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Aquatic Nuisance Species: A multi-stage approach to understanding the invasion ecology of exotic crayfish in Northern and Southern California.

Introduction

Biological invasions are widely thought to have major negative impacts on native communities and ecosystems (Vitousek et al. 1996; Parker et al. 1999; Mack et al. 2000). Exotic species are the second most important cause of species extinctions (after habitat destruction) in the United States (Enserink 1999) and an important cause of losses in biodiversity worldwide (Sala et al. 2000). From an economic, resource management view, exotic species can have major direct and indirect impacts on commercially-important natural resources – e.g., fisheries, crops (Pimentel et al. 2000). Although exotic species can impact native species via various mechanisms (e.g., competition, spread of disease, hybridization), for aquatic animals, a key mechanism is clearly predation (Moyle and Light 1996; Gamradt and Kats 1996; Knapp et al. 2001). Thus an important goal on the interface between basic and applied ecology is to understand the ecology of potentially damaging invasive predators (including omnivores), in order to minimize their negative impacts.

To understand the ecology of invasions, it is useful to distinguish and study dynamics in each of several stages in an invasion and potential recovery (Moyle and Light 1996; Kolar and Lodge 2001, 2002).

1. Establishment and spread – what is the basic pattern of establishment and spread of an exotic species? What factors allow or even facilitate establishment and spread, and what conditions pose barriers to further spread?
2. Impacts on native biota – does a given invader have strong (or weak) impacts on the native community, and what characteristics of the invader or invaded species tend to result in stronger (or weaker) impacts?
3. Restoration and recovery – if we can remove and exclude exotics, how rapidly and effectively does the native biota recover after exotics are removed, and what factors influence the pattern of recovery?

In each stage, the first step towards understanding the system and ultimately towards informed management is to document patterns. What is the pattern of establishment and spread? Which invaders have greater impacts on which prey? How well do prey communities recover after exotic predators are removed? Step two is to then study mechanisms explaining these patterns. For example, for impacts, if two exotic predators differ in their impacts on native communities, and each has greater impacts on some prey than others, what aspects of the predator-prey interaction explain these patterns? A time honored method for explaining population/community patterns is to study behavioral interactions among focal species (Sih et al. 1992; Hill and Lodge 1999). For example, to explain relative impacts of different invaders on various prey, it is important to understand predator-prey behavior. A recent review noted the potentially great value of more detailed study of behavior in invasion ecology (Holway and Suarez 1999). Overall, a mechanistic, multi-stage approach seems clearly valuable for addressing issues in both the basic and applied ecology of invasions..

Our focus is on the invasion ecology of exotic crayfish in California. Throughout much of the world, crayfish are key invaders that are having large impacts on freshwater communities (Lodge

et al. 2000). Crayfish are active, generalist omnivores (they consume plants, animals and detritus) that can thus function as keystone consumers that both directly and indirectly impact multiple trophic levels. Since they are avid predators on eggs and larvae, they can have important, negative effects on animals that, as adults, are much larger than crayfish. Part of the strong impact of crayfish might come from their potentially large per capita effects, but the overall effect appears to be due in part to their capacity to become very abundant. We are thus interested in evaluating both their per capita impacts and how their overall impacts might depend on their ability to attain high densities.

In California, different exotic crayfish species are spreading throughout northern vs. southern California. In northern California, the signal crayfish, *Pacifasticus leniusculus*, has been introduced from the north primarily through bait bucket introduction. In southern California, the red swamp crayfish, *Procambarus clarkii*, has been introduced from the eastern United States via aquaculture and bait bucket introductions. Both species are having strong, negative effects on native taxa – in particular, on amphibian larvae and native crayfish (Gamradt et al. 1997; Ellis 1999; Light et al. 1995). In northern California, the spread of the signal crayfish is considered the single, greatest threat to the continued existence of the federally and state-listed endangered Shasta crayfish, *Pacifasticus fortis*. In both northern and southern California, invasive crayfish appear to be important contributors to amphibian decline (Gamradt et al. 1997; Kerby et al. 2005). Amphibian decline is, of course, an issue of global concern (Houlahan et al. 2000).

We used a blend of field surveys, landscape-level, GIS-based distributional analyses, controlled experiments in mesocosms, and field experiments to study the invasion ecology of exotic crayfish in both northern and southern California. Specifically, we examined the following key factors influencing dynamics in each of the stages of the invasion. In brief, we:

- 1) Developed a quantitative model for assessing factors that influence patterns of crayfish spread across the landscape using sophisticated statistical analyses of GIS-based, landscape level databases coupled with crayfish distributional data. Our analyses examined the effects of human recreation sites (as a source of crayfish introduction), basic stream physical characteristics, and stream connectivity on patterns of crayfish presence in focal regions of both northern and southern California.
- 2) Compared the impacts of two exotic crayfish on a range of prey. In particular, we contrasted the effects of two exotic, nuisance crayfish, the signal crayfish (in northern California), and the red swamp crayfish (in southern California) on representative prey found in both regions. These effects were evaluated using a blend of field surveys and mesocosm experiments. Extensive behavioral observations elucidated the mechanisms underlying relative impacts of different crayfish on different prey.
- 3) Examined the recovery of native communities following removal of exotic crayfish. Specifically, we conducted removals of crayfish from streams containing natural or artificial barriers and monitored the change in the native stream communities for two years following the initial removal. Because our focal exotic crayfish are often found in small streams, it was physically feasible to remove the great majority of them from relevant stream stretches. We hypothesized that the prey community's evolutionary history with crayfish (or lack of it) might

affect the pattern of recovery. Therefore, we addressed this issue by comparing community recovery in two regions where crayfish were historically absent (southern California, and some areas of northern California) versus where exotic crayfish have recently replaced native crayfish (other regions of northern California). In all three regions, we quantified the pattern of recovery over 2 years after initial crayfish removal.

Together, these studies should yield both a substantial increase in our mechanistic understanding of the ecology of crayfish invasions, and provide practical information for managers on preventing spread, predicting impacts, and targeting sites for restoration. Furthermore, this research should significantly enhance our general understanding of animal invasions and impacts in a spatially patchy environment, and illustrate a general framework for an integrative, multi-stage study of invasion ecology.

Study Design & Methods

Component 1: Establishment and Spread

Goals: To understand the roles of human recreation (fishing and release of crayfish as bait), basic stream physical characteristics, and stream connectivity in explaining the present distribution and spread of exotic crayfish.

The basic methodology involved collecting and organizing information on the distribution of crayfish, and on factors that could influence crayfish introduction and spread. Factors being explored include: 1) commonly used recreational fishing sites; 2) stream slope and upstream area; 3) stream substrates; 4) stream connectivity; and 5) locations of potential barriers to crayfish spread (e.g., waterfalls, culverts). Standard distributional mapping statistics will then be used to find the best model for explaining observed crayfish distributions. This basic design is being implemented in two regions: 1) the region of northern California where the signal crayfish and Shasta crayfish are both found; and 2) another region in north-central California where signal crayfish are present, but not Shasta crayfish.

Component 2: Impacts on Prey

Goals:

- 1. To compare the impacts of two exotic crayfish on typical California stream communities.*
- 2. To evaluate whether differences among crayfish species in their impacts on a standardized prey community are due to differences in individual predator abilities or to differences in typical densities.*
- 3. To examine key predator-prey and aggressive behaviors underlying variations among crayfish species in their impacts on different prey.*

We addressed the above issues using a blend of field surveys and mesocosm experiments:

A) Field surveys:

Detailed field surveys were conducted to estimate exotic crayfish impacts by contrasting aquatic communities in stream stretches with vs. without exotic crayfish, and with varying abundances of exotic crayfish. Six, evenly spaced transects were established in an approximately 90m stretch of stream. Within each transect, several types of samples were taken. In northern California streams, estimates of fish and crayfish densities were obtained by visual, snorkel surveys in 3, 1-m² plots within each transect (18, 1-m² plots total per stream stretch).

All crayfish seen were captured, identified to species, sexed, measured (carapace and chelae length) and released. Fish were identified to species and their size estimated by observation.

In southern California, fish, crayfish and amphibians were sampled using a standard kick-net sample within each transect. If the transect was less than 5 meters, only one sample was taken per transect. Otherwise, three 1-m² samples were taken within each transect. All crayfish captured were identified to species, sexed, measured (carapace and chelae length) and released. Fish and amphibians were also identified to species, measured (standard length for fish, snout vent length for amphibian larvae) and released.

In both northern and southern California, benthic invertebrates were sampled using a d-frame net (1 um mesh net). Three, 1 ft², evenly spaced samples were taken within each transect (18 samples total) and preserved in 95% ethanol for identification in the laboratory. Snail densities were estimated by visual counts in three 0.25-m² plots within each transect. Additionally, periphyton samples (10 cm diameter) from 3 randomly sampled rocks per transect. Periphyton samples were taken to the laboratory for algal biomass (using Ash Free Dry Mass) measurements.

The stream's profile (width and depths) was quantified at three spots in each transect, and various abiotic variables (flow velocity, temperature, pH, conductivity, salinity, dissolved oxygen, and alkalinity) were measured (using a flow meter and a YSI meter) at three evenly spaced points along each transect. Substrate type was characterized in three 1 –m² plots along each transect. Finally, the GIS coordinates of each site were recorded.

Statistical analyses will include MANCOVAs comparing aquatic communities in stream stretches with versus without crayfish, using physical variables as covariates, non-metric multi-dimensional analyses (NMDAs) to characterize communities in different stream stretches in a coordinate space, and multiple regressions to examine relationships between crayfish density and measures of either the density of specific taxa or of the entire community.

These field surveys were done in 6 stream stretches with exotic crayfish and 6 stretches without crayfish in each of the same three regions of southern and northern California where we did surveys and removals for components 1 (northern CA only) and 3 (i.e., a total of 36 stream stretches).

B) Mesocosm experiments: The three goals of this component are to evaluate the impacts of two invasive crayfish species, examine effects of crayfish density, and study underlying behavioral mechanisms. Because of thermal tolerance differences between the two invasive crayfish species, experiments on each species had to be run separately.

1. Northern California species, Pacifastacus leniusculus

Our basic experimental design for the northern CA species, *P. leniusculus* was a two factor design manipulating crayfish density (4 and 12/ m²) and crayfish population (American River & Crystal Lake), along with a no crayfish control. Two populations of *P. leniusculus* were collected by hand from the American River (Sacramento Co., CA) and from the outflow of Crystal Lake (Shasta Co., CA). Prior to the start of the experiment, crayfish were held in aerated aquaria and fed daily with TetraMin Granules.

The prey community used represented a typical prey community in northern California streams invaded by *P. leniusculus*. Snails were collected by sweep nets in Hat Creek (Shasta Co. CA). The two dominant snail species were used; *Fluminicola sp.* and *Juga sp.* The two species were added to the tanks in a 3:1 ratio, as indicated from field surveys across ~30 streams in

northern California. Benthic invertebrates used in the experiment included chironomids, water boatman, zooplankton and damselflies that had naturally colonized the mesocosm tanks from nearby streams in the Sacramento River drainage.

We used a one-factor design, manipulating crayfish density (4 crayfish/pool & 12 crayfish/pool), along with a no crayfish control in replicate mesocosm pools. Experiments were run in four outdoor, semi-natural streams housed at the Center for Aquatic Biology and Aquaculture at the University of California at Davis. Each stream consists of 5 pools (each 1.5 m diameter filled to a depth of 40 cm; a total of 20 pools) connected by gravel-filled riffles (1.3 m long, 30 cm wide). Pumps recirculate water through each stream. Water cascades into each pool, and exits through a screen thus preventing benthic prey from dispersing from a given pool. Each pool thus serves as a replicate unit. Each pool was also provided with 6 PVC pipes that served as refuge for crayfish and prey. The set of streams are housed under a screen tent (to keep out birds and reduce overheating) with natural lighting augmented if necessary by fluorescent lights. Such streams have been used for conducting numerous experiments on predator-prey interactions among aquatic organisms (e.g., Sih and Krupa 1995; Sih et al. 2002).

Snails were added to each pool in equal densities and allowed to acclimate and disperse throughout for two days prior to the addition of crayfish. Crayfish were measured (carapace and chelae length, mm), weighed (grams) and individually marked prior to being added to the experiment. Crayfish were segregated by sex into a small (25-35mm carapace length) and large (40-50mm carapace length) group. Crayfish were added in equal proportions of sex and size group in the appropriate treatment densities, (i.e. low density treatment: one small male and female and one large male and female). Experiments looking at the agonistic behavior of crayfish typically size match pairs of crayfish within 5mm of each other. However, we felt that size matching all crayfish within 5mm of each other would inflate aggression estimates as it would likely take more interactions and higher levels of aggression to establish a dominance hierarchy within the tank. Therefore, we chose to use a wider range of sizes to better reflect the range of sizes in natural communities. Treatments were randomly assigned to the tanks and replicated six times over two time blocks (3 replicates/block).

a) Impacts on Typical Prey Community & Algae

To assess the impacts of the crayfish treatments on prey, snails and benthic invertebrates were sampled prior to the addition of crayfish and at the end of the experiment. For snails, three samples were taken; two on the sides of the tanks and one on the bottom. Three benthic invertebrate samples were taken using an aquarium net in a transect across the middle of the pool. Drift nets at the end of the riffles were sampled during the second week of the experiment. Drift nets were cleaned and then sampled 24 hours later. Impacts on algal biomass were also estimated by sampling 3, 1 ft-long, 1 ½ inch PVC pipes in each replicate pool. PVC pipes were scrubbed clean and bleached prior to the start of the experiment. At the end of the experiment, algae was scraped from each PVC pipe and analyzed by estimating Ash Free Dry Mass.

b) Baiting Experiment

Baiting assays were conducted over the course of the two week experiment (four replicates total). Prior to the start of the assay, crayfish location and activity was recorded. The trial started after a piece of bait (1/3 of a canned sardine) was placed in the middle of the tank. Observations were made for 15 minutes. Behaviors recorded included: time until a crayfish recruited the bait, proportion of active crayfish, the number of interactions between crayfish and

the highest level of aggression attained during the interaction. Aggression was scored based on scoring adapted from Karavanich & Atema (1998).

c) Measurement of Crayfish Dispersal

Crayfish dispersal out of the tanks was estimated by counting the number of crayfish missing from the tanks after the first three mornings of the experiment. After three days, nets were securely placed over each tank to prevent crayfish from dispersing.

d) Crayfish Growth

No crayfish molted over the course of the two week experiment. Therefore, at the end of the experiment only weight was measured and used to calculate growth over the experiment. Also, densities of crayfish were monitored each morning and any individual that was missing after two days was replaced to maintain equal densities of crayfish throughout the experiment. However, crayfish that were replaced were not included in final growth measurements.

*2. Southern California species, *Procambarus clarkii**

For the southern CA species, *P. clarkii* we used the same experimental design, but instead had three levels of crayfish density (4, 8 and 12/m²), along with a no crayfish control. Crayfish were collected from Trancas Creek in Los Angeles County, CA). The same experimental set-up was applied as described for the experiment with *P. leniusculus*, but with the following additions or changes:

1. Each treatment was stocked with 30 *Hyla regilla* tadpoles. Numbers of tadpoles remaining were counted and staged.
2. One additional snail species was added to the prey community; *Physa heterostropha*.

Component 3: Removals, Barriers and Recovery

Goals:

1) To document the pattern of community recovery following the removal and exclusion of exotic crayfish.

2) To compare community recovery following removal of exotic crayfish from streams in southern versus northern California, and in northern California, from streams that originally had native crayfish (before invasion by the signal crayfish) versus those that did not.

3) To generate information on the efficacy of natural and artificial barriers in blocking recolonization of stream stretches by exotic crayfish.

We conducted removal experiments in 6 stream stretches in each of three regions (a total of 18 stream stretches): 1) the Santa Monica Mountain watershed (in southern California) where *P. clarkii* is invading streams that previously had no crayfish; 2) the Pit and Fall River, and Hat Creek drainage (in northern California) where signal crayfish are invading streams where Shasta crayfish were historically present; and 3) the Pit and Fall River, and Hat Creek drainage (in northern California) where signal crayfish have invaded into previously crayfish-free streams. In each region, 3 stream stretches had exotic crayfish removed, while the other three served as

controls with no crayfish removal. All stream stretches were associated with existing barriers which limited crayfish recolonization. In total, we removed exotic crayfish from 9 stream stretches, and compared these to 9 stream stretches with no crayfish removed.

In northern California, exotic *P. leniusculus* were removed from a stream stretch by snorkeling and hand removal. This method proved to be the most effective at removing crayfish, as *P. leniusculus* appear to avoid baited crayfish traps (Pintor & Ellis, personal observation). Additionally, hand removal was the most sensitive removal method for site that contained the endangered Shasta crayfish (*P. fortis*). In southern California, exotic *P. clarkii* were removed from a stream with baited traps and nets. In both locations, removals took place over a series of three days in order to estimate the initial density of crayfish present in this reach. Although ideal, complete removal was not necessary as previous studies have indicated that organisms, such as amphibians, can co-exist with invasive crayfish as long as crayfish densities are reduced. Baseline conditions (i.e., numbers of crayfish, amphibians, fish, other invertebrates, algae, and basic physical variables) were assessed prior to crayfish removal as part of the field survey described in component 2. All treatments were applied in the first year of the project and continued for one additional years to measure the cumulative impacts of crayfish removal. During the main field season (May- October), aquatic communities and physical variables in each stream stretch were resampled (and exotic crayfish numbers re-reduced, as necessary), every 3 weeks. Because recovery within the streams will be measured repeatedly over time a repeated-measures MANOVA with planned contrasts will be used to test for the effects of crayfish removal and region on community recovery.

Preliminary Results & Analyses to Date

Component 1: Establishment and Spread

Use of geographical information systems (GIS) in support of the project has been implemented in three distinct arenas: data compilation, watershed characterization, and site selection. Data compilation has consisted of standardizing existing geodatasets into a common analytical framework using the ArcGIS personal geodatabase format with a common coordinate projection and datum. These synoptic data include many comprehensive data stores available from partnering land management agencies, such as vegetation and lakes. Value-added geodata are largely derived from digital elevation models developed by United States Geological Survey at a 10m resolution; slope, aspect, flow direction, and drainage area are a few of the value-added data in the compilation that are comprehensive for the upper Sacramento and lower Pit River complexes. From these data, we generated a suite of watershed characteristics that we feel are indicative of process and land use on the landscape, including dominant land use / land cover, drainage area, and stream gradient. Furthermore, we leveraged these watershed characteristics to identify spatial gaps in our coverage of field collection activities; thus, we were able to augment and complement prior collection efforts with GIS-derived site selections that created a more balanced field collection framework.

Component 2: Impacts on Prey

Field Surveys:

All field surveys have been completed related to assessing the impacts of both species of exotic crayfish, *P. leniusculus* and *P. clarkii*. Field data for both the northern and southern CA components have been entered into a database. Invertebrate samples collected as part of the surveys have been processed and analyzed for the southern CA surveys. For the northern

CA surveys, invertebrate samples have all been processed. Algae samples for both the northern and southern CA surveys have also been processed and analyzed.

To date, exploratory data analyzes for some of the data from the northern California surveys have been conducted. Initial results indicate that unfortunately for the endangered *P. fortis*, densities of *P. leniusculus* are significantly higher in streams with *P. fortis* than in streams that historically did not have crayfish prior to the invasion of *P. leniusculus* (Figure 1). Initial analyses of snail densities from the stream surveys indicates that snail densities are highest in streams that have endemic *P. fortis*, but have not yet been invaded by *P. leniusculus* (Figure 2). Sites that contain *P. fortis*, but have now been invaded by *P. leniusculus* had significantly lower densities of snails, suggesting that *P. leniusculus* has a negative impact on snail prey. Sites that historically did not contain crayfish had very low densities of snails overall. Sites that had been invaded by *P. leniusculus*, however, did have higher snail densities in comparison to sites that had not been invaded by *P. leniusculus*. This might suggest that snail densities (a preferred prey item of crayfish) might limit the establishment of *P. leniusculus* in some streams. Specific analyses for the field surveys from both regions are on-going and are anticipated to be completed within the year.

Mesocosm Experiment:

Northern California: Impacts of P. leniusculus

There were no population level differences therefore, populations were combined and analyzed for differences between density treatments. Results of the mesocosm experiment indicate that *P. leniusculus* does have a negative impact on typical prey communities and that as density of crayfish increases, so does the impact on both benthic invertebrates and snails. Specifically, *P. leniusculus* had a significant negative impact on benthic invertebrate prey (chironomids, water boatman & zooplankton), and that impacts were greatest in the high density treatment (Figure 3). *P. leniusculus* also had a significant impact on the proportion of benthic invertebrates that drifted downstream from the mesocosm pool (Figure 4). This indicates that not only do they directly impact the density of prey through consumption, but also affect the behavior of prey as well. The same general pattern was seen for the two snail species in the experiment, *Fluminicola sp.* and *Juga sp.* More snails were consumed in the high density treatment in comparison to the low density or control treatment (Figure 5). Additionally, there did not appear to be a preference for either snail species as there were no significant differences in the proportion of snails consumed between the two species. For *Juga sp.* there was not a significant difference in the proportion of snails consumed between the low and control treatment. *Juga sp.* is a much larger species than *Fluminicola sp.* and might have a slight size refuge from crayfish predators at low densities when predation pressure is not as high on *Juga sp.*

However, the per capita consumption per crayfish did not differ between the low and high density treatments. This indicates that an individual crayfish was consuming the same number of prey regardless of the density of crayfish competitors. Specifically, there was not a significant difference in the per capita consumption of benthic invertebrates between the low and high density treatments of crayfish (Figure 6). The same was true for both snail species; there was no significant difference in per capita consumption of either species of snails, nor an interaction between density and snail species (Figure 7). The lack of a difference in the per capita consumption of prey between the low and high density treatments likely contributed to

crayfish in low and high density treatments growing the same amount by the end of the experiment (Figure 8).

Results of the behavioral assays provided some indication of the mechanisms underlying the patterns of impact by *P. leniusculus* on prey communities. During the behavioral assays, there were significantly more aggressive interactions between crayfish in the high density treatment as compared to the low density treatment (Figure 9). The null expectation was that there would be three times as many interactions between crayfish in the high density treatment than in the low density treatment given that there were three times as many crayfish. However, results indicated that there were twenty-six times more interactions between crayfish in the high density treatment in comparison to the low density treatment. During these interactions, crayfish in the high density treatment were significantly more aggressive in interactions in comparison to the low density treatment (Figure 10). Specifically, crayfish were seven times more aggressive than crayfish in the low density treatment. Additionally, crayfish in the high density treatment were faster to recruit to the bait than crayfish in the low density treatment (Figure 11). Along with that result, crayfish in the high density treatment were also more active than crayfish in the low density treatment (Figure 12).

Together these behavioral results suggest that density acts synergistically with behavior to exacerbate the impacts that *P. leniusculus* have on native prey communities. As density of crayfish increases, their behavior shifts and crayfish become more aggressive and active. This aggressive and increased activity likely underlies the maintenance of per capita consumption of prey as competition between crayfish increases at high densities. Additionally, these behavioral shifts also may influence the rate of dispersal by *P. leniusculus*. During the experiment, crayfish in the high density treatment dispersed more from the tanks than crayfish in the low density treatment (Figure 13). Therefore, not only do these shifts in behavior lead to larger impacts on native communities, but they also increase the rate of spread of this invasive crayfish.

Southern California: Impacts of P. clarkii

Data for the mesocosm experiment on *P. clarkii* have been processed and entered, but have not yet been analyzed. However, impressions from the experiment suggest that *P. clarkii* have more negative impacts on native prey communities than *P. leniusculus*, particularly at high densities. *P. clarkii* appeared to be much more aggressive than *P. leniusculus*, particularly as density of crayfish increased. There seemed to be a significantly high level of interactions between crayfish, as well as a higher level of activity, particularly as density of *P. clarkii* increased. This shift in behavior likely led to higher total impacts, as well as the higher per capita impacts by *P. clarkii*. Sampling of the benthic invertebrate community & the snail community at the end of the experiment found many replicates of the high density treatments with densities near zero. Additionally, analysis of the algae samples from the experiment suggest that *P. clarkii* cause a trophic cascade. Impressions from analysis of the algae samples suggest that algal biomass was highest in the high density treatment and lowest in the low density treatment. Therefore, high densities of crayfish reduce densities of grazing invertebrates, thereby increasing biomass of algae. Finally, surprisingly, despite this higher level of activity, aggression, along with the depletion of prey resources, *P. clarkii* did not disperse from the tanks at all in comparison to *P. leniusculus*.

Component 3: Removals, Barriers and Recovery

Removal experiments were conducted in both northern and southern California over the 2004 and 2005 field seasons. Exotic crayfish were removed over the course of two field seasons with 6 streams in northern CA and 3 streams in southern California. Removal and control stretches of all streams were sampled once before removal and twice following the removal in both years. Field data collected during the pre & post-removal surveys has been entered into a data base. Periphyton samples from both northern and southern California have been processed and entered into the database. Invertebrate samples from the southern California removal experiment have been processed, analyzed and entered into the database. Invertebrate samples from northern California have been processed.

Our impressions from the experiment are that the removals were effective at reducing the densities of invasive crayfish and that the barrier present at each site were also effective in limiting the recolonization by crayfish. Additionally, our impressions are that sites that had the highest densities of invasive crayfish will likely have the greatest degree of recovery of the native prey community.

Literature Cited

- Ellis, M.J. Species invasions and replacements in a native crayfish community. Dissertation. University of Michigan, Ann Arbor, Michigan, USA.
- Enserink, M. 1999. Biological invaders sweep in. *American Association for the Advancement of Science* 285: 183
- Gamradt, S.C. and L.B. Kats. 1996. Effect of introduced crayfish and mosquitofish on California newts. *Conservation Biology* 10(4): 1155-1162.
- Gamradt, S.C., L.B. Kats and C.B. Anzalone. Aggression by non-native crayfish deters breeding in California newts. *Conservation Biology* 11(3): 793-796.
- Hill, A.M. and D.M. Lodge. 1999. Evaluating competition and predation as mechanisms of crayfish species replacements. *Ecological Applications* 9:678-690.
- Holway, D.A. and A.V. Suarez. 1999. Animal behavior: an essential component of invasion biology. *Trends in Ecology and Evolution* 14(8): 328-330.
- Houlahan, J., C. S. Findlay, B. R. Schmidt, A. H. Meyer and S. L. Kuzmin. Quantitative evidence for global amphibian population declines. *Nature* 404 (6779): 752-755.
- Karavanich, C. and J. Atema. 1998: Individual recognition and memory in lobster dominance. *Animal Behaviour* 56: 1553-1560.
- Kerby, J. L., S. Riley, L. B. Kats and P. Wilson. 2005. Barriers and flow as limiting factors in the spread of an invasive crayfish (*Procambarus clarkii*) in southern California streams. *Biological Conservation* 126(3): 402-409.
- Knapp, R. A., K. R. Mathews and O. Sarnelle. 2001. Resistance and resilience of alpine lake fauna to fish introductions. *Ecological Monographs* 71:401-421.
- Kolar, C.A. and D.M. Lodge (2001). Progress in invasion biology: Predicting invaders. *Trends in Ecology and Evolution* 16(4): 199-204.
- Kolar, C. S. and D. M. Lodge (2002). "Ecological Predictions and Risk Assessment for Alien Fishes in North America." *Science* 298(5596): 1233-1236.
- Light, T., D.C. Erman, C. Myrick and J. Clarke. 1995. Decline of the Shasta crayfish (*Pacifastacus fortis* Faxon) of Northeastern California. *Conservation Biology* 9(6): 1567-1577.
- Lodge, D.M., M.W. Kershner, J.E. Aloï, and A.P. Covich. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology* 75(5): 1265-1281.
- Lodge, D.M., C.A. Taylor, D.M. Holdich, and J. Skurdal. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: Lessons from Europe. *Fisheries* 25(8): 7-19.
- Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout and F. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications* 10:689-710.
- Moyle, P.B. and T. Light. 1996. Fish invasions in California: Do abiotic factors determine success? *Ecology* 77(6): 1666-1670.
- Parker, J.M., D. Simberloff, W.M. Lonsdale, K. Goodell, M. Wonham, P.M. Kareiva, M.H. Williamson, B. Von Holle, P.B. Moyle, J.E. Byers and L. Goldwasser. 1999. Impact: assessing the ecological effects of invaders. *Biological Invasions* 1:3-19.
- Pimentel, D., L. Lach, R. Zuniga and D. Morrison. 2000. Environmental and economic costs of non-indigenous species in the United States. *Bioscience* 50:53-65.

- Sala, OE, FS Chapin III, JJ Armesto, R Berlow, J Bloomfield, R Dirzo, E Huber-Sanwald, LF Huenneke, RB Jackson, A Kinzig, R Leemans, D Lodge, HA Mooney, M Oesterheld, NL Poff, MT Sykes, BH Walker, M Walker, DH Wall 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770-1774.
- Sih, A., Lauer, M. and Krupa, J. J. 2002. Path analysis and the relative importance of male-female conflict, female choice and male-male competition in water striders. *Animal Behaviour* 63(6): 1079-1089.
- Sih, A. and Krupa, J. J. 1995. Interacting effects of predation risk and male and female density on male/female conflicts and mating dynamics of stream water striders. *Behavioral Ecology* 6 (3): 316-325.
- Sih, A., L.B. Kats and R.D. Moore. 1992. Effects of predatory sunfish on the density, drift and refuge use of stream salamander larvae. *Ecology* 73: 1418-1430.
- Vitousek, R.M., C.M. D'Antonio, L.L. Loope and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468-479.

Figures

Figure 1.

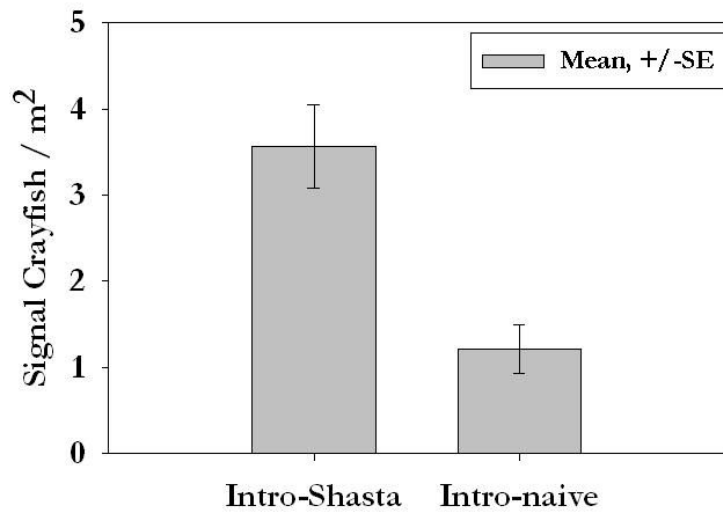


Figure 2.

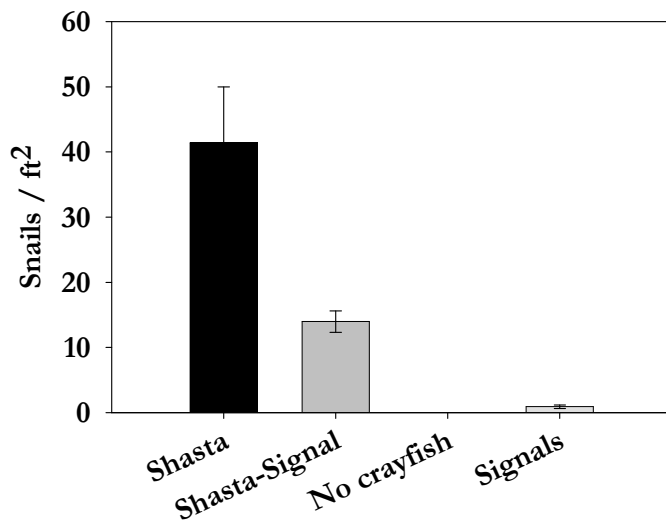


Figure 3.

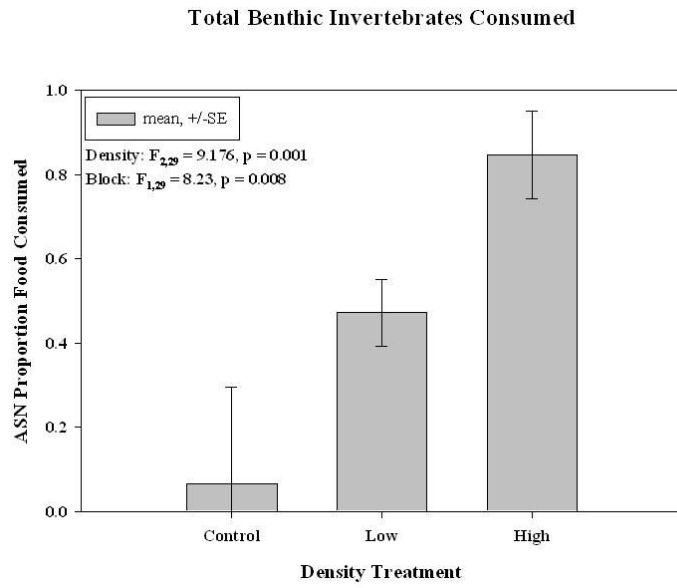


Figure 4.

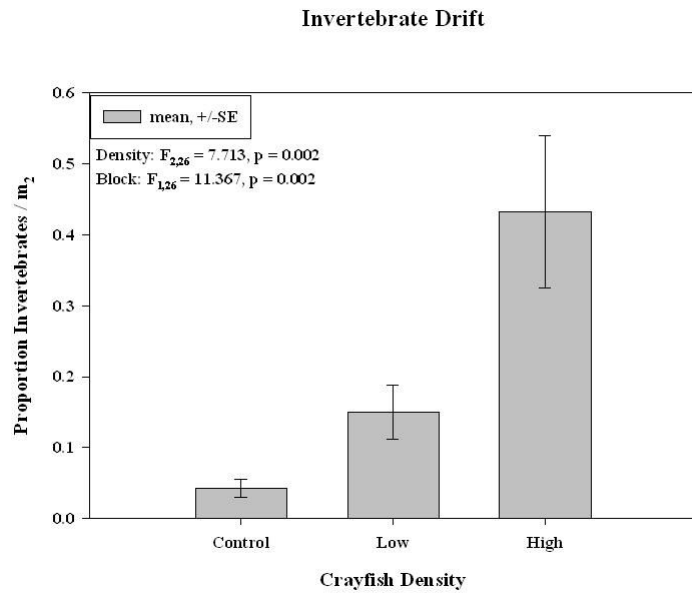


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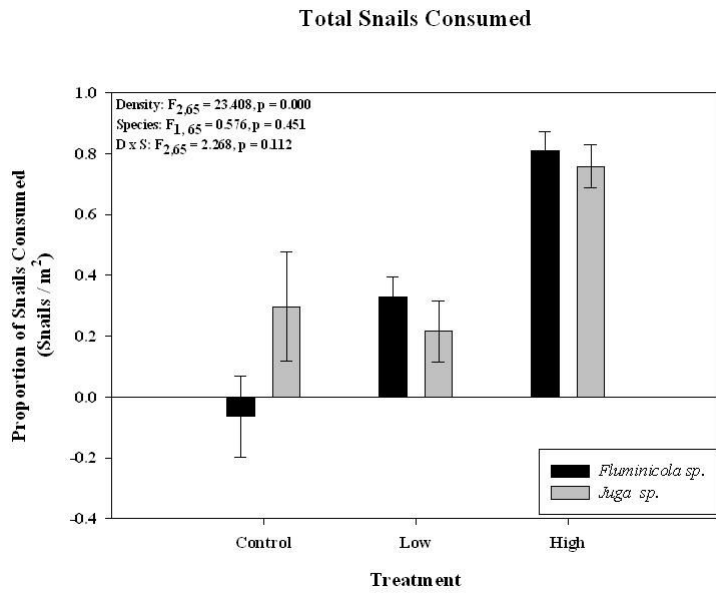


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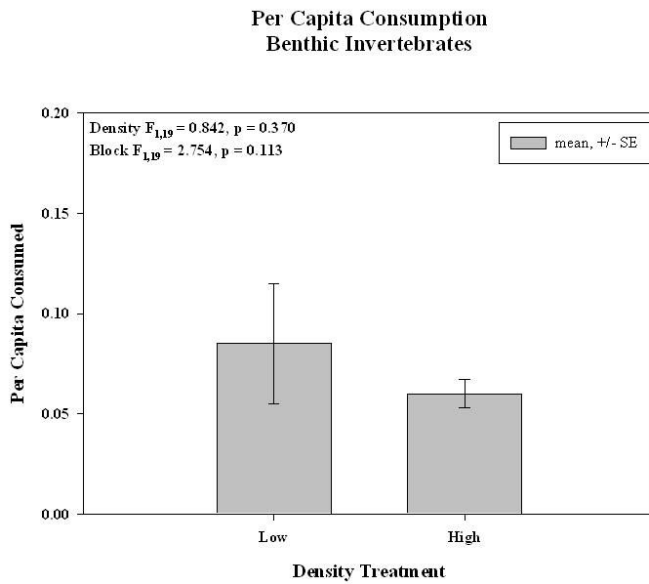


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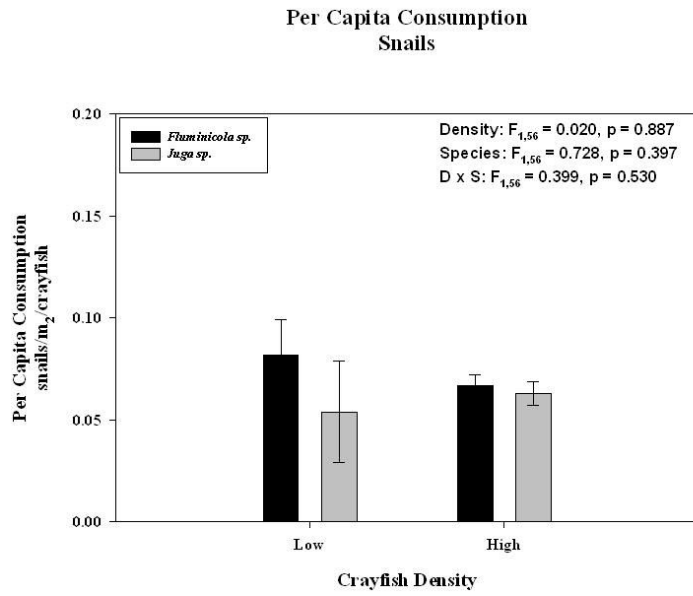


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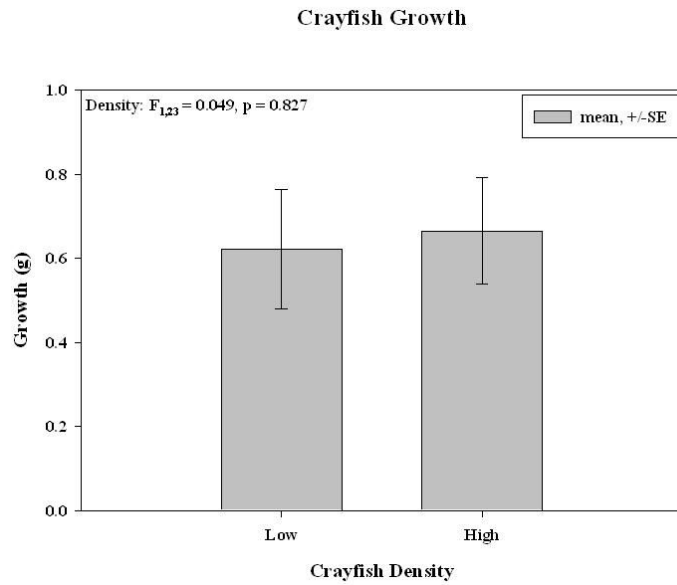


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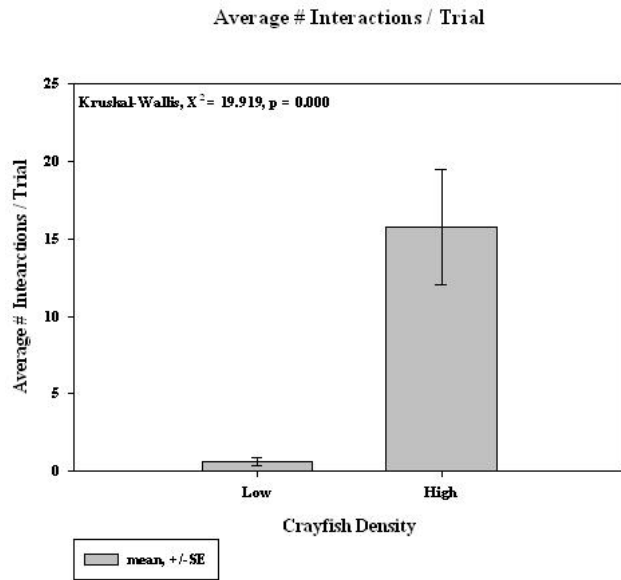


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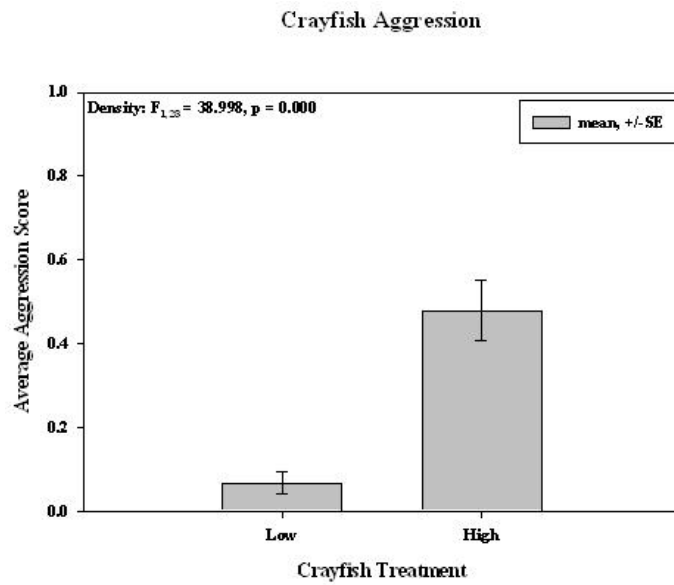


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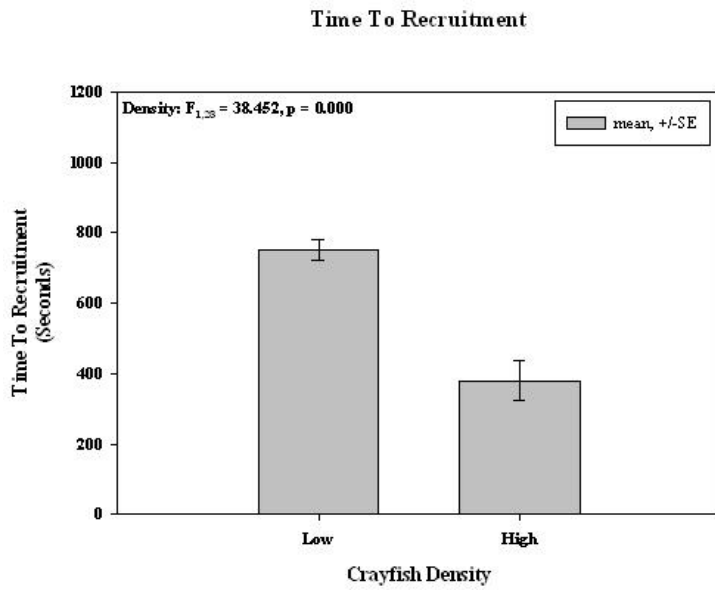


Figure 12.

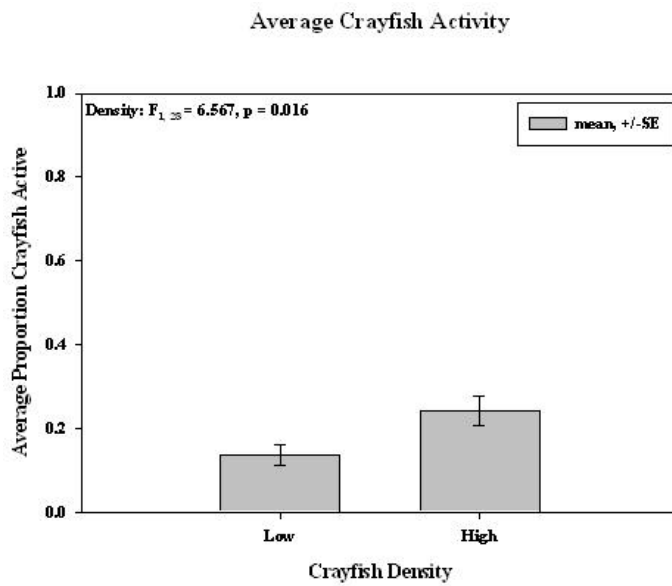


Figure 13.

