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Barriers and flow as limiting factors in the spread of an invasive crayfish (*Procambarus clarkii*) in southern California streams

Jacob L. Kerby [a,*], Seth P.D. Riley [b], Lee B. Kats [c], Paul Wilson [d]

[a] *Department of Environmental Science and Policy, 1 Shields Ave., University of California, Davis, CA 95616, USA*
[b] *Santa Monica Mountains National Recreation Area, National Park Service, 401 W. Hillcrest Dr., Thousand Oaks, CA 91360, USA*
[c] *Natural Science Division, 24255 Pacific Coast Highway, Pepperdine University, Malibu, CA 90263-4321, USA*
[d] *Department of Biology, 18111 Nordhoff St., California State University, Northridge, CA 91330-8303, USA*

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Abstract

Invasive crayfish are a major threat to stream ecosystems, yet research has seldom identified successful ways of preventing their spread. Thirty-two stream sections were surveyed during 2000 and 2001 in the Santa Monica Mountains of southern California to determine the distribution of the invasive crayfish *Procambarus clarkii*. Streams with large barriers (waterfalls, culverts) often did not have crayfish present upstream of barriers. A mark-recapture study indicated that *P. clarkii* moved both up and downstream between pools, but that barriers significantly reduced movement between pools. Seasonal high flow velocities likely increase passive movement downstream and reduce movement upstream. Results indicate that crayfish mainly spread downstream from a point of colonization and are restricted in their movement to adjacent upstream sections by both natural and artificial barriers. We suggest management strategies for removing invasive crayfish and reducing their spread by focusing on smaller stream segments that are bounded by a downstream barrier and by timing removal efforts to follow large flow events.

Keywords: Exotic; Barriers; Dispersal; Amphibian; Crayfish; Invasive

1. Introduction

Invasive species pose a threat to the integrity of many natural communities, and limiting their spread is a major challenge to conservation (Elton, 1958; Simberloff and Stiling, 1996). There is extensive documentation of the negative impacts of predatory invasive species that extend across several trophic levels (Carpenter et al., 2001). For example, non-native predators can influence prey abundance and distributions (Fraser et al., 1995; Schoener et al., 2001), as well as increase competition between top consumers (Nakano et al., 1998). Although generalities about the effects of non-native predators have emerged from such research, practical information on how to control invasive populations is lacking and must be sought on a case-by-case basis. For many invasive species, eradication or limiting spread might prove impossible. Indeed, some populations have become well established and now function as an integral part of the community such that eliminating them would cause further degradation (Simberloff and Stiling, 1996; Zavaleta et al., 2001). While elimination may be difficult, removal efforts could contain or reduce some invasive populations, potentially lessening negative impacts. Understanding factors that limit the distribution of invasive species could play a key role in reducing their effects on native communities.

Previous studies indicate that barriers such as waterfalls limit the movement of aquatic species within streams. Both natural and artificial barriers in rivers and streams negatively affect many native organisms

* Corresponding author. Fax: +1 530 752 3350.
E-mail address: jlkerby@ucdavis.edu (J.L. Kerby).

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by interfering with dispersal mechanisms (Utzinger et al., 1998; Benstead et al., 1999; Luttrell et al., 1999; Joy and Death, 2001). Although barriers in lotic systems are known to negatively influence native species, the same barriers may protect many systems from invasion by non-native species. Waterfalls prevent the upstream dispersal of invasive fishes (Sabo and Pauley, 1997) and often are used as presumed barriers in comparative stream studies of non-native predators (Endler, 1991; Fraser et al., 1995). Intentionally introduced barriers have been effective at limiting upstream movement of lampreys and fishes (Novinger and Rahel, 2003; Porto et al., 1999). Another type of "barrier" to upstream movement may be high water velocities. Several studies have linked water flow patterns to abundances of non-native aquatic species (Acosta and Perry, 2001; Light, 2003). In this study, we examine the role of barriers in the distribution of an invasive crayfish species in the Santa Monica Mountains of southern California.

Crayfish possess many characteristics of successful invaders and can greatly alter native communities (Lodge, 1993; Holway and Suarez, 1999). They are able to live in a wide variety of harsh, abiotic conditions (Holdich, 2002) and are highly aggressive, often actively antagonizing native organisms (Hill and Lodge, 1999). Crayfish are predatory omnivores and can have impacts across multiple trophic levels. For example, non-native crayfish can alter the biomass of native aquatic plants (Chambers et al., 1990; Creed, 1994), and can reduce populations of native invertebrates through predation and competition (Olsen et al., 1991; Lodge and Hill, 1994).

One invasive crayfish of increasing concern is the red swamp crayfish, *Procambarus clarkii*. This species is native to the southeastern United States but has been introduced worldwide. It is spreading throughout the US and in many other countries, including Japan, Italy, and Portugal (e.g., Adao and Marques, 1993; Lane and Fujioka, 1998; Gherardi et al., 2000). Much of the spread may be attributed to the popularity of crayfish as a food item and as a source of fish bait. For example, this species is harvested for commercial use and accounts for 85–90% of the world's annual crayfish consumption (Huner, 1997).

The introduction of *P. clarkii* has had a significant negative effect on invaded communities at several trophic levels. This species adversely affects native flora and fauna through both predation and competition (Carral et al., 1993). *P. clarkii* can also be a vector for disease and can alter native crayfish populations (Gil-Sanchez and Alba-Tercedor, 2002). The presence of *P. clarkii* can significantly alter amphibian species assemblages (Beja and Alcazar, 2003), and impact both aquatic invertebrates and macrophyte communities (Ilheu and Bernardo, 1993; Ilheu et al., 2000).

P. clarkii is found in many streams in the Santa Monica Mountains (Los Angeles and Ventura Counties, California). Stream surveys in the area indicate that newts have been replaced by invasive crayfish in several streams (De Lisle et al., 1987; Gamradt and Kats, 1996). Concern over the decline of the California newt in southern California is increasing, and experimental studies have shown that *P. clarkii* actively deter newts during the breeding season in several southern California streams (Gamradt et al., 1997). There has been little research on the impacts of crayfish on other native animals in the Santa Monica Mountains, yet it is likely that the impacts are manifold. Given these potential effects and the fact that crayfish represent a relatively recent introduction, efforts to control *P. clarkii* populations should be examined and successful methods incorporated into land management. Although there is considerable literature on the impacts of *P. clarkii* as an invasive species, little of it has focused on how to control its spread.

The goal of this study was to identify methods for the containment of *P. clarkii* and for its removal from streams already occupied. We conducted extensive surveys of southern California streams to determine patterns of distribution and spread of *P. clarkii.* Using these surveys, we designed a field study to determine the effectiveness of possible physical barriers to crayfish dispersal in streams. Finally, we measured the ability of *P. clarkii* to endure various flow rates and how that ability depends on the texture of the stream bottom.

2. Methods

2.1. Stream surveys

During the spring of 2000 and 2001, we surveyed 32 stream stretches in the Santa Monica Mountains for the presence or absence of crayfish and amphibians. A stream stretch was approximately 500 continuous meters (length) of a stream. Some streams were surveyed more than once in different reaches above and below barriers (e.g., north and south Las Virgenes; Fig. 1). We attempted to survey all the major streams in the area. Streams varied in human influence from areas with little or no impact (i.e., protected areas with few visitors) to areas with possible large impacts (i.e., areas near roads, popular hiking spots, or downstream of suburban runoff). Crews of 3–5 people searched for crayfish and amphibians. We identified and recorded any apparent large physical barriers (waterfalls, culverts) that might inhibit movement of crayfish between stream stretches.

We quantified the abundance of crayfish and amphibians present both in the water and within 2 m of the surrounding stream banks. When exact counts were difficult to make, quantities were assigned to categories

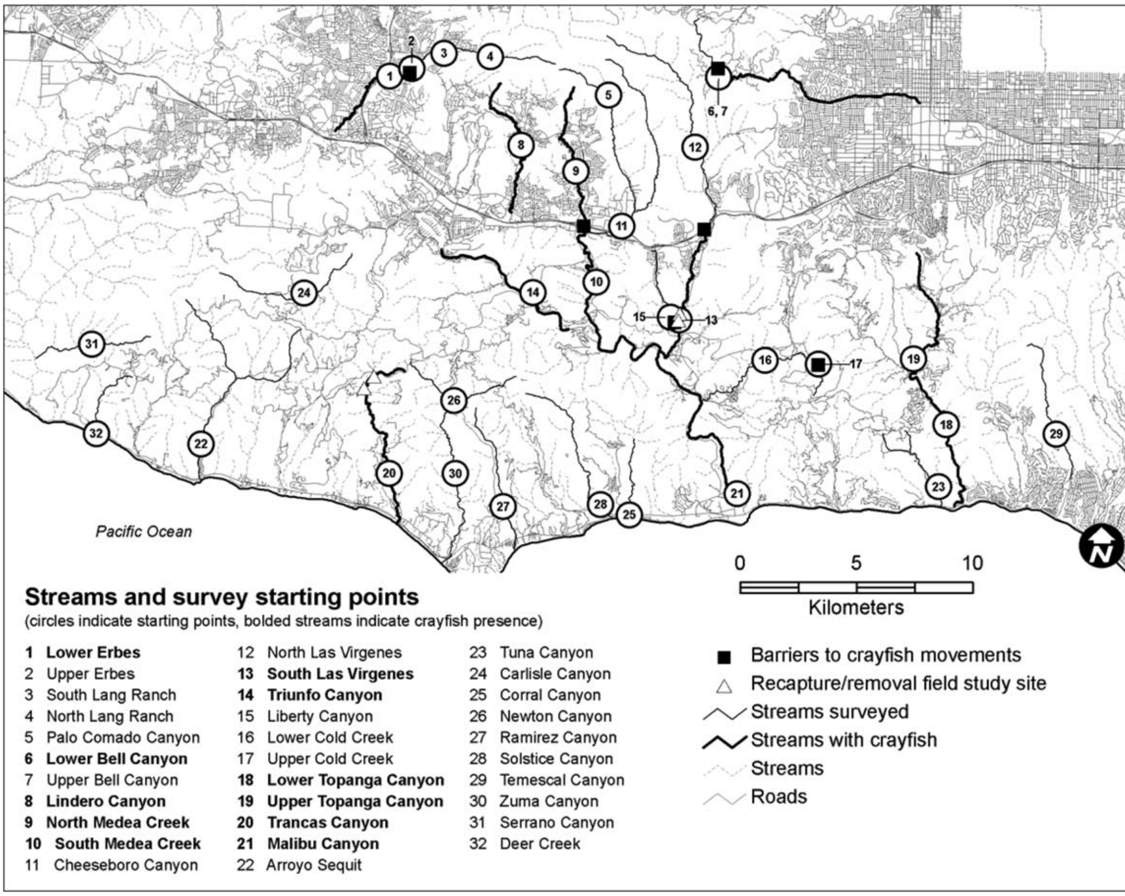

Fig. 1. Map of streams surveyed for crayfish presence. Bold lines and text indicate stream areas where crayfish were found. Mark-recapture and removal study was conducted in Trancas and Las Virgenes.

of >20, >50, >100, or >500 individuals. We also visited streams at areas outside of the surveyed stretches to determine whether patterns in crayfish and amphibian presence persisted throughout the rest of the stream both above and below barriers.

2.2. Mark-recapture and removal study

We conducted a field study using mark-recapture techniques to determine whether: (1) continual crayfish removal resulted in a significant reduction in densities of crayfish; (2) individual crayfish tended to move upstream or downstream between pools; (3) certain presumed barriers deterred movement of crayfish between pools. The field study was conducted in two of the above surveyed streams, Trancas and Las Virgenes creeks (Fig. 1). Since only a few large physical barriers were located in the survey and most of these had no crayfish above them, we examined movement over smaller barriers. We presume that the introduction of crayfish likely occurred above these smaller barriers and crayfish then spread downstream. The goal was to determine the ability of crayfish to move upstream over small barriers.

Each stream was partitioned into four sections, each containing three pools (Fig. 2). In each section, we monitored movement upstream (lower to center pool) and downstream (upper to center pool) and examined the effects of removal (from center pool only). Stream sections

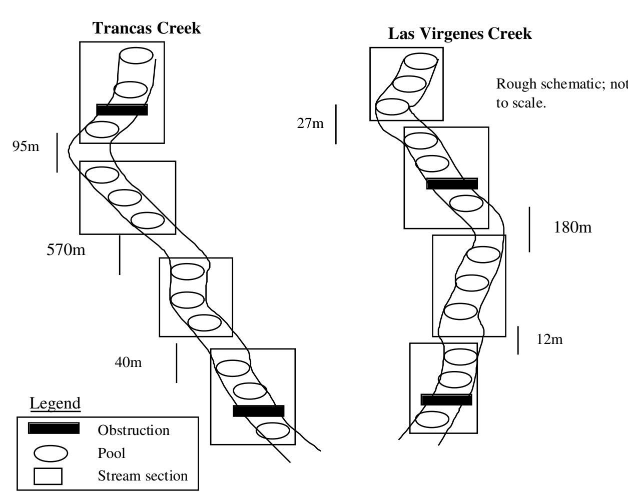

Fig. 2. Diagram of mark-recapture and removal study. Actual distances between each stream section are provided.

were determined by identifying the presence of three successive pools within 15 m of each other half with barriers. Each section was surveyed 12 times over the course of five weeks (11 June–13 July 2001).

2.2.1. Crayfish capture

To capture crayfish, a single steel, 1-cm mesh, vinyl-coated crayfish trap (30 cm × 20 cm × 13 cm) was placed in each pool. Each trap was baited using a black film canister filled with wet cat food. Traps were left open for 2–4 nights and then inspected during the day. Crayfish were removed each time traps were inspected and fresh bait was placed in traps. Any other crayfish seen in the pool at the inspection time were caught with 15 cm standard aquarium nets. We limited our netting effort in each pool to 30 min (with two people). If no crayfish were observed for a 5-min period, we stopped short of the 30 min period and moved to the next pool. Each captured crayfish was catalogued (carapace length, carapace width, total length, gender, and location), and any distinguishing characteristics were noted.

2.2.2. Removal and movement between pools

To monitor movements of crayfish, captured individuals were marked (tail notched) with patterns specific to each pool and stream section. Except for crayfish removed from the center pools, we then released marked individuals back into the pool where they were caught. If an individual with an upper or lower pool mark was found in the center pool, its movement was recorded and it was removed. Any individual that moved through the center pool without being recaptured there was marked to indicate both its original and recapture pool. Recaptured individuals from the same pool were measured and noted as recaptured. Due to the limited number of notching patterns, individuals could not be uniquely marked. Therefore, repeatedly recaptured individuals were recorded the same as novel recaptures.

To examine the effect of barriers on crayfish movement, two of the four sections in each creek were chosen to include stream sections with barriers that were located between the lower and center pools of the set (Fig. 2). Both upstream and downstream movements were monitored between all three pools (upper to center, upper to lower, lower to center, and lower to upper). Since crayfish in center pools were removed, data on movement from center to either upper or lower pools could not be obtained. Movements between pools in sections with and without barriers were analyzed using exact binomial sign tests to determine whether barriers deterred movement between pools. Finally, the effectiveness of crayfish removal was evaluated by regressing square-root transformed counts over the five-week period for each pool. Resulting regression coefficients were then analyzed by a two-way ANOVA to compare removal success by stream and by the existence of a barrier.

2.3. Flow experiments

A flow experiment was done to determine the effect of water velocity on crayfish movement. We measured upstream and downstream movement of individual crayfish on different substrates and at different flow velocities. The flow experiment was conducted in Trancas Creek within plastic rain gutters (150 cm × 8 cm) with either a rocky pebble substrate or no substrate using natural stream velocities. The rocky substrate was obtained from the streambed and was arranged so that there was a consistent flow throughout the gutter length. Water depth was maintained approximately at the gutter height (11 cm).

Immediately preceding the experiment, we captured individual crayfish and placed each one in a plastic bag containing stream water. Individuals missing appendages were not used and each crayfish was used only once. Each crayfish was set in the middle of the gutter facing upstream. We noted the direction of movement, either with or against the flow, when an individual had moved 40 cm from its starting point. Tests were done at flows of 10, 30, and 60 cm/s with no substrate (six trials) and at 30 and 60 cm/s with a rocky substrate (12 trials). We manipulated flow velocity by moving the gutter among different parts of a naturally flowing stream. Flow rates were consistently measured 4 cm from gutter bottom using an electromagnetic flow meter (©Marsh-McBurney Flo-mate 2000).

3. Results

3.1. Stream surveys

Several species of amphibians were detected in streams throughout the Santa Monica Mountains (*Taricha torosa, Hyla regilla, Hyla cadaverina, Bufo boreas, Rana catesbeiana*). Stream surveys showed a wide distribution of crayfish in streams (11 of 32) across the Santa Monica Mountains (Fig. 1). In six of the surveyed streams, crayfish were present in downstream stretches while absent in upstream stretches separated by a barrier (Table 1). The opposite pattern was not detected in any of the surveyed streams. In all cases where one stretch contained crayfish but an adjacent section did not, a barrier existed. Other possible obstructions (small waterfalls) to crayfish movement were identified within stretches that contained crayfish.

At two of the six barriers separating stretches of crayfish presence and absence (Bell Canyon and Cold Creek), newts were present above the barrier where no

Table 1
Description of barriers separating invaded and non-invaded reaches

Reaches	Barrier type	Height (m)	Length	Newts above barrier
Erbes (S), Erbes (N)	Culvert	1	600 m	No
Las Virgenes (S), Las Virgenes (N)	Culvert	0	200 m	No
Las Virgenes (S), Liberty	Small falls	2	N/A	No
Medea Creek (S), Cheeseboro	Culvert	0	500 m	No
Malibu Canyon, Cold Creek	Underpass pipe	1	N/A	Yes
Bell Canyon (S), Bell Canyon (N)	Large falls	20	N/A	Yes

crayfish were present but were not found below the barrier in the presence of crayfish. At the other four sites, newts were not present either above or below the barriers. In Trancas creek crayfish and newts co-occurred (see Gamradt and Kats, 1996).

3.2. Mark-recapture and removal study

Over the course of five weeks, we captured and marked 1696 individuals. We recaptured 31.6% (536) of the marked individuals. Captures exhibited a fairly equal male-to-female ratio (Las Virgenes 474:469; Trancas 364:369). In terms of carapace length, crayfish in Las Virgenes Creek (mean = 5.51 cm, SD = 0.51) were significantly larger than those in Trancas Creek (mean = 4.45 cm, SD = 0.78; $t = 33.55$, df = 1694, $p < 0.001$).

Movement between pools within each section occurred (Table 2), but no movement between sections was ever recorded. Movement was recorded upstream across only one presumed barrier. In this section, one crayfish moved up to the center pool across the barrier, and another crayfish moved to the upper pool across this barrier. These two observations of movement across a barrier upstream were compared to 12 observations in which a crayfish moved upstream between control pools not separated by a barrier (exact binomial sign test, $p = 0.013$). Barriers also inhibited downstream movement of crayfish: when there was a barrier between the center and lower pools, 19 crayfish moved from the upper pool to the center pool (not through a barrier) and only two moved on to the lower pool (across the barrier), whereas in control sections six crayfish moved down to the center pool and seven moved to the lower pool (Fisher's exact 2×2 test, $p = 0.013$). In the absence of any barrier, there was no statistically significant difference between upstream movement and downstream movement (12 vs. 13 instances; exact binomial sign test, $p = 1.0$).

Table 2
Movement of marked crayfish between pools with and without barriers

Movements between pools	Section with barrier between center and lower pools	Control section
Lower to center	1	6
Lower to upper	1	6
Upper to center	19[a]	6
Upper to lower	2	7

[a] Movement not over a barrier.

Removal effectiveness varied according to stream ($F_{1,5} = 10.164$, $p = 0.024$) but not by treatment ($F_{1,5} = 0.947$, $p = 0.375$). Trancas Creek exhibited a negative trend (mean regression coefficient = −0.41, SE = 0.06) in crayfish number over the five weeks, while Las Virgenes Creek gave no downward trend (mean regression coefficient = 0.13, SE = 0.16; Fig. 3). There was no difference in removal counts between barrier (mean regression coefficient = −0.06, SE = 0.23) and control stream sections (mean regression coefficient = −0.22, SE = 0.13). Las Virgenes Creek pools (mean = 1.17 m, SE = 0.22) were significantly deeper than Trancas pools (mean = 0.59 m, SE = 0.08, $t = 2.25$, df = 22, $p = 0.02$), a likely cause of a significantly lower capture success rate per visit over the last four weeks (Trancas: 592/791, 75%; Las Virgenes: 730/1129, 65%; t-test on arcsine-square-root transformed proportions for each center pool $t = 2.72$, df = 14, $p = 0.02$).

3.3. Flow experiments

In trials without natural substrate, all six crayfish were pushed downstream at flows of 60 cm/s (exact binomial sign test, $p = 0.031$) and 30 cm/s ($p = 0.031$).

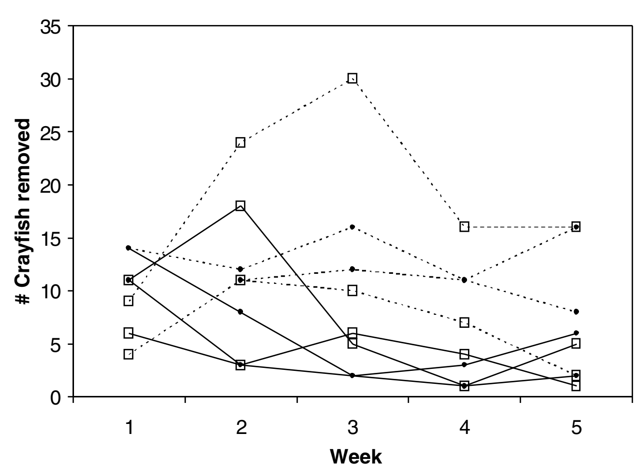

Fig. 3. Number of crayfish removed from center pools by week in mark-recapture and removal study. Solid lines for Trancas Creek; dotted lines for Las Virgines Creek. Open squares for stream segments without barriers; solid circles for stream segments with barriers.

At 10 cm/s there was no significant difference from a 1:1 ratio of upstream (five) and downstream (three) movements ($p = 0.727$). In pebble substrate trials, all 12 crayfish were pushed downstream at flows of 60 cm/s ($p = 0.0004$), but there was no significant pattern in movement at the lower flow of 30 cm/s (five upstream, six downstream; $p = 1.0$).

4. Discussion

In the Santa Monica Mountains, large-scale patterns of crayfish distribution suggest that spread typically occurs downstream from initial points of introduction. Downstream movement was detected in field study observations of crayfish movement between pools in stream sections. These observations also reveal that crayfish can move upstream, either within the stream or occasionally over land. However, our data indicate that both velocity and height barriers reduce, and in many cases evidently eliminate, the movement of crayfish into some upstream reaches of the watershed. These limiting factors have repercussions for both the conservation of native amphibians and the restoration of stream habitats.

4.1. Limiting factors

Height barriers (natural and artificial) along with high velocity flow seem to be limiting the distribution of crayfish in upstream stream stretches of the Santa Monica Mountains. Height barriers discovered in our surveys were typically waterfalls that ranged from 1 to 20 m in height. To move over these barriers, crayfish would need to climb directly up the face of the barrier against a current of running water, or crawl around them on dry land. An important consideration with height barriers is the surrounding banks. *P. clarkii* are able to easily crawl out of the water and move upstream before re-entering the water. Hence, steep terrain surrounding the barrier must also exist to reduce upstream movement. In our mark-recapture study, only two of the 146 crayfish caught in pools below barriers were found in pools upstream of the barrier. Both of these individuals moved over the same barrier; a 3-m high dam where we later observed a crayfish climbing up its algae-covered sloping face. Thus, the selection of barriers to use for conservation efforts must be carefully considered (i.e., surface material, surrounding banks) and barriers may not always completely eliminate movement upstream. Interestingly, data from our field study suggest that crayfish movement downstream may also be hampered by barriers. Occasionally, we have seen crayfish retreat from confrontations with other crayfish by drifting into a fast-flowing current, but generally crayfish avoided the faster flowing water that would cascade over a barrier.

Stream flow likely also plays a large part in crayfish distribution. High velocity flows resulting from infrequent storms may contribute to crayfish removal (Gamradt and Kats, 1996), and lower flows may facilitate re-establishment. Light (2003) found that signal crayfish (*Pacifastacus leniusculus*) abundances declined in years following floods in tributaries of Lake Tahoe (Placer County, California), and that more crayfish were found in lower gradient streams. In several surveyed sections, ponds or reservoirs exist upstream where precipitation increases water volume and depth but not velocity. This may allow crayfish populations to be "stored" in upstream ponds during storms, and then slowly migrate downstream after the flows decrease. Light (2003) found that *P. leniusculus* were positively associated with reservoirs. Concrete paved culverts that run under roads drastically alter flow patterns in streams and further increase the effectiveness of flow velocity as a barrier. Due to the seasonality of rain in southern California, these culverts typically had very little water in them most of the year, and during storms contain large volumes of fast flowing water. This pattern presumably prevents the passage of crayfish during dry periods due to the risk of desiccation and in wet periods because high velocities cause individuals to be forced downstream.

Other factors contribute to the establishment and maintenance of crayfish populations, such as water volume, water quality, and urban proximity (Light, 2003; Riley et al., in press), but our surveys suggest that barriers are paramount in limiting crayfish distribution. Since sections of stream separated by barriers are obviously otherwise contiguous, no other habitat quality factor is likely leading to the end of the distribution. This is further reinforced by the diversity of habitats this species has invaded throughout the world. Although additional criteria should be evaluated to determine the most effective barriers to the spread of *P. clarkii*, we have identified two significant factors that limit crayfish movement; high water velocity and abrupt vertical drops. Admittedly, other factors (continued introductions, seasonal patterns, water levels, etc.) must also be considered in managing crayfish spread.

4.2. Removal

Physical removal of crayfish can also limit crayfish distribution and be a major component to stream restoration. In the Santa Monica Mountains, the most effective method of removal in smaller high gradient streams is likely through heavy winter storms. Alternatively or in addition to this, removal through trapping and netting may also increase success. Our intensive netting and trapping efforts to remove crayfish in specific pools were somewhat effective after five weeks, although complete eradication was not achieved. The traps used in our study did not seem to be very effective, suggesting the use of a different type of trap might increase removal success. Beyond this, in our setup eradication was theoretically impossible due to the ability of crayfish to move into the center pools from adjacent pools. Any concerted effort to physically remove crayfish from a stream reach must include efforts to prevent movement back into the reach by new individuals. Our data strongly suggest that removal from a stream section in combination with a barrier would help to reduce re-colonization from downstream. Recent efforts in Trancas creek (using different trap types) have shown this to be true (Watters et al., 2004). Artificial barriers could also be used to prevent crayfish from re-colonizing stream stretches where eradication efforts have taken place.

Although eradication efforts are labor intensive, prolonged heavy removal could serve to at least lower crayfish numbers. Complete removal might be achievable in shallower streams where capture rates are higher. While complete removal may not be possible in all streams, it also may not be necessary for the partial protection of native animals. California newts and Pacific treefrogs are both able to breed and reproduce successfully in the presence of low crayfish abundance as exhibited in Trancas creek (Gamradt and Kats, 1996). High velocity natural flows in this creek provide a feasible way to allow removal of many crayfish individuals. Subsequent and continuous removal effort following high flow periods could then have a large impact on crayfish abundance.

4.3. Restoration

Restoration efforts are important in re-establishing natural communities but also must be executed with caution in riparian systems. There has been significant interest nationwide in barrier removal to promote the migration of anadramous fish (Doyle et al., 2003). However, allowing the upstream passage of fish may also allow non-native crayfish to move upstream into reaches that had been formerly blocked. Alteration or removal of barriers for restoration could actually reduce biodiversity if the impacts from newly introduced crayfish are considered. The removal or replacement of barriers that increase water velocity, such as culverts, must be carefully considered for the same reasons. Water flow over a smooth surface sweeps out crayfish more easily than those over a rocky substrate. Other studies have also documented the barrier to movement that channelized monotonous flows have on crayfish (Renz and Breithaupt, 2000). Although the loss of connectivity in stream habitats may negatively impact some native species, the introduction of crayfish may prove more damaging. Further research should be done on the construction of barriers that allow passage by some species but prohibit invasive crayfish movement upstream.

Restoration of certain Santa Monica Mountain streams does seem plausible. The use of both barriers to limit spread and seasonal water velocities to aid in removal are promising components of a restoration effort. Concerted trapping and netting efforts could also contribute to a reduction in crayfish abundances, but must be maintained for several years if a lasting effect is to be achieved. Other studies have shown that removal of crayfish can cause a dramatic return to former conditions (Gamradt and Kats, 1996). Long-lived newts are able to return and breed, and other amphibians and invertebrates are able to re-establish from other areas. Alternatively, if crayfish are allowed to remain in streams and continually spread to new areas, natural re-colonization of former habitats by native animals may become impossible.

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