will aid in ongoing management to better inform risk, climatic match, and range mapping models of these snails, so as to aid in the ongoing management of these invasive snails in both Australia and other countries facing similar biosecurity risks associated with these species.

Materials and methods

Collection and storage of snails

Snails of *Pomacea* sp. were collected from Springfield Lakes, Queensland (27°40'1"S, 152°55'15"E) in September, October and December 2019. Individual snails attached to submerged vegetation were removed at night. Identification was based on Cowie (2005) and Cowie *et al.* (2006) and was aided by an absence of any closely related species in Australia (Ponder *et al.* 2016).

Given the status of *Anentome* sp. as high-risk ornamental species that are not yet established in the wild in Queensland waterways, they were sourced from ornamental traders in Queensland under General Biosecurity Obligation. All individuals were held at a biosecure laboratory at Griffith University.

All organisms were initially kept in storage aquaria containing dechlorinated tap water and a fine-gravel substrate, with the temperature maintained at 25°C. The tanks were oxygenated using aerators and high calcium concentrations were maintained by the addition of powdered calcium carbonate to promote growth. Deceased snails were removed immediately, and water received a one-third change every 2 weeks. Water quality was tested during each water change, using multiparameter test strips, to ensure that nitrate/nitrite and chlorine concentrations remained constant throughout the experiment. Because low numbers of snails were available, it was necessary to reuse individuals across experiments. Snails of *Pomacea* sp. were marked using a waterproof metallic acrylic marker, and those of *Anentome* sp. were marked using beekeeper tags glued to their shells (because of their smaller size). To prevent the confounding effect of retesting, individuals were rested for a minimum of 2 weeks before reuse to ensure that the snail recovered from the previous testing. After completion of the experiment, individuals were euthanised by chilling, then freezing, and disposed of as per the biosecurity protocols approved by Biosecurity Queensland. Further treatment protocol included bleach-treating tank water prior to disposal and cleaning equipment to ensure that species spread was not facilitated.

Thirty random individuals were separated into each acclimation group for either a temperature acclimation (20, 25 or 30°C) or a salinity acclimation (1 or 2 ppt), with 10 individuals from each acclimation being used for each experiment. Acclimation occurred at a rate of 1°C h⁻¹ or 1 ppt h⁻¹. Acclimation groups were fed once the acclimation level had been reached. Each of the groups was given 7 days to acclimate prior to commencing experiments, because acclimations were not significantly outside the natural range for either species group. Experimentation took place over the 5 days following the acclimation week.

Testing was performed using a dynamic method of evaluating environmental tolerance, such that temperature or salinity was slowly raised, while the organism's behavioural response was monitored (following Lutterschmidt and Hutchison 1997). Behaviour responses were categorised as follows: 'detachment', when the individual retracted its foot, causing it to detach from the substrate; and 'coma', when the individual did not demonstrate any response to probing with a blunt glass rod. Probing was performed at 5-min intervals following detachment from the substrate. The snails were returned to their acclimation tank after experiments, allowing time to reacclimate to tank conditions.

Thermal tolerance

Maximum and minimum thermal tolerances were tested by placing individuals into separate 2-L containers, each containing 1 L of water from their associated acclimation tank. These were then placed into a temperature-controlled water bath, consisting of a cooling basin and water-circulating heating unit, to allow for precise temperature control. The temperature of the water bath was then increased or decreased at a rate of 4°C h⁻¹, depending on the treatment, with temperature adjustments occurring every 30 min ($\pm 2^\circ\text{C}$). Measurements of container water temperature were taken at the time of detachment from the substrate and when snails no longer responded to probing. Container water temperature was measured using a fluid-glass thermometer. The resulting temperature measurements, snail-size data (Fig. 1), and snail number were recorded.

Salinity tolerance

Maximum salinity tolerance was tested by removing individuals from their acclimation tanks and placing them in separate 2-L containers, each containing 1 L of water from their associated acclimation tank. The salinity of the water was then increased at a rate of 2 ppt h⁻¹, with salinity adjustments occurring every 30 min by the introduction of increasing volumes of a stock saline solution (NaCl and water) at a concentration of 100 ppt. Salinity was calculated both at the point at which the snails became detached and when they entered coma, on the basis of the volume and concentration of the added solution, and verified using an

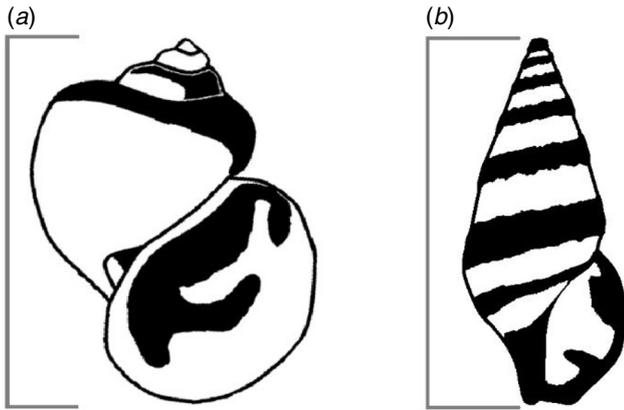


Fig. 1. Shells of (a) *Pomacea* sp. (adapted from Business Queensland 2016) and (b) *Anentome* sp. (adapted from Ponder et al. 2016), with grey lines indicating the size measurement used.

optical refractometer. Resulting salinity measurements, along with snail size (Fig. 1) and snail number, were recorded.

Data analysis

A linear mixed-effects model was used to determine whether there was an interaction between snail size and acclimation regime on detachment and coma responses for each species. Normality and the equality of variances were tested using Levene's test. Once non-significant variables were removed and data were determined to be normal, statistical significance of difference was evaluated between the acclimation groups, within each experiment and species. This was determined using Chi-Square pairwise tests using the 'phia' package in RStudio (ver. 3.6.2, RStudio, Inc., Boston, MA, USA, see <http://www.rstudio.com>). The comparison was completed using acclimation as a pairwise character vector and test as a fixed character vector.

Results

Snail mortality was low and occurred prior to the onset of acclimation treatments.

Snail size

The 55 snails of *Pomacea* sp. had a size range of 35.2–48.3 mm, with a mean of 43 mm (s.d. = 2.7 mm), whereas the 32 snails of *Anentome* sp. had a size range of 8.2–19.5 mm, with a mean of 13.4 mm (s.d. = 2.5 mm). Linear mixed-effects modelling found that size was not significant for either detachment (*Pomacea* sp., $P = 0.87$; and *Anentome* sp., $P = 0.12$) or coma response (*Pomacea* sp., $P = 0.84$; and *Anentome* sp., $P = 0.15$) and was not further investigated.

Response to increased temperature

Pomacea sp. demonstrated a median detachment response of 39°C and a median coma response of 39.5°C for increasing temperatures. Acclimation regimes affected both the point of detachment and coma for *Pomacea* sp. in response to experimental temperatures. Compared with the control (25°C), snails acclimated at 20°C demonstrated a higher temperature resistance before coma was observed than did those in the control of 25°C (coma, $P = 0.03$). Acclimation at 30°C also led to a greater ability to withstand higher temperatures (detachment, $P = 0.01$; and coma, $P = 0.01$) when compared to the control of 25°C (Fig. 2a, 3, 4). There was no significant effect of salinity on upper thermal limit; however, the 1-ppt acclimation group was much more variable than were other acclimation groups (Fig. 2a).

Anentome sp. demonstrated a median detachment response of 38.5°C and a median coma response of 39.5°C for increasing temperatures. Their ability to withstand higher temperatures was positively affected by a higher-temperature acclimation (detachment, $P = 0.001$; and coma, $P = 0.01$). Lower-temperature acclimations did not significantly decrease their tolerance to high temperatures (detachment, $P = 0.535$; and coma, $P = 0.285$; Fig. 2b, 3, 4). Salinity did not have a significant effect on their ability to withstand higher temperatures.

Response to decreased temperature

Pomacea sp. demonstrated a median detachment response of 16°C and a median coma response of 13.5°C for decreasing temperatures. The lower thermal limit of the low temperature acclimation (20°C) was similar to that of the control 25°C in *Pomacea* sp.; however, the lower-temperature acclimation had a slightly higher median (Fig. 2c). The acclimation of 30°C (detachment, $P > 0.001$; and coma, $P > 0.001$) and 1-ppt salinity (detachment, $P > 0.001$; and coma, $P > 0.001$) demonstrated significantly reduced lower thermal limits than in the 25°C acclimation group (Fig. 2c, 3, 4). The 2-ppt salinity acclimation group demonstrated a slightly lower thermal limit than the 30°C group and 1-ppt salinity acclimations for the detachment response ($P = 0.01$ and $P = 0.001$ respectively; Fig. 2c, 3). This lower thermal limit was observed further through the coma response ($P > 0.001$ and $P > 0.001$; Fig. 2c, 4).

Anentome sp. demonstrated a median detachment response of 13°C and a median coma response of 12.5°C for decreasing temperatures. The ability of *Anentome* sp. to withstand lower temperatures was negatively affected by both acclimations above (detachment, $P = 0.008$; and coma, $P = 0.017$) and below (detachment, $P = 0.554$; and coma, $P = 0.059$) the control of 25°C (Fig. 2d, 3, 4). Salinity acclimation also impaired their ability to withstand lower temperatures at both the low (detachment, $P = 0.049$; and coma, $P = 0.014$) and

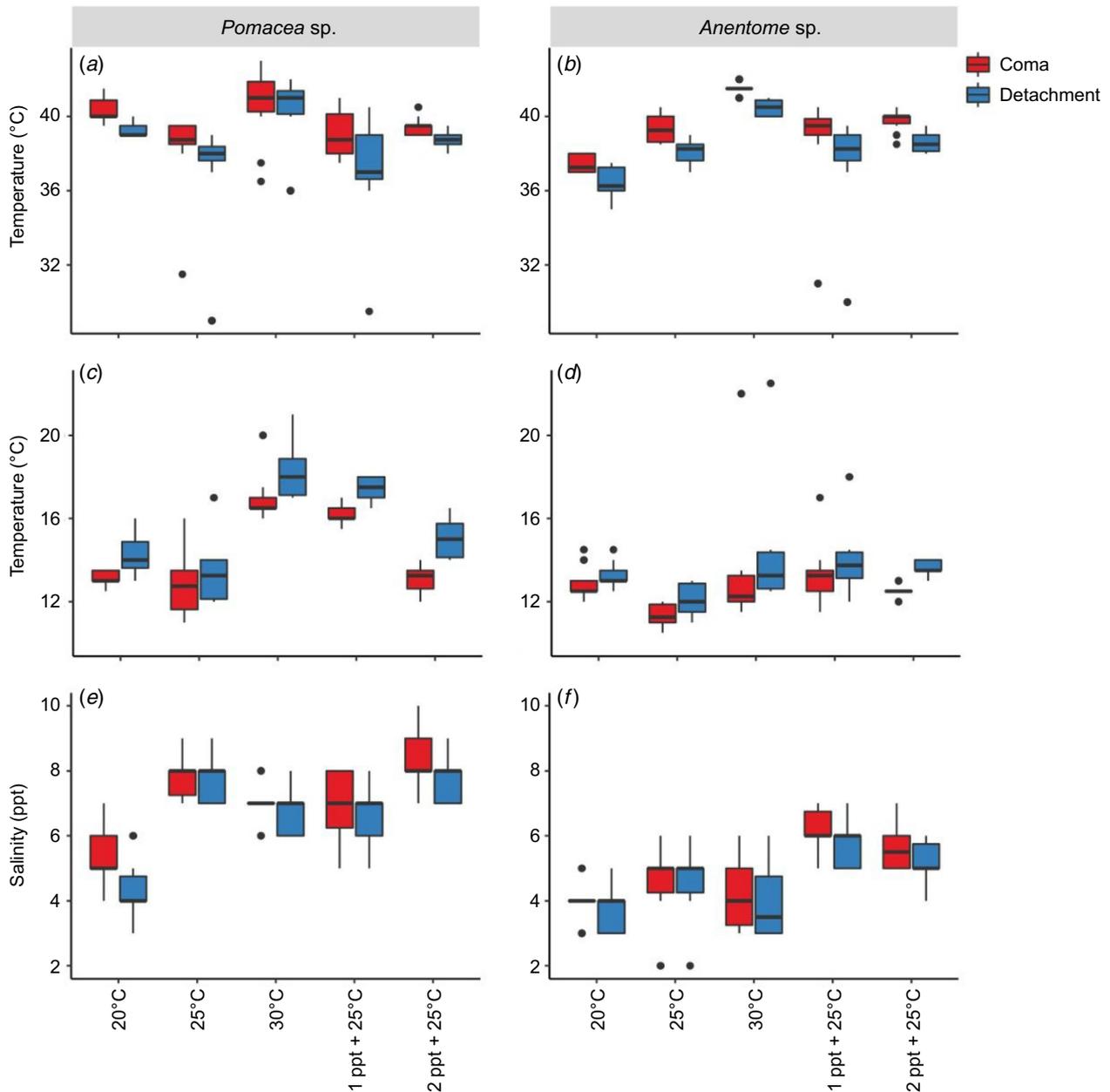


Fig. 2. Box plots of the temperature and salinity tolerances of *Pomacea* sp. and *Anentome* sp. representing the point of detachment and point of coma ($n = 10$). Each species is separated into water-condition acclimations (*Pomacea* sp., 20, 25, 30, 25°C + salinity of 1 ppt and 25°C + salinity 2 ppt; *Anentome* sp., 20, 25, 30, 25°C + salinity of 1 ppt and 25°C + salinity 2 ppt). (a, b) Temperature increase experiment. (c, d) Temperature decrease experiment. (e, f) Salinity increase experiment.

high (detachment, $P = 0.067$; and coma, $P = 0.217$) acclimation levels (Fig. 2d, 3, 4).

Response to salinity

Pomacea sp. demonstrated a median detachment response of 7 ppt and a median coma response of 7 ppt for increasing environmental salinity. *Pomacea* sp. in the 20°C acclimation group demonstrated a significantly lower tolerance to salinity compared to those in the 25°C group (detachment,

$P > 0.001$; and coma, $P > 0.001$) and the other acclimation groups (Fig. 2e, 3, 4).

Anentome sp. demonstrated a median detachment response of 5 ppt and a median coma response of 5 ppt for increasing environmental salinity. Of the salinity acclimations for *Anentome* sp., the lower acclimations had a positive effect on their ability to withstand higher salinities (detachment, $P = 0.534$; and coma, $P = 0.033$; Fig. 2f, 3, 4). All other salinity treatments had no significant effect on either species.

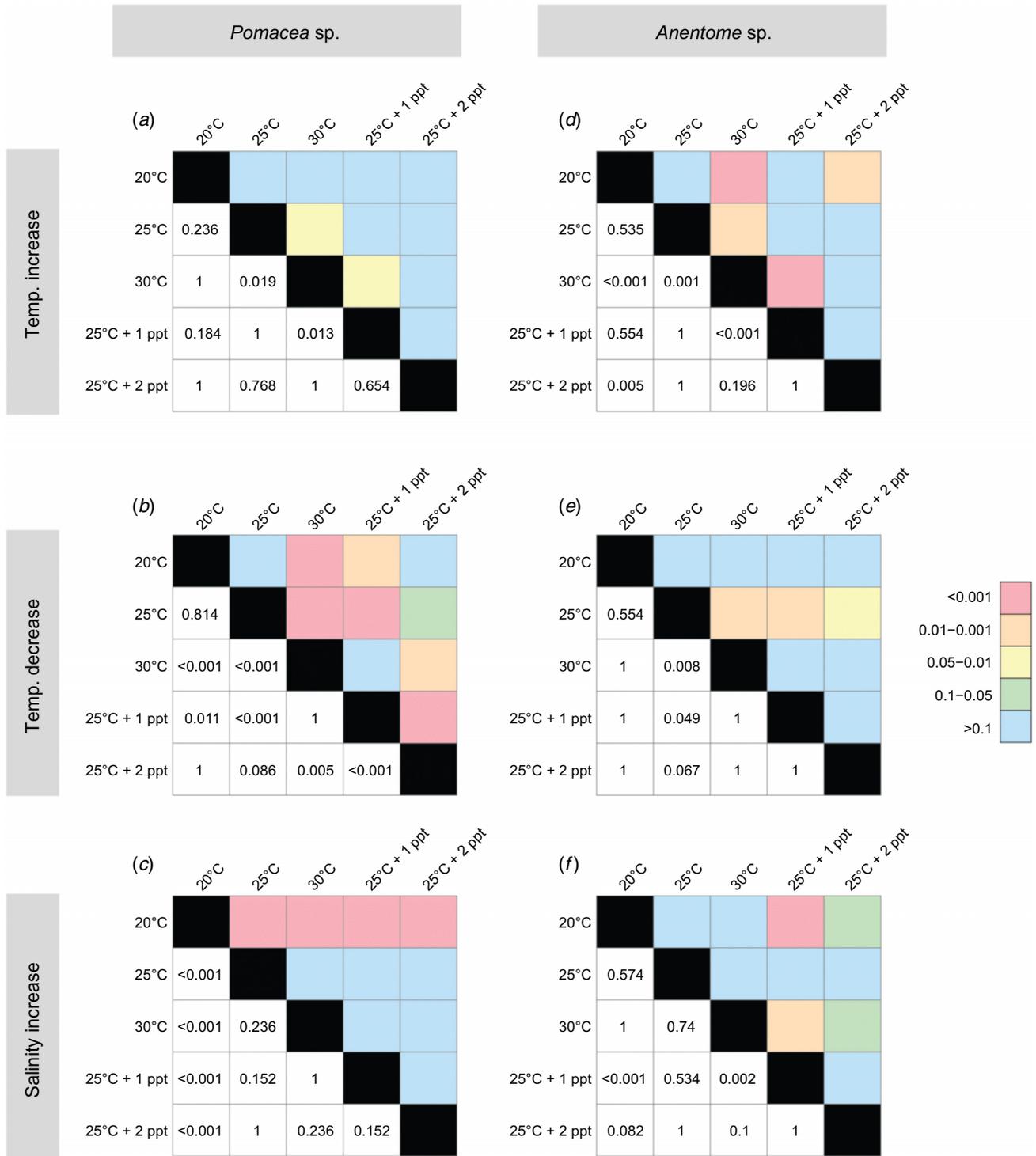


Fig. 3. The statistical relationship between the five acclimation groups based on *P*-values generated from a Chi-Square pairwise test. The data represent the point where individuals detached from the substrate. Data used are for *Pomacea* sp.: (a) temperature increase, (b) temperature decrease and (c) salinity increase; and *Anentome* sp.: (d) temperature increase, (e) temperature decrease and (f) salinity increase. The bottom half demonstrates the significance values generated, and the top half demonstrates this significance visually.

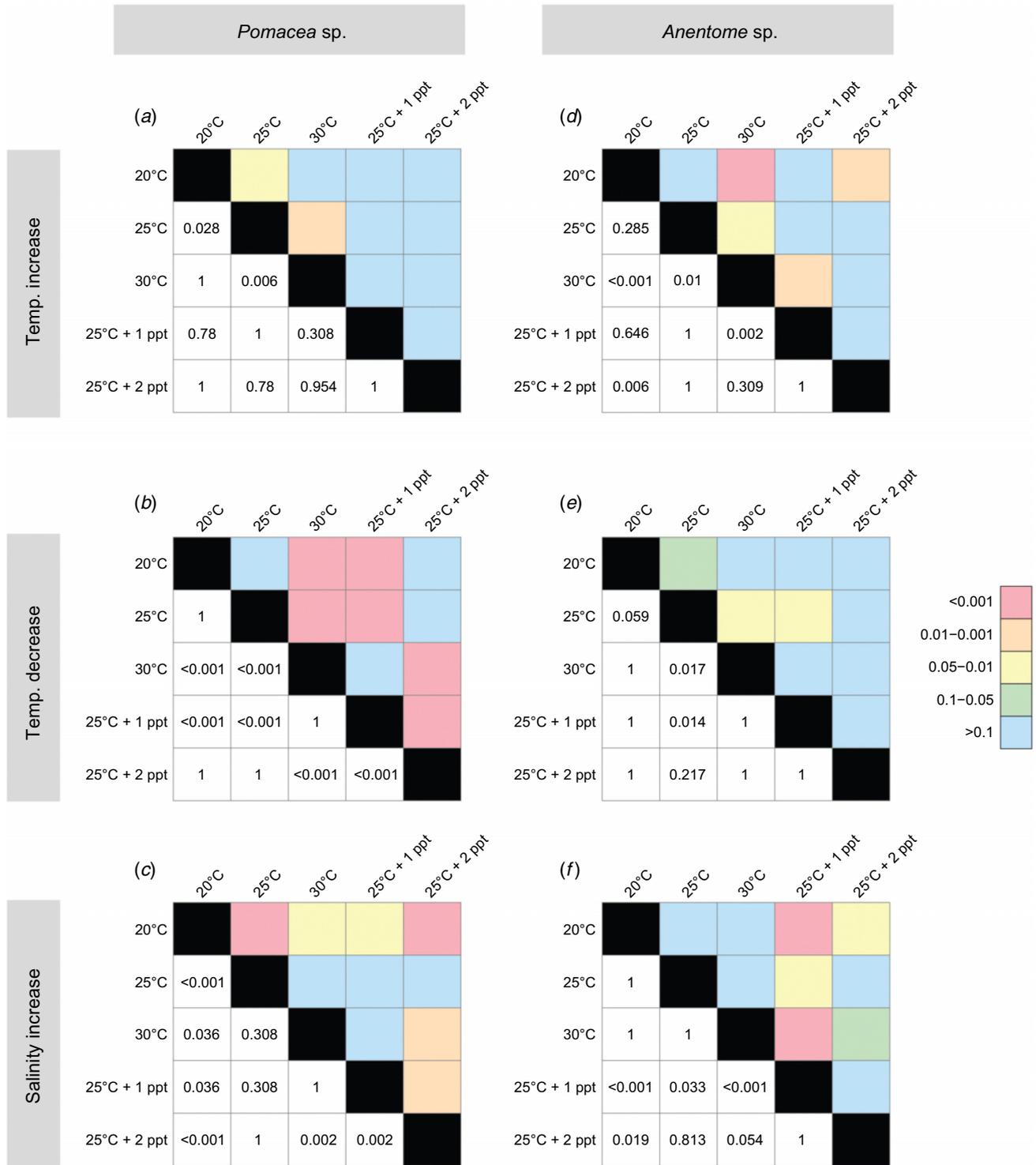


Fig. 4. The statistical relationship between the five acclimation groups based on P-values generated from a Chi-Square pairwise test. The data represent the point where individuals entered a coma. Data used are for *Pomacea* sp.: (a) temperature increase, temperature decrease (b) temperature decrease and salinity increase (c), and *Anentome* sp.: (d) temperature increase, (e) temperature decrease and (f) salinity increase. The bottom half demonstrates the significance values generated, and the top half demonstrates this significance visually.

Discussion

This study was the first to critically investigate the physiological limitations of Australian *Pomacea* sp. and *Anentome* sp. Both species demonstrated a thermal range that would allow a wide range of potential habitats in Australian freshwater environments. Our results also indicated that low-salinity environments may not be a barrier to their range extension. Given the clear risk that both represent, these outcomes are important for both national and international management of impacts from current and further invasions (Aditya and Raut 2001; Ng et al. 2016; Ponder et al. 2016). The results of this study have provided a foundation for biosecurity policy and further research into these species.

As expected, both species groups demonstrated a thermal range that reflected their tropical origins. Their lower temperature limits (onset of coma), based on the acclimations used in our experiments, were 12°C for *Pomacea* sp. and 11°C for *Anentome* sp. By contrast, the upper thermal limits for both species exceeded 40°C. This is not surprising because tropical species tend to demonstrate limited ability to adapt to temperatures outside of their thermal range because of their evolution under stable conditions (Tewksbury et al. 2008; Sunday et al. 2011). Although some intraspecific variation was detected, our results suggested that their ability to spread to more temperate climates would probably be limited (Sunday et al. 2011).

Both species displayed varying responses among acclimation groups in their ability to respond to temperature stress. The higher-temperature acclimation of 30°C assisted both to cope with higher test temperatures, in terms of attachment to the substrate, and delaying the point of onset of coma. However, the lower-temperature acclimations of 20°C did not appear to have any major impact on the ability to respond to lowered environmental temperature in either species when compared with the control of 25°C. This may be because of physiological thermal limitations on the species, suggesting that the species may be unable to adjust sufficiently to lower-temperature environments (Tewksbury et al. 2008; Sunday et al. 2011). The higher-temperature acclimation (30°C) limited the response to lower temperatures for *Pomacea* sp. but not *Anentome* sp. Further, the lower temperature-acclimated (20°C) *Pomacea* sp. were significantly better able to withstand higher temperatures. No other studies have reported such a response in freshwater snails.

Salinity acclimation generated different responses in the two species groups. In *Anentome* sp., the medium salinity acclimation (1 ppt) granted a significant advantage in their ability to cope with elevated salinity, whereas *Pomacea* sp. demonstrated no significant benefit from either salinity acclimation. Previous studies have reported that some snails increase the free amino acid content of their tissues as a method of reducing osmotic gradient; however, this is

effective only at low salinity (Matsushima et al. 1989; Jordan and Deaton 1999). In the case of *Pomacea* sp., this may suggest that their limited plasticity in salinity tolerance is a result of a limited compensation capability, rather than cellular volume regulation. The salinity acclimation of 1 ppt was detrimental at lower temperatures for both species; however, *Pomacea* sp. experienced no negative effect when acclimated to 2 ppt. Further study would be needed to explain this phenomenon. In addition, the lower-temperature acclimation of *Pomacea* sp. resulted in their decreased ability to cope with increasing environmental salinity. This interaction between salinity and temperature may be attributed to metabolic demand (Chen and Stillman 2012; King and Sardella 2017). Matsukura et al. (2009) demonstrated that lower temperatures alter the metabolic pathways of the congener *Pomacea canaliculata*. This alteration of the metabolic system is likely to be the cause of the decreased ability to tolerate salinity increase.

Our study used a dynamic method of evaluating environmental tolerance because this informs how the organism can respond to changing environments (Lutterschmidt and Hutchison 1997), but also because this method accommodates the scarcity of test organisms. To better understand the potential environmental range of *Pomacea* sp. and *Anentome* sp. a combination of methods (i.e. including those considered herein with measures of activity, reproduction or oxygen consumption) should be combined with studies of the survival of their eggs and larvae, because all of these factors have the potential to promote or inhibit their dispersal (Ebner et al. 2020). *Anentome* sp., although currently not established in the wild, has the potential to invade a geographic range similar to that of *Pomacea* sp. This highlights the significant negative effects that these species could have on the native fauna of tropical and subtropical Queensland waterways, along with other similar climatic regions.

Supplementary material

Supplementary material is available [online](#).

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