

The effect of manual removal on movement distances in populations
of signal crayfish (*Pacifastacus leniusculus*).

TOM P. MOORHOUSE*

tom.moorhouse@zoo.ox.ac.uk

*Wildlife Conservation Research Unit, Department of Zoology,
University of Oxford, The Recanati-Kaplan Centre,
Tubney House, Abingdon Road
Tubney, Abingdon OX13 5QL, UK*

DAVID W. MACDONALD

*Wildlife Conservation Research Unit, Department of Zoology,
University of Oxford, The Recanati-Kaplan Centre,
Tubney House, Abingdon Road
Tubney, Abingdon OX13 5QL, UK*

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*Corresponding author

SUMMARY

1. Crayfish are amongst the most frequently introduced non-native aquatic organisms, with well-documented negative effects on a large number of freshwater taxa. Many crayfish-control strategies make use of manual removal by trapping, a method known preferentially to remove the largest individuals, leaving the juvenile population almost entirely untrapped.
2. Removal by trapping may be used in an attempt to delay colonisation of new stretches by invasive crayfish. It is, however, unclear what effects trapping may have on movement distances of crayfish in wild populations. We examine the impacts of removal by trapping on the movements of American signal crayfish in two UK rivers.
3. We studied four 100m stretches of two rivers, the Evenlode and Thame, comprising two removal and two non-removal stretches. Each river supported both treatments. Half of the crayfish captured from the removal sections were removed and humanely destroyed by freezing, and half were marked with their trap location and released there. All crayfish captured from the non-removal sections were marked and returned at the point of capture.
4. Mean movement distances were smaller in the removal stretches than the non-removal stretches, both within capture sessions (10.8 m and 16.0m, respectively) and between sessions (14.5 m and 24.6 m, respectively), suggesting that removal trapping resulted in the remaining crayfish making smaller movements. Crayfish with larger carapace lengths under both treatments made substantially larger movements than those with smaller carapace lengths, both within capture sessions (range 7.6 - 19.6 m) and between range capture sessions (range 8.9 - 32.6 m).
5. The results of this study are consistent with expectations if removal by trapping lowered population densities, which we speculate may have affected movement distances directly, or indirectly through increasing the availability of food and shelter.
6. This study suggests that trapping at the margins of a population may be sufficient to delay colonisation of new stretches by: 1) maintaining low densities and therefore reducing movements, and 2) preferentially reducing the population of large individuals, which make the largest movements. However it remains unlikely that any trapping programme can entirely prevent emigration/dispersal, and therefore colonisation, by signal crayfish.

Introduction

The introduction and spread of non-native species has become of major global ecological and conservation concern (Simberloff, 2005). Crayfish are amongst the most frequently introduced non-native aquatic organisms, and invasive crayfish have great potential to disrupt the freshwater ecosystems into which they are translocated (Holdich, 1999). Documented detrimental effects of introduced crayfish include potential negative impacts upon amphibian eggs and larvae (Axelsson *et al.*, 1997; Gamradt & Kats, 1996), macroinvertebrates (Hanson, Chambers & Prepas, 1990; McCarthy, 2006; Guan & Wiles, 1998), algae (Guan, 1995, cited in Guan & Wiles, 1998; Hanson *et al.*, 1990), macrophytes (Creed Jr., 1994; Lodge, Kershner, Aloï *et al.*, 1994), fish, and their eggs and larvae (Guan & Wiles, 1997; Guan & Wiles, 1998; Peay *et al.*, 2009).

Controlling the numbers of invasive crayfish poses significant problems for habitat managers. Crayfish population densities can be extremely high; estimates of signal crayfish (*Pacifastacus leniusculus*, Dana) densities in US and British habitats range from 0.9 - 20 individuals m⁻² (Abrahamsson & Goldman, 1970; Bubb, 2004; Goldman & Rundquist, 1977) and where present they typically dominate the invertebrate biomass (Momot, 1995). A variety of methods exist, or have been proposed, for crayfish population control, including manual removal, trapping, electrofishing, biological control agents such as fish predators, microbial insecticides and diseases, physical measures such as de-watering and habitat destruction, and chemical means such as pheromone traps or biocides (see Freeman *et al.*, 2010; Hyatt, 2004; Holdich, Gydemo & Rogers, 1999; Peay, 2001), but no single or simple solution is currently available (Freeman *et al.*, 2010). Many control attempts continue to make use of manual removal, which is relatively cheap to implement and arguably has fewer impacts on non-target species and their habitats. However these methods (in particular hand searching, seine netting and trapping) have a well reported bias towards removal of the largest individuals (e.g. Abrahamsson, 1966; Moorhouse & Macdonald, 2010; Westman, Savolainen & Pursiainen, 1999; Holdich *et al.*, 1999) and leave the juvenile population almost entirely intact (Holdich *et al.*, 1999; Bills & Marking, 1988). Even with reduced trap mesh size (e.g. Guan & Wiles, 1996) smaller size classes may avoid contact with larger crayfish, probably due to the possibility of cannibalism, and therefore prove difficult to catch until the larger size classes have been removed (Holdich *et al.*, 1999).

Few studies of wild populations have examined the consequences of removal trapping on the movements of the remaining crayfish. This issue has significant implications for the effectiveness of any removal-by-trapping campaign, particularly if the campaign seeks to limit further colonisation at population margins, but it remains unclear what the predicted effects on movement distances would be. Bubb, Thom & Lucas (2006) suggest that, since signal crayfish of all ages appear to make movements of similar extent, the removal of mainly large individuals during trapping may have limited success in reducing colonisation at the edges of populations. This implies that crayfish removal would have little effect on movement distances. However alterations in population density due to trapping may affect movements: Moorhouse & Macdonald (2010) found that signal crayfish immigrating into areas in which the population density had been reduced by trapping moved significantly further than they did into control areas where no removal had occurred. They speculated that this finding indicated that the relative absence of large individuals from the removal sites reduced the potential for interference competition, permitting the immigrants to disperse larger distances. It is therefore possible that removal trapping may result in larger movement distances in crayfish. It is also possible, however, that removal trapping may result in smaller movement distances. Capelli & Hamilton (1984) observed that rusty crayfish (*Orconectes rusticus*, Girard) in the field can converge from long distances on freshly killed fish, but that when food was well dispersed and abundant most crayfish occupied shelters, ventured out only short distances to obtain it, and showed a reduction in aggressive activity. Similarly, crayfish are able to perceive, and move away from, areas containing a high density of conspecifics (Bovbjerg, 1959). If removals sufficiently lowered the population density it is therefore possible that crayfish may make smaller movements, either in direct response or due to a decrease in competition for food and shelters.

We examine the movement distances of signal crayfish from four sites on two UK rivers in a replicated experiment to examine the impacts of removal by trapping on the movements of the non-removed component of the population.

Methods

Study sites and design

We studied four stretches of river, each 100 m in length, representing two removal and two non-removal stretches. These stretches were divided between two rivers, the Evenlode and

the Thame, both in Oxfordshire, UK, such that each contained a removal and non-removal stretch, separated by a minimum distance of 800 m. From the removal stretches half of the crayfish captured were marked and returned at the point of capture and half were removed and humanely killed by freezing (see RSPCA, 2003; RSPCA, 2009), whereas in the non-removal stretches all crayfish captured were marked and returned at the point of capture (conducted under Natural England licence NNR/2008/0004). The study therefore comprised a replicated removal experiment with two treatment (removal) and two control (non-removal) stretches.

The rivers Thame and Evenlode were selected because both rivers were sufficiently deep and slow flowing throughout the selected stretches to permit crayfish traps to be deployed down both banks simultaneously to within a 1 - 2 m accuracy of trap placement. No instance of a trap moving from its previously-set position was noted at any point during the experiment. The substratum of each stretch was predominantly silt, bordered by earth banks supporting stands of riparian macrophyte vegetation. UK national grid references for the sites were: Evenlode 51°47'53.49"N 001°22'01.14"W; 51°48'09.62"N 001°21'50.47"W and Thame: 51°45'25.96"N 001°01'37.50"W; 51°45'16.03"N 001°01'11.63"W. In both cases the non-removal site was located downstream of the removal site to minimise the possibility of effects from the removals being propagated downstream and affecting the non-removal stretch.

Trapping protocol

Each river was trapped in separate capture sessions for eight consecutive days per month during spring/summer 2010, with the removal and non-removal stretches within a river being trapped simultaneously. All stretches were therefore trapped once in May, June, July and August, making a total of 64 days of trapping (32 days per river). Trapping sessions at a given river were separated by a three week period. Crayfish were trapped with commercially available cylindrical, plastic crayfish traps (TrappyTM crayfish trap, Virserum, Sweden), 50 cm long and 20 cm in diameter with 25 x 35mm mesh and a 51 mm diameter aperture, under Environment Agency licenses C/WA/17052010/S2 and C/WA/20052010/S3. Half of the traps were covered with 4 x 4 mm plastic mesh (Guan & Wiles, 1996; Guan & Wiles, 1999) to increase the proportion of small crayfish captured. The remaining traps were left uncovered for the purposes of a separate study to be reported elsewhere. In a given capture session, traps were set on Monday afternoon and removed on the next but one Tuesday,

allowing eight nights of trapping. Traps were checked early each morning, the contents handled and either returned at the point of capture or removed according to the experimental design. Traps from the separate treatments were checked separately each day, so that all of the traps from one stretch were checked before progressing to the next. To avoid bias, the starting stretch was alternated between days. Traps were baited with fish (sections of frozen whole sardines) and re-baited daily. Traps were set symmetrically down both banks of each stretch at a spacing of 5 m along the length of the river and 5 m across the width of the river. The spacing was measured accurately in the field using a tape measure. Twenty one traps were set down each bank, making 42 per stretch and 84 combined between the removal and non-removal stretches in a given session. Each stretch was sufficiently narrow (range 5 - 8 m for all stretches) that no crayfish within a given 100 m stretch was more than 2.5 m away from a trap.

Handling of captures

In the non-removal stretches all crayfish captured were given a semi-permanent mark which identified the stretch (non-removal) and capture session (one to four) in which they were captured, using methods adapted from Guan (1997). Marks were made by holding the crayfish on a piece of polystyrene mounted in a sturdy plastic tray and piercing the uropod with a sterile needle. In addition, crayfish from every second trap were marked on the carapace with the trap number (1 – 21 on side A or B of the river) and the day (2-8) in which they were captured using a permanent marker (Brite-Mark fine valve-action paint marker, Dykem, UK). This marking with capture location was alternated between odd and even numbered traps each day to avoid bias.

In the removal stretches crayfish from every second trap were marked by tail-piercing and with their capture location, as above, and returned at the point of capture. All captures from the alternate traps at the removal stretch were transported off site and destroyed by chilling in air to -15°C (RSPCA, 2003) on the day of removal. Again the removals alternated between odd and even numbered traps each day.

In both removal and non-removal stretches, on both sides of the river, crayfish from every fourth trap were weighed and measured prior to being marked and released. Weighing and measuring efforts were distributed equally across all traps over the eight days by varying the first trap to be weighed amongst the first four traps. Measurements taken were CL (carapace length), measured from the rostral apex to the posterior median edge of the

cephalothorax, measured to the nearest 1 mm with Vernier callipers, the wet mass, measured to the nearest g, and a note of any missing chelae. In addition, all recaptured individuals carrying capture location information were weighed and measured and the position and day of their last capture noted. To prevent pseudoreplication these individuals were removed and destroyed at the removal sites, and at the non-removal sites were countermarked with a clear “X” through the previous mark before returning at the point of capture. Alternative semi-permanent individual marking methods, such as those described by Guan (1997) and Abrahamsson (1965), were discounted since these methods would have required much additional field time and marks were required for the short term only.

In addition to the morning captures crayfish were removed from the removal stretch in three afternoons during each capture session. During these removals all crayfish captured in all traps were removed and destroyed.

Measuring distance moved and statistical analysis

Traps were spaced at 5 m intervals both across the width of the river and down the length of a line on one side. Distance moved for an individual was calculated assuming that the individual had travelled in a straight line between the start and end trap. Traps were set with an accuracy of within 2 m. The maximum error for any measure of distance moved was therefore 4 m but is expected to be lower than this in the majority of cases.

We wished to examine the impact of the removals upon the movements of the remaining crayfish, both within a given capture session, and between sessions. We constructed generalised linear models with a negative binomial error function (GLM.NB in Program R, version 2.12.0, The R foundation for Statistical Computing) with distance moved as the response variable and sex, treatment, river, session (covariate), CL (covariate), damage (missing one or more chelae, yes or no), and the number of days over which the movement was made (covariate – within sessions analysis only) as the explanatory variables. We included an interaction of session * treatment to test for increasing effects of treatment over the course of the experiment.

Results

Number of captures

In total 27,354 captures were made of 15,793 individual crayfish. Of these, 7,594 were captured in non-removal stretches and 8,199 from removal stretches. A total of 6,181 crayfish was removed from the two 100 m removal stretches over the course of the study, 4,478 from the morning trap checks and a further 1,703 from afternoon removals.

Size of recorded movements

Of the 4429 movements within capture sessions, 53% were < 10 m, and 69 % were < 15 m in length (Fig. 1a). Almost all (94%) movements were < 40 m. Only five recorded movements (0.1%) were > 90 m. The distribution of frequency of movement between capture sessions was similar to that within capture sessions (Fig. 1b), but with a slightly higher percentage (1.6%) of the 577 movements being > 90 m. These data suggest that a relatively small proportion of the population would have made (unrecorded) movements of greater than 100 m in length, either within or between capture sessions.

Effect of removals on movements within capture sessions

Mean distance moved was smaller at removal than at non-removal sites (GLM.NB, $n = 4363$, effect of treatment, $P < 0.001$; Table 1a); back transformed marginal mean movements were 10.8 m and 16.0 m, respectively. Larger crayfish moved further than smaller crayfish (GLM.NB, effect of CL, $P < 0.001$; Table 1a): marginal mean movements of crayfish of the smallest size for which movements were recorded (CL = 30 mm) were 12 m smaller (7.6 m as opposed to 19.6 m) than for the largest size class (CL = 78 mm). Movement distances in both treatments increased with increasing session and varied between rivers (Table 1a). There was no evidence that mean distances moved varied with sex, damage, or the number of days over which the movement took place (Table 1a). There was no evidence for an interaction of session * treatment in a separate model in which this was included (GLM.NB, effect of treatment * session, $z = 0.09$, $P > 0.9$). There was also no evidence for an effect of direction (upstream or downstream) moved in a separate model in which this was included (GLM.NB, $n = 3323$, effect of direction, $z = -0.29$, $P > 0.77$). This latter analysis excluded individuals which were recaptured in the same trap since these moved in neither direction.

Effect of removals on movements between capture sessions

Movements made between capture sessions were smaller at the removal sites than at the non-removal sites ($n = 564$, GLM.NB, effect of treatment, $P = 0.004$; Table 1b); marginal mean distances moved were 14.5 m and 24.6 m, respectively. Again, movement distances increased with increasing size (GLM.NB, effect of CL, $P < 0.001$; Table 1b); marginal mean movement distances for crayfish with CLs of 30 mm and 78 mm were 8.9 m and 32.6 m, respectively. There was no evidence for significant effects of session, river, sex or damage on between-sessions movement distances (Table 1b).

Discussion

Movement distances of signal crayfish in the removal stretches were significantly smaller than in the non-removal stretches. We were unable specifically to determine the cause of this reduction in movement distances but they are likely to result from one, or a combination of, increased availability of food and shelter, and / or a direct response to decreasing population density. Both food and shelters are important resources for crayfish, and changes in the availability of both could alter movement distances (Capelli & Hamilton, 1984). Fights are of higher intensity in the presence of a particularly valuable food resource (Bergman & Moore, 2003), and are more intense (Hazlett, Rubenstein & Rittschof, 1975) and likely to be escalated (Stocker & Huber, 2001) when crayfish are hungry. Hungry *Orconectes virilis* (Hagen, 1870) have been shown to demonstrate increased locomotory behaviour (Hazlett *et al.*, 1975), and their movements are less reduced by alarm odours than those of relatively satiated individuals (Hazlett, 2003). Davis & Huber (2007) noted in rusty crayfish that time outside their shelter was mainly used for feeding, individuals frequently returned to the same shelter from which they had emerged and that agonistic encounters generally occurred in the context of shelter acquisition or defence. Conflicts over shelters can be more intense than those over some food resources (Bergman & Moore, 2003), and could plausibly have consequences for movement distances if evicted crayfish needed to locate an alternative shelter.

Our signal crayfish removals could plausibly have decreased competition for resources and therefore increased the availability of both food and shelter for the remaining population. We were unable directly to measure these effects in the field, but they could explain observed decrease in movement distances. It is also possible, however, that the crayfish reacted directly to lower population densities. Crayfish are able to perceive, and move away from, areas containing a high density of conspecifics (Bovbjerg, 1959). It may,

therefore, be that densities in the removal stretches in this study were lowered sufficiently to diminish the dispersal impulse. We speculate that a combination of some, or all, of the above effects led to the observed decrease in movement distances in this study.

In this study crayfish with larger CLs made substantially larger movements than smaller crayfish, both within a given session, and between sessions. This finding is at odds with previous studies (e.g. Bubb, 2004; Bubb, Lucas & Thom, 2002; Bubb *et al.*, 2006; Moorhouse & Macdonald, 2010) which have demonstrated no effect of crayfish size on movement distance using a variety of techniques (radio-tracking, PIT telemetry and trapping, respectively). This discrepancy possibly derives from the larger sample sizes in the present study: 4363 individuals for the within-sessions analysis and 564 for the between-session analysis, compared with 356 individuals from Bubb *et al.* (2006), 64 in Bubb (2004), 20 in Bubb *et al.* (2002) and 124 from Moorhouse & Macdonald (2010). The discrepancy may also derive from differences in the range of CLs observed. Bubb *et al.* (2006) present data from only 29 crayfish captured with CLs > 50 mm, but from 120 individuals with CLs < 30 mm. In the present study, in the within-sessions analysis, 3,325 individuals had CLs in the range 50 - 78mm, 1,104 individuals between 30 - 49 mm and no individuals < 30 mm. Conversely in Moorhouse & Macdonald's (2010) study only one individual had a CL < 50 mm, with the majority (67%) of captures having CLs between 60 - 80mm, due to these movements being made by relatively large, individuals immigrating into a removal stretch. It is possible that the smaller sample sizes, the shift towards smaller CLs in the study of Bubb *et al.* (2006), and the contraction of the range examined and the shift towards larger CLs in Moorhouse & Macdonald's (2010) study may have meant that any relationship between CL and movements was missed in these previous analyses.

It is unlikely that either the reduction in movement distances in the removal stretches or the correlation between CL and movement distance were artefacts of our use of baited traps to attract crayfish. It is possible that, if densities in the removal stretches were reduced such that trapped crayfish consumed more bait than in non-removal areas, then recaptured individuals (those for which movement distances were able to be measured) may be less willing to make large movements to access fresh bait. However movements between sessions, when trapping did not occur and when no bait was therefore available, were still smaller in removal areas, suggesting that differential access to bait was not a determining factor. Also no crayfish in our study stretches was further than 2.5 m from a trap, and the mean movement distances were substantially larger than this in both removal and non-removal sites, indicating that crayfish were not merely competing for access to the nearest bait. The size differences

between treatments, and of movements across the range of CLs, within and between sessions, were sufficiently large that these differences are unlikely to be due to any consistent error in trap placement (maximum error for any recorded distance 4 m).

The implications of this study for the use of removal by trapping to control populations of signal crayfish are that trapping may be useful to slow the rate of spread of signal crayfish populations. Bubb *et al.* (2006) concluded from their study that all signal crayfish of both sexes which are one year of age (typical CL = 28-34 mm; Guan & Wiles, 1999) or over might contribute to dispersal, and so trapping, which preferentially captures large adults (CL > 50mm, > 3 years old, and an increasing probability of capture with increasing size/age; Moorhouse & Macdonald, 2010; Guan & Wiles, 1999), may have only limited success in reducing colonisation because the preferential removal of large adults would leave a large relatively untrapped cadre of potential dispersers. The observations from the present study, however, imply that trapping at the edge of a river population may be sufficient to delay colonisation of new stretches by: 1) maintaining low densities and therefore reducing movement distances and; 2) preferentially reducing the population of the large individuals which make the largest movements. This conclusion requires substantiation, however, possibly through a replicated experiment across several signal crayfish invasion fronts, with removal and non-removal treatments. It remains unlikely that any trapping programme can entirely prevent, rather than merely delay, colonisation by signal crayfish.

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References

- Abrahamsson, S.A.A. (1965) A method of marking crayfish *Astacus astacus* Linné in population studies. *Oikos*, **16**, 228-231.
- Abrahamsson, S.A.A. (1966) Dynamics of an Isolated Population of the Crayfish *Astacus astacus* Linné. *Oikos*, **17**, 96-107.

Abrahamsson, S.A.A. & Goldman, C.R. (1970) Distribution, density and production of the crayfish *Pacifastacus leniusculus* Dana in Lake Tahoe, California - Nevada. *Oikos*, **21**, 83-91.

Axelsson, E., Nystrom, P., Sidenmark, J. & Bronmark, C. (1997) Crayfish predation on amphibian eggs and larvae. *Amphibia-Reptilia*, **18**, 217-228.

Bergman, D.A. & Moore, P.A. (2003) Field observations of intraspecific agonistic behavior of two crayfish species, *Orconectes rusticus* and

Orconectes virilis, in different habitats. *Biological Bulletin*, **205**, 26-35.

Bills, T.D. & Marking, L.L. (1988) Control of nuisance populations of crayfish with traps and toxicants. *The Progressive Fish-Culturalist*, **50**, 103-106.

Bovbjerg, R.V. (1959) Density and dispersal in laboratory crayfish populations. *Ecology*, **40**, 504-506.

Bubb, D.H. (2004) Movement and dispersal of the invasive signal crayfish *Pacifastacus leniusculus* in upland rivers. *Freshwater Biology*, **49**, 357-368.

Bubb, D.H., Lucas, M.C. & Thom, T.J. (2002) Winter movements and activity of signal crayfish *Pacifastacus leniusculus* in an upland river, determined by radio telemetry. *Hydrobiologia*, **483**, 111-119.

Bubb, D.H., Thom, T.J. & Lucas, M.C. (2006) Movement patterns of the invasive signal crayfish determined by PIT telemetry. *Canadian Journal of Zoology*, **84**, 1202-1209.

Capelli, G.M. & Hamilton, P.A. (1984) Effects of food and shelter on aggressive activity in the crayfish *Orconectes rusticus* (Girard). *Journal of Crustacean Biology*, **2**, 252-260.

Creed Jr., R.P. (1994) Direct and indirect effects of crayfish grazing in a stream community. *Ecology*, **75**, 2091-2103.

Davis, K.M. & Huber, R. (2007) Activity patterns, behavioural repertoires, and agonistic interactions of crayfish: A non-manipulative field study. *Behaviour*, **144**, 229-247.

Freeman, M.A., Turnbull, J.F., Yeomans, W.E. & Bean, C.W. (2010) Prospects for management strategies of invasive crayfish populations with an emphasis on biological control. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 211-223.

Gamradt, S.C. & Kats, L.B. (1996) Effect of introduced crayfish and mosquitofish on California newts. *Conservation Biology*, **10**, 1155-1162.

Goldman, C.R. & Rundquist, J.C. (1977) A comparative ecological study of the California crayfish, *Pacifastacus leniusculus* (Dana), from two subalpine lakes (Lake Tahoe and Lake Donner). *Freshwater Crayfish*, **3**, 51-80.

Guan, R.Z. (1995) *Ecological studies on the crayfish Pacifastacus leniusculus (Dana)*. . Ph.D., The University of Buckingham, UK.

- Guan, R.Z. (1997) An improved method for marking crayfish. *Crustaceana*, **70**, 641-652.
- Guan, R.Z. & Wiles, P.R. (1996) Growth, density and biomass of crayfish, *Pacifastacus leniusculus*, in a British lowland river. *Aquatic Living Resources*, **9**, 265-272.
- Guan, R.Z. & Wiles, P.R. (1997) Ecological impact of introduced crayfish on benthic fishes in a British lowland river. *Conservation Biology*, **11**, 641-647.
- Guan, R.Z. & Wiles, P.R. (1998) Feeding ecology of the signal crayfish *Pacifastacus leniusculus* in a British lowland river. *Aquaculture*, **169**, 177-163.
- Guan, R.Z. & Wiles, P.R. (1999) Growth and reproduction of the introduced crayfish *Pacifastacus leniusculus* in a British lowland river. *Fisheries Research*, **42**.
- Hanson, J.M., Chambers, P.A. & Prepas, E.E. (1990) Selective foraging by the crayfish *Orconectes virilis* and its impact on macroinvertebrates. *Freshwater Biology*, **24**, 69-80.
- Hazlett, B., Rubenstein, D. & Rittschof, D. (1975) Starvation, energy reserves and aggression in the crayfish *Orconectes virilis* (Hagen, 1870) (Decapoda, Cambaridae). *Crustaceana*, **28**, 11-16.
- Hazlett, B.A. (2003) The effects of starvation on crayfish responses to alarm odor. *Ethology*, **109**, 587-592.
- Holdich, D. (1999) The negative effects of established crayfish introductions. In: *Crayfish in Europe as alien species: How to make the best of a bad situation?* (Ed^Eds F. Gherardi & D. Holdich). A.A. Balkema, Rotterdam.
- Holdich, D.M., Gydemo, R. & Rogers, W.D. (1999) A review of possible methods for controlling nuisance populations of alien crayfish. In: *Crayfish in Europe as alien species: How to make the best of a bad situation?* (Ed^Eds F. Gherardi & D.M. Holdich). A.A.Balkema, Rotterdam.
- Hyatt, M.W. (2004) Investigation of crayfish control technology. Vol. COOPERATIVE AGREEMENT NO. 1448-20181-02-J850.
- Lodge, D.M., Kershner, M.W., Aloï, J.E. & Covich, A.P. (1994) Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology*, **75**, 1265-1281.
- Mccarthy, J.M., Hein, C.L., Olden, J.D. & Vander Zanden, M.J. (2006) Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biology*, **51**, 224-235.
- Momot, W.T. (1995) Redefining the role of crayfish in aquatic ecosystems. *Reviews in Fisheries Science*, **3**, 33-63.
- Moorhouse, T.P. & Macdonald, D.W. (2010) Immigration rates of signal crayfish (*Pacifastacus leniusculus*) in response to manual control measures. *Freshwater Biology*.

Peay, S. (2001) Eradication of alien crayfish populations. Vol. R&D Technical Report W1-037/TR1. Environment Agency.

Peay, S., Guthrie, N., Spees, J., Nilsson, E. & Bradley, P. (2009) The impact of signal crayfish (*Pacifastacus leniusculus*) on the recruitment of salmonid fish in a headwater stream in Yorkshire, England. *Knowledge and Management of Aquatic Ecosystems*, **394-395**, 1-15.

RSPCA (2003) Humane killing and processing of crustaceans. *RSPCA*, <http://kb.rspca.org.au/file/3/>, accessed 10/2010.

RSPCA (2009) Humane electrical stun/killing of Crustacea. *RSPCA*, <http://www.rspca.org.uk/servlet/BlobServer?blobtable=RSPCABlob&blobcol=urlblob&blobkey=id&blobwhere=1223294842888&blobheader=application/pdf>, accessed 10/2010.

Simberloff, D. (2005) Non-native species *do* threaten the natural environment! *Journal of Agricultural and Environmental Ethics*, **18**, 595-607.

Stocker, A.M. & Huber, R. (2001) Fighting strategies in crayfish *Orconectes rusticus* (Decapoda, Cambaridae) differ with hunger state and the presence of food cues. *Ethology*, **107**, 727-736.

Westman, K., Savolainen, R. & Pursiainen, M. (1999) Development of the introduced North American signal crayfish, *Pacifastacus leniusculus* (Dana), population in a small Finnish forest lake in 1970–1997. *Boreal Environment Research*, **4**, 387-408.

Tables

Table 1. Results of (a) generalised linear model analysis of factors affecting distance moved by crayfish between consecutive captures within a session (n = 4363) and (b) generalised linear model analysis of factors affecting distance moved by crayfish between capture sessions (n = 564).

a.

Source	z value	P
Treatment	-5.764	<0.001
Sex	0.882	0.38
Session	1.966	0.05
River	-3.485	<0.001
CL	7.562	<0.001
Damage	0.426	0.67
Days over which movement occurred	1.518	0.13

b.

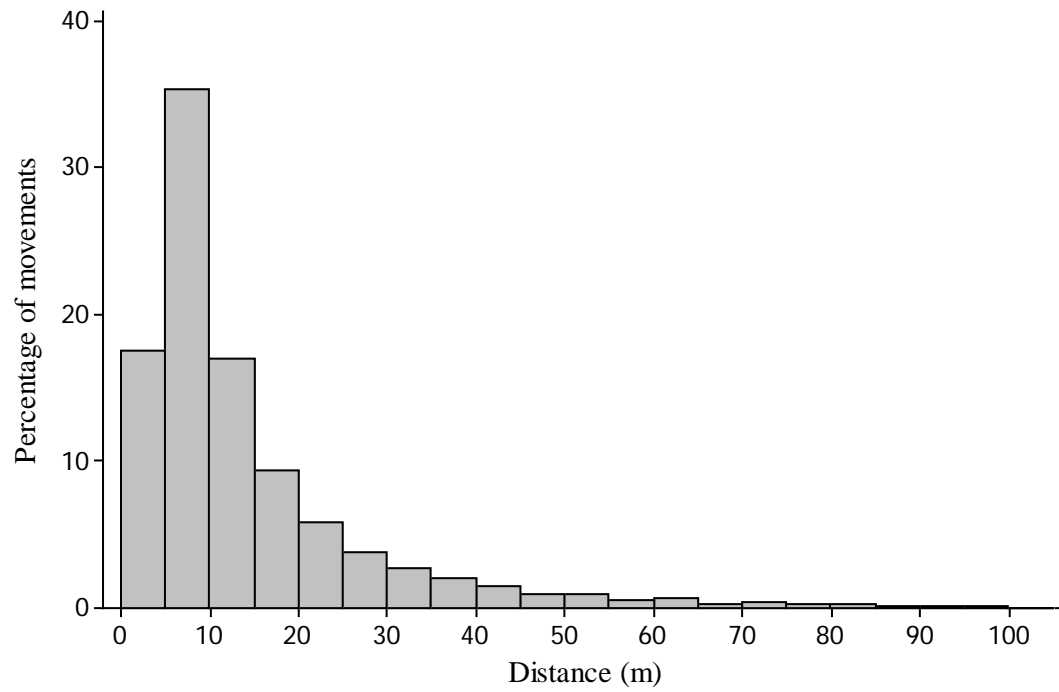
Source	z value	P
Treatment	-2.904	0.004
Sex	0.076	0.94
Session	0.254	0.79
River	0.736	0.46
CL	4.204	<0.001
Damage	-0.655	0.51

Figure legends

Figure 1. The percentage of movements of a given size made by signal crayfish: a) within a capture session ($n = 4363$) and; b) between capture sessions ($n = 564$).

Figure 1.

a.



b.

