

Aggressive interactions between two invasive species: the round goby (*Neogobius melanostomus*) and the spinycheek crayfish (*Orconectes limosus*)

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Abstract The invasion success of introduced species may be limited by competitive interactions with phylogenetically unrelated invaders. The round goby (*Neogobius melanostomus*) and spinycheek crayfish (*Orconectes limosus*) are invasive benthic predators that occupy and defend similar cryptic microhabitats, and thus may compete for shelter. The round goby expanded throughout the North American Great Lakes within 8 years of introduction, whereas another 6 years passed before it had spread through the upper St. Lawrence River. Here, we explore the premise that dense established populations of the invasive spinycheek crayfish slowed round goby colonization of the St. Lawrence River. We performed a series of videotaped laboratory experiments to determine if round gobies suffer from aggressive attacks or alter their behaviour (e.g. use of shelter and movement) in the presence of spinycheek crayfish. We also assessed the prolonged effects of food and shelter competition

by comparing changes in the submerged mass of juvenile round gobies and spinycheek crayfish in conspecific and heterospecific pairs. Contrary to our predictions, round gobies more frequently initiated aggressive encounters with spinycheek crayfish, whereas the crayfish were more likely to flee or be evicted from their shelters. Furthermore, round gobies gained more body mass than spinycheek crayfish, regardless of conspecific or heterospecific pairing. Rather than impeding round goby colonization, spinycheek crayfish appear more likely to suffer energetic costs and an increased exposure to predation in the presence of round gobies.

Keywords Aggression · Agonistic behaviour · Interspecific competition · Crustacean · Freshwater fish · Invasive species

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Introduction

The invasion success of introduced species is influenced greatly by behavioural interactions with the pre-existing community (Holway and Suarez 1999). Aggression is a key behaviour that can drive the competitive displacement of resident species by an invader (Butler and Stein 1985; Chucholl et al. 2008; Janssen and Jude 2001; Karlson et al. 2007; Pintor et al. 2008). Conversely, intra- and interspecific aggression can limit an invader's abundance,

distribution, and rate of spread (Blight et al. 2010; Thompson et al. 2012; Hudina et al. 2014). Previous studies that investigated competition among invaders have tended to focus on phylogenetically related species (Dubs and Corkum 1996; Griffen et al. 2008; Piscart et al. 2011), and prior work examining the effects of crayfish aggression have not assessed reciprocal aggression towards crayfish (Carpenter 2005; Light 2005; Bubb et al. 2009). Here, we consider the potential for mutually aggressive interactions between two unrelated species: a freshwater fish—the round goby (*Neogobius melanostomus*), and a crustacean—the spinycheek crayfish (*Orconectes limosus*). Both species are ecologically similar in that they are aggressive, high-impact invasive predators with overlapping habitat and food requirements (Bergstrom and Mensinger 2009; Hirsch and Fischer 2008).

The round goby, a Ponto-Caspian species, was discovered in North America in 1990 in Lake Superior, and by 1998 it had invaded all five Great Lakes (Walsh et al. 2007). However, another 6 years passed before it was found established in the St. Lawrence River (Hickey and Fowlie 2005). Abundant populations were not observed near the Island of Montreal until 2008 (Kipp and Ricciardi 2012). This delay is surprising, given that (1) the round goby expanded rapidly throughout the lower Great Lakes, (2) there are no physical barriers to its dispersal between eastern Lake Ontario and the St. Lawrence River, (3) the St. Lawrence River drains Lake Ontario, and (4) the physical environment of the upper St. Lawrence River is well suited to the life history requirements of the species (Charlebois et al. 1997; Ricciardi et al. 1997; Kipp and Ricciardi 2012; Kipp et al. 2012). The apparently slow colonization of the river could conceivably have been the result of aggressive interactions with the spinycheek crayfish, which is present in high abundance throughout the upper St. Lawrence River, having become established in the early to mid-1970s (Dubé and Desroches 2007).

The success of an invader often varies with the strength and direction of its interactions with native species and previously established invaders (Mooney and Cleland 2001). In freshwater habitats with multiple invasive species, invaders are frequently found to have negligible or weakly negative effects on each other, while exerting stronger negative effects on the native community (Preston et al. 2012; Johnson et al.

2009). However, the success and impact of an invading species can be limited by aggressive behavioural interactions with other invaders (e.g. Zheng et al. 2008; James et al. 2016; Kobak et al. 2016).

The round goby and several *Orconectes* species of crayfish are highly successful invaders owing, in part, to their aggressive behaviour (Dubs and Corkum 1996; Phillips et al. 2003; Balshine et al. 2005; Kozák et al. 2007; Usio et al. 2001). Round gobies can displace native and invasive fishes through competition for food and spawning sites (Dubs and Corkum 1996; Bauer et al. 2007; Cooper et al. 2007; Savino et al. 2007; Bergstrom and Mensinger 2009). Similarly, invasive crayfish have often replaced resident species through aggressive interactions and interference (Capelli and Munjal 1982; Söderbäck 1991; Nakata and Goshima 2003; Gherardi and Cioni 2004; Klockner and Strayer 2004), and are generally more aggressive than native crayfishes (Hill and Lodge 1999; Nakata and Goshima 2003; Gherardi and Cioni 2004; Gherardi and Daniels 2004; Klockner and Strayer 2004). Such behaviour can limit the abundance of a subordinate species by reducing its access to key resources (Holway and Suarez 1999). Indeed, introduced species are likely to be more successful if they are sufficiently aggressive to co-opt resources from resident species (Duckworth and Badyaev 2007). Larger individuals and those with prior residency may have a competitive advantage over smaller intruders. Expressed aggression increases with prior residency (Dubs and Corkum 1996; Figler et al. 1999), and individuals are most aggressive towards conspecifics of the same size, for both the round goby (Stammler and Corkum 2005) and crayfishes (Peeke et al. 1995; Bergman and Moore 2003).

Here, we examined how prior residency and relative size differences between interspecific pairs of round gobies and spinycheek crayfish affect their aggressive behaviour, shelter use, and movement. We also assessed the potential population-level effects of food and shelter competition between round gobies and spinycheek crayfish by examining change in mass in conspecific and heterospecific pairs. Specifically, we tested the following predictions: (1) size-matched spinycheek crayfish display higher levels of aggression towards round gobies than vice versa; (2) prior residents exhibit more aggression than intruders; and (3) round gobies grow at a lesser rate when paired with spinycheek crayfish than when paired with conspecific individuals.

Methods

Round gobies and spinycheek crayfish were collected throughout the summers of 2008 and 2009 from five sites along the St. Lawrence River, near the Island of Montreal for the behavioural experiments (Beauhar-nois: 45°19'7.1"N, 73°52'58.6"W; Châteauguay: 45°22'31.7"N, 73°46'34.3"W; Les Coteaux: 45°15'13.9"N, 74°12'43.7"W; Melocheville: 45°19'9.2"N, 73°55'39.8"W; and Summerstown: 45°2'45.7"N, 74°35'36.6"W). Adult male round gobies in reproductive condition were excluded because they exhibit heightened aggressive behaviour (Dubs and Corkum 1996; MacInnis and Corkum 2000). Following behavioural experiments, we assessed the potential for long-term effects of competitive interactions by measuring individual growth of round gobies and spinycheek crayfish. Round goby and spinycheek crayfish juveniles were collected in September 2013 from Châteauguay and Parc Rene-Levesque (45°25'43"N 73°40'50"W), respectively, for growth experiments. Fish and crayfish were separated by species and kept in 75 L holding tanks (72.64 cm × 40.64 cm × 25.4 cm) containing de-chlorinated tap water, gravel, and tube shelters (5 cm diameter, 6 cm length PVC pipe) and were fed one sinking fish food pellet (Hikari sinking wafers) per individual per day during the holding period. Animals were not kept in isolation, in order to mimic natural conditions. The number of tube shelters always exceeded the number of individuals to ensure all individuals had access to shelter. Holding and experimental tanks were kept in a climate-controlled room at 16–20 °C with a photoperiod of 12:12.

Behavioural experiments

Residency and size trials

We assessed the effect of prior residency and relative size differences on the aggressive behaviour, use of shelter, and cryptic movement (see description in *Analysis of recordings*) of round goby and spinycheek crayfish. Animals were held for a minimum of 7 days and were not fed for 18 h prior to each trial. Experiments were conducted during the daytime, as both species are more active at night and shelter use is greatest during the day to reduce predation risk (Griffiths et al. 2004; Eros et al. 2005; Holdich and Black 2007). Body mass, total body length (TL,

crayfish with chelae fully extended along the axis of the body), and gender of each animal were recorded before each trial. Experimental arenas consisted of 75 L tanks with three sides covered with brown paper to minimize disturbance, and contained only a PVC tube shelter in the center of the experimental arena to maximize the visibility of the animals. Water in the experimental arenas was replaced between trials.

Prior residency was established by placing either species into the experimental arena 24 h prior to the addition of the other species. This is sufficient time for spinycheek crayfish to establish residency (Figler et al. 1995), and round gobies acclimate to aquaria rapidly and show consistent activity patterns 1–72 h after initial introduction (Stammler and Corkum 2005). In no-residency treatments, animals were placed into the experimental arena at the same time. Controls were run to assess the solitary behaviour of round gobies and spinycheek crayfish, with and without prior residency.

In each set of residency treatments, round gobies were paired with spinycheek crayfish of the same total length (“equal crayfish”), 75 % of the length (“medium crayfish”), or half of the length (“small crayfish”) of the round gobies. As round gobies can achieve maximum sizes that are twice that of spinycheek crayfish (Jude 2001; Holdich and Black 2007), we selected spinycheek crayfish sizes that were either equal to or smaller than the round gobies. Round goby size has also been found to vary across stages of colonization (MacInnis and Corkum 2000; Gutowsky and Fox 2011; Brandner et al. 2013), which is represented in our use of different round goby:spinycheek crayfish size ratios. A size difference of 25 % is sufficient to promote dominance between two crayfish owing to resource holding potential (Figler et al. 1999), whereas a size difference as little as 3 % has been found to convey immediate dominance between round gobies (Stammler and Corkum 2005).

Videotaping began immediately upon introduction of both animals in the no-residency trials, and after the introduction of the second animal in the prior residency trials. The camera faced the uncovered side of the tank, and was located approximately 1 m away. Recordings were taken for a period of 60 min. Animals were used only once in the experiments. Each of the size and residency combinations were replicated ten times, for a total of 90 pairwise trials, while there were 20 solitary controls per species, with ten replicates of two residency treatments.

Analysis of recordings

Aggressive behaviour was observed for a 20 min period beginning immediately after the animals began to interact. An ethogram of aggression was adapted from Karanavanich and Atema (1998) (Table 1), and scores (−2 to 3) were assigned to each individual every 5 s.

Shelter use and cryptic movement of paired and solitary individuals were observed within three time periods: at the beginning (0–10 min), middle (25–35 min), and end (50–60 min) of each trial. The use of shelter and type of movement was noted for each individual every 10 s. An individual was considered to be using the shelter if it was inside or within half of a body length from the shelter, and movement was classified as either “cryptic” or “non-cryptic”. For a round goby, cryptic movement included moving only slightly such that it remained on the bottom of the tank, whereas swimming in the water column was considered to be non-cryptic. For spinycheek crayfish, remaining motionless or climbing slowly over objects were considered cryptic behaviours, whereas walking or crawling out in the open, or sudden tail-flipping were considered to be non-cryptic behaviours.

Growth experiments

Newly collected juveniles of round gobies and spinycheek crayfish were acclimated to laboratory conditions in single-species holding tanks (10 indiv/tank) for 3 weeks, and then were tagged with one of two colors of visible implant elastomer (VIE, Northwest Marine Technology). VIE does not affect fish growth

(Malone et al. 1999; Olsen and Vollestad 2001; Astorga et al. 2005) and has been successfully used in crayfish growth studies (Parkyn et al. 2002). The elastomer was injected into the caudal peduncle of round gobies and the tail muscle of spinycheek crayfish with a 0.3 ml hypodermic syringe. Animals were then placed back into the holding tanks and observed for 4 days before beginning the experiment; no mortality or visible signs of stress were observed during this time.

Gender was not identified for these experiments as this was not considered to be an important factor affecting competition between juveniles. Gender differences in round gobies do not emerge until adulthood when males become significantly more aggressive (Dubs and Corkum 1996; MacInnis and Corkum 2000), and juvenile crayfish have not been found to have gender-related competitive advantages (Figler et al. 1999).

Treatments

The effect of competition on growth was compared between conspecific and heterospecific pairs of round gobies and spinycheek crayfish, with five replicates per treatment. We measured growth in terms of body mass, rather than length, and thus focus here on weight measures. For these experiments, we paired juveniles of round gobies (1.17 ± 0.07 g) and spinycheek crayfish (1.13 ± 0.08 g) based on equivalent body mass, whereas the behavioural experiments paired adult round gobies (4.22 ± 0.21 g) and spinycheek crayfish (2.66 ± 0.20 g) based on body length ratios. One month after collection, two individuals were

Table 1 Ethogram of aggressive behaviours of round gobies and spinycheek crayfish during dyadic interactions (adapted from Karanavanich and Atema 1998)

Rank scores	Behaviour	Spinycheek crayfish	Round goby
−2	Fleeing	Tail flip	Swim escape
−1	Avoidance	Walking, turning, facing away	Move just out of the way, facing away
0	Not interacting	More than one body length between	More than one body length between
1	Initiation	Facing, approaching, turning toward	Facing, approaching, turning toward
2	Threat display	Meral spread, claws forward	Blocking path, swooping
3	Physical contact	Attempted grab with claw, claw pushing, tapping	Head bump

All interactions were videotaped for 60 min, and aggressive behaviour was observed for a 20 min period after the animals began to interact. Aggression scores were assigned to each individual every 5 s

paired within ± 0.1 g submerged mass, as well as by VIE color identification for conspecific pairings. Each pair was put into a 20.8 L (40.64 cm \times 20.32 cm \times 25.4 cm) tank containing a layer of gravel mixed with limestone sand (to provide calcium in case of molting crayfish), a PVC tube shelter, and an air bubbler. Tanks were separated by opaque barriers and covered with mesh screens. Animals were first fed one food pellet/individual six times a week for 1 week, but this accumulated too much excess food in the tanks, so thereafter feeding was reduced to a half pellet/individual. All animals were fed to satiation and remaining food was removed from tanks daily. Experiments were completed after 8 weeks when all animals were reweighed. No mortality occurred during the experiments. Experiments were not run for a longer duration to ensure survival of all individuals, as determined by pilot trials (J.C. Iacarella, pers. obs.).

Data analysis

Separate models were constructed to assess the effect of species, prior residency, size pairing, and gender on aggression, shelter use, and cryptic behaviors of round gobies and spinycheek crayfish. We verified that body sizes (length and weight) were similar between genders for each species and for each size pairing treatment separately, using Welch two-sample *t* tests ($p > 0.05$; “Appendix”, Tables 4 and 5). Aggression scores were analyzed using a cumulative logit mixed-effects model for ordinal data (“ordinal” in R, Christensen 2015), with trial number and experimental time (minutes) as random effects. Additional models were constructed to assess the effect of total body length, fork length or carapace length, and weight, on overall aggression; these models were run separately for each species. The binary time series for shelter use and cryptic behaviour were compiled to obtain a total number of times the behaviour was observed out of 180 observational time steps for each individual within each trial. The number of times shelter use or cryptic movement was observed was analyzed using maximum likelihood generalized linear mixed-effects models with binomial distributions (“lme4” in R, Bates et al. 2014) and trial number as a random effect. Separate generalized linear models were used to assess the effect of species, residency, and gender on shelter use and cryptic behavior of solitary individuals.

Backwards stepwise multiple regression with analysis of variance likelihood ratio tests were used to determine variable retention ($\alpha = 0.05$) for all interaction and main effects terms, beginning with four-way (paired treatments) and three-way interactions (solitary treatments). Final model selection was verified using Akaike information criterion for small sample sizes (AICc, Bolker et al. 2009; “MuMIn” in R, Bartoń 2015). Post-hoc tests were conducted on all retained interaction terms using least squares means comparisons (“lsmeans” in R, Lenth 2016) with Bonferroni corrections. Least squares means were plotted for visualization of contrasts between interaction terms as estimated by the models.

A linear maximum likelihood mixed-effects model was used to compare the growth of individual round gobies and spinycheek crayfish in conspecific and heterospecific pair treatments (“lme4” in R, Bates et al. 2014). Tank was treated as a random effect, and model selection was performed as described previously. Tukey’s post hoc tests with Bonferroni corrections were used to test the significance of retained model terms. Data were normally distributed (Shapiro–Wilk, $p > 0.05$) and variances were homogenous (Fligner–Killeen test, $p > 0.05$).

Results

Aggression, paired trials

Aggression was explained by a four-way interaction between species, prior residency, size pairing, and gender (see Table 2 for all model selection results). Across all trials, gobies displayed more aggressive behaviour than crayfish ($z = 2.36$, $p = 0.018$; Fig. 1), although no differences were found between female gobies and male crayfish when medium crayfish were prior residents, or when resident gobies were paired with small crayfish. Aggression levels were often significantly different between genders within species, but a consistent pattern was not observed across treatments (Fig. 1; Table 3). In addition, larger animals of both species exhibited more aggression. Round gobies with longer body size were more aggressive ($z = 2.16$, $p = 0.031$), as were heavier crayfish ($z = 2.07$, $p = 0.039$). Body weight was not related to aggression in gobies, whereas aggression in crayfish was unrelated to body or carapace length.

Table 2 Model selection results using backwards stepwise elimination with analysis of variance likelihood ratio tests (deviance and *p* value) and Akaike information criterion for small sample sizes (AICc)

Behaviour	Trial	Model comparison: full versus reduced	Δ AICc (full-reduced)	Deviance value	<i>p</i> value
Aggression	Paired	Full model, 4-way interaction versus No 4-way interaction	-12.00	19.61	<0.001
Shelter	Paired	Full model, 4-way interaction versus No 4-way interaction	-127.40	135.43	<0.001
Cryptic	Paired	Full model, 4-way interaction versus No 4-way interaction	-48.10	56.07	<0.001
Shelter	Solitary	Full model, 3-way interaction versus No 3-way interaction (“Mod1”)	1.94	1.21	>0.10
		Mod1, 2-way interactions versus No species × gender interaction	-74.02	78.92	<0.001
		Mod1, 2-way interactions versus No residency × gender interaction	-12.77	17.66	<0.001
		Mod1, 2-way interactions versus No species × residency interaction	-42.33	47.22	<0.001
Cryptic	Solitary	Full model, 3-way interaction versus No 3-way interaction	-47.33	50.48	<0.001

Trials either contained a round goby and spinycheek crayfish (“paired”) or a single individual of either species (“solitary”). Final, best-fit model is indicated in bold under “Model comparison”, as are statistically significant *p* values (*p* < 0.05)

Fig. 1 Aggression of male (light grey) and female (dark grey) round gobies (circle) and spinycheek crayfish (square) in pairwise trials, showing post hoc estimations of least squares means for an interaction between species, residency, size, and gender. Axis labels are as follows: *NR* no prior residency, *RC* crayfish residency, *RG* goby residency. Different letters represent significant differences (*p* < 0.05) only within the same size and residency trials. Error bars are ±1 SE

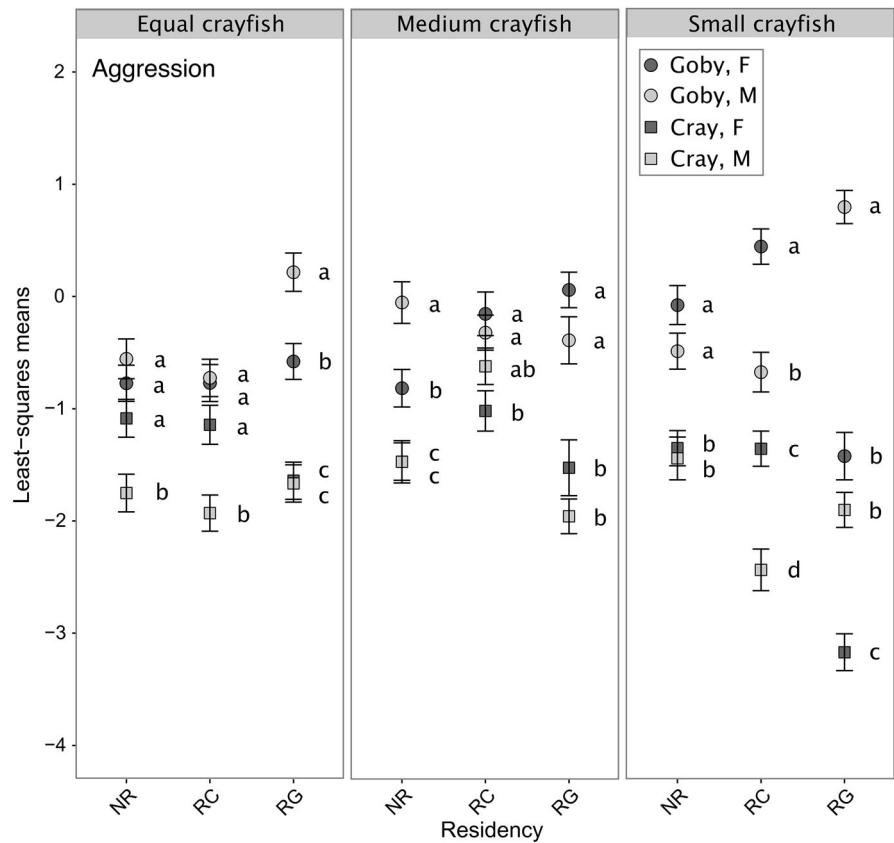


Table 3 Comparison of behaviour (aggression, shelter use, cryptic movement) between males and females of round gobies and spinycheek crayfish in different size pairing and prior residency treatments

Behaviour	Size	Residency	Species	z-ratio	<i>p</i> value	
Aggression	Equal	NR	Goby	1.34	>0.10	
			Crayfish	-4.21	0.016	
		RC	Goby	0.30	>0.10	
			Crayfish	-5.05	<0.001	
	Medium	RG	Goby	5.23	<0.001	
			Crayfish	-0.16	>0.10	
		NR	Goby	4.01	0.038	
			Crayfish	-0.01	> 0.10	
	Small	RC	Goby	-0.92	>0.10	
			Crayfish	2.33	>0.10	
		RG	Goby	-2.11	>0.10	
			Crayfish	-1.74	>0.10	
	Shelter use	Equal	NR	Goby	-2.61	>0.10
				Crayfish	-0.53	>0.10
			RC	Goby	-7.02	<0.001
				Crayfish	-6.55	<0.001
		Medium	RG	Goby	11.88	<0.001
				Crayfish	9.47	<0.001
			NR	Goby	-7.74	<0.001
				Crayfish	-4.18	0.019
Small		RC	Goby	-9.99	<0.001	
			Crayfish	-17.33	<0.001	
		RG	Goby	-6.79	<0.001	
			Crayfish	-6.45	<0.001	
Cryptic movement	Equal	NR	Goby	-1.69	>0.10	
			Crayfish	4.25	0.014	
		RC	Goby	-3.57	>0.10	
			Crayfish	5.14	<0.001	
	Small	RG	Goby	-0.65	>0.10	
			Crayfish	2.10	>0.10	
		NR	Goby	-9.96	<0.001	
			Crayfish	3.22	>0.10	
Small	RC	Goby	-7.84	<0.001		
		Crayfish	-0.37	>0.10		
	RG	Goby	-1.51	>0.10		
		Crayfish	-3.14	>0.10		
Equal	NR	Goby	2.42	>0.10		
		Crayfish	-0.81	>0.10		
	RC	Goby	-15.07	<0.001		
		Crayfish	-6.61	<0.001		
Small	RG	Goby	-4.02	0.037		
		Crayfish	1.71	>0.10		

Table 3 continued

Behaviour	Size	Residency	Species	z-ratio	<i>p</i> value
Residency categories are as follows: <i>NR</i> no prior residency, <i>RC</i> crayfish residency, <i>RG</i> goby residency. Positive z-value indicates male displays higher level of behaviour than female, and statistically significant differences ($p < 0.05$) are indicated in bold	Medium	NR	Goby	7.83	<0.001
			Crayfish	0.85	>0.10
		RC	Goby	-2.59	>0.10
			Crayfish	3.30	>0.10
		RG	Goby	0.41	>0.10
			Crayfish	0.79	>0.10
	Small	NR	Goby	-4.67	0.002
			Crayfish	0.17	>0.10
		RC	Goby	-8.13	<0.001
			Crayfish	-5.88	<0.001
		RG	Goby	-3.33	>0.10
			Crayfish	-7.02	<0.001

Shelter use, paired trials

Shelter use was best explained by a four-way interaction between species, residency, size, and gender (Table 2). Round gobies engaged in more shelter use than spinycheek crayfish overall ($z = 10.27$, $p < 0.001$; Fig. 2). In particular, female round gobies consistently used shelter more than male gobies and either gender of crayfish across residency and size pairings, with the exception that equal female crayfish used the shelter more when prior residents ($p < 0.001$; Fig. 2; Table 3).

Cryptic movement, paired trials

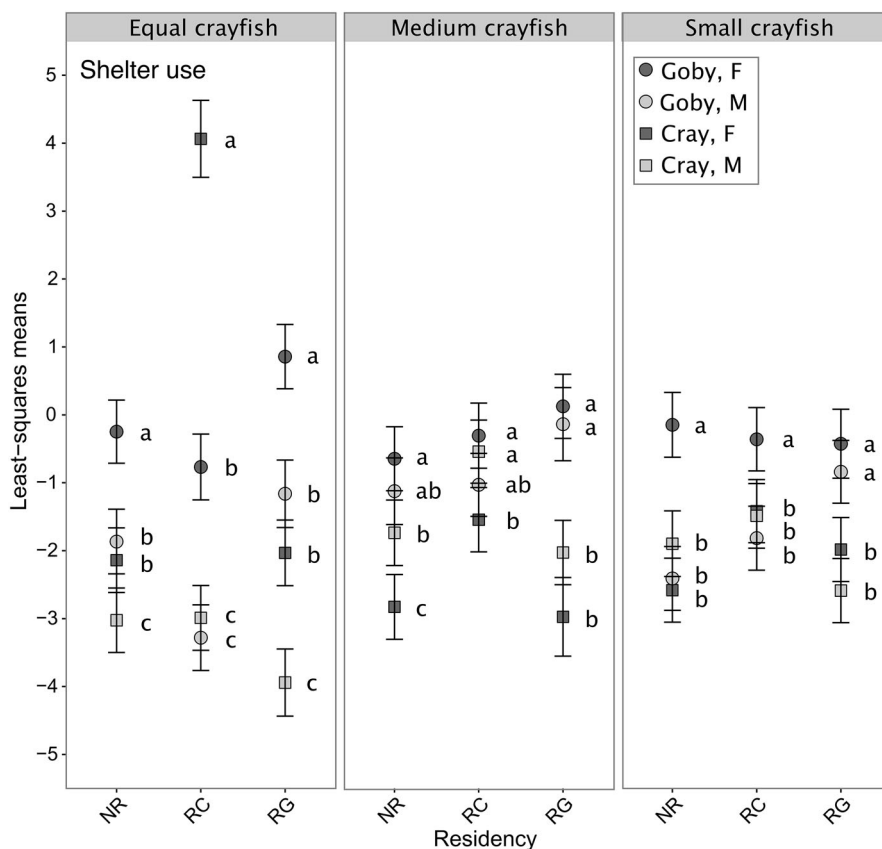
Cryptic movement was also determined by a four-way interaction between species, residency, size, and gender (Table 2). Round gobies generally engaged in more cryptic movement than spinycheek crayfish ($z = 8.01$, $p < 0.001$). When equal crayfish were prior residents, however, both male ($z = 9.13$, $p < 0.001$) and female crayfish ($z = 13.55$, $p < 0.001$) displayed more cryptic movement than male gobies (Fig. 3). Male gobies were also less cryptic than small female, resident crayfish ($z = -5.80$, $p < 0.001$), whereas female gobies were more cryptic ($z = 5.51$, $p < 0.001$). When small crayfish were paired with gobies, female gobies tended to be the most cryptic across residency treatments, but no clear pattern was observed with equal or medium crayfish pairings (Fig. 3; Table 3).

Shelter use and cryptic movement, solitary trials

Shelter use of solitary round gobies and spinycheek crayfish was best explained by a model retaining all two-way interactions between species, residency, and gender (Table 2). Shelter use by solitary round gobies was greater than that of spinycheek crayfish ($z = 2.01$, $p = 0.045$; Fig. 4a), and was higher with prior residency for gobies (residency vs. no residency, $z = 3.49$, $p = 0.003$), but lower for crayfish (residency vs. no residency, $z = -5.59$, $p < 0.001$). Females of both species used shelter more than males with ($z = -9.91$, $p < 0.001$) and without prior residency ($z = -6.65$, $p < 0.001$). In particular, female gobies used the shelter more than male gobies ($z = -11.99$, $p < 0.001$), though crayfish showed no difference with gender ($p > 0.10$; Fig. 4a).

Cryptic behaviour of solitary individuals was determined by a three-way interaction between species, residency, and gender (Table 2). Round gobies were observed to engage in more cryptic behaviour than spinycheek crayfish ($z = 3.79$, $p < 0.001$), particularly female gobies compared to others without prior residency ($p < 0.001$; Fig. 4b). Prior residents were generally more cryptic compared to non-residents ($z = 3.86$, $p < 0.001$)—except for male crayfish, who were less cryptic as residents (resident male vs. female crayfish, $z = -6.53$, $p < 0.001$).

Fig. 2 Shelter use of male (light grey) and female (dark grey) round gobies (circle) and spinycheek crayfish (square) in pairwise trials, showing post hoc estimations of least squares means for an interaction between species, residency, size, and gender. Axis labels are as follows: *NR* no prior residency, *RC* crayfish residency, *RG* goby residency. Different letters represent significant differences ($p < 0.05$) only within the same size and residency trials. Error bars are ± 1 SE



Change in body mass

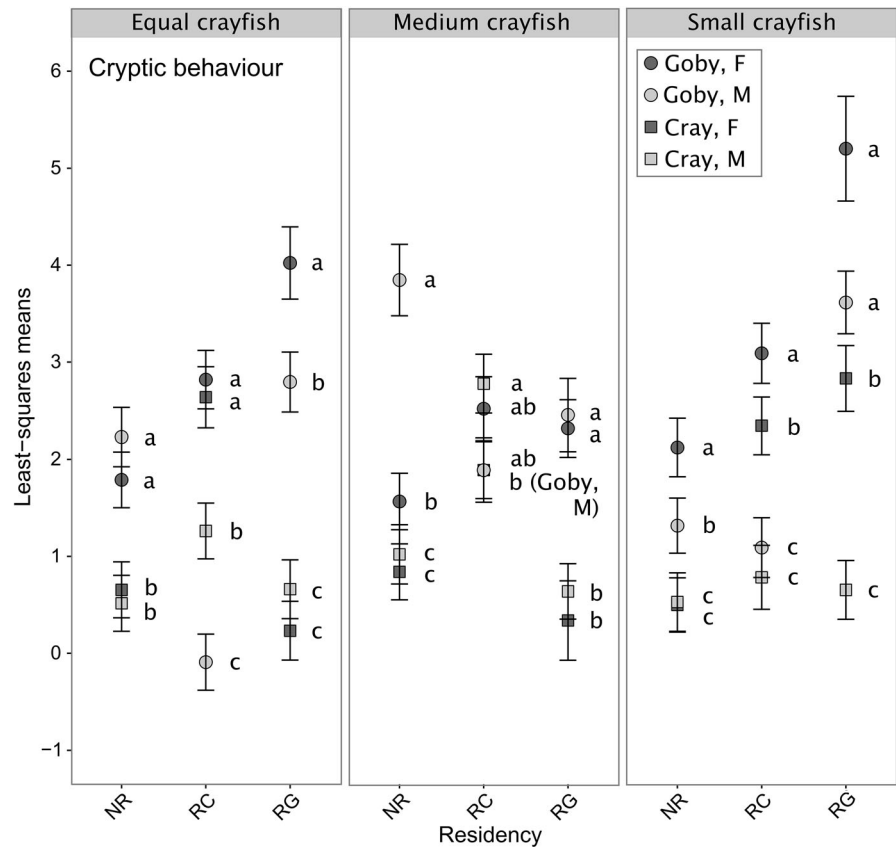
In growth experiments, round gobies gained more mass than spinycheek crayfish ($z = 9.15, p < 0.001$; Fig. 5). Though conspecific or heterospecific pairing was not a significant predictor of growth (likelihood ratio test, $p > 0.10$), spinycheek crayfish tended to grow less in the presence of gobies than in the presence of conspecifics.

Discussion

Our results suggest important ecological consequences arising from aggressive interactions between phylogenetically unrelated, but functionally similar invaders. Contrary to our predictions, round gobies were more aggressive than spinycheek crayfish and tended to suppress their growth. Round gobies also exhibited atypical aggressive behaviour, such that

higher levels of aggression occurred amongst individuals with larger size differentials, in contrast to the expectation of heightened levels between individuals similarly matched in size (Figler et al. 1999; Vorburger and Ribi 1999; Balshine et al. 2005). Combined with their rapid growth and larger adult body size, this trait appears to result in a distinct size-based competitive advantage in the majority of aggressive interactions with spinycheek crayfish. In addition, round gobies displayed greater boldness—that is, they initiated and escalated the vast majority of aggressive interactions—which may also confer a competitive advantage, particularly when they invade habitats already occupied by crayfish. Overall, round gobies used shelter more and engaged in more cryptic movement, whereas spinycheek crayfish exhibit higher levels of exploration and lower crypsis, which may lead to increased exposure to predation in the presence of round gobies. We speculate that this could have a population-level

Fig. 3 Cryptic behaviour of male (*light grey*) and female (*dark grey*) round gobies (*circle*) and spinycheek crayfish (*square*) in pairwise trials, showing post hoc estimations of least squares means for an interaction between species, residency, size, and gender. Axis labels are as follows: *NR* no prior residency, *RC* crayfish residency, *RG* goby residency. *Different letters* represent significant differences ($p < 0.05$) only within the same size and residency trials. *Error bars* are ± 1 SE



consequence for crayfish in areas where round gobies are abundant.

Round gobies were initially recorded in Lake Ontario in 1998 (Dietrich et al. 2006), so their earliest possible forays into the St. Lawrence River were met with spinycheek crayfish populations that had been established for more than a decade. We first collected round gobies from our St. Lawrence River sites soon after they were discovered around the Island of Montreal; to their competitive advantage, these individuals tended to be larger than the spinycheek crayfish (Kipp and Ricciardi 2012; A. Ricciardi, pers. obv.). Adult round gobies can obtain a maximum length of 25 cm (Jude 2001), whereas adult spinycheek crayfish rarely exceed 10 cm (Holdich and Black 2007). We did not run trials with a combination of large spinycheek crayfish/small round gobies, as the present size distributions of round gobies and spinycheek crayfish suggests that this type of interaction would be rare in the field.

Behavioural differences

Gender-based differences in aggression, shelter use, and cryptic behaviour were observed for both gobies and crayfish. However, neither species showed consistent differences across the size or residency trials, except for the high level of shelter use by female gobies. Our exclusion of reproductive adults from the experiments may account for the lack of consistency in gender differences. Reproductive male round gobies have been found to be more aggressive than females, as they engage in nest guarding and territorial defense (MacInnis and Corkum 2000). Similarly, reproductive male crayfish have larger chelae and often win aggressive interactions with females, although maternal female crayfish carrying eggs or young are more aggressive than males and outcompete them for shelter (Figler et al. 1995). It is possible that the gender-based differences that we observed corresponded to a pre- or post-reproductive stage that affected the behaviour of

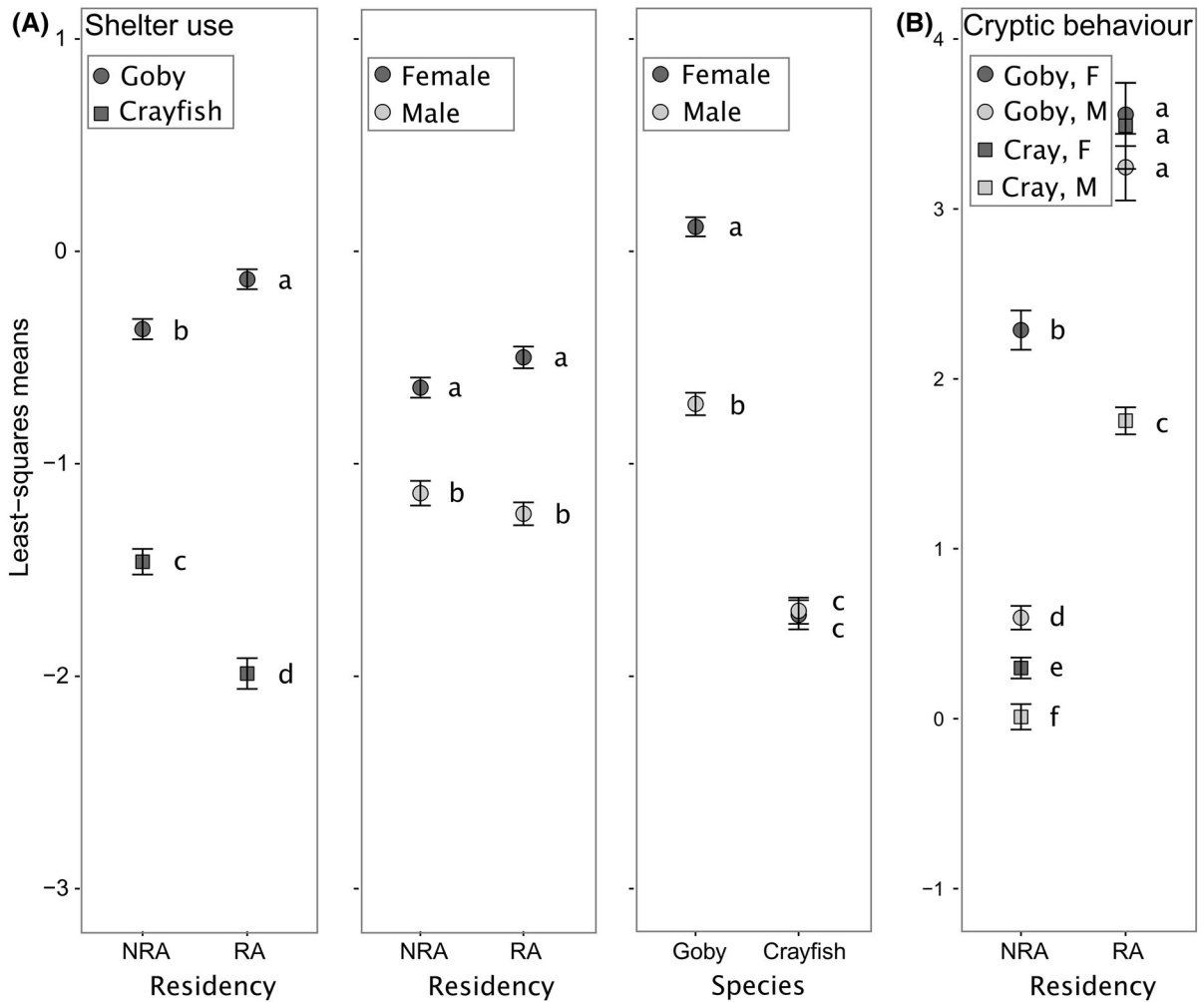


Fig. 4 Solitary trials of male (light grey) and female (dark grey) round gobies (circle) and spinycheek crayfish (square) showing post hoc estimations of least squares means for A) shelter use, for interactions between species and residency, gender and residency, and species and gender (from left to

right), and B) cryptic behaviour, for an interaction between species, residency, and gender. Axis labels are as follows: NRA no prior residency and alone, RA prior residency and alone. Different letters represent significant differences across all trials within each panel. Error bars are ±1 SE

the animals differently depending on their individual life histories.

Round goby stomach content analysis shows that small crayfish may be vulnerable to predation when they are “soft-shelled” immediately following a molt (Ray and Corkum 1997). Although no crayfish suffered injuries or mortalities during our behavioural trials, none of the crayfish used had recently molted and were thus not vulnerable. The increased aggression observed in trials with larger size differentials may have reflected predatory, rather than competitive behaviour. Conversely, round goby aggression toward

spinycheek crayfish may have been atypical simply because crayfish are morphologically and behaviourally dissimilar.

Crayfish engage in substantial thigmotactic navigation, particularly in novel environments (McMahon et al. 2005; Patullo and Macmillan 2006). The reduced shelter use and cryptic movement of spinycheek crayfish in our experiments could reflect the need for crayfish to gather information about their environment, and it may be these behavioural differences, rather than direct competition with the round goby, that lead to greater predator exposure for crayfish.

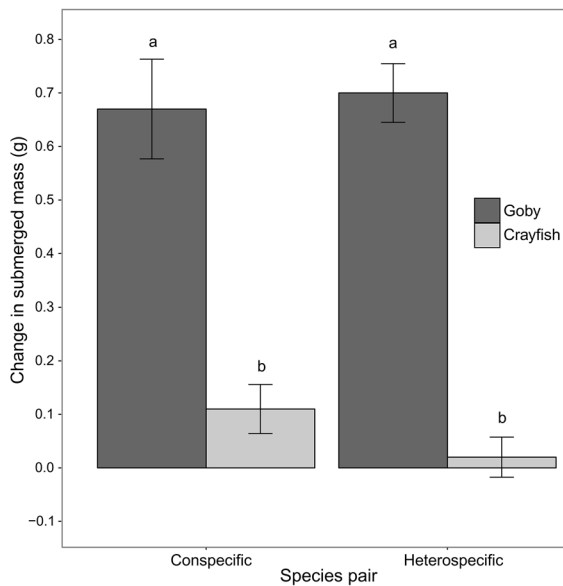


Fig. 5 Growth of round gobies (*dark gray*) and spinycheek crayfish (*light gray*) in conspecific and heterospecific pairs. Different letters represent significant differences ($p < 0.05$), and error bars are ± 1 SE

Shelter as a limiting resource

Shelter availability has been described as the principal limiting resource in crayfish populations (Gherardi and Daniels 2004). Although rocky littoral areas along the shoreline of the St. Lawrence River offer an abundance of interstitial habitat, round goby territoriality has the potential to negatively impact spinycheek crayfish populations by making them more vulnerable to predation and reducing their ability to obtain food resources. Round gobies have been found to be significantly more aggressive in rocky habitats than in vegetated or open habitat, perhaps owing to the higher perceived value of the former (Savino et al. 2007). Such aggressive behaviour did not preclude round gobies from experimental shelter use, suggesting that they are not likely to increase their predation risk in the presence of spinycheek crayfish. Although spinycheek crayfish in our experimental system were more exposed than in natural habitats, we did not test their behaviour in the presence of an actual predator, which may have resulted in significant behaviour changes, such as increasing shelter use and reducing conspicuous behaviours, like walking and climbing (Stein and Magnuson 1976).

Recognizing that shelter size may affect the perceived value of the habitat resource, we used the same shelter size throughout the trials instead of scaling to body size. A previous study found that round goby shelter selection does not vary with body size and that non-reproductive males displayed no preference whatsoever (Stammler and Corkum 2005). Conversely, crayfish may display a preference for smaller shelters relative to body size, to more effectively block intrusion by a predator or competitor (Steele et al. 1999). Our experimental shelters were small enough that the vast majority of crayfish were able to brace themselves against its walls when confronted by a conspecific intruder. Smaller shelters may cause overestimation of self-assessed resource holding potential in crayfish, and thus lead to longer fights at higher intensities (Percival and Moore 2010). However, in our study, heavier crayfish and gobies of greater body length were more aggressive overall, which may reflect a general tendency amongst larger individuals, rather than enhanced self-assessments of fighting ability owing to relative shelter size.

We found that solitary spinycheek crayfish reduced their use of shelter over time (residents vs. non-residents), whereas the converse was true for round gobies. Overall, round gobies had a higher affinity for the shelters; similarly, in the growth experiments, juvenile round gobies were often found using the shelters, whereas spinycheek crayfish—particularly those paired with round gobies or with a dominant crayfish—were observed to hide at the tank edges underneath gravel. We did not find the resource value of shelters to be strongly size-dependent for spinycheek crayfish; larger crayfish did not use the shelters more than small crayfish when paired with round gobies.

Crayfish may become more aggressive in defense of shelters they already occupy (Tricarico and Gherardi 2010), though we only found this to be the case when they were of medium size; in any case, their aggressive behaviour remained much lower than the round goby. Prior residency conferred the greatest advantage to round gobies in aggressive interactions, whereas spinycheek crayfish engaged in more risky and energetically costly flee behaviour when gobies were prior residents. Balshine et al. (2005) found that although round gobies were more aggressive than native logperch (*Percina caprodes*), residency had no effect on the amount of aggression displayed, which

perhaps contributed to the observed dramatic increase of the round goby population in Hamilton Harbour. Our results confirm that the round goby is highly aggressive to heterospecific competitors, and suggest that they become an even greater opponent once they have established residency.

Species differences in growth rate

Round gobies grew more than spinycheek crayfish and were unaffected by species pairing, whereas spinycheek crayfish growth was diminished in the presence of round gobies. The experimental density we used (4.4 individuals m^{-2}) is within the range of densities found in the field (e.g. 0.1–6.4 m^{-2} at invaded sites in the St. Lawrence River; Kipp et al. 2012). Round goby populations can reach enormous levels, owing to early maturity, high fecundities (Corkum et al. 1998), and multiple spawning events over a prolonged reproductive season (MacInnis and Corkum 2000). For example, in western Lake Erie, the round goby population comprises nearly 10 billion individuals (Savino et al. 2007). To our knowledge, spinycheek crayfish population densities have not been measured systematically in the St. Lawrence River, although in some local areas near the Island of Montreal and at downstream sites they exceed 5 m^{-2} (A. Ricciardi, pers. obs.), which is within the range of densities of *Orconectes* spp. populations recorded elsewhere (0.04–33 m^{-2} ; Momot et al. 1978; Haertel-Borer et al. 2005). We suspect that spinycheek crayfish experienced some level of stress during the experiments, as none molted; in past laboratory holding situations, when spinycheek crayfish were held individually in tanks and fed the same diet they have always been observed to molt.

Ecological implications

Despite being outcompeted by round gobies in our study, invasive crayfish have been found to negatively impact the populations of benthic fishes through aggressive behaviour and shelter competition. Signal crayfish (*Pacifastacus leniusculus*) can displace native Atlantic salmon (*Salmo salar*), Paiute sculpin (*Cottus beldingi*), and bullheads (*Cottus gobio*) from their shelters, thereby increasing the risk of predation and energetic costs (Griffiths et al. 2004; Light 2005; Bubb et al. 2009). However, signal crayfish are more aggressive and better shelter competitors than

spinycheek crayfish when paired in laboratory trials (Hudina et al. 2011). Spinycheek crayfish are highly invasive in Europe, where they have been shown to evict juvenile burbot (*Lota lota*) from the latter's preferred shelters; round gobies were also found to be superior habitat competitors in comparison to these smaller benthic fish, especially during daylight hours when both species seek refuge from visual predators (Hirsch and Fischer 2008).

Aggressive behaviour in established populations may limit the establishment or spread of introduced species. For example, the expansion of the invasive Argentinean ant (*Linepithema humile*) in Corsica is believed to be limited by a species of native ant (*Tapinoma nigerrimum*) that exhibited superior competitive ability and heightened interspecific aggression in laboratory assays (Blight et al. 2010). Similarly, eastern mosquitofish (*Gambusia holbrooki*) native to Florida, readily attacks and kills introduced poeciliid fishes and drives them from their cover in mesocosm experiments, possibly reflecting a form of biotic resistance that explains why few small-bodied fishes are among the over 30 invasive species established in Florida's inland waters (Thompson et al. 2012). To our knowledge, our study is the first to examine aggressive interactions between two unrelated invasive species that occupy similar niches.

It is plausible that the presence of dense spinycheek crayfish populations in the upper St. Lawrence River may have slowed round goby colonization, owing to their prior residency, initially larger population density, and perhaps a larger body size relative to the smaller round gobies that tend to disperse into new territory (Ray and Corkum 2001; Brownscombe and Fox 2012). Over time, the age and size structure of round goby populations increased in the river (Kipp and Ricciardi 2012), eroding any size and residency advantage of spinycheek crayfish populations. More detailed explorations of the trade-offs between intra- and interspecific aggression and foraging style may determine the extent to which the aggressive behaviour of an established species is advantageous in limiting the invasion success and impact of an invader.

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Appendix: Summary results of size comparisons between genders of round gobies and spinycheek crayfish used in behavioural experiments

See Tables 4 and 5.

Table 4 Summary of Welch two-sample *t* tests comparing size measurements of male and female round gobies used in pairwise ($n = 30$) and alone experimental treatments ($n = 20$)

No significant differences in size were found between round goby genders within treatments ($p > 0.05$)

Experimental treatment size category	Measurement	<i>t</i> value	<i>df</i>	<i>p</i> value
Small crayfish	Total length	0.776	19.700	0.447
	Fork length	-0.079	17.762	0.938
	Weight	0.855	24.780	0.401
Medium crayfish	Total length	0.772	27.360	0.447
	Fork length	0.817	27.030	0.421
	Weight	1.057	27.921	0.299
Equal crayfish	Total length	-0.301	27.180	0.766
	Fork length	0.168	26.516	0.868
	Weight	0.229	27.958	0.821
Solitary	Total length	-0.637	15.472	0.534
	Fork length	1.805	16.694	0.089
	Weight	1.193	13.828	0.253

Table 5 Summary of Welch two-sample *t* tests comparing size measurements of male and female spinycheek crayfish used in pairwise ($n = 30$) and alone experimental treatments ($n = 20$)

No significant differences in size were found between spinycheek crayfish genders within treatments ($p > 0.05$)

Experimental treatment size category	Measurement	<i>t</i> value	<i>df</i>	<i>p</i> value
Small crayfish	Total length	0.698	25.325	0.491
	Fork length	0.490	27.429	0.628
	Weight	0.526	25.075	0.604
Medium crayfish	Total length	-0.572	27.772	0.572
	Fork length	-1.319	26.087	0.199
	Weight	1.408	26.773	0.171
Equal crayfish	Measurement	0.579	27.963	0.568
	Total length	0.082	27.977	0.935
	Fork length	0.590	23.814	0.561
Solitary	Measurement	-1.539	8.543	0.160
	Total length	-1.415	8.488	0.193
	Fork length	-1.521	8.118	0.166

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