Antipredator defence mechanism in the amphidromous shrimp *Xiphocaris elongata* (Decapoda: Xiphocarididae): rostrum length

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Predators may affect prey through inducible defences that can alter prey phenotype. The shrimp *Xiphocaris elongata* exhibits a short rostrum (SR) in the absence of fish predators and a long rostrum (LR) in their presence. The long rostrum in *X. elongata* is inducible by the predatory fish *Agonostomus monticola* (mountain mullet). Our objective was to test whether the long rostrum is an effective antipredator defence against *A. monticola* in different stages of predator–prey interactions (i.e. choice, attacks, bites, rejections, handling time and survival). We conducted behavioural experiments in fish tanks in which we fed *A. monticola* simultaneously with (1) one LR shrimp and one SR shrimp, or (2) one LR shrimp and one shrimp which originally had a long rostrum but whose rostrum was cut (LR[S]). We scored the fish behaviours in terms of choice, unsuccessful attacks, bites, rejections and handling time. We also conducted mortality experiments in closed artificial pools in which we exposed (1) 10 LR and 10 SR shrimp or (2) 10 LR and 10 LR[S] shrimp to *A. monticola*, and quantified shrimp survival after 24 h. In the trials with LR and SR shrimp, *A. monticola* tended to attack SR shrimp first. LR shrimp were unsuccessfully attacked, bitten and rejected more than SR individuals. Handling time was higher for LR shrimp. The mortality experiments show higher survival of LR shrimp. In the trials with LR and LR[S] shrimp, *A. monticola* tended to attack LR[S] shrimp first. Unsuccessful attacks were similar for LR and LR[S]. There were more bites and rejections and longer handling time for LR shrimp. Survival was similar for LR and LR[S] shrimp in the mortality experiments. This study provides evidence in support of the hypothesis that the long rostrum in *X. elongata* is an effective antipredator defence against *A. monticola* by conferring benefits in most stages of the predator–prey interactions.

Keywords: antipredator strategies; Caribbean streams; freshwater macroinvertebrates; inducible defenses; predator–prey interactions

Prey may reduce their vulnerability to predation through either constitutive or inducible defences (Adler and Harvell 1990; Harvell 1990). Constitutive defences are those that are fixed (Oda et al. 2007), while inducible defences are environmentally triggered phenotypic modifications that are activated through a previous encounter with a predator (Harvell 1990). These phenotypic modifications in response to predator cues may consist of alterations in prey behaviour (e.g. temporal or spatial segregation, changes in activity and movement patterns, vigilance, refuge use and escape), life-history (e.g. growth delay), physiology (e.g. immune responses to pathogens) or morphology (e.g. changes in shape or structure) (Ives and

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Dobson 1987; Adler and Harvell 1990; Crowl and Covich 1994; Nilsson et al. 1995; Wisenden 2003; Oda et al. 2007; Creel and Christianson 2008; Hein and Crowl 2010); and have associated costs that are minimised or avoided in the absence of the predator’s visual, mechanical or chemical cues (Harvell 1986, 1990; Dodson 1989; Creel and Christianson 2008; Aránguiz-Acuña et al. 2010).

Morphological inducible defences are common in aquatic invertebrates like snails (e.g. crawl-out behaviour or thickened shells), rotifers, barnacles and bryozoans (e.g. spines in their exoskeletons), and crustaceans such as Daphnia (Adler and Harvell 1990; Crowl and Covich 1990, 1994; Covich et al. 1994; Dodson et al. 1994; Oda et al. 2007; Ferrari et al. 2010). In the presence of the predatory midge larvae Chaoborus, backswimmers (i.e. Notonectidae) and predatory fishes, different species of Daphnia elongate their heads or produce neck teeth and helmets in their exoskeletons (Dodson et al. 1994; Oda et al. 2007). These induced morphologies have been found to be effective antipredator defences in terms of evasion and escape efficiency (Grant and Bayly 1981; Havel and Dodson 1984; Mort 1986). The amphidromous shrimp Xiphocaris elongata exhibits a phenotypic polymorphism (i.e. long or short rostrum) that has been linked to the presence or absence of predatory fishes (Covich et al. 2009). Covich et al. (2009) found that X. elongata shrimp possess a short rostrum in headwater streams of Caribbean rivers where predatory fishes are absent, but have a long rostrum in stream reaches below waterfalls where diadromous predatory fishes are present. Natural barriers such as steep waterfalls limit the upstream migration of diadromous predatory fishes like mountain mullets, Agonostomus monticola, and American eels, Anguilla rostrata, to headwater streams (Fievet et al. 2001). No genetic differentiation among the different morphological varieties of X. elongata has been found for two mitochondrial genes (Reuschel 2008), and exposure experiments indicate that the presence of A. monticola induces the long rostrum in juvenile, long-rostrum adult shrimp (LR) and short-rostrum adult shrimp (SR) (Ocasio-Torres et al. 2014). Xiphocaris elongata may avoid fish predation by migrating above waterfalls and by altering their morphology where predatory fishes are present (Covich et al. 2009; Hein 2009; Ocasio-Torres et al. 2014).

Morphological inducible defences may confer benefits in different stages of predator–prey interactions. Perception of a long rostrum of X. elongata may deter an experienced (i.e. non-naïve) visual predatory fish from attacking it. A long rostrum may also increase the probability of an unsuccessful attack or of a rejection if the predator cannot handle the shrimp. Given a successful attack, a long rostrum may be of benefit at the population level by increasing handling time, decreasing their profitability (i.e. energy intake per unit time) and increasing the chance that nearby shrimp can escape. The objective of our research was to examine whether the long rostrum in X. elongata is a successful defence mechanism against the predatory fish A. monticola by any of the four modalities described above. We hypothesised that the long rostrum is an effective defence for X. elongata against A. monticola in terms of choice, unsuccessful attacks, bites, rejections, handling time and survival. We first conducted behavioural experiments to examine whether A. monticola limit feeding on LR shrimp when presented with a choice between LR and SR shrimp. In these tests we also measured the attack success on LR and SR shrimp, as well as handling time of both shrimp morphs. We also conducted an experiment to measure predation-related mortality rate of LR and SR shrimp co-occurring in an artificial environment in the
presence of *A. monticola*. Given that in another study we found that shrimp differ morphologically in ways other than rostrum length (i.e. abdomen length and weight) (Ocasio-Torres 2014), we also ran behavioural and mortality trials with LR shrimp and shrimp which originally had a long rostrum but whose rostrum was cut before the trials (LR[S] shrimp). This study will help to demonstrate that the long rostrum in *X. elongata* fits the criterion of a morphological inducible defence in an amphidromous macroinvertebrate.

**Methods**

**Study organisms**

*Xiphocaris elongata* are amphidromous shrimp, spending most of their adult life in fresh water, where females carry their eggs until hatching (Fievet et al. 2001). Newly hatched larvae drift to the estuary, where they spend 50–110 days before migrating upstream as post-larval juveniles (Benstead et al. 1999; March and Pringle 2003; Kikkert et al. 2009; Pérez-Reyes et al. 2013). *Xiphocaris elongata* are mostly detritivores, using their small cheliped pincers to shred leaf matter, periphyton and particulate organic matter (March and Pringle 2003; Cross et al. 2008; Covich et al. 2009). Their distribution is limited to the West Indies (Fryer 1977).

Mountain mullets, *Agonostomus monticola*, are diadromous, spending most of their adulthood in fresh waters (Fievet et al. 2001; Hein et al. 2011; Smith and Kwak 2014). *Agonostomus monticola* are generalist consumers feeding on shrimps, aquatic insects, algae and plant material (Cruz 1987; Phillip 1993; Aiken 1998; March et al. 1998; March and Pringle 2003; Matamores et al. 2009). *Agonostomus monticola* are some of the main predatory fishes in streams in Puerto Rico (Holmquist et al. 1998; Benstead et al. 1999; Cross et al. 2008; Covich et al. 2009). Their distribution has been reported in the West Indies, South American countries like Venezuela and Colombia, Central America, and as far north as Florida and North Carolina, USA (Aiken 1998; Matamores et al. 2009).

**Animal collection**

We collected all fish and shrimp via backpack electrofishing in two Puerto Rican rivers. *Xiphocaris elongata* with a short rostrum (SR) were collected in pools upstream of waterfalls in Río Espíritu Santo (18.3227°N, 65.8188°W) where fish are absent, and *X. elongata* with a long rostrum (LR and LR[S]) were collected in pools downstream of waterfalls in Río Espíritu Santo (18.3423°N, 65.8255°W) where predatory fishes are common. *Agonostomus monticola* were collected in riffles and pools downstream of waterfalls in Río Sabana (18.3647°N, 65.7193°W). Río Espíritu Santo and Río Sabana have large waterfalls that impede the passing of diadromous predatory fishes to the headwaters (Pringle et al. 1999; Kikkert et al. 2009). The sizes of the fish and the shrimp chosen for the experiments were the most common sizes collected. These sizes (i.e. mentioned in the next two subheadings of the methods section) are comparable to fish sizes reported by Cooney and Kwak (2010; e.g. total length: 3–29 cm) and shrimp sizes reported by Covich et al. (2009; e.g. post-orbital length: 8–11 mm for LR and SR; rostrum length: 10–14 mm for LR, 2–4 mm for SR).
Behavioural experiments

We kept individual *A. monticola* fish in 75.7-L tanks with clear filtered water and gravel (9 kg of CaribSea Instant Aquarium Gravel; CaribSea, Fort Pierce, Florida, USA) for 3 days to acclimate them before conducting the behavioural experiments in the same tanks. The fish were fed commercial fish flakes (i.e. Aqueon Tropical Flakes; Central Garden and Pet Company, Walnut Creek, California, USA) every day up to 48 hr prior to the first testing day to control for hunger level. Prior to the experiments we kept up to 40 *X. elongata* shrimp in 75.7-L tanks with clear water and gravel. The shrimp were also fed fish flakes (Aqueon Tropical Flakes) every day prior to the experiments. We ran trials in which we simultaneously presented 15 *A. monticola* with one LR and one SR shrimp. Fish had an average standard length of 19.08 ± 0.3 cm. LR and SR shrimp had similar post-orbital length (*Table 1*: Student’s *t* test: *t*28 = −0.01, *P* = 0.99) but different rostrum length (*Table 1*: Student’s *t* test: *t*28 = −14.15, *P* < 0.0001). To eliminate the effect of other possible morphological or behavioural differences between LR and SR shrimp, we also ran trials where we simultaneously presented 15 *A. monticola* with one LR shrimp and one LR[S] shrimp (i.e. shrimp which originally had a long rostrum but whose rostrum was cut before the trials). Fish had an average standard length of 19.7 ± 0.3 cm. The rostrum of the LR[S] shrimp was cut by hand 5 minutes prior to the trials. LR and LR[S] shrimp had similar post-orbital length (*Table 1*: Student’s *t* test: *t*28 = −0.042, *P* = 0.97) but different rostrum length (*Table 1*: Student’s *t* test: *t*28 = −16.58, *P* < 0.0001). The abdomen length in the trials with LR and LR[S] shrimp was also measured and was similar for both morphs (*Table 2*: Student’s *t* test: *t*28 = 0.13, *P* = 0.90).

No refugia were provided for the shrimp in the trials. Trials started when we added the shrimp to the tanks and finished 15 minutes later or when the fish consumed both shrimp if consumption occurred before the end of the 15 minutes. All trials were conducted in the morning or early afternoon (i.e. 7:00 am–1:00 pm) under 200-V fluorescent light bulbs. We recorded all trials with video equipment (Panasonic Lumix DMC-FZ60, Panasonic Corporation, Kadoma, Osaka Prefecture, Japan) and scored the predatory behaviour of the fish towards the shrimp by watching the video recordings from the trials.

The following behaviours were quantified: attacks – the number of times the fish approached the shrimp in a predatory manner; choice – the shrimp phenotype attacked first; unsuccessful attacks – attacks that did not result in consumption; bites – the number of times the fish opened its mouth, engulfed a shrimp and then closed its mouth; rejections – when after taking a bite, the fish spat the shrimp away; consumption – ingestion of the shrimp; and handling time – the period between the capture and complete ingestion (Wahl and Stein 1988; Nilsson et al. 1995).

After the trials, the fish and the surviving shrimp were kept in captivity for research not associated to this study.

Mortality experiments

We conducted trials to measure mortality of *X. elongata* shrimp by *A. monticola* in 150-L pools (diameter: 57 cm) with clear water. These pools contained three rocks (diameter: 15 cm) to provide refuge to *X. elongata* shrimp. The pools also had a mesh cover to prevent the fish and shrimp from jumping outside the pools.
Table 1. Measures of *Xiphocaris elongata* shrimp used for the behavioural and the mortality experiments.

| Experiments | Trials       | Morphs | Post-orbital length* | Rostrum length* | Abdomen length* |
|-------------|--------------|--------|----------------------|-----------------|-----------------|
| Behavioural | LR and SR    | LR     | 8.62 ± 0.17 mm       | 9.80 ± 0.37 mm  | n/a             |
|             |              | SR     | 8.61 ± 0.17 mm       | 3.25 ± 0.31 mm  | n/a             |
|             | LR and LR[S] | LR     | 8.61 ± 0.28 mm       | 9.60 ± 0.38 mm  | 21.92 ± 0.51 mm |
|             |              | LR[S]  | 8.59 ± 0.30 mm       | 2.74 ± 0.16 mm  | 22.02 ± 0.50 mm |
| Mortality   | LR and SR    | LR     | 8.75 ± 0.14 mm       | 10.26 ± 0.21 mm | n/a             |
|             |              | SR     | 8.78 ± 0.16 mm       | 3.17 ± 0.10 mm  | n/a             |
|             | LR and LR[S] | LR     | 8.28 ± 0.13 mm       | 11.01 ± 0.19 mm | 20.56 ± 0.29 mm |
|             |              | LR[S]  | 8.16 ± 0.10 mm       | 2.36 ± 0.09 mm  | 20.14 ± 0.26 mm |

Notes: *Mean ± standard error (SE) for each measure. LR[S] = shrimp which originally had long rostrums but whose rostrums were cut.
Prior to experiments, individual *A. monticola* were placed in 75.7-L tanks with clear filtered water and fed with fish flakes (Aqueon Tropical Flakes) every day, including the day prior to each trial, to avoid excessive feeding during the trial due to starvation. Before trials, we acclimated 10 *X. elongata* from each morph for 24 h in each pool and fed them with fish flakes (Aqueon Tropical Flakes). After the acclimation period, we added one *A. monticola* to each pool and quantified the number of surviving shrimp of each of the two rostrum sizes after a 24-h feeding period.

There were 10 trials with 10 LR *X. elongata* and 10 SR *X. elongata*. In these trials, fish had an average standard length of 19.9 ± 0.2 cm. LR *X. elongata* and LR[S] *X. elongata* had similar post-orbital length (Table 1: Student’s *t* test: *t*198 = −0.73, *P* = 0.47) but different rostrum length (Table 1: Student’s *t* test: *t*198 = −41.77, *P* < 0.0001). We measured the abdomen length for LR and LR[S], which was similar between morphs (Table 2: Student’s *t* test: *t*198 = −1.08, *P* = 0.28).

All the fish and surviving shrimp were kept in captivity after the trials for experimentation not related to this study.

### Statistical analysis

In the behavioural experiments, we used the Chi-square goodness-of-fit test to compare the total number of times that each morph was the first attack choice for the predatory fish. We also used 2 × 2 contingency table analysis to examine the relation between (1) the number of shrimp unsuccessfully attacked and the number of shrimp consumed for each morph, (2) the number of bites and the number of consumptions for each morph and (3) the number of shrimp consumed and the number of shrimp

| Behaviours               | *N* for each phenotype | *df* | *X*^2^ | *P*  |
|--------------------------|------------------------|------|--------|------|
| Attacked first           | 12                     | 3    | 5.40^a_ | 0.020 |
| Consumptions             | 12                     | 9    |        |      |
| Unsuccessful attacks     | 31                     | 100  | 10.00^b_ | 0.0016 |
| Bites                    | 21                     | 48   | 4.95^b_ | 0.026 |
| Rejections               | 0                      | 13   | n/a^c_  | 0.0006 |

Notes: ^a_Chi-square goodness-of-fit test results.  
^b_Pearson’s Chi-square test results.  
^c_Fisher’s exact tests results.
rejected for each morph, in the trials with LR and SR shrimp and the trials with LR and LR[S] shrimp. We used Pearson’s Chi-squared test when an expected value was ≥ 5 and Fisher’s exact test when an expected value was < 5 in the contingency tables. We also ran a Student’s t-test (two-tailed) to test for differences in mean handling time of A. monticola for each morph, in the trials with LR and SR shrimp and the trials with LR and LR[S] shrimp. For the mortality experiments, we also used Chi-square goodness-of-fit test for the number of shrimp that were alive for each X. elongata morph.

Results

Behavioural experiments

When presented with LR and SR shrimp, A. monticola was significantly more likely to first attack SR shrimp than LR shrimp (Table 2). The likelihood of an attack being successful (i.e. ending in consumption) was significantly greater for SR shrimp relative to LR shrimp (Table 2). Following an attack, LR X. elongata were bitten and rejected significantly more than SR shrimp (Table 2). Handling time (HT) of A. monticola consuming shrimp was significantly higher for LR shrimp (HT + standard error, SE = 22.00 ± 7.95 s, N = 9) than for SR X. elongata (HT + SE = 2.42 ± 0.51 s, N = 12).

When presented with LR shrimp and LR[S] shrimp, A. monticola attacked significantly more LR[S] X. elongata first (Table 3). However, the likelihood of an attack being successful was statistically similar for LR[S] and LR shrimp (Table 3). Following an attack, LR X. elongata were bitten and rejected more than LR[S] shrimp (Table 3). Handling time of A. monticola consuming shrimp was significantly higher for LR shrimp (HT + SE = 30.83 ± 12.79 s, N = 6) than for LR[S] X. elongata (HT + SE = 3.43 ± 1.15 s, N = 7).

Table 3. Chi-square goodness-of-fit analysis for the fish choice trials (i.e. first shrimp phenotype attacked); Pearson’s Chi-square analysis in terms of consumptions and unsuccessful attacks; and Fisher’s exact test in terms of consumptions and bites and in terms of consumptions and rejections for trials with shrimp which originally had a long rostrum but whose rostrum was cut (LR[S]) and LR shrimp.

| Behaviours           | N for each phenotype | df  | $X^2$ | P   |
|----------------------|----------------------|-----|-------|-----|
|                      | LR[S] | LR  |       |     |
| Attacked first       | 13    | 2   | 1     | 8.07$^a$ | 0.0045 |
| Consumptions         | 7     | 7   |       |      |    |
| Unsuccessful attacks | 64    | 55  | 1     | 0.07$^b$ | 0.79  |
| Bites                | 5     | 58  | 1     | n/a$^c$ | 0.0007 |
| Rejections           | 0     | 9   | 1     | n/a$^c$ | 0.014  |

Notes: $^a$Chi-square goodness-of-fit test results.

$^b$Pearson’s Chi-square test results.

$^c$Fisher’s exact tests results.
Mortality experiments
The *A. monticola* consistently consumed more SR *X. elongata* in the trials with SR and LR *X. elongata*; 38 SR *X. elongata* and 66 LR *X. elongata* survived these trials. In the trials with LR[S] and LR *X. elongata*, nonetheless, there was similar survival for both morphs when in the presence of *A. monticola*; 69 SR *X. elongata* and 69 LR *X. elongata* survived these trials).

Discussion
We found that long rostrums provide *X. elongata* an effective defence against predation by *A. monticola*. First, when presented with an LR and an SR shrimp, *A. monticola* consistently attacked first the SR *X. elongata*. Second, *A. monticola* were more unsuccessful in their attacks and rejected more LR than SR shrimp. Third, handling time was significantly longer in LR *X. elongata*. Fourth, more LR shrimp survived predation by *A. monticola* than SR shrimp did during a 24-h predation experiment in closed and artificial conditions. Because we did not control for morphological variability between LR and SR shrimp, we cannot state that the more effective antipredator strategies of LR shrimp against *A. monticola* in these experiments is solely due to their long rostrums. Additionally, results from another study attest that the LR *X. elongata* have longer and heavier abdomens than the SR *X. elongata* (Ocasio-Torres 2014). We thus repeated the experiments with LR shrimp and shrimp that had long rostrums previous to the trials (LR[S]) to remove any possibility of variability between the two morphs (e.g. abdomen length or weight) other than the rostrum length.

The behavioural and mortality experiments with LR and LR[S] shrimp reveal that having a long rostrum significantly benefited *X. elongata* at most stages of the predator–prey interactions. First, *A. monticola* repeatedly attacked first the LR[S] *X. elongata*. *Agonostomus monticola* are visual predators (March et al. 1998), and so they may perceive the long rostrum before attacking and choose to avoid LR *X. elongata*, selecting instead other prey in a natural setting. Second, LR shrimp were rejected more than LR[S] shrimp. These responses may give the shrimp the opportunity to escape predation in natural streams, given their rapid movements and leaping capacity (Fryer 1977). Third, *A. monticola* required more bites and more time to consume the LR shrimp than the LR[S] shrimp. Less profitable prey are unlikely to be targeted by predators seeking to maximise their energy intake (Emlen 1966, 1968; Schoener 1971; Pyke 1984). We conclude that the long rostrum in *X. elongata* fits the criteria of an inducible defence against the predatory fish *A. monticola* in terms of choice, rejections, bites and handling time.

The unsuccessful attacks in the behavioural experiments and the survival in the mortality experiments were similar for LR and LR[S] *X. elongata*. Because LR shrimp have larger abdomens than SR shrimp with similarly-sized post-orbital carapace lengths (Ocasio-Torres 2014), the larger fraction of unsuccessful attacks on LR versus SR shrimp is likely due to the larger abdomen of the LR shrimp rather than their larger rostrum. *Xiphocaris elongata* may escape from capture by flexing their abdomen (Fryer 1977). The larger abdomen of LR shrimp could have translated into a more efficient flex and a better possibility of escaping predation by *A. monticola* in the trials with SR shrimp. In terms of the equal survival of LR and LR[S] in the mortality experiments, we argue that the long rostrum is not
sufficient to lower the predation risk of *X. elongata* in situations where they are under constant predation (i.e. 24 h) and they do not have the ability to escape by migrating to other areas. Because our experiments were run in artificial pools that did not allow shrimp emigration, we recommend running similar experiments in natural settings. In the trials with LR and SR *X. elongata*, other antipredator defences, such as having a larger abdomen, may have been sufficient for LR *X. elongata* to have had lower predation rates than SR *X. elongata*. Experiments focusing on the antipredator behaviours of *X. elongata* against *A. monticola* are also recommended. Additionally, because the SR shrimp used in our experiments were collected from stream sections above waterfalls where predatory fishes cannot access, their inexperience with predatory fishes could have increased their chance of mortality when compared to the experienced LR shrimp. However, because *X. elongata* shrimp are amphidromous, SR shrimp most certainly migrated as juveniles and possibly as adults through streams with predatory fishes. Therefore, we argue that their inexperience with predatory fishes is only relative to the time they have spent above waterfalls.

As mentioned earlier, the sizes of the fish and the shrimp used in both the behavioural and mortality experiments were representative of the average sizes of the fish and shrimp that inhabit local streams. Therefore, we also expect that the behaviours of the *A. monticola* used in our experiments represent the behaviours of most *A. monticola* in natural settings towards adult *X. elongata*. Nonetheless, we also infer that the long rostrum in smaller *X. elongata* (i.e. perhaps smaller than shrimp with a post-orbital length of 9.0 mm) may not be an effective defence against *A. monticola* of a standard length greater than 19.0 cm because of large size differences between the predators and the prey. Our results, therefore, should not be used to interpret predator–prey interactions between *A. monticola* with larger sizes and *X. elongata* with smaller sizes than the ones used in our experiments. Juvenile or small-sized adult shrimp may possibly be using other anti-predator strategies (e.g. abdomen flexing) not assessed in our experiments. The results from these experiments should also not be used to infer that the long rostrum in *X. elongata* is an effective defence mechanism against other predatory fishes like American eels, *Anguilla rostrata*, and the bigmouth sleeper, *Gobiomorus dormitor*. Predation experiments with these and other predatory fishes, including exotic fishes, are recommended to test if the long rostrum is effective in minimising predation risk against predatory fishes other than *A. monticola*.

Although our sample sizes in both the behavioural and the mortality experiments may be considered small, the statistical power of our analyses was relatively high due to the consistent results obtained. Thus, even with small sample sizes, the behaviours of the fish towards shrimp with long rostrums were consistently different than those towards shrimp with short rostrums (SR and LR[S]), and this provides statistical evidence for an important and strong biological phenomenon.

Studies on the effectiveness of behavioural and morphological defences of tropical stream macroinvertebrates are relatively scarce (Covich et al. 1994; Crowl and Covich 1994; Dodson et al. 1994; Hein and Crowl 2010). In contrast, research on the efficiency of morphological defences (e.g. spines) of invertebrates in marine and lentic environments is more extensive (Krueger and Dodson 1981; Havel and Dodson 1984; Hebert and Grewe 1985; Harvell 1986; Lively 1986; Mort 1986;
Adler and Harvell 1990; Crowl and Covich 1990; Parejko and Dodson 1990; Dodson et al. 1994). Isopods *Asellus aquaticus* that inhabit Swedish lakes are more streamlined and have higher escape speeds when they live in reed (*Phragmites australis*) habitats where invertebrate predators are dominant than when they inhabit stonewort (*Chara tomentosum*) habitats where fish predators are dominant (Eroukhmanoff and Svensson 2009). Havel and Dodson (1984) also found that spined morphs of *Daphnia pulex* have greater escape efficiency than the morph without spines. Their study, nonetheless, did not find differences in the handling time of *Chaoborus* for both phenotypes (Havel and Dodson 1984). Spines in *Daphnia* seem to confer an advantage at an earlier stage of predator–prey interactions (i.e. before the predator has bitten the prey), whereas in *X. elongata* the long rostrum seems to be an effective defence in most stages of predator–prey interactions. Another example in which spines appear to reduce predation occurs in the colonial bryozoans *Membranipora* spp. (Harvell 1984). Through field observations, Harvell (1984) found that the feeding rate of the predatory nudibranch *Doridella steinbergae* for spined colonies of *Membranipora* was significantly lower than that for unspined colonies. In these bryozoans, as in *X. elongata*, the morphological defence seems to operate by lowering prey profitability.

In cave shrimps of the subgenus *Troglocaris*, individuals that inhabit caves where the predatory amphibian *Proteus anguinus* is present exhibit a longer rostrum than individuals that are not in contact with *P. anguinus* (Jugovic et al. 2010). In these shrimps, as in *X. elongata*, predatory presence or absence seems to explain the variability in the length of the rostrum. Prior to their experiments, Jugovic et al. observed that all the long-rostrum *Troglocaris* that were attacked from the front by *P. anguinus* were rejected, while all the successful attacks (i.e. that resulted in consumption) occurred from behind or from the side of the shrimp (Jugovic et al. 2010). Although in our experiments we did not quantify whether fish attacks occurred from the front, the side or the back, we found that the predatory fish *A. monticola* had significantly more rejections for LR *X. elongata* than for SR and LR[S] *X. elongata*. In their behavioural experiments, *P. anguinus* was presented with an individual without rostrum (i.e. individual whose short rostrum was previously cut) and an individual with a long rostrum simultaneously (Jugovic et al. 2010). In these experiments, *P. anguinus* took longer to swallow the individuals with a long rostrum (Jugovic et al. 2010). In both the cave shrimps *Troglocaris* and the amphidromous shrimp *X. elongata*, elongation of the rostrum seems to represent a defence mechanism against predation, in terms of rejections and in terms of handling time.

We demonstrate that rostrum polymorphism in *X. elongata* alters interactions with predators at the organismal level. In addition, rostrum polymorphism is also likely to have significant impacts at the community and ecosystem levels. At the community level, long rostrum in *X. elongata* may cause generalist predatory fishes to feed on other species of shrimp that do not possess effective anti-predator defences against these fishes and may also cause them to shift diets and eat aquatic insects, algae, plants, fruits and shrimps, but also on algae and plant material (Cruz 1987; Phillip 1993; Aiken 1998; March et al. 1998; Matamores et al. 2009). *Xiphocaris elongata* is one of the dominant macroconsumers in Caribbean streams (Crowl and Covich 1994; March et al. 1998) and its role as shredder and omnivore
also influences ecosystem processes like detrital processing, assimilation of organic matter, nutrient cycling and energy flow (March et al. 1998; Benstead et al. 1999; Pringle et al. 1999; Crowl et al. 2001; Hein 2009). The prevalence of LR *X. elongata* in areas where predatory fishes are present may allow considerable numbers of these shrimp to survive and contribute significantly to shredding leaf litter and to the processing and assimilation of particulate organic matter, which in turn may influence the decomposition rates of leaf litter and the export of particulate organic matter downstream (Crowl et al. 2001, 2006). *Agonostomus monticola* is one of the top predatory fishes in Caribbean streams (Holmquist et al. 1998). Studies of the interactions between fishes and shrimp help to understand the importance of predation in controlling not only the morphology, but the behaviour, antipredator strategies, distribution and abundance of shrimp, which in turn determine the structure of stream communities (March et al. 1998; Creed 2006). Studying predator–prey interactions, thus, is essential for the general understanding of community dynamics and ecosystem processes that occur in Caribbean streams. Predator–prey interaction studies are also important because they aid in gaining understanding of the evolution of antipredator adaptations in relation to the presence or absence of their potential predator.

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