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# Optimising control of invasive crayfish using life-history information

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## SUMMARY

1. Optimisation of control methods of invasive species using life-history information may increase probability that techniques will be effective at reducing impacts of nuisance species.

2. The northern crayfish, *Orconectes virilis*, has negatively affected native flora and fauna throughout the world in areas where it is non-native. Yet, life history of invasive populations has rarely been studied.

3. We investigated the life history of three introduced populations of *O. virilis* within Arizona streams using mark–recapture methods and a laboratory investigation of reproduction to identify times and techniques to maximise effects of mechanical control.

4. We show the most effective time to implement crayfish control efforts is in autumn during their mating season, prior to onset of colder temperatures, at which time the majority of *O. virilis* become inactive. To improve crayfish survival, recapture and population density estimates, we suggest a mark–recapture programme using a robust sampling approach concentrated during spring and autumn.

5. Identification of vulnerable points in the life history of nuisance species may aid in control efforts.

*Keywords*: invasive crayfish, invasive species, life history, mechanical control, *Orconectes virilis*

## Introduction

Biological, chemical and mechanical control methods are all used to minimise the often catastrophic effects of invasive species on native ecosystems (Myers *et al.*, 2000; Roberts & Pullin, 2008; Gherardi *et al.*, 2011). Unfortunately, control methods are frequently ineffective or cost-prohibitive. Therefore, means to optimise the effectiveness of techniques are critically needed.

Careful study of the life history of the invasive organism may identify the most vulnerable points of the life history for control. Applying control on these vulnerable life-history stages may improve their efficacy. Here, we show how use of life-history information of invasive crayfish might be used in just such a manner.

Negative effects of non-indigenous crayfishes on native flora and fauna are well documented (reviewed in Lodge *et al.*, 2000; Gherardi *et al.*, 2011; Larson & Olden, 2011). Invasive crayfish can significantly reduce abundance of macroinvertebrates, aquatic vascular plants and molluscs (Fernandez & Rosen, 1996; Childs, 1999). There are many invasive crayfishes, with most research focusing on two of the most notorious and widespread crayfishes: the red swamp crayfish, *Procambarus clarkii*, and the signal crayfish, *Pacifastacus leniusculus* (Delivering Alien Invasive Species for Europe; European Invasive Alien Species Gateway, 2010; Chucholl, 2011). Two other species are becoming more widespread and problematic, the rusty crayfish, *Orconectes rusticus*, and the northern or virile crayfish, *Orconectes virilis*. The rusty crayfish is currently a problem only in North America (Olden *et al.*, 2006), while the northern crayfish has been introduced throughout North America (Global Invasive Species Database, 2010; U.S. Geological Survey, 2012) and Europe (Ahern, England & Ellis, 2008; Holdich *et al.*, 2009; Filipová *et al.*, 2010).

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In areas without native crayfish or other functionally similar decapods, the ecological impacts of non-indigenous crayfishes may be severe as native organisms have not evolved in the presence of large aggressive omnivorous invertebrates. Arizona is unique as the only state (in the United States) without native crayfish. The Southwest and Arizona in particular are home to a variety of endemic aquatic species (Williams *et al*., 1985); thus, aquatic systems in Arizona are particularly vulnerable to crayfish introductions.

Ecosystem effects of northern crayfish have been previously studied in Arizona (Fernandez & Rosen, 1996; Childs, 1999; Carpenter, 2005). Northern crayfish can prey on a variety of sensitive species found in Arizona, such as juvenile Sonoran mud turtles, *Kinosternon sonoriense*, Chiricahua leopard frogs, *Rana chiricahuensis*, and newborn narrow-headed garter snakes, *Thamnophis rufipunctatus* (Fernandez & Rosen, 1996). Northern crayfish also compete with and prey on many native fish species, such as Little Colorado spinedace, *Lepidomeda vittata* (White, 1995), Gila chub, *Gila intermedia*, flannelmouth sucker, *Catostomus latipinnis* (Carpenter, 2005), and rainbow trout, *Oncorhynchus mykiss* (Hepworth & Duffield, 1987).

Because of negative effects of non-indigenous crayfish, control or eradication techniques are needed. Efficacy of currently available control methods for crayfish has been reviewed in a variety of publications (Hyatt, 2004; Peay, 2009; Freeman *et al*., 2010; Gherardi *et al*., 2011). Frequently, mechanical techniques are the methods of choice because of social, logistical or biological constraints associated with biological or chemical techniques (Myers *et al*., 2000).

Often, mechanical capture techniques are applied with little regard for many critical aspects of the organism's life history, the major goal simply being to capture or kill as many as possible. However, without appropriate life-history knowledge, efforts may not be effective or efficient. Perhaps, this contributed to the reported lack of success of many removal efforts for invasive crayfish (Childs, 1999; Hyatt, 2004; Freeman *et al*., 2010). Most life-history information about northern crayfish comes from studies of native populations and investigations of their potential for aquaculture (e.g. Weagle & Ozburn, 1972; Momot & Gowing, 1977a,b,c; Richards *et al*., 1996). Little is known about the life history of nuisance populations of northern crayfish, especially in the American Southwest where their potential for ecological damage is considerable.

Most mechanical control efforts have relied on catch per unit effort (CPUE) as a means to evaluate their effectiveness (e.g. Somers & Green, 1993; Richards *et al*., 1996). While CPUE can provide some help when ranking effectiveness of various capture techniques, it does not provide information on the impact of those efforts on a population because crayfish population size can fluctuate greatly over the year. Ideally, one would measure the percent of the population removed, and for that, one needs an accurate population estimate before and after control efforts to adequately evaluate effectiveness of removal techniques (Zabala, Zuberogoitia & González-Oreja, 2010; Zuberogoitia *et al*., 2010).

Identifying the most vulnerable life stages of the northern crayfish is important for applying control methods with maximum impact and cost-effectiveness. Therefore, the primary objective for this study was to examine life-history characteristics of introduced populations of northern crayfish and how such information could be used to direct management efforts.

## Methods

### *Crayfish*

Currently, two species of crayfish have been introduced to Arizona, the red swamp crayfish and the northern crayfish (Fernandez & Rosen, 1996). The northern crayfish is native to Missouri, Mississippi, Ohio, the Great Lakes drainages of the United States, and in southern Canada from Alberta to Quebec. The northern crayfish is thought to have entered Arizona through bait-bucket introductions and from deliberate introductions to control aquatic weeds (Dean, 1969). The northern crayfish can be found in higher altitudes throughout Arizona, particularly in the White Mountains of Arizona (Fernandez & Rosen, 1996; Inman *et al*., 1998; Childs, 1999; Carpenter, 2005; Benson, 2012).

### *Study sites*

We investigated life histories of three introduced populations of northern crayfish in Arizona. One population was the San Pedro River at Charleston (31.627014°W, −110.1747°N), located between Tombstone and Sierra Vista in southern Arizona. The other two populations were both located in the White Mountains of east-central Arizona, Silver Creek near Show Low (34.333042°W, −109.931131°N), and Porter Creek near Pinetop-Lakeside (34.170275°W, −109.969389°N). In each stream, a segment length of about 20–50 m was intensively sampled. The San Pedro River has highly variable flow, and our sampling site was located at an approximate altitude of

1200 m above mean sea level (m asl). Sampling sites at Porter Creek and Silver Creek were at 2000 and 1860 m asl. Silver Creek is spring-fed, while Porter Creek is downstream of a small reservoir (~32 ha Scott Reservoir). Both Porter Creek and the San Pedro River had intermittent flow for a couple of hundred metres followed by no flow downstream of our sampling sites. Both San Pedro and Porter Creek were dominated by non-native fishes, while Silver Creek has a relatively intact native fish fauna.

### *Field study*

Sample sites were monitored for a year (May 2007–May 2008) to obtain site-specific life-history information on northern crayfish. Mark–recapture techniques were used to estimate survival and recapture probabilities (Lebreton *et al.*, 1992). Each site was sampled every 4–6 weeks with the exception of December through February, as most northern crayfish become inactive when temperatures drop in wintertime. In lieu of monitoring one site over multiple seasons, we monitored three populations over a shorter time period. Congruence among populations would indicate fairly stable life-history strategies.

For each sampling event, water temperature (°C), specific conductance ($\mu$m S cm$^{-1}$) and pH were measured using a hand-held monitor (EC-400-Exstik®, Extech Instruments Corporation, Waltham, MA, U.S.A.). Total hardness ($CaCO_3$) was measured with a Hach Model 5B test kit (Hach Company, Loveland, CO, U.S.A.).

A sampling event consisted of 2–3 days of sampling every 4–6 weeks. Standard minnow traps (galvanised steel, 6.4 mm mesh, 2.54 cm opening, 42 cm long) were the primary means used to collect northern crayfish. Traps were baited with either dead fish (mortalities from a trout hatchery) or small cans of fish-based cat food. Total number of traps deployed at one time varied from 10 to 14 in the San Pedro River, 8–9 in Porter Creek and 10–14 in Silver Creek. One to three traps were generally set outside the designated sampling area to capture crayfish that might have moved out of the immediate study site. During each sampling event, traps were deployed in the evening of the first day of sampling and checked the next morning. Traps were then reset by early afternoon the second day, left overnight again and checked the following morning (day 3). During June when northern crayfish were abundant and CPUE was high, traps were checked and crayfish processed multiple times throughout the day (at 2- to 4-h intervals). For calculation of CPUE for minnow traps, we used the number of crayfish divided by the number of traps and hours traps were in the water. To compare the various capture methods, CPUE was calculated differently (explained in statistical analyses).

Alternative methods of capture were also conducted (dipnetting, hand collecting and electrofishing). For dipnetting (22.8 × 40.6 cm, 4.7-mm-mesh aquaculture dip net), we walked along the shore sweeping within vegetation, along the bank and/or underneath cut banks. When the water was clear, crayfish were caught by hand. This entailed slowly moving through the water, closely examining holes, crevices and under rocks for crayfish. Crayfish were then collected directly by hand or with the help of a small aquarium net (10 × 15 cm). Electrofishing was conducted using a Smith-Root LR-24 battery-powered backpack unit (Smith-Root Incorporated, Vancouver, WA, U.S.A.), walking upstream sweeping with the electrode from the centre to the shoreline and repeating the process on the opposite shore. Settings used for electrofishing were as follows: pulsed DC, between 30 and 50 Hz, 100 ± 20 volts and 12% duty cycle (~5 millisecond pulse width).

All northern crayfish collected above 13 mm were sexed and measured (cephalothorax length) before being released at the site of capture. Crayfish above 18 mm were marked with individually numbered visible implant alpha fluorescent elastomer (VIA) tags (Northwest Marine Technology Inc., Shaw Island, WA, U.S.A.) injected into abdominal tissue (Parkyn, Collier & Hicks, 2002). Only crayfish collected within the defined sampling site were tagged. Crayfish caught outside the defined study site were examined for previous tags, and those not previously marked were released without being tagged. Male crayfish were identified as to their Form (Form I, II) (Tierney *et al.*, 2008), and the degree of glair gland development of females was noted to evaluate reproductive maturity. Breeding males or Form I males can be identified by the presence of a larger and a more developed first pleopod (a hardened terminal projection) that is not present in non-breeding males (juveniles or Form II males). For each trap set, we measured water depth and sex ratios of captured crayfish.

### *Laboratory experiments*

A laboratory experiment was conducted to examine the effect of tags on crayfish survival. Twelve crayfish were injected with VIA tags, and 25 were used as controls. Crayfish were held in individual plastic containers holding about 500 mL of water. Crayfish were fed pelletised commercial fish food, and the water was replaced weekly. A semi-nonparametric survival analysis model (proportional hazards model [Cox, 1972]) was used to assess differences in survival between tagged crayfish and controls.

A field and laboratory approach was used for estimating number of attached eggs and number of free-swimming juveniles. In spring, we collected females with eggs at each site and counted number of attached eggs. To estimate number of free-swimming juveniles produced by individual females, crayfish were collected in autumn and maintained in the laboratory over winter with the hope that they would then produce eggs and subsequently free-swimming juveniles the following spring. Additional crayfish ($n$ = 88) were collected from Rose Canyon Lake (32.387389°W, −110.710323°N) located at 2100 m above mean sea level, approximately 17 miles NE from Tucson in the Coronado National Forest. Crayfish were collected from Rose Canyon Lake for logistical ease, as well as not to impact study areas with crayfish removal. Crayfish need 4 months of cold water (less than 12 °C) and darkness for ovarian development and egg laying (Aiken, 1969a; Portelance & Dubé, 1995). Approximately 43 female crayfish were placed in a cool room (12 °C), while others ($n$ = 80) were kept in a laboratory at ambient room temperature (mean = 19.06 SD = 3.17 °C, range = 13–23 °C). Crayfish were monitored for eggs produced and/or the number of free-swimming crayfish produced (3rd instar). All eggs that are laid do not remain attached to the female, nor do all attached eggs hatch and survive to become free-swimming juveniles (Dean, 1969; Momot & Gowing, 1977a).

### *Statistical analyses*

To test length differences between the sexes, we conducted a matched pair $t$-test using the mean cephalothorax length by sample date and site and compared the observed paired $t$-test statistic with a $t$-test statistic distribution generated using a Monte Carlo technique with 4999 simulations (resampling of actual values with replacement). Length differences among capture methods, controlling for sex and time of year (e.g. month captured), were tested using an ANOVA with Tukey's HSD for multiple comparisons.

To test whether the minnow traps were sex-biased, we compared the observed paired $t$-test statistic with a $t$-test statistic distribution generated using a Monte Carlo technique with 4999 simulations (resampling with replacement) for each site. This approach was used as many traps contained only one sex (precluding G or chi-square tests), and distributions were not normally distributed. To investigate the efficiency of the capture methods, we used CPUE. For electrofishing, hand collecting and dipnetting, we used the actual amount of time it took to collect crayfish. With traps, we used the amount of time it took to bait and set the traps once we arrived on site. We did not include the time it took to arrive at the study sites to calculate CPUE as time varied by site (nearest road access). This may have resulted in a relative inflated CPUE for the trap method as one has to make a return trip to pick up the traps, which was not necessary for the other techniques. Hand collection was only attempted on days when water clarity was sufficient and crayfish were readily observed; thus, hand sampling may also have inflated CPUE, as hand sampling was only attempted during ideal conditions. As capture results were unbalanced and not normally distributed, we used a Monte Carlo technique to compare the actual $F$ value of an analysis of variance (ANOVA) with a distribution of $F$ values generated with 4999 simulations (resampling with replacement).

To investigate capture efficiency and temporal differences, we investigated the percent of the population that was composed of recaptures to CPUE, site and time. We used minnow trap CPUE for this analysis as conditions did not allow us to electrofish or catch crayfish by hand for each sampling occasion. Although the distributions were not normal, they were relatively equivalent in shape; consequently, we conducted an ANOVA.

Our field sampling protocol was designed with the intent to use the "robust model" within program MARK to obtain apparent survival, recapture probabilities and population estimates (White & Burnham, 1997). A robust model involves sampling at two temporal scales incorporating a closed population and an open population component (Nichols, 2005). We had few recaptures in spring and early summer of 2007, and thus, program MARK was unable to arrive at a solution based on the robust model parameters. Consequently, we used an open population model [Cormack–Jolly–Seber (CJS)] within program MARK (Nichols, 2005). Apparent survival is the probability of surviving between successive sampling occasions, with the assumption that the animal has not permanently emigrated from the sampling site. Permanent emigration is indistinguishable and treated the same as mortality. The recapture probability is the probability of an individual being captured at a site given that it is alive. The CJS model does not differentiate between emigration and death, nor provide population size estimates.

A variety of different candidate models were developed within MARK using the CJS framework to estimate apparent survival and recapture probability. Within the convention of MARK, apparent survival is represented by 'Phi' and recapture probabilities by '*P*'. We use this notation throughout this article. We used parameter size –adjusted Akaike's information criterion (AIC$_c$) values to identify the best model based on maximum likelihood (Burnham, White & Anderson, 1995; Burnham & Anderson, 1998). Candidate models tested included various permutations with factors such as sex, sampling date, length (at first capture), flow and temperature. Once the most parsimonious model(s) was selected within MARK, we then used Markov Chain Monte Carlo (MCMC) sampling (~30 000–50 000 samples) in a Bayesian framework to estimate model parameters. Maximum-likelihood values generated from the model with the most support in MARK were used as prior beta estimates and standard errors for the MCMC analysis (Brooks, 1998). The MCMC analyses result in distributions of possible solutions for survival and recapture probabilities. MCMC posterior distributions were examined using Convergence Diagnostic and Output Analysis software (CODA©: Best, Cowles & Vines, 1997) to optimise the MCMC sampling and to ensure that stationarity and convergence were reached. The CODA program analyses result from MCMC posterior distributions to ensure that enough samples were run in the MCMC and that an acceptable solution was reached.

## Results

### *Water quality*

Water quality varied among sites, and here, we report the minimum and maximum values. The San Pedro River generally had higher pH (8.2–10), specific conductance (SP = 274–499 μmS cm$^{-1}$) and total hardness (TH = 154–239 mg L$^{-1}$) than the other two sites. Porter Creek had a pH of 7.0–9.5; SC = 78.8–207 μmS cm$^{-1}$; and TH = 103–205 mg L$^{-1}$. Values for Silver Creek were as follows: pH = 7.1–9.4; SP = 93.8–155 μmS cm$^{-1}$; and TH = 68.4–103 mg L$^{-1}$.

### *Crayfish collection*

Crayfish were not collected at any of the sites in July because of prohibitive high water flow. There was a significant difference in CPUE for the four capture methods (ANOVA: MS = 64420, $F_{3,41}$ = 18.8, $P$ = 0.002), with minnow traps being the most effective (Table 1). Crayfish length significantly varied by collection method (ANOVA: MS = 0.627, $F_{18,2737}$ = 106, $P$ = 0.0059), with minnow traps capturing significantly longer crayfish than any other method (Tukey's HSD, $P < 0.05$) (Fig 1.).

We marked 832, 704 and 908 individual crayfish at San Pedro River, Porter Creek and Silver Creek, respectively. Mean minnow trap CPUE changed dramatically throughout the year, although Silver Creek and Porter Creek had similar temporal patterns (Fig. 2).

### *Northern crayfish biology*

Minnow traps set in Silver Creek on average captured significantly more females (6.3 ± 6.5, mean ± SD) than males (4.1 ± 5.1), as the observed *t*-test statistic of absolute value of −5.1 was only equalled or exceeded in 22 instances in the Monte Carlo simulation ($P$ = 0.0046). In the San Pedro River, there was no difference as 1395 simulated *t*-test statistics were equal to or less than the absolute value of the observed *t*-test statistic of −1.22 ($P$ = 0.28). In Porter Creek, there was no difference, as 3365 simulations were equal to or greater than the observed *t*-test statistic absolute value of 0.46 ($P$ = 0.67).

Female crayfish were significantly larger than males (mean cephalothorax length = 34.4 and 32.8 mm respectively) in Silver Creek (matched pair *t*-test: d.f. = 14, *t*-ratio = −2.28, $P$ = 0.0380). There was no significant difference between sexes at Porter Creek (matched pair *t*-test: d.f. = 15, *t*-ratio = 0.664, $P$ = 0.518) or in the San Pedro River (matched pair *t*-tests: d.f. = 15, *t*-ratio = −1.57 = 0.137, $P$ = 0.137).

**Table 1** Crayfish catch per unit effort (CPUE) by method and total number of crayfish collected by waterbody (includes recaptures)

| Collection method | CPUE (SD) | San Pedro R. | Porter Creek | Silver Creek | Total |
|---|---|---|---|---|---|
| Dipnetting | 46.3 (46.7) | 12 | 38 | 59 | 109 |
| Electrofishing | 6.39 (7.31) | 57 | 31 | 28 | 116 |
| By hand | 39.2 (19.2) | 132 | 0 | 235 | 367 |
| Minnow traps | 232 (163) | 795 | 680 | 679 | 2154 |
| Total | | 996 | 749 | 1001 | 2746 |

CPUE is crayfish per hour, based on time to set and collect traps and time spent collecting crayfish via dipnetting, hand collecting or electrofishing.

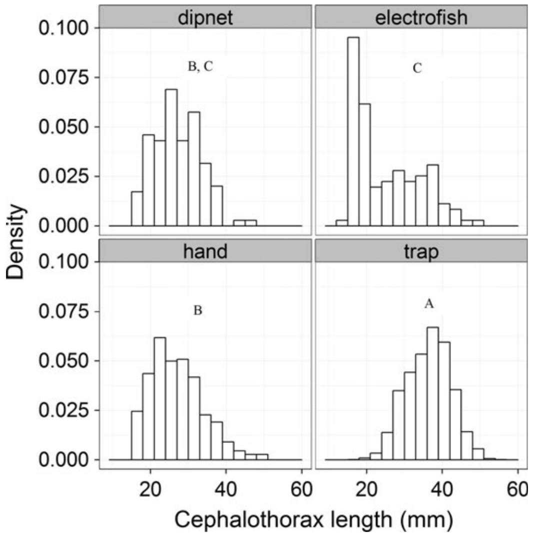

**Fig. 1** Length frequency graphs of crayfish by collection method, differing letters indicate significant differences ($P < 0.05$).

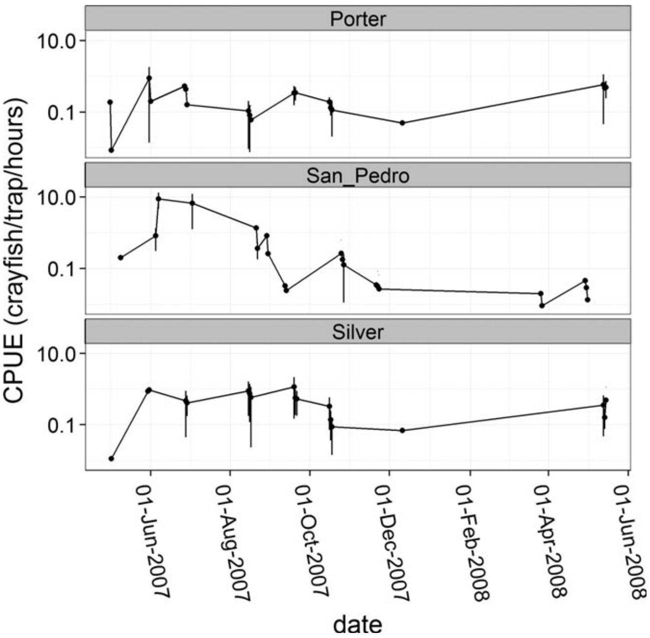

**Fig. 2** Mean catch per unit effort of northern crayfish over time by sample sites, Porter Creek, San Pedro River and Silver Creek from baited minnow traps (error bars are standard deviations)

## *Reproduction*

Male Form (I or II) and the presence of the glair gland in females were recorded from August till May and from September till May, respectively (Table 2). In Porter and Silver Creek, the greatest percentage of males in reproductive form was in September; while for the San Pedro River, which is further south and at a much lower altitude, the highest percentage was from October to December. Per cent of females in glair followed a similar pattern as males in Form I.

**Table 2** Proportion of reproductive Form (I) male crayfish and of females with visible glair glands, by month (sample size in parentheses)

| Date | Porter Creek | Silver Creek | San Pedro R. |
|---|---|---|---|
| Male | | | |
| 8/21/2007 | 0.16 (38) | 0.36 (107) | 0.12 (109) |
| 9/15/2007 | 0.93 (84) | 0.92 (106) | 0.20 (5) |
| 10/20/2007 | 0.52 (63) | 0.55 (38) | 1.00 (49) |
| 12/11/2007 | 0.80 (5) | 0.20 (5) | 1.00 (15) |
| 3/25/2008 | – | – | 0.37 (8) |
| 4/30/2008 | – | – | 0.00 (8) |
| 5/14/2008 | 0.04 (160) | 0.00 (49) | – |
| Female | | | |
| 8/21/2007 | – | – | – |
| 9/15/2007 | 0.87 (38) | 0.93 (136) | 0.20 (93) |
| 10/20/2007 | 0.40 (25) | 0.74 (42) | 1.00 (9) |
| 12/11/2007 | 0.43 (7) | 1.00 (1) | 1.00 (1) |
| 3/25/2008 | – | – | 0.00 (7) |
| 4/30/2008 | – | – | 0.00 (21) |
| 5/14/2008 | 0.00 (60) | 0.00 (81) | – |

Collection dates are not exact, but are within 1 week of actual collection. A dash indicates that sampling did not occur during that time period. Crayfish were collected May-June; however, reproductive state was not recorded.

Juvenile crayfish were only observed from approximately May through the end of June, suggesting that northern crayfish in Arizona have one reproductive season a year. We had little success collecting crayfish with attached eggs at our sampling sites in spring, with only three crayfish collected that were in berry (had attached eggs).

Maintaining northern crayfish in a cold room (at 10 °C) did not stimulate egg production in females. Only four of 30 northern crayfish produced eggs after 5 months in the cold room. A higher percentage (35%) of crayfish kept in a laboratory (at ambient room temperature) produced eggs compared with those in the cold room. Only nine of the 29 crayfish in the laboratory retained their eggs to hatching. The majority (83%) of northern crayfish that produced eggs in the laboratory were collected at Rose Canyon Lake, in the Santa Catalina Mountains (Pima County, AZ, U.S.A.). These crayfish were collected later in the year (December) than those crayfish from the research sites that were retained for fecundity measurements (July–October). Counts of pleopod eggs ranged from 1 to 662 ($n = 16$) (Table 3), while the range of juveniles surviving to the 3rd instar (free-swimming stage) was 46–416 ($n = 11$). The average and standard deviation

**Table 3** Comparison of reported mean fecundity values (attached eggs) of *Orconectes virilis* and standard deviations (SD)

| Source | Location | Mean (SD) | Range | *n* |
|---|---|---|---|---|
| This study | Arizona | 214.5 (186.5) | 1–662 | 16 |
| Weagle & Ozburn, 1972; | Lakehead Univ., Thunder Bay, Ontario, Canada | 214 (?) | 115–320 | 16 |
| Corey, 1987; | Bruce Peninsula, Ontario, Canada | 139.11 (51.79) | 20–310 | 38 |
| Momot, 1967; * | West Lost Lake, Pigeon River State Forest, Otsego Co., Michigan | 162 (41$^{\dagger}$) | 92–276$^{\dagger}$ | 29$^{\dagger}$ |
| Momot, Gowing & Jones, 1978 | Pigeon River State Forest, Otsego Co., Michigan | 100 (?) | 1–443 | ? |

*values reported are ovarian eggs, not attached eggs.

$^{\dagger}$SD, *n* and range were not reported; these values were derived from the data points presented in Figure 6 in Momot (1967) using ImageJ (http://rsbweb.nih.gov/ij/).

? values not reported.

(in parentheses) of the number of pleopod eggs and free-swimming juveniles produced per crayfish were 214.5 (186.5) and 179.8 (138.08), respectively.

Number of eggs attached to pleopods was positively correlated with female cephalothorax length ($R^2 = 0.54$, $P = 0.026$), while number of free-swimming juveniles was not ($R^2 = 0.21$, $P = 0.18$). Cephalothorax length of females producing eggs ranged from 27.4 to 47.8 mm. One female collected in July and maintained in isolation in the laboratory successfully extruded eggs and hatched 266 juveniles over winter.

### *Capture probability and survival*

The VIA tags did not appear to affect survival or growth of crayfish (proportional hazards model: d.f. = 3, chi-square = 149, $P = 0.6835$). Eleven of 12 marked crayfish in the laboratory survived (355 days). Of the 25 control crayfish, six died (three within the first 3 days), and one escaped its container. Three of the 12 tagged crayfish moulted, and two of those moulted twice. Tags were retained and readable in all laboratory crayfish.

The overall model investigating percent recaptures of female crayfish to CPUE, site and time was significant (MS = 0.257, $F_{42,14} = 2.66$, $P = 0.0252$), with time as the only significant factor (SS = 9.82, d.f. = 39, $F = 2.61$, $P = 0.0282$) and site and CPUE were not significant ($P > 0.2$) (Fig. 3). The overall model investigating percent recaptures of male crayfish to CPUE, site and time was not significant (MS = 0.0864, $F_{42,14} = 0.706$, $P = 0.812$).

For each population, model 1 was the most parsimonious based on AICc, and this was used in the MCMC analysis to estimate survival and recapture probabilities (Table 4). Of the 832 northern crayfish marked in the San Pedro River, 111 individuals were recaptured, and 39 of those were recaptured more than once. For the San Pedro River, twenty models were examined in program MARK with the top five presented in Table 4. Apparent mean daily survival (Fig. 4) varied across time and with age (Table 4). Crayfish were classified as being either age 1 or age 0 based on length at first capture. Time and length were the two factors that were identified as most important in the two best models for recapture probabilities (Table 4).

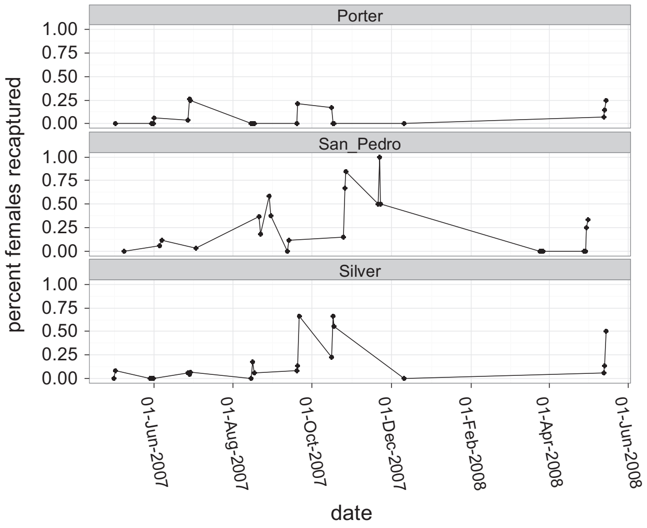

**Fig. 3** Percent of female crayfish captured that were recaptures over time by sample sites, Porter Creek, San Pedro River and Silver Creek.

Of the 704 crayfish marked within Porter Creek, 77 individuals were recaptured once, and eight of those, more than once. Five of the sixteen open population models examined in program MARK are presented in Table 4. Recapture probabilities varied across time (Fig. 5), but survival probabilities did not (Fig. 4). Apparent mean daily survival differed by sex; for females and males, it was 0.979 (SD = 0.00613) and 0.992 (SD = 0.00152), respectively.

Of the 908 crayfish marked at Silver Creek, 84 were recaptured at least once, and of those, 13 crayfish were recaptured two or more times. Recapture probabilities varied across time (Fig. 5), but apparent mean daily

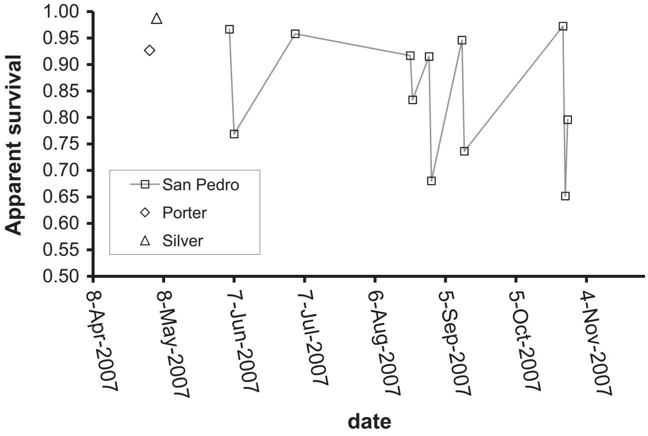

**Fig. 4** Female northern crayfish apparent survival estimates for three populations from an Markov Chain Monte Carlo (MCMC) analysis of the best-fitting open population model selected from Program MARK. For the population at Porter Creek and Silver Creek, survival did not vary temporally; thus, there is only one survival estimate.

survival did not. Apparent mean daily survival differed by sex. Apparent mean daily survival for female crayfish was 0.9876 (SD = 0.001740), and for males, it was 0.9841 (SD = 0.002510). In Silver Creek, precise location data were available before and after recapture for 73 northern crayfish. Forty-five northern crayfish had a net downstream movement, 22 moved upstream, and six had no net movement, indicating a general trend for downstream movement.

## Discussion

To control or eradicate crayfish populations, implementation of efforts when they have the greatest impact on the population is important. For all three studied populations, time was an important factor for recapture probability. Thus taking into account activity levels, mating behaviour and recapture rates, it appears that the best time to implement crayfish control efforts is in the autumn (September through October) prior to the onset of colder temperatures.

Of the methods we tested, minnow trap sets in the autumn have the best chance of impacting northern crayfish populations. Trapping should begin in autumn when the majority of crayfish are reproductively active. Reproductive activity can be inferred when female crayfish are in glair (white coloration on telson and uropods) and males are in Form I. Northern crayfish are very active during mating season and susceptible to trapping at this time. We would suggest trapping before temperatures reached 10–12 °C, after which crayfish movement is severely reduced. Unfortunately, in this study, we were unable to estimate whether intense autumn trap-

**Table 4** Cormack–Jolly–Seber open population model selection result summary for three northern crayfish populations in Arizona from program MARK (only top five models presented)

| | AICc | Delta AICc | AICc weights | Model likelihood | Num. par. | Deviance |
|---|---|---|---|---|---|---|
| San Pedro model | | | | | | |
| Phi(time + age) p(time + length) | 970.5 | 0.000 | 0.505 | 1.000 | 46 | 873.9 |
| Phi(time) p(time + length) | 971.3 | 0.813 | 0.336 | 0.666 | 45 | 876.9 |
| Phi(time + age + flow) p(time + length) | 974.6 | 4.11 | 0.0648 | 0.128 | 47 | 875.8 |
| Phi(time + age) p(time + length + age) | 975.2 | 4.70 | 0.0483 | 0.0957 | 46 | 878.5 |
| Phi(time + age + length) p(time) | 977.0 | 6.51 | 0.0194 | 0.0385 | 46 | 880.4 |
| Porter Creek model | | | | | | |
| Phi(sex) p(time) | 724.2 | 0.000 | 0.487 | 1.000 | 21 | 680.9 |
| Phi(sex + length) p(time) | 725.3 | 1.02 | 0.293 | 0.602 | 22 | 679.8 |
| Phi(g*length) p(time) | 725.9 | 1.61 | 0.218 | 0.447 | 23 | 678.2 |
| Phi(.) p(time) | 735.3 | 11.1 | 0.002 | 0.004 | 20 | 694.1 |
| Phi(sex + temp) p(time + length) | 741.6 | 17.4 | 0.000 | 0.0002 | 39 | 658.9 |
| Silver creek model | | | | | | |
| Phi(sex) p(time + length) | 974.1 | 0.00 | 0.999 | 1.000 | 23 | 927.0 |
| Phi(sex + length) p(time + length) | 989.3 | 15.12 | 0.00052 | 0.0005 | 24 | 940.0 |
| Phi(sex) p(time) | 992.6 | 18.48 | 0.0001 | 0.0001 | 22 | 947.5 |
| Phi(sex + length) p(time) | 996.2 | 22.07 | 0.00002 | 0.000 | 24 | 946.9 |
| Phi(time) p(time) | 998.0 | 23.89 | 0.00001 | 0.000 | 40 | 914.5 |

Variables: survival factors (Phi), recapture factors (p), sampling date (time), number of parameters (num. par.), volume of water (flow), crayfish cephalothorax length (length); one factor for a parameter is indicated by (.).
AICc, Akaike's information criterion.

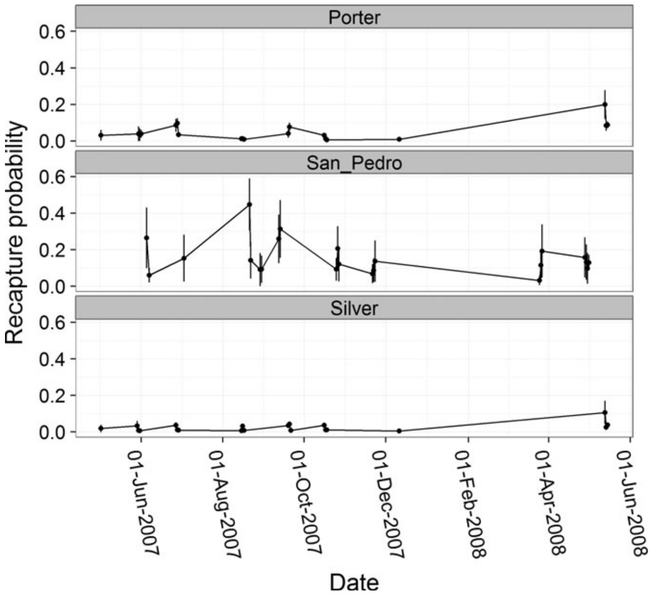

**Fig. 5** Recapture probabilities and standard deviations for female northern crayfish from Porter Creek, San Pedro River and Silver Creek derived from an Markov Chain Monte Carlo (MCMC) analysis of the best-fitting open population model selected from program MARK. For Porter Creek, recapture probabilities for three dates were not estimable.

ping would be able to control or eradicate populations, as we could not estimate population levels.

There is a size bias for capturing larger individuals when using trapping methods only; thus, utilising an additional technique that is biased for smaller adults and juveniles would be beneficial. This approach was used to control invasive rusty crayfish (*Orconectes rusticus*), with intensive trapping for adults and using smallmouth bass to predate on juvenile and small adult crayfish (*Micropterus dolomieu*: Hein, Vander Zanden & Magnuson, 2007). However, this method would be unfeasible in most Arizona locations, as smallmouth bass are not native, and could possibly create additional problems if they were introduced. In this study, other capture methods examined were biased for smaller crayfish (Fig. 1), and the use of any other method where feasible would increase the size distribution of captured crayfish and overcome any size bias associated with using only traps.

The success of electrofishing, dipnetting and collecting by hand was dependent on water clarity. If water was too turbid to see crayfish on the stream bottom, then these methods were unsuccessful. High turbidity was characteristic of our streams from July to September and in December. We found electrofishing ineffective for collecting crayfish, which contrasted with the results of others (Westman, Sumari & Pursiainen, 1978; Rabeni *et al.*, 1997; Alonso, 2001). Crayfish did not respond in the same manner as fish to pulsed direct current (DC). We could not adjust the levels to successfully stun and/or draw crayfish to the electrode as one can with fish. The response of most crayfish was to swim down and away, towards the substratum. The crayfish behaviour of hiding in shelters also contributed to the ineffectiveness of electrofishing. Additionally, electrofishing is not an option commonly available to volunteer groups that may be recruited to control or eradicate invasive crayfish. Compared with setting traps, electrofishing is expensive and requires training to capture target organisms while minimising injury to other species (Snyder, 2003, 2004).

Life history of introduced populations of northern crayfish appears to be similar to native populations with slight differences in timing. Male crayfish in Arizona seem to moult to the reproductive form (Form 1) later in the year September-October compared with native populations moulting July–September (Momot, 1967; Aiken, 1969b; Weagle & Ozburn, 1972). A delayed moult is probably a function of a later autumn season in lower latitudes, as crayfish moulting and reproduction are determined by a combination of temperature and photoperiod (Aiken, 1969a,b). Based on length frequency data, field collections and observations, introduced populations of northern crayfish in Arizona reproduce once annually. Our estimates of northern crayfish reproductive potential were based on individuals that were collected in the wild in berry (eggs attached) as well as from crayfish that were brought into the laboratory and subsequently laid eggs. Counts of attached eggs (fecundity) in our crayfish populations correspond to what is reported in the literature for other northern populations (Table 3). However, the majority of our data comes from captive crayfish, which may not accurately reflect wild populations. One of our goals was to estimate the percentage of females that reproduced. While the majority of female crayfish brought into the laboratory developed glair glands, few extruded eggs, and even fewer produced free-swimming juveniles (3rd instar or moult). Additionally, we caught very few females in berry in the wild; thus, we could not reliably estimate the percentage of females that reproduced in the wild.

An interesting observation in the laboratory was the production of eggs and juveniles by a female that was collected in July and kept in isolation. This would suggest that females can maintain viable sperm for an extended period, potentially over 1 year (Reynolds, 2002), or that they will produce viable eggs even if they are not fertilised. Other crayfish have been known to reproduce clonally, for example *Orconectes limosus* (Buřič *et al.*, 2011) and the marbled crayfish *Procambarus fallax* (Scholtz *et al.*, 2003). Whether this individual maintained sperm from a previous mating or whether it was parthenogenetic is unknown.

While reproduction occurs in spring and early summer, mating occurs in the autumn. Most males collected in autumn were of Form I (reproductive form), and most females had visible glair glands. Recapture rates were relatively high during this period as crayfish were active and moving around presumably in search of mates. High activity levels and movement have been associated with mating in *Orconectes limosus* (Buřič, Kouba & Kozak, 2009). As winter progressed and water became colder, fewer crayfish were reproductively active (e.g. glair glands, percent of Form I males) and CPUE declined, as did recapture rates. It is not clear at what temperature northern crayfish become inactive, but based on our trapping data and the literature (Aiken, 1969a; Portelance & Dubé, 1995), we believe it to be in the range of 10–12 °C. Temperatures below 12 °C are necessary for ovarian development (Aiken, 1969a; Portelance & Dubé, 1995), while temperatures above 12–13 °C are thought to be necessary for crayfish to become active in spring (Momot, 1967; Aiken, 1969a).

Recapture probabilities were highest in the spring for crayfish in Porter Creek and Silver Creek (Fig. 5), suggesting that spring might be a good time to apply control efforts. However, crayfish have already reproduced at this time as evidenced by the presence of free-swimming juveniles. Juveniles, that is, crayfish <18 mm, were not marked and not included in calculations of apparent survival or recapture. High recapture rates in the spring do not reflect the combined population of adults and very small juveniles. Thus, while CPUE may be relatively high in the spring, the percent of the population caught would be relatively low, and as our results show, there was not a significant relationship between CPUE and percent recaptures. It must be noted that the analysis comparing the percent of the captured population that were recaptures to CPUE is not the best approach for analysing recaptures. While it provides a generalised view, it is biased, as the percent of the population that is marked (captured) increases with time. The results generated from Program Mark are more appropriate to analyse recapture data.

The results of this investigation depend on the assumption that northern crayfish captured and marked were representative of the general population. The CJS model also assumes that all crayfish were equally likely to be captured. In one respect, this was not true, as the few crayfish smaller than 18 mm cephalothorax length we captured were not marked. Also, when female crayfish are carrying eggs, they are less likely to be captured (Hazlett, Rittschoff & Ameyaw-Akumfi, 1979). Females in berry generally find a safe refuge to allow eggs and juveniles to develop and, consequently, are inactive. Whether the sex ratio of northern crayfish obtained primarily from minnow traps accurately represents the sex ratio of northern crayfish in the wild is unclear. Bias of traps towards male northern crayfish has been reported (Momot & Gowing, 1977b; Somers & Green, 1993), but we did not see a consistent pattern of sex bias using minnow traps. We tried to account for differences associated with reproduction and crayfish inactivity by not sampling December through March. However, some females still had eggs or attached young beyond March (April–June).

Stream flow (volume/velocity) and temperature were not important factors explaining northern crayfish survival or recapture. However, this does not mean these variables have no effect on survival or recapture. We used flow measurements collected on the day of capture and did not sample in unsafe flood conditions. Additionally, flow was highly seasonal, and effects could have been masked by temporal differences. After the monsoon season (July), when high water flows were present, crayfish densities appeared to be significantly lower. Prior to the high flows of the monsoon season, crayfish were very abundant and easily observed. Many of the smaller crayfish may have been swept away and/or did not survive high flows during the monsoon season. After the monsoon season, our CPUE declined and length frequency increased. Any differences in survival related to temperature may have also been accounted for by the temporal differences included in the models, which were significant for recaptures, as temperature is typically correlated with time of year.

Life-history information is vital to control and eradicate invasive species (Nylin, 2001). These data are particularly relevant for organisms with high reproductive capacities such as insects and crustaceans. For an effective eradication or control programme, rate of removal must exceed rate of population increase and all reproductive animals must be at risk (Bomford & O'Brien, 1995), both criteria requiring life-history information to be employed. Knowledge of northern crayfish reproductive potential at various population densities and an ability to capture all reproductive individuals is essential. Characteristic of the species, reproductive individuals are only at risk during certain times of the year. Past attempts at crayfish control may have been less effective because they did not use life-history information. Control and eradication of invasive species are expensive (Myers *et al.*, 2000), and much time, effort and money can be expended without achieving desired goals if life-history information is unknown.

To improve crayfish survival and recapture estimates, as well as to estimate population densities, we suggest a mark–recapture programme using a robust (two-tiered) sampling approach concentrated during spring and autumn. Adult northern crayfish recapture probabilities are at the highest during the spring and autumn, while adult population size is probably at its lowest. Our results with mark–recapture are similar to the conclusions reached by Nowicki *et al.* (2008), who suggest a similar approach to mark–recapture techniques for the white-clawed crayfish (*Austropotamobius pallipes*) native to Western Europe.

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