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Size-dependent impacts of the endangered white-clawed crayfish (*Austropotamobius pallipes*) (Lereboullet) on the littoral community

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ABSTRACT

Key-words: *crayfish, mesocosm, ontogenic diet-shift,* Austropotamobius pallipes*, conservation*

The demise of Britain's only native crayfish (*Austropotamobius pallipes* (Lereboullet)) has prompted conservation-led translocations to safe isolated stillwaters (Ark sites). Many translocations represent introductions rather than re-stocking; hence it is important to ensure that there will not be a detrimental impact on communities already present. Current knowledge is insufficient to predict likely effects, although gut contents analyses suggest that *A. pallipes* is omnivorous and exhibits ontogenic diet shifts. A mesocosm study was conducted with the aim to first, determine community impacts of introducing *A. pallipes* on the benthic invertebrate community, and second investigate if impacts vary with crayfish life-stage. All crayfish life-stages strongly reduced shredder and grazer abundance, particularly thin-shelled *Lymnaea* snails. The small snail *Physa fontinalis* was preferentially consumed by juveniles, perhaps reflecting different prey-handling ability. Adults showed greater reliance on terrestrially derived detritus compared to juveniles. There were limited effects on other trophic levels, although by reducing shredders that process basal resources, crayfish impacts may be felt through the community in the long-term.

RÉSUMÉ

Impacts dépendant de la taille de l'écrevisse à pattes blanches (*Austropotamobius pallipes*) (Lereboullet) sur la communauté littorale

Mots-clés : *écrevisse, mésocosmes, changement ontogénique de régime,* Austropotamobius pallipes*, conservation*

L'effondrement en Grande-Bretagne de la seule espèce indigène d'écrevisse *Austropotamobius pallipes* (Lereboullet) a incité les transferts à but de conservation dans des milieux aquatiques isolés et sûrs (sites Ark). De nombreuses translocations représentent des introductions plutôt que la reconstitution de stocks, et il est important de s'assurer qu'il n'y aura pas un impact négatif sur les communautés déjà présentes. Les connaissances actuelles sont insuffisantes pour prévoir les effets probables, bien que les analyses des contenus stomacaux suggèrent que *A. pallipes* est omnivore et présente des changements ontogéniques de régime. Une étude en mésocosmes a été menée dans le but d'abord, de déterminer les impacts de l'introduction d'*A. pallipes* sur la communauté d'invertébrés benthiques, puis d'étudier si les effets varient en fonction du stade de vie des écrevisses. Tous les stades de vie de l'écrevisse ont fortement réduit l'abondance des déchiqueteurs et des brouteurs, en particulier les escargots *Lymnaea* à coquilles minces. Le petit escargot *Physa fontinalis* a été préférentiellement consommé par les jeunes,

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reflétant peut-être une capacité de capture de proie différente. Les adultes ont montré une plus grande dépendance à l'égard des détritus d'origine terrestre par rapport aux juvéniles. Il y avait des effets limités sur les autres niveaux trophiques, mais en réduisant les broyeurs qui consomment des ressources de base, les impacts de l'écrevisse peuvent être ressentis par la communauté dans le long terme.

INTRODUCTION

Translocation of animals, whether it be movement of imminently threatened populations or reintroduction to restored habitats, is a widely used tool for the conservation of both terrestrial and aquatic species (Seddon *et al.*, 2007; Armstrong and Seddon, 2008). The endangered white-clawed crayfish (*Austropotamobius pallipes* (Lereboullet)) has declined across its range since the introduction of the invasive signal crayfish (*Pacifasticus leniusculus*) to Europe in the 1960s (Lewis and Holdich, 2002). *Pacifastacus leniusculus* outcompetes *A. pallipes* and is a vector of *Aphanomyces astaci*, the cause of 'crayfish plague', which is fatal to *A. pallipes* (Alderman *et al.*, 1990; Peay and Rogers, 1998). In the absence of effective means to control the spread of invasive crayfish or plague, translocation of imminently threatened populations of *A. pallipes* to isolated locations (Ark sites) has become a key part of current conservation strategy for the species (Kozák *et al.*, 2011).

Two of the five most important criteria for the selection of recipient Ark sites are absence of non-native crayfish and low risk of future invasion (Peay, 2009). Isolated waterbodies, such as natural lakes and restored quarries or gravel pits, represent the most biosecure sites available and the majority do not hold existing crayfish populations (Kindemba *et al.,* 2009). Translocations to Ark sites therefore commonly represent introductions, i.e. attempts to establish a species outside its recorded distribution. Recommendations from the International Union for Conservation of Nature (IUCN) state that such introductions are a feasible conservation tool, though assessment of likely impacts on the existing ecosystem is necessary to avoid unforeseen ecological consequences (IUCN, 2012).

Introduced species have potential to impact the existing ecology, for example through predation, habitat modification or release of pathogens (Conant, 1988; Hodder and Bullock, 1997), and the need to exercise caution during translocations is frequently voiced (*e.g.* Hodder and Bullock, 1997; Carter and Newbery, 2004). Crayfish are opportunistic omnivores, yet selective consumers; hence community impacts are predominantly mediated through dietary choices, causing direct and indirect effects at a range of trophic levels (Nyström *et al.*, 1999; Usio and Townsend, 2002; Dorn and Wojdak, 2004). Presence of crayfish of *Astacus* sp. has been associated with reduction in submerged macrophytes (Nyström and Strand, 1996; Nyström *et al.*, 1999), reduced biomass of grazers, particularly gastropods, and shifts in community composition towards predatory invertebrates (Nyström *et al.*, 1999). Some crayfish species are also significant bioturbators, modifying sediment transport and increasing turbidity (Harvey *et al.*, 2011; Johnson *et al.*, 2011), with indirect effects on algae and macrophyte cover (Dorn and Wojdak, 2004; Usio *et al.*, 2009). Palatability and preference tests suggest dietary choices of crayfish are dependent on nutritional content (Adams *et al.*, 2005), past experience (Gherardi and Barbaresi, 2007), and ease of capture (Brown, 1998); while field-based foraging patterns reflect a complex balance between food preference and competition (Gherardi *et al.*, 2001).

The diet of *A. pallipes*, examined indirectly through gut content analyses of field-caught specimens or through laboratory preference and predation tests, indicates generalist omnivory with a wide range of food types including terrestrially derived detritus, algae, molluscs, isopods, fish and fish eggs, amphipods and insect larvae (Gherardi *et al.*, 2001; Reynolds and O'Keeffe, 2005; Scalici and Gibertini, 2007). Gut analysis also provides evidence of an ontogenic diet shift in *A. pallipes*, as evidenced for other crayfish species e.g. *P. leniusculus* (Guan and Wiles, 1998) and *Procambarus clarkii* (Correia, 2003), with juvenile diet comprising a greater proportion of micro-crustaceans, whereas adults consume more vegetal items such as macrophytes, woody fragments and aufwuchs (Reynolds and O'Keeffe, 2005). In view of this, it may be predicted that crayfish impacts on existing communities will vary with population structure. The influence of *A. pallipes* on the littoral community has been previously investigated by Matthews *et al.* (1993) who found a reduction in *Chara*, Chironomidae, *Gammarus* and Hemiptera biomass when *A. pallipes* were reintroduced to enclosures in a mesotrophic marl lake system; though the size range of crayfish studied was not indicated. We used a field-based mesocosm experiment to assess the short-term impacts of *A. pallipes* introduction on the benthic invertebrate community, and to test the hypothesis that impacts differ between juvenile and adult life-stages of crayfish.

MATERIALS AND METHODS

The experiment was conducted August–September 2010 using outdoor mesocosm pools (n = 12) to mimic lentic Ark sites. Mesocosms overcome some of the limitations of gut contents analyses such as providing only a snapshot of diet at the moment of capture, and bias due to over representation of less digestible diet items (Correia, 2003). Pools were seeded with identical communities of plants, detritus and invertebrates to reflect flora and fauna which are widespread in the UK. Individuals of *A. pallipes* were introduced to the pools at the start of the experiment within four treatments: juvenile crayfish, adult crayfish, mixed juvenile and adult crayfish, and a no crayfish control, using a randomised-block design with 3 replicates in each. The experiment lasted 5 weeks after which we recovered and counted all the remaining invertebrates in each pool, and weighed the macrophytes and detritus.

> *MESOCOSM SETUP*

Plastic pools (0.78 m^2, 1 m diameter, 0.65 m depth) were sunk into a meadow at the University of Leeds Field Research Unit, UK. The rim of each pool was positioned 15 cm above ground level to prevent accidental drowning by insects and small mammals. Pools were filled to 35 cm depth with groundwater and seeded with additional lake water (3 L) to facilitate the development of phytoplankton and zooplankton communities. Lids were placed over the pools, each with a central circular opening (50% area) to enable light penetration yet limit extreme temperature fluctuations. Netting (20 mm mesh) was secured over the opening to prevent both crayfish escaping and predation by birds, and to reduce leaf litter inputs.

Macrophytes, *Ceratophyllum demersum* (65 g wet mass), *Elodea nuttallii* (65 g) and *Potamogeton natans* (25 g) were added to the pools on 5th August. Stems were secured within 12 shallow circular trays (300mm diameter, 40mm depth) filled with 60:40 mix of pure sand and dried loam soil. These were placed in the centre of each pool and covered with a layer of gravel. A slope of gravel extended approximately 10 cm beyond the margin of the tray to the floor of the pool, thereby enabling crayfish access to the plants. Allochthonous detritus (100 g wet mass), as leaves of beech (~80%) and alder (~20%) soaked for over 2 months, was also added to each pool.

Pools were left to stabilise for 3 weeks before stocking the invertebrates and crayfish. The following macro-invertebrates were added to each pool: 6 *Lymnaea stagnalis* (20–30 mm, total length (TL)), 10 *Planorbarius corneus* (15–22 mm, TL), 60 *Physa fontinalis* (6–9 mm, TL), 8 *Bithynia tentaculata* (9–14 mm, TL); 57 *Gammarus pulex* (9–16 mm, TL), 52 *Asellus aquaticus* (10–14 mm, TL) and 80 chironomid larvae. All were collected from still or slow-flowing waters nearby, except the chironomid larvae which were purchased live from a local pet retailer, and densities within the pools approximately reflected those found in the source sites.

Crayfish were collected from the Aire catchment, Yorkshire, held within the laboratory for at least one week under 16:8 light/dark regime at 16 °C and fed crab pellets (Hinari) *ad libitum*, before being placed in the pools. All crayfish were numbered on the cephalothorax using non-toxic correction fluid to enable recognition of individuals, then weighed (wet weight) and measured (carapace length, CL). Eight sections of PVC pipe (2 × 50 mm dia meter, 120 mm length; 6 × 25 mm dia meter, 80 mm length) were also added to serve as refugia, with a view to reducing aggressive interactions and post-moult cannibalism.

> *EXPERIMENTAL DESIGN*

Crayfish were assigned to the three treatments based primarily on mass, with the aim to reduce variation in total mass between treatments. Juvenile treatment comprised 6 juveniles (2.1–5.5 g, 16.1–24.2 mm CL), adult treatment comprised 2 adults (12–22.7 g, 31.6−38.9 mm CL), and mixed treatment comprised 1 adult (12.1–16.1 g, 33.2– 36.1 mm CL) and 4 juveniles (1.87–2.78 g, 17.5–20.4 mm CL). Crayfish densities in the pools ranged from 2.56 to 9 individuals m^{-2}. Mean total mass of crayfish did not vary significantly between pools within the same treatment (23.4 ± 3.8 g S.D., $F = 2.8$, $p = 0.09$ (juveniles); 33.7 ± 3.5 g S.D., $F = 0.223$, $p = 0.81$ (adults); 21.8 ± 1.9 g S.D., $F = 2.24$, $p = 0.98$ (mixed), ANOVA). The limited availability of study animals meant sex ratios could not be fully balanced between treatments. While there is some evidence for sex-dependent feeding patterns for crayfish in the wild (Gherardi *et al.*, 2004), most studies report no dietary differences due to sex (*e.g.* Renai and Gherardi, 2004; Reynolds and O'Keeffe, 2005; Stenroth *et al.*, 2008).

Pools were checked weekly for crayfish mortalities and evidence of moult. In the event of mortality, crayfish were replaced with equivalent sized individuals. In the event of ecdysis, moults were removed and identification numbers repainted on post-moult individuals once the carapace had hardened. Water temperature and dissolved oxygen were measured in each pool at weekly intervals during mid-afternoon and sub-surface water samples were also collected at the end of the experiment for subsequent laboratory analyses of nitrate, phosphate, ammonium, calcium, potassium, magnesium and sulphate.

Pools were emptied at the end of the experiment. Macrophytes were removed, blotted dry and reweighed, and all water and sediment were passed through a net of mesh 1 mm to recover remaining invertebrates and detritus. Invertebrates and detrital fragments were separated from the gravel by hand sorting and then identified to species and counted. Detrital fragments exceeding approximately 4 mm diameter were collected and weighed.

> *STATISTICAL ANALYSIS*

We tested for a treatment effect on the overall change in crayfish mass, and for a difference in percentage mass change between juveniles and adults using an independent samples median test. Treatment effects on the remaining biomass of macrophytes and absolute abundances of macro-invertebrate taxa were tested using one way ANOVA with treatment as a factor. All data were tested for normality using Shapiro-Wilk test and were log 10 + 1 transformed where necessary. Levene's test was used to determine compliance with the assumption of homogeneity of variance between groups. Tukey's HSD post-hoc test was use to identify differences between groups if there was a significant overall treatment effect. The Shannon diversity (H) and evenness (E_H) indices were calculated for the macro-invertebrate communities present in the pools after 5 weeks and compared across treatments using Kruskal-Wallis independent samples test with 0.05 significance level. All analyses were performed using PASW Statistics 18 (IBM).

RESULTS

> *WATER CHEMISTRY*

Water temperature in the pools varied from 14 to 17 °C over the study period and there was no significant temperature difference between treatments ($F_{3,56} = 0.48$, $p = 0.70$). Dissolved oxygen saturation ranged from 89 to 116% at the weekly checks, and did not differ significantly between treatments ($F_{3,56} = 0.11$, $p = 0.96$). Treatments did not differ for any other water chemistry parameters measured.

Table I

One way ANOVA and Tukey's HSD post-hoc test comparing the biomass of macrophytes and abundances of invertebrate taxa remaining in pools after 5 weeks under 3 crayfish treatments (juveniles only (J); Adults only (A); and mix of juveniles and adults (M), and control (C) with no crayfish.

	Treatment		J vs. A	J vs. M	A vs. M	J vs. C	M vs. C	A vs. C
	$F_{3,8}$	p	p	p	p	p	p	p
Macrophyte biomass								
Potamogeton natans	2.23	0.16	–	–	–	–	–	–
Ceratophyllum demersum	1.52	0.28	–	–	–	–	–	–
Elodea nutallii	3.87	0.06	–	–	–	–	–	–
Detrital leaves	10.78	<**0.01**	0.30	0.09	0.80	0.14	<**0.01**	<**0.01**
Grazers								
Bithynia tentaculata	2.149	0.17	–	–	–	–	–	–
Physa fontinalis	20.03	<**0.01**	<**0.05**	0.74	<**0.01**	<**0.01**	<**0.01**	0.50
Planorbarius corneus	17.37	<**0.01**	0.11	0.59	0.58	<**0.05**	<**0.01**	<**0.01**
Lymnaea sp.	11.62	<**0.01**	0.78	0.89	0.40	<**0.01**	<**0.05**	<**0.01**
Shredders								
Gammarus pulex	4.22	<**0.05**	0.97	0.79	0.95	0.16	<**0.05**	0.09
Asellus aquaticus	32.24	<**0.01**	0.96	0.98	0.99	<**0.01**	<**0.01**	<**0.01**
Filterers/collectors								
Chironomid larvae	10.18	<**0.01**	0.99	0.72	0.55	<**0.05**	<**0.01**	<**0.05**

> *CRAYFISH*

Two juvenile crayfish were found dead on day 28 of the experiment, both in small treatment pools, and one was partially consumed. Both were removed and replaced with crayfish of similar mass. Four individuals, all juveniles, successfully moulted during the 35 day study period. Change in total crayfish biomass was highly variable between pools within the same treatment. Mean total mass increase per pool was 5.51 ± 7.8 g (20.4%), 1.21 ± 1.3 g (5.8%) and 2.34 ± 1.5 g (7.3%) for the juvenile, mixed and adult treatments respectively, with no treatment effect ($T_2 = 4.56$, $p = 0.10$, Independent samples median test); however juvenile crayfish experienced a significantly higher percentage change in mass compared to adults, irrespective of treatment ($T_1 = 7.26$, $p < 0.05$, Independent samples median test).

> *MACROPHYTES AND MACRO-INVERTEBRATES*

There was no treatment effect on the biomass of the 3 macrophyte species, however the mass of detrital leaves was significantly reduced relative to control in both treatments where adults were present (mean overall reduction of 70 and 74% in adult and mixed treatments, respectively), though not when only juveniles were present (mean 63% reduction) ($F_{3,8} = 10.78$, $p < 0.01$) (Table I). Detrital leaves in the control treatment were reduced on average by 53% (Figure 1).

With the exception of the gastropod *B. tentaculata,* there was a treatment effect on the abundances of all benthic invertebrates at the end of the 35 day period (Table I). Of the grazers, abundance of the small gastropod *P. fontinalis* was significantly lower in the juvenile and mixed treatments, relative to the adult treatment ($p < 0.05$ and $p < 0.01$, respectively), but there was no difference in abundance between adult treatment and control ($p = 0.50$) (Table I) (Figure 2). Mean abundance of *B. tentaculata* increased in all treatments by an average of 40%; these were all comprised of juveniles. For the other gastropod species (*P. corneus* and *Lymnaea* sp.) there was no difference in remaining abundances between the different crayfish treatments (Table I).

The shredder *Asellus aquaticus* was significantly reduced in all treatments relative to control ($F_{3,8} = 32.24$, $p < 0.01$), whereas *Gammarus pulex* was only reduced in the mixed treatment relative to control ($F_{3,8} = 4.2$, $p < 0.05$) (Figure 2). There was no difference in shredder abundances between crayfish treatments (Table I). The abundance of *Chironomid* larvae was

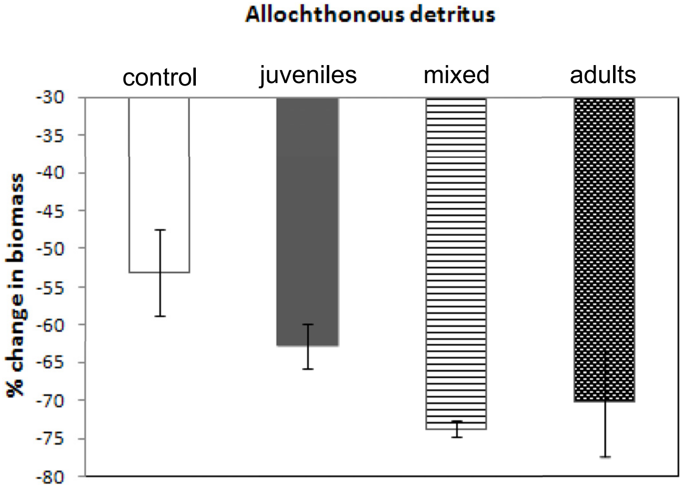

Figure 1
Percentage change (±S.D.) in biomass of allochthonous detritus over 5 weeks in mesocosms under 3 crayfish treatments: juveniles; mixed (juveniles and adults), and adults only, and with no crayfish (control).

significantly reduced in all crayfish treatments relative to the control ($F_{3,8} = 10.18$, $p < 0.01$), with no differences between crayfish treatments (Table I, Figure 2).

Several other species colonised the pools during the experiment including *Callicorixa praeusta* and damselfly larvae (*Coenagrion* sp.); however they occurred only at low abundances with generally less than 4 individuals per pool.

The Shannon diversity index in each pool ranged from 0.87 to 1.44, and did not vary between treatments ($H_{3,12} = 7.78$, $p = 0.05$). Shannon evenness ranged from 0.24 to 0.49, and again did not vary between treatments ($H_{3,12} = 6.08$, $p = 0.11$).

DISCUSSION

Presence of the crayfish *A. pallipes* had a strong influence on the abundances of benthic invertebrates and on the biomass of detritus in the littoral community over the short-term. However, their presence did not have an influence on the macrophytes. Ontogenic differences were apparent in a species shift among grazers.

The 3 macrophyte species present within the pools did not appear to be important food items for either adults or juveniles of *A. pallipes*, although terrestrially derived detritus was reduced in the presence of adult crayfish. Both *G. pulex* and *A. aquaticus* function as shredders processing these basal resources within freshwater systems; *A. aquaticus* was significantly reduced in all crayfish treatments, and *G. pulex* in the mixed treatment, which infers that reduction in detrital leaves was predominantly due to direct consumption from crayfish. Previous results of gut content analysis similarly infer greater consumption of detritus among adults (Reynolds and O'Keeffe, 2005) which may be explained by lower energy demands for growth within the adult life-stage compared to juveniles (Whitledge and Rabeni, 1997); indeed, our juvenile crayfish showed a three fold higher increase in mass than adults during the experiment. However, adults have been shown to adopt a more protein rich diet comprising a greater proportion of macroinvertebrates during times of high energy demand (*e.g.* breeding) (Stenroth *et al.*, 2008).

In a study of *P. leniusculus*, Nyström *et al.* (1996) concluded that the activity level of a prey type is the most important determinant on their consumption by crayfish, with a shift towards a community dominated by sediment dwelling taxa in the presence of crayfish. In accord with this, *A. aquaticus* was more reduced than *G. pulex* in all treatments, which likely reflects the ease of capturing this slow moving isopod (Nyström *et al.*, 1996); and also, since there

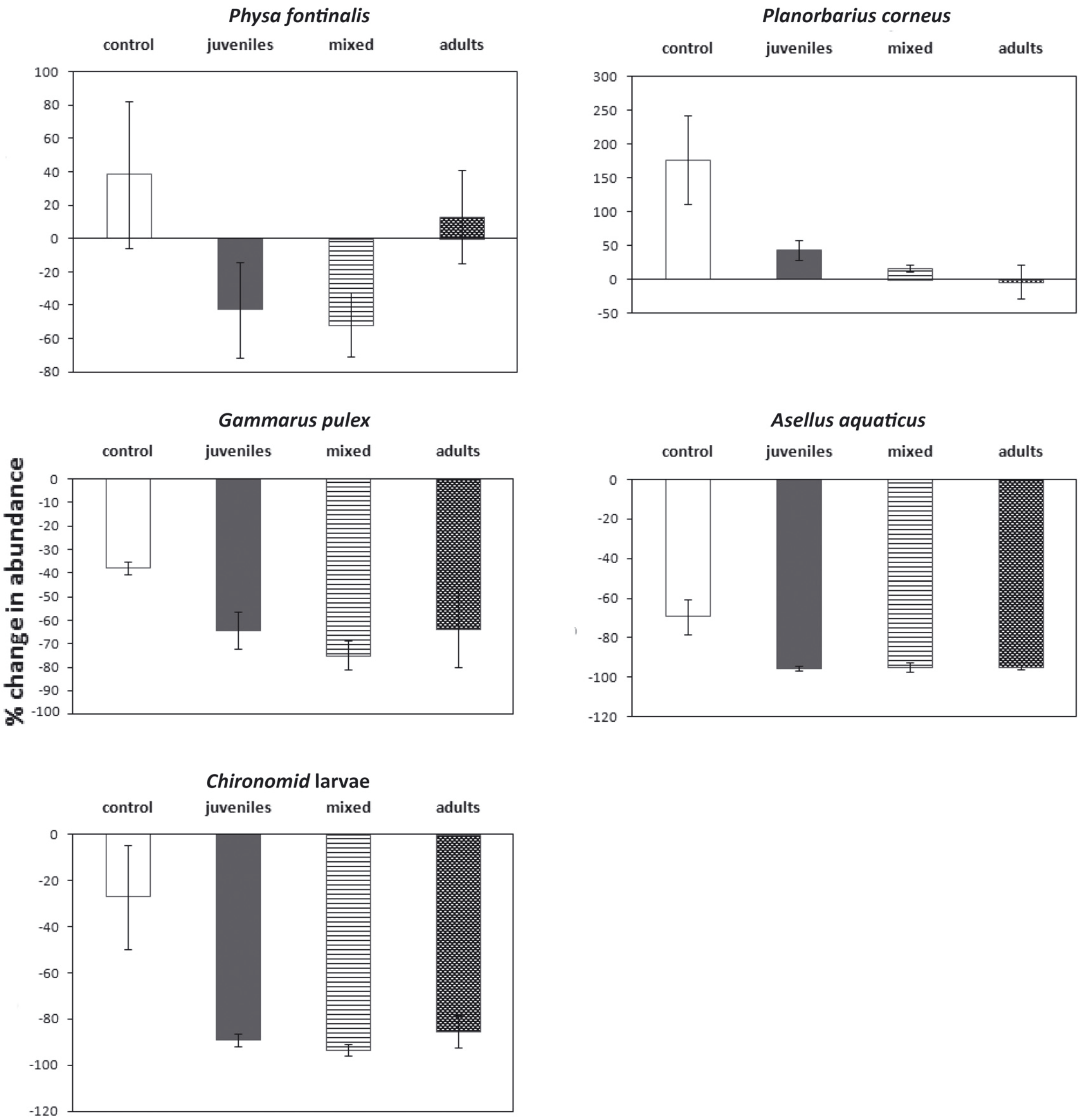

Figure 2

Percentage change (±S.D.) in abundance of grazers (gastropods Physa fontinalis and Planorbarius corneus), shredders (Asellus aquaticus and Gammarus pulex) and filterers (Chironomid larvae) over 5 weeks in mesocosms under 3 crayfish treatments: juveniles; mixed (juveniles and adults), and adults only, and with no crayfish (control).

was a decrease in the controls, perhaps predation by other invertebrates such as *G. pulex* (Macneil *et al.*, 1997). The reduction of *G. pulex* in the control pools, though to a lesser degree than *A. aquaticus*, may reflect post-moult cannibalism (Dick, 1995), or reduced survival due to unfavourable conditions (*e.g.* food or shelter). The high predation level of sediment-dwelling *Chironomid* larvae in the crayfish treatments (81 to 87%) is likely to be higher than in natural environments due to the relatively shallow depth of sediment in the pools, and therefore less opportunity to escape predation.

As slow moving species, snails are highly vulnerable to crayfish predation (Lodge *et al.*, 1994; Nyström *et al.*, 1996). This was apparent in the current study, with the exception of *B. tentaculata* which increased in abundance, presumably as a consequence of reproduction by adults, or perhaps hatching of eggs present on plants at the start of the experiment. It is suggested that the presence of the operculum and thicker shell of this species makes it less preferable to crayfish compared to the thinner-shelled species such as *Lymnaea* spp. (Brown, 1998; Nyström *et al.*, 1999). Predation upon *P. fontinalis* was dependent upon crayfish size, with greater consumption among juveniles. One possible explanation for this may be the differential ability of adults and juveniles to handle these small snails. Reynolds and O' Keeffe (2005) supposed that the size of *A. pallipes* is inversely related to motility of its prey, yet the current study suggests that physical size of the prey is also important. This finding highlights that once crayfish are introduced to an Ark site, the influence on specific species such as the shift towards predation resistant gastropods, is likely to change as the crayfish population structure changes from that dominated by the adult donor stock (Souty-Grosset and Reynolds, 2009), to greater representation by the smallest size classes.

Over the 5 week period of study, we observed a large reduction in the abundance of shredders. Although it is acknowledged that the use of mesocosms may lead to overestimation of predation rates due to more homogenous habitat than in the wild (Nilsson *et al.*, 2008), the changes observed, even if at lower magnitude, are likely to have longer term cascading effects on the community. The predatory impact on shredders may lead to a change in the processing of basal resources, with implications for nutrient cycling and therefore availability to primary producers (Vanni, 2002). However, the current study also highlighted the role of crayfish, particularly adults, in processing basal resources, which may compensate for the loss of shredders in this regard; although a reduction in smaller shredders will likely have knock on effects on other higher order predators that compete with crayfish, for example, fish.

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