



## Responses to chemical cues indicative of predation risk by the freshwater shrimp *Palaemon argentinus* (Nobili, 1901) (Caridea: Palaemonidae)

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### ABSTRACT

Many prey species detect predators through chemoreception, particularly in low-visibility aquatic environments. Moreover, injury-released chemical cues from conspecifics are often perceived as a reliable indicator of predation threat. We examined whether males of the freshwater caridean shrimp *Palaemon argentinus* (Nobili, 1901) react to different types of infochemicals associated with predation threat. Shrimp were exposed to chemical stimuli from starved individuals of a predatory fish (*Australoheros facetus* (Jenyns, 1842)) and from crushed conspecific shrimp. Our experiment showed that *P. argentinus* reacts to waterborne substances associated with predation threat, indicating that chemical cues mediate behavioural anti-predator responses. Shrimp adopted an appropriate antipredator behaviour (reduced swimming activity) in response to chemical stimuli from *A. facetus*, and from crushed conspecifics, relative to a distilled-water control. The chemical stimuli from crushed conspecifics elicited the strongest reduction in swimming activity. Reduced movement, a common response in prey animals to the presence of predators, was not entirely consistent because shrimp increased their walking time in response to the chemical stimuli that were investigated. The ability to alter behaviour based on vision-independent perception of ambient risk would be highly useful for macroinvertebrate prey species such as *P. argentinus* living in eutrophic shallow lakes where visibility is often reduced. Our results demonstrated chemosensory recognition of predation risk highlighting the important role of chemical cues in the behavioural ecology of this shrimp, especially with regards to predator-prey interactions.

**Key Words:** alarm cues, antipredatory responses, *Australoheros facetus*, behaviour, chemoreception, kairomones, predator-prey interactions

### INTRODUCTION

There has been an increasing interest in understanding the importance of non-visual signals for communication and information in aquatic systems. Many studies have shown that aquatic animals use chemical cues to locate food, detect the presence of predators, find a partner or host, and for precise migration and navigation (Dodson *et al.*, 1994; Brönmark & Hansson, 2012). Chemoreception depends primarily on the senses of taste and smell, and is probably one of the most common type of perception used by animals to exploit valuable resources and/

or detect danger. Several crustacean groups have highly developed chemosensory systems (Hay, 2011), with chemical cues mediating numerous behavioural processes including foraging, reproduction, and antipredator responses (Dodson *et al.*, 1994; Bauer 2011; Hay 2011; Hazlett, 2011; Brooker & Dixon, 2016, 2017). Among decapods, crabs, lobsters, and crayfishes have been shown to be capable of recognising and reacting to chemical substances indicative of predation risk (Dodson *et al.*, 1994; Hazlett, 2011), and such responses have also been recently reported in some caridean shrimps (Huang *et al.*, 2011; Brooker & Dixon 2016, 2017).

In many aquatic animals, chemical cues from predators and cues from injured conspecifics have the potential to provide important information about the current risk of predation for prey (Tollrian & Harvell, 1999; Ferrari *et al.*, 2010; Paterson *et al.*, 2013; Wisenden, 2015). Chemical substances released by predators, defined as kairomones, can be important indicators of risk and elicit antipredatory responses in several aquatic taxa (Tollrian & Harvell, 1999; Wisenden, 2015). Moreover, when attacked by predators, diverse animals actively or passively release molecules that trigger alarm and related antipredatory behaviour by nearby conspecifics (Shabani *et al.*, 2008; Derby & Zimmer, 2012). The actively released molecules are pheromones, whereas the passively released molecules are alarm cues (Shabani *et al.*, 2008). It is believed that alarm cues which leak from injured or freshly killed preys warn conspecifics of an immediate danger (e.g., active predators) and elicit similar responses as predator odour when received by nearby conspecifics (Chivers & Smith, 1998; Shabani *et al.*, 2008). After detecting these chemical cues, preys usually reduce their activity and/or their shelter-seeking. The reduction of overall activity and/or shelter-seeking may result in reduced foraging, mating activity or less investment in offspring (Holomuzki & Short, 1988; Lima & Dill, 1990). Therefore, prey species should be able to distinguish chemical cues as indicators of predation threats to ensure escape behaviour is not unnecessarily initiated, thus representing a cost in terms of decreased opportunities for foraging, mating activity, and other fitness-related behaviours (Åbjörnsson *et al.*, 1997).

The freshwater caridean shrimp *Palaemon argentinus* (Nobili, 1901) (= *Palaemonetes argentinus*, see DeGrave & Ashelby, 2013) inhabits shallow lakes and streams in southeastern South America, and breeds in spring and summer (from October to March). This shrimp is found sympatrically with predatory fishes such as cichlids, characids, and cyprinodonts in shallow lakes in the Pampa plains of Argentina (González Sagrario *et al.*, 2009). Littoral fishes, such as the cichlid *Australoheros facetus*, are omnivores that feed on aquatic plants, zooplankton, smaller fishes, and macroinvertebrates such as *P. argentinus* (Yafé *et al.*, 2002). Some shallow lakes in the Pampas are dominated by submersed macrophytes, have a relatively low phytoplankton biomass, and the water is clear, but in general, most water bodies exhibit high phytoplankton biomass and scarce macrophyte development, and are typically turbid (Allende *et al.*, 2009). A third type of lake that can be encountered in this region corresponds to shallow lakes in which turbidity is mostly due to inorganic material, and in which both phytoplankton and macrophyte development is low (Allende *et al.*, 2009). Nowadays, there is a gradual shift from clear to turbid-water conditions, which along with decreases in macrophyte abundance, has been shown to affect trophic interactions (Quirós, 1998; Quirós *et al.*, 2002; Coops *et al.*, 2003; González Sagrario *et al.*, 2009; Sosnovsky *et al.*, 2010). The prevailing low visibility during the turbid water condition suggests that macroinvertebrate prey species like *P. argentinus* probably rely almost completely on chemical senses to detect predators. Although *P. argentinus* is likely to play a key role in trophic interactions of these shallow lakes, chemosensory recognition of predation risk by adults of this shrimp has not yet been reported.

We performed a short-term laboratory experiment to examine whether adults of *P. argentinus* can detect and react to chemical cues indicative of predation threat. We examined the ability of male shrimp to modify locomotor activities (swimming and walking) in response to chemical cues from starved individuals of a predatory fish (kairomones) and from crushed conspecific shrimp (alarm cues). We predicted that adults of *P. argentinus* will decrease their activity level when exposed to alarm cues, a reliable indicator of predation threat. Reduced movement to the presence of predators is a common response in prey taxa, including shrimps (e.g., Heck & Thoman, 1981). We exposed shrimp to chemical stimuli from the known predator (*A. facetus*) to verify that the response of

shrimp to stimuli from crushed conspecifics represents antipredator behaviour.

## MATERIALS AND METHODS

### Sampling

In March 2014, January and December 2015, mature individuals of *P. argentinus* and *A. facetus* were collected from La Brava Lake (37°52'52"S, 57°58'38"W), Buenos Aires province, Argentina. Both species co-occur in shallow lakes in the Pamapas, so the tested population of shrimp had previous experience with the experimental predator (Ituarte *et al.*, 2014). Specimens were obtained from the littoral zone using a hand net (45 cm width, 30 cm deep; 1 mm mesh). In the laboratory, each group of animals was held in separate 50 l aerated aquaria (22 °C, 10:14 h light dark cycle) filled with dechlorinated tap water for at least five days before being included in experiments. During acclimation, shrimp and fish were fed daily on TetraMin Pro® (lipids 12%; proteins 46%) (Tetra GmbH, Melle, Germany).

In order to avoid the possibility of sex differences in behavioural responses to predation risk during the breeding season, only males of *P. argentinus* were used for experimentation (Gancedo, 2015). As in many caridean shrimps, *P. argentinus* shows a 'pure searching' mating tactic, in which males are continually on the prowl for a receptive female (Bauer, 2004). In this type of mating, often referred to as promiscuous, males do not defend territories, are highly mobile, smaller than females, cryptic, and less obvious to visually oriented predators (Bauer, 2004). Male shrimp 4–6 mm carapace length were used in the experiments. Individuals were checked for the presence of metacercarial cysts of microphallid parasites (Trematoda, Microphallidae; Merlo *et al.*, 2016), and only non-parasitized shrimp were used.

### Experimental procedure

We tested the responses of male shrimp to chemical cues from three starved individuals of the fish *A. facetus* (collections made in March 2014, and January and December 2015; fork length = 14.1; 13.2 and 10.5 cm, respectively), and from crushed conspecific shrimp. Different male shrimp were used for each trial. Chemical stimuli from fish individuals were used as predator odour as suggested by Gelowitz *et al.* (1993), Wisenden *et al.* (1997), and Wudkevich *et al.* (1997) following the procedure described by Wisenden *et al.* (1997). During acclimation, approximately 12 h after the final feeding, each fish individual was placed in an aquarium (volume 3.5 l; 22 °C, 14:10 h light dark cycle) filled with dechlorinated tap water and was held there without food for three days. Specimens were then removed and the stimulus water was immediately used. The collection aquaria were well-aerated but contained no filtration system to avoid filtering active compounds. Chemical cues from conspecifics were prepared by crushing one adult shrimp using a mortar and pestle in 10 ml of distilled water; the stimulus preparation was immediately used.

We tested the responses of male shrimp in an acrylic aquarium (10 × 10 × 10 cm) filled with 800 ml dechlorinated tap water. A video camera was installed on the side of the experimental aquaria to record shrimp behaviour. Each shrimp was left to acclimatise for 30 min before the beginning of each trial. Different male shrimp were used for each trial ( $N = 34$  per trial). Shrimp behaviour (pre-stimulus activity) was recorded for 5 min before 3 ml of treatment water (Wisenden *et al.*, 1997) were carefully introduced with a syringe into a corner of the aquarium. Twenty seconds after injection, behaviour was recorded for another 5 min (post-stimulus activity). Aquaria were thoroughly rinsed and cleaned between test trials to remove any trace of chemical stimuli from previous trials.

All the recordings were randomly assigned to a video code and were blindly analysed by the same experimenter (BJG). From the recordings, we obtained the time in which each shrimp swam and walked in each of the two 5 min periods before and after adding a chemical stimulus to the water.

### Statistical analyses

Shrimp response to a particular stimulus was defined as the difference between post- and pre-stimulus activity. All values were expressed as arithmetic mean  $\pm$  standard error (SE). The effects of fish odour on changes in the swimming and walking time of shrimp were tested with mixed-model nested ANOVA with fish nested within control using InfoStat 2017 (Di Rienzo *et al.*, 2017). Water treatment condition (distilled water and predator odour) was a fixed factor and fish identity was a random factor in the model. We compared behavioural changes in 34 male shrimp (8, 12, and 14 shrimp for each respective fish individual). The effects of the three treatment conditions (distilled water, predator odour, and crushed conspecifics) on the changes in time performing each activity were analysed by one-way ANOVA using SigmaStat v 4.0. Shrimp reactions to all three fish individuals tested were pooled as the predator odour treatment. We tested 102 male shrimp, 34 in each of the three treatment conditions. All ANOVAs were performed after checks for normal distribution and equality of variance (Shapiro-Wilk and Brown-Forsythe tests, respectively). When ANOVA indicated significant differences between treatments, they were tested with a post hoc Tukey test.

## RESULTS

Basal behaviours of *P. argentinus* during the pre-stimulus period (before adding any water treatment) involved moving and stationary activities. Shrimp spent most of their time either swimming in the water column, motionless, or walking on the bottom of the aquarium. We focused our data analysis on the most frequently observed activities involving movement: swimming and walking. The two types of swim behaviour included slow forward motion by swimming through the water column with pereopods extended downward, and swimming up-side-down just below the surface of the water. To facilitate data recording, both types of swimming behaviour were grouped into a single activity category ("swimming").

Chemical cues from different fish individuals did not affect changes in swimming time of male shrimp relative to distilled water control (nested mixed-model ANOVA:  $F_{(1; 62)} = 0.62$ ;  $P = 0.48$ ), whereas their walking time was affected ( $F_{(1; 62)} = 25.44$ ;  $P = 0.007$ ). Shrimp increased their walking time in response to fish stimuli ( $P < 0.05$ ). Data for all three fish were pooled as predator

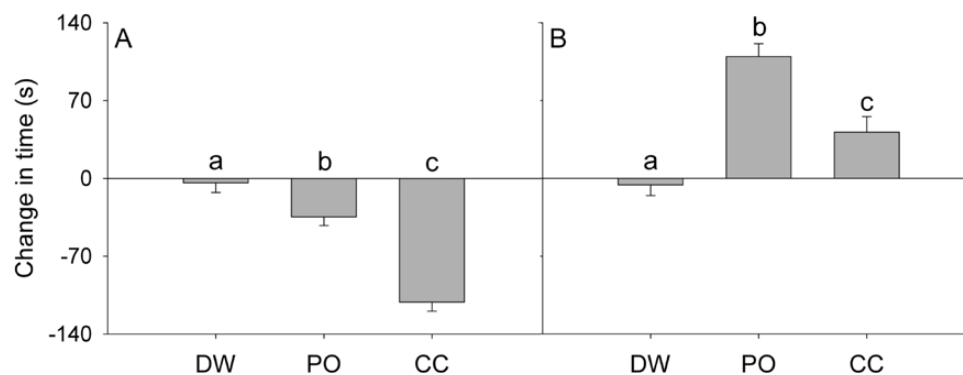
odour although variance for fish individuals differed from zero (swimming time:  $F_{(4; 62)} = 34.4$ ;  $P < 0.0001$  and walking time:  $F_{(4; 62)} = 2.52$ ;  $P = 0.049$ ).

Changes in swimming time of male shrimp was affected by water treatment conditions (ANOVA:  $F_{(2; 101)} = 46$ ;  $P < 0.001$ ). Male shrimp reduced their swimming time in response to chemical stimuli from predator odour (pooled data) and crushed conspecifics relative to distilled water, and the strongest reduction occurred in response to chemical stimuli from crushed conspecifics (Fig. 1A). Moreover, the amount of time that shrimp spent walking increased in response to both predator odour (pooled data) and conspecific stimuli relative to distilled water (ANOVA:  $F_{(2; 101)} = 24$ ;  $P < 0.001$ ). Such increase was stronger in response to the predator odour treatment (Fig. 1B).

## DISCUSSION

The ability to recognise and respond to a potential predator is an essential component of antipredator behaviour because failure to do so increases the probability of the predator capturing or injuring the prey (Lima & Dill, 1990). The importance of chemical cues in aquatic predator-prey systems is well known and chemical cues recognition has already been demonstrated in some caridean shrimps (e.g., Dunlop-Hayden & Rehage, 2011; Huang *et al.*, 2011; Ocasio-Torres *et al.*, 2014; Brooker & Dixon, 2016, 2017). Shrimps seem to have evolved a chemosensory ability that allows them to distinguish different organisms in their environment (Brooker & Dixon, 2016). Our experiment showed that the *P. argentinus* reacts to waterborne substances indicative of predation risk suggesting that chemical cues mediate behavioural antipredator responses in this species as well.

Reduced swimming behaviour has been reported in palaemonids shrimps upon non-chemical detection of predatory fish (Heck & Thoman, 1981; Carson & Merchant, 2005; Kunz *et al.*, 2006). By decreasing swimming activity, benthic prey such as *P. argentinus* can possibly be less vulnerable to predation by reducing the rate of encounter with potential predators (e.g., Wisenden *et al.*, 1997; Chivers & Smith, 1998; Ferrari *et al.*, 2010). Non-significant changes in the swimming behaviour of *P. argentinus* along with the high variability in shrimp behaviour when exposed to waterborne substances from each fish individual may be due to the small sample size for each fish. When data for all three fish were pooled, however, there was a clear reduction in the swimming time of shrimp. In turbid water and/or physically complex environments, preys able to detect predator odours will certainly be better suited to deal with predators than preys which solely rely on visual detection (Kats & Dill, 1998). Since many fishes feeding in light-limited environments locate their prey following hydrodynamic stimuli in the wake (e.g., Pohlmann *et al.*, 2004; Schwalbe *et al.*, 2012),



**Figure 1.** Mean ( $\pm$  SE) change in time devoted to swimming (A), and walking (B) by males of *Palaemon argentinus* following exposure to a control of distilled water (DW), predator odour (PO, chemical stimuli from starved individuals of the predatory fish *Australoheros facetus*, or crushed conspecific shrimp (CC). For each behaviour, bars with different letters indicate significant differences (post-hoc Tukey test,  $\alpha = 0.05$ );  $N = 34$  in each treatment.

a decrease in swimming activity will presumably be a good anti-predatory response.

Benthic invertebrate preys generally decrease their activities in response to predatory vertebrates (review by Wooster & Sih, 1995); however, some reports have shown an opposite response. Williams (1986) found in laboratory trials that larvae of the stonefly *Paragnetina media* (Walker, 1852) increase their movement when exposed to trout (*Oncorhynchus mykiss* (Walbaum, 1792)) odour. Moreover, response to predator odour is known to depend upon the presence or absence of a refuge (Sih & Kats, 1991). We found that male shrimp increased their walking time in response to predator odour and the crushed-conspecific treatment, suggesting that such reaction depends on the context of habitat (e.g., seeking for refuge). The increased walking time and the reduced swimming behaviour could provide protection against fish predators, but further experimental studies are needed to understand whether these observed reactions in males of *P. argentinus* are adaptive.

The chemical characterization of predator-specific cues is still scarce (von Elert, 2012; Weiss *et al.*, 2012), although faeces are often the source of predator odour (Kats & Dill, 1998). The fish in our experiments were starved for three days, indicating that shrimp reactions could be triggered by other metabolites of *A. facetus* rather than by faeces and/or by predator-associated bacteria that release specific metabolites (probably present in the mucus cover of fish; see Ringelberg & Van Gool, 1998). Almost every invertebrate species tested has shown an increase in antipredator behaviour when odours of crushed conspecifics were presented (e.g., Wisenden & Millard, 2001; Hazlett, 2011; Schaum *et al.*, 2013), but the chemical identity of alarm cues has been determined in only a few species of sea anemones (Howe & Sheikh (1975) and ostariophysan fishes (e.g., Smith, 1992). There is no indication of specialized crustacean cells that could produce alarm cues (such as the epidermal club cells in ostariophysan fishes), but peptides found in the hemolymph have been suggested as alarm cues (Acquistapace *et al.*, 2005; Shabani *et al.*, 2008; Hazlett, 2011). Since multiple cues can act in an additive or synergistic fashion to provide additional information for risk assessment by prey (e.g., Schoeppner & Relyea, 2009), the observed reduction in swimming time of male *P. argentinus* could translate into a stronger learned response to the predator when the predator odour is paired with alarm cues. Future studies should test this hypothesis.

The ability in small benthic species to identify other animals within proximity without visual cues would be highly useful (Brooker & Dixon, 2016). Since most of the shallow lakes in the Pampas are permanently limited by light (Quirós *et al.*, 2002; Torremorell *et al.*, 2007; Allende *et al.*, 2009), macroinvertebrate prey such as *P. argentinus*, probably rely almost completely on chemical senses to detect the risk of predation. The fact that *P. argentinus* can distinguish between chemical exuded by a predatory fish and from crushed conspecifics highlights the important role of chemical cues in the behavioural ecology of caridean shrimps, especially with regards to predator-prey interactions (see Brooker & Dixon, 2016, 2017).

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