

Rusty crayfish (*Orconectes rusticus*) movement within and between habitats in Trout Lake, Vilas County, Wisconsin

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Abstract. The exotic rusty crayfish, *Orconectes rusticus*, has invaded northern Wisconsin watersheds and is causing severe ecological alterations. We investigated the processes of rusty crayfish dispersal and movement within Trout Lake, Vilas County, Wisconsin, using a mark and recapture technique. We examined the effects of crayfish size, gender, and original location on distance traveled. Some *O. rusticus* moved up to 221 m in 2 d, but most crayfish remained in their original habitat (distances ranged from 0–58 m). Distances traveled were similar for both male and female crayfish. Crayfish size did not affect the patterns of movement. Crayfish did not travel greater distances over time, which may be an artifact of 2 groups of crayfish: those that stayed in their local habitat and those that moved far distances. Comparisons with published dispersal and movement data suggest that large movements are observed occasionally in both lotic and lentic habitats. For rusty crayfish, these movements have important implications for invasion rates.

Key words: *Orconectes rusticus*, dispersal, invasion, crayfish, Wisconsin, habitat.

In many northern Wisconsin lakes, the exotic crayfish *Orconectes rusticus* has replaced the native *O. virilis* and another invader *O. propinquus* (Capelli 1982, Lodge et al. 1986, Lodge and Hill 1994). *Orconectes rusticus* is a successful invader because it is larger and more aggressive than its congeners, and is a better competitor for food and habitat (Capelli and Munjal 1982, Lodge et al. 1994, Hill and Lodge 1999). It can limit the growth of macrophytes (Lodge and Lorman 1987, Lodge et al. 1994), thereby affecting fish habitat and nutrient cycling in the littoral zone of lakes (Carpenter and Lodge 1986).

Orconectes rusticus were first brought to northern Wisconsin ~35 y ago by anglers from Indiana and Illinois (Capelli and Magnuson 1983, Hobbs et al. 1989) and have continued to disperse between and within lakes. They were 1st detected in Trout Lake in 1981 (Lodge et al. 1986), but took >16 y to completely disperse around Trout Lake's 30 km of shoreline (Magnuson and Kratz 1999). In this study, we look at short-term *O. rusticus* movement in the context of the influence of daily movements on invasion rates.

Several factors influence the dispersal and site affinity of crayfish within a lake. For instance,

cobble and macrophyte habitats may represent different levels of food resources for crayfish. Macrophytes typically have more invertebrates than cobble (Resh and Rosenberg 1984); invertebrates are a favored food source for crayfish because they are high in protein (Momot 1995). However, if invertebrates are scarce, crayfish depend on detritus (Chambers et al. 1990, Momot 1995, Nystrom and Strand 1996), which does not facilitate rapid growth but does allow moderate to high survival (Hill et al. 1993, Lodge and Hill 1994). If a stretch of shoreline receives equivalent amounts of terrestrial detritus, then a nearby offshore macrophyte habitat would be expected to collect more detritus than an equidistant cobble habitat because of the additional inputs of macrophyte-derived detritus. Thus, we might expect to see short-term foraging movements from cobble to macrophyte habitats.

Predation risk may also be a factor that affects habitat preference of crayfish. Crayfish prefer refuge-providing substrates (Hill and Lodge 1994, Lodge and Hill 1994) and are most abundant in cobble substrates (Lorman 1980, Capelli and Magnuson 1983). Large crayfish are protected by size from gape-limited predators, whereas small crayfish experience high predation risk (Stein 1977, DiDonato and Lodge 1993, Garvey et al. 1994, Kershner and Lodge 1995).

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Because small crayfish experience high predation risk, they congregate in cobble substrate where they are better concealed from predators (Kershner and Lodge 1995, CJB and KAW, unpublished observations). Conversely, larger crayfish can be found in less protected areas of sand or macrophytes in addition to cobble (Kershner and Lodge 1995).

Sex may also influence crayfish movement. Male crayfish tend to be more aggressive than female crayfish (Lodge and Hill 1994, Hill and Lodge 1999), which suggests increased movement among males to reduce encounter rates with each other (Bovbjerg 1959). However, Hill and Lodge (1994) found *O. rusticus* females to be equally aggressive in one-on-one competition experiments for limited food. In addition, female crayfish are sedentary when they are carrying extruded eggs or young, usually in the months of May and June (Thorp and Covich 1991). Adult male *O. rusticus* also molt twice during the summer months, during which time they are inactive. As such, we expected sex to be of minimal importance in explaining distances traveled by individual crayfish.

We evaluated distances traveled by marked crayfish within and between cobble and macrophyte habitats. We predicted that habitat, in conjunction with size and sex, may affect the distance *O. rusticus* travels. We hypothesized that: 1) crayfish would travel towards macrophyte-dominated areas, 2) larger crayfish would be more likely to travel greater distances than smaller crayfish, 3) crayfish would travel farther over time, and 4) there would be no difference in distance traveled between female and male crayfish of similar size.

Methods

Study site

Our experiment was conducted along the shoreline of an undeveloped island in Trout Lake, Vilas County, Wisconsin, USA, where terrestrial vegetation consisted of small shrubs and 2nd-growth deciduous forest. Habitats consisted of both a macrophyte and a cobble patch on firm sand substrate. The patches were 120 m apart, separated by a slightly raised sandy underwater bar. Only *O. rusticus* are present in this area (Magnuson and Kratz 1999). At the time of the study, adult male *O. rusticus* had completed

their final molt of the summer to Form 1. The water was calm with a temperature around 20°C during the study period.

Experimental design

Crayfish were captured in macrophyte and cobble habitats using modified minnow traps (hole diameter ~5 cm) arranged in a grid. We placed traps 10 to 20 m apart (depending on the recapture effort, Fig. 1) to ensure that the effective trapping area of traps (12 m, Capelli 1975) did not overlap.

For the 1st recapture effort (48-h recapture effort, Fig. 1), the trap configuration was elongated to sample a larger spatial extent along the shoreline and to determine whether crayfish were traveling outside of the original grid areas. This trap configuration may have under-sampled crayfishes that moved <10 m (e.g., they would have been recaptured in the same place that they were originally marked) because the traps were farther apart than in the original configuration (although 4 traps in each habitat were in their original position, Fig. 1). We saw no obvious pattern of movement away from the original grids, so for the 2nd recapture effort (96-h recapture effort, Fig. 1), trap configuration was returned to a pattern resembling the original configuration and trapping effort to make the 96-h recapture and original marking efforts more comparable.

Each trap was baited with 120 g of beef liver for the initial capture and 60 g of beef liver for each subsequent recapture effort and set for ~24 h in 1 to 1.5 m of water. Bait was reduced on subsequent recapture efforts because of cost and because there was excess liver in the traps after the initial trapping effort.

Trapping with bait is biased because traps select for larger, more aggressive individuals (Capelli 1975, Olsen et al. 1991). Bait also can attract crayfish, potentially biasing movement distances. However, we removed our traps for 24 h between trapping efforts to allow crayfish to redistribute without the influence of bait, and our low recapture rate suggested that crayfish were not remaining in the same place. Furthermore, because weather was calm and strong underwater currents generally occur only with strong wind events, we assumed that the effective trapping area of each trap was roughly circular, and

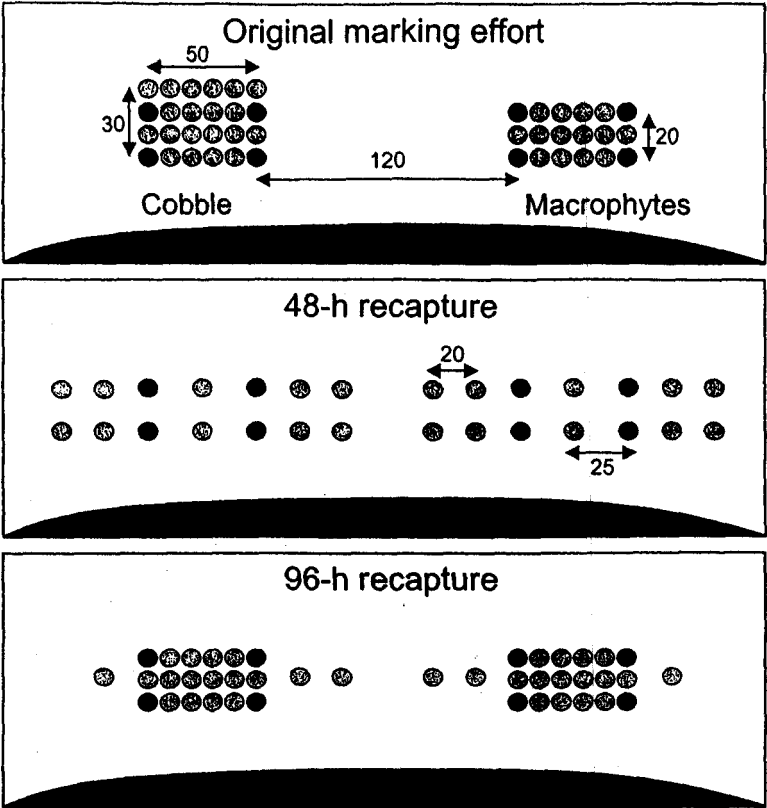


FIG. 1. Trap placement in the cobble and macrophyte grids for each trapping effort. Dark circles indicate traps that were placed in the same location for all 3 trapping efforts. Light circles indicate traps that were moved in each subsequent trapping effort. Dimensions of grids (in meters) given with double-headed arrows.

that the smell of bait did not travel differentially in any direction.

Crayfish were marked by poking a series of small holes in their uropods with a safety pin (Guan 1997). This method of marking lasts for up to a year and does not harm or inhibit crayfish movement (Guan 1997). Two of 105 recaptured crayfish were discarded from the data set because markings were unclear. All crayfish from an individual trap had the same unique uropod marking so that we could identify the initial location of each crayfish. We measured and sexed all crayfish (marked or unmarked) caught in the 1st recapture effort, but only sexed and counted the unmarked crayfish caught in the 2nd recapture effort. Crayfish were released at the same location where they were trapped. To minimize fright responses (Robinson et al. 2000) and escape swimming, crayfish were released by gently flooding and then overturning

their holding pan into the water. Most crayfish sank straight to the bottom without swimming.

Data analysis

We were concerned that the distribution of the observed distances traveled was an artifact of the trap configuration. Thus, we calculated all possible Euclidean distances a marked crayfish could travel between all pairwise combinations of original and recapture traps given the layout of the 3 different trapping grids. We then compared the expected distribution of distance traveled with the distribution of observed distances traveled by the marked crayfish using a Kolmogorov-Smirnov 2-sample test, which is a nonparametric test that measures the discrepancy between 2 distributions (in this case, the expected and observed distances traveled) with the null hypothesis that the 2 distributions are

TABLE 1. Mean size (mm carapace length) of crayfish caught initially and in each successive recapture. There was no significant difference in the size of all marked crayfish recaptured in 48 h or 96 h ($t = -0.008$, $p = 0.994$).

	Mean (SE) size		
	Initial captures	48-h recaptures	96-h recaptures
Males	39.1 (0.16)	39.2 (0.51)	39.5 (0.66)
Females	38.5 (0.33)	41.7 (1.66)	41.1 (1.01)
All crayfish	39.0 (0.14)	39.8 (0.60)	39.8 (0.56)

identical (Sokal and Rohlf 1995). The D statistic represents the maximum unsigned difference between the relative cumulative frequencies of expected and observed distances.

The grids were not perfectly square to each other because the shoreline curved slightly and we wished to keep all traps along the 1 to 2 m contour. However, we calculated Euclidean distances between traps as if the grids were exactly square to each other to simplify calculations. Note that the calculation of distances between traps accounts for the relative placements of traps in the original marking effort as compared to the 2 successive recapture attempts.

Results

Original marking effort

A total of 1127 crayfish were originally caught, of which 852 were males, 250 were females, and 25 were unknown because we failed to note their sex. There was no significant difference in mean size between crayfish originally marked in the macrophyte grid (mean \pm SE: 40 ± 0.19 mm carapace length [CL], range = 27–53) and in the cobble grid (38 ± 0.21 mm CL, range = 15–53) ($t = 1.98$, $p = 0.157$). Males and females did not differ in mean size (male = 39 ± 0.16 mm CL, range = 15–53, female = 38 ± 0.33 mm CL, range = 25–53) ($t = 1.666$, $p = 0.097$).

Recaptured crayfish

A total of 643 crayfish (434 male, 209 female) were caught during the 48-h recapture effort, and 905 crayfish were caught during the 96-h recapture effort. The reduction in bait seemed to have little significant effect on the number of crayfish caught per trap in the 2 later trapping efforts; we found no significant reduction in the

mean number of crayfish caught per trap between the original capture (mean \pm SE: 27.5 ± 1.49 crayfish/trap) and the 48-h recapture effort (23.3 ± 1.65 crayfish/trap) ($t = 1.843$, $p = 0.07$) or between the 48-h recapture and the 96-h recapture effort (21.5 ± 1.25 crayfish/trap) ($t = 0.857$, $p = 0.394$). However, there was a significant difference in the mean number of crayfish caught between the original capture and the 96-h recapture ($t = 3.062$, $p = 0.003$). Mean sizes of marked crayfish for all 3 trapping efforts were similar (Table 1).

In total, we recaptured 9.2% of all marked crayfish. No crayfish were recaptured twice because, when compared to our original marking records, the recaptured crayfish had unique combinations of uropod markings, sex, and size.

Distances moved

Mean distances traveled between release and recapture did not differ significantly between the 48-h recapture (mean \pm SE: 58 ± 8.87 m) and the 96-h recapture (54 ± 7.73 m) ($t = 0.918$, $p = 0.362$). Mean distance traveled was similar for male, female, or both genders combined for either 48 h or 96 h after release (Table 2). Size did not affect the distance crayfish moved ($R^2 = 0.027$, $p = 0.204$).

We categorized distances traveled as near (<100 m) and far (>100 m), which roughly corresponded to within- and between-habitat movements, depending on the trapping configuration (Fig. 2). Distances traveled within the same habitat over the 48-h period were significantly different from the possible distances that could have been traveled ($D = 0.340$, $p = 0.001$), and appeared to be skewed towards smaller distances (mean_{observed} = 32.4, median_{expected} = 45.5). All other comparisons were not significantly different: 48-h period between habitats

TABLE 2. Mean distance traveled (m) by crayfish in 48- and 96-h periods. None of the distances traveled were significantly different from each other.

	Distance traveled				<i>t</i> -statistic	<i>p</i> -value
	48 h		96 h			
	Mean distance (SE)	No. of crayfish caught	Mean distance (SE)	No. of crayfish caught		
Males	60.44 (11.41)	32	47.96 (8.11)	45	0.918	0.362
Females	52.08 (12.01)	12	72.29 (19.35)	14	-0.852	0.403
All crayfish	58.16 (8.87)	44	53.73 (7.73)	59	0.376	0.708

($D = 0.273$, $p = 0.506$), 96-h period within habitats ($D = 0.095$, $p = 0.811$), and 96-h period between habitats ($D = 0.213$, $p = 0.682$).

In general, crayfish were more likely to stay within their original habitat than to travel into neighboring habitat. Directional movement was apparent in the crayfish that moved the farthest distances. Of the 20 marked crayfish that moved from one habitat to the other during the study, all but 4 moved from macrophytes to cobble. More recaptured crayfish than expected were originally marked in the macrophyte habitat ($\chi^2 = 4.28$, $0.025 < p < 0.05$, Table 3). Also, more crayfish stayed in their original habitat rather than moved to a different habitat ($\chi^2 = 38.5$, $p < 0.001$, Table 3). Average distances traveled within macrophyte habitat (27 ± 2.4 m) did not differ from distances traveled within cobble habitat (34 ± 4.2 m) ($t = -1.485$; $p = 0.143$).

Discussion

Limitations of baited traps

The efficacy of baited traps has been long debated (Capelli 1975, Collins et al. 1983, Somers and Stechey 1986, Olsen et al. 1991), but most crayfish studies in lentic habitats have used baited traps for mostly practical reasons. Rusty crayfish orient accurately and rapidly to carrion odors in slow currents (Moore and Grills 1999), so it is possible that odors from the beef liver dispersed by currents could have attracted crayfish to the study. This attraction might increase the recruitment of crayfish to the site, resulting in an overestimate of the number of crayfish present in the area and distances traveled. However, our recapture rates were within the variability (7.1–21.4%) found by Camougis and Hichar (1959) in a small (180×45 m) pond over

a 36-h period. In contrast, Flint (1977) had a recapture rate of 0.02% over a 2- to 4-wk period in a much larger area in Lake Tahoe. Previous studies showed that the use of baited traps accurately estimated local crayfish density (Lorman 1980) but, in lakes with *O. rusticus*, crayfish densities were accurately estimated only if *O. rusticus* was the dominant crayfish species (Olsen et al. 1991). Current-based odors may increase the directional movement to the study site, but we did not detect patterns in trap catches that would suggest that crayfish originated down-current from the traps. In addition, strong directional currents should have been at a minimum because of calm weather during the trapping period. We accounted for possible trap affinity by removing the traps and bait from the water for a 24-h period between each successive recapture to allow crayfish to move uninfluenced by the odor of the bait. We assumed that our traps captured individuals closest to each trap when the traps were set. Several alternatives to baited traps exist, but all have their own associated biases. Unbaited traps catch fewer crayfish. More active techniques such as hand netting by SCUBA divers tends to frighten neighboring crayfish away while an individual is netted. Radiotelemetry may be the most ideal method in lentic habitats because one individual's location can be mapped over time and recapture points are not fixed. Radiotelemetry, however, is costly and, consequently, sample sizes are low.

Movement rates and distances

Average movement rates by marked crayfish over 48 h (1.2 m/h) and 96 h (0.56 m/h) were within the range of movement studies conduct-

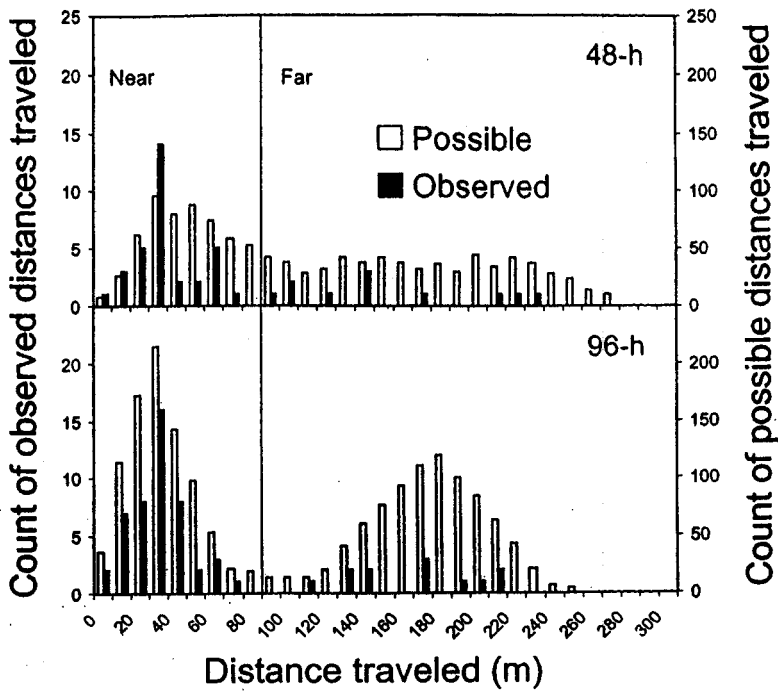


FIG. 2. Distributions of observed and possible distances traveled for the 48- and 96-h time periods. Possible distances (i.e., those distances crayfish could have traveled between the original trapping point and recapture) depended on trap placement. In general, near distances (<100 m) correspond to within-habitat travel and far distances correspond to between-habitat travel. Only near movements in the first 48 h suggested movement patterns that differed significantly from expected based on the trapping configurations (see text).

ed in small ponds (0.625–0.83 m/h, Camougis and Hichar 1959; 2.58 m/h, Momot and Gowing 1972), but these studies, like ours, were limited in their sampling extent. Our longest distance traveled was not unusual. Flint (1977) found that most crayfish released from a single point dispersed ~50 m from the release point in 2 to 4 wk, but that many individuals went considerably further. Another published account (Fürst

1977) suggested that crayfish can travel up to 600 m in 24 h. These movement rates are generally higher than those observed in stream crayfishes, where daily movements are often within 10 m of the last recapture, but individuals occasionally move >50 m.

Studies by Camougis and Hichar (1959), Momot and Gowing (1972), and ours represent potentially large underestimates of crayfish

TABLE 3. Recaptured crayfish within and between the macrophyte and cobble grids over a 48-h and a 96-h period. A total of 543 crayfish were initially marked in the macrophyte habitat and 577 crayfish were marked in the cobble habitat.

Original habitat (marked)	Final habitat (recaptured)	% Recaptured (no. recaptured)	
		48 h	96 h
Macrophyte	Macrophyte	3.68 (20)	4.79 (26)
	Cobble	1.29 (7)	1.66 (9)
	Total	4.97 (27)	6.45 (35)
Cobble	Cobble	2.60 (15)	3.81 (22)
	Macrophyte	0.35 (2)	0.35 (2)
	Total	2.95 (17)	4.16 (24)

movement in lentic environments because the spatial extent of crayfish movement was, in all 3 cases, greater than the spatial extent of sampling points. In our study, the distribution of observed distances traveled within habitats during the first 48 h was skewed toward shorter distances relative to the expected distances. We thus concluded that crayfish were generally moving within the area sampled by our traps. However, for the 96-h recapture effort, we concluded that our sample area was too small to adequately measure the net distance traveled in 96 h because the observed distribution of distances traveled was the same as the expected distances traveled. In this case, the movements measured may have simply been a function of where individual crayfish were located when the traps were dropped into the water. Consequently, even our maximum estimate of dispersal rate (221 m/48 h) is likely an underestimate of crayfish movement. To fully assess the gradual dispersal of marked crayfish, we would have required a sample area of hundreds of meters and a longer time period.

It is possible that we measured movements by 2 groups of crayfish: one that stayed (at least for the period of our study) in the same area, and one that moved long distances (>100 m). This interpretation agrees with many studies of crayfish movement in lotic and lentic habitats, in which most individual crayfishes appear to occupy a general area for some time (days or weeks) before moving, sometimes relatively long distances, to another site. For instance, Robinson et al. (2000) used radiotelemetry in a small creek to identify "home sites" at which *Austropotamobius pallipes* would remain for up to a week, but then leave for another site; experimentally displaced crayfish showed no affinity for their former haunts. Similar home sites in a stream system were observed by Hazlett et al. (1974), who found that most recaptures occurred from 0 to 5 m from the last capture, but infrequent large movements as great as 308 m suggested that *O. virilis* remained stationary for some time and then moved long distances. Flint (1977) found most crayfish stayed within 50 m of their release point in Lake Tahoe in a 2 to 4 wk period, but that a few individuals traveled much further. These occasional far movements could very well represent the leading edge of rusty crayfish invasion fronts.

Implications for invasions

Rusty crayfish are clearly capable of moving long distances, with critical implications for estimates of invasion rates. Unlike streams, crayfish in lakes are much less restricted in the direction of travel. However, our (minimum) movement estimates are the cumulative distance traveled by an individual crayfish under realistic conditions of predation risk and food availability, and so should give a reasonable estimate of possible invasion rates around the shoreline of Trout Lake. Assuming that *O. rusticus* is active only during the months of June, July, and August (Lorman 1980) and using our most conservative dispersal estimate of 0.56 m/h, our results suggest a potential invasion rate of 1.2 km/y, much faster than the observed rate of 0.68 km/y (Magnuson and Kratz 1999). Large single movements by some individuals could greatly increase dispersal by the population as a whole, especially movements by the large females observed in our study. These females mate in late summer and carry a spermatophore (sperm plug) until they extrude their fertilized eggs in early spring (Thorp and Covich 1991) and therefore might act as epicenters for dispersal.

There are many possible mechanisms for the observed slower-than-expected invasion of Trout Lake: predation pressure by fishes (Garvey et al. 1994), density-dependent processes (Bovbjerg 1959), habitat availability (e.g., cobble for shelter, especially during molting periods) and connectivity (Kershner 1992), the width or area of colonizable littoral zone, and interactions with congeners (Hill and Lodge 1994). The relative importance of these processes in determining invasion rate (versus invasion success) is largely unknown.

In conclusion, we did not see any effect of size, sex, or time on distances traveled by rusty crayfish. Among crayfish moving long distances, more moved towards cobble substrate than towards macrophytes. The observed distances traveled most likely represent minimum distances traveled by these crayfishes, both the majority that remained in the same general location, and the few individuals that traveled >100 m. We suggest that future work on rusty crayfish dispersal in lentic environments would benefit from careful tracking of individually marked crayfish without baited traps, over ex-

tents >250 m. Our work suggests that rusty crayfish are quite mobile and invasions of water bodies could be rapid. However, the invasion of Trout Lake by rusty crayfish was slower than expected given our measured distances. We expect that this discrepancy was caused not by dispersal ability, but by multiple interactions between crayfish, predators, and habitat. Correlations between local movement rates and interactions with environmental factors may help explain and predict local invasion rates.

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Literature Cited

- BOVBJERG, R. V. 1959. Density and dispersal in laboratory crayfish populations. *Ecology* 40:504-506.
- CAMOUGIS, G., AND J. K. HICHAIR. 1959. Some studies on crayfish distribution in a small pond. *American Midland Naturalist* 62:227-231.
- CAPELLI, G. M. 1975. Distribution, life history, and ecology of crayfish in northern Wisconsin with emphasis on *Orconectes propinquus* (Girard). PhD Dissertation, University of Wisconsin, Madison, Wisconsin.
- CAPELLI, G. M. 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). *Limnology and Oceanography* 27:741-745.
- CAPELLI, G. M., AND J. J. MAGNUSON. 1983. Morphoedaphic and biogeographical analysis of crayfish distribution in northern Wisconsin. *Journal of Crustacean Biology* 3:548-564.
- CAPELLI, G. M., AND B. L. MUNJAL. 1982. Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. *Journal of Crustacean Biology* 2: 486-492.
- CARPENTER, S. R., AND D. M. LODGE. 1986. Effects of submerged macrophytes on ecosystem processes. *Aquatic Botany* 26:341-370.
- CHAMBERS, P. A., J. M. HANSON, J. M. BURKE, AND E. E. PREPAS. 1990. The impact of crayfish *Orconectes virilis* on aquatic macrophytes. *Freshwater Biology* 24:81-91.
- COLLINS, N. C., H. H. HARVEY, A. J. TIERNEY, AND D. W. DUNHAM. 1983. Influence of predatory fish density on trapability of crayfish in Ontario Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1820-1828.
- DiDONATO, G. T., AND D. M. LODGE. 1993. Species replacements among *Orconectes* crayfishes in Wisconsin lakes: the role of predation by fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1484-1488.
- FLINT, W. R. 1977. Seasonal activity, migration and distribution of the crayfish, *Pacifastacus leniusculus*, in Lake Tahoe. *American Midland Naturalist* 97: 280-292.
- FÜRST, M. 1977. Introduction of *Pacifastacus leniusculus* (Dana) into Sweden: methods, results and management. Pages 229-247 in O. V. Lindquist (editor). *Freshwater crayfish 3: papers from the Third International Symposium on Freshwater Crayfish, August 1976, Kuopio, Finland*. University of Kuopio, Kuopio, Finland.
- GARVEY, J. E., R. A. STEIN, AND H. M. THOMAS. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. *Ecology* 75:532-547.
- GUAN, R. Z. 1997. An improved method for marking crayfish. *Crustaceana* 70:641-652.
- HAZLETT, B., D. RITTSCHOFF, AND D. RUBENSTEIN. 1974. Behavioral biology of the crayfish *Orconectes virilis* 1. Home range. *American Midland Naturalist* 92:301-319.
- HILL, A. M., AND D. M. LODGE. 1994. Diel changes in resource demand: competition and predation in species replacement among crayfishes. *Ecology* 75:2118-2126.
- HILL, A. M., AND D. M. LODGE. 1999. Replacement of resident crayfishes by an exotic crayfish: the roles of competition and predation. *Ecological Applications* 9:678-690.
- HILL, A. M., D. M. SINARS, AND D. M. LODGE. 1993. Invasion of an occupied niche by the crayfish *Orconectes rusticus*: potential importance of growth and mortality. *Oecologia (Berlin)* 94:303-306.
- HOBBS, H. H. I., J. P. JASS, AND J. V. HUNER. 1989. A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). *Crustaceana* 56:299-316.
- KERSHNER, M. W. 1992. The impact of landscape pattern on the invasion of northern Wisconsin lakes by the crayfish, *Orconectes rusticus*. MS Thesis, University of Notre Dame, Notre Dame, Indiana.
- KERSHNER, M. W., AND D. M. LODGE. 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. *Journal of the North American Benthological Society* 14:414-422.
- LODGE, D. M., AND A. M. HILL. 1994. Factors governing species composition, population size, and pro-

- ductivity of cool-water crayfishes. *Nordic Journal of Freshwater Resources* 69:111-136.
- LODGE, D. M., M. W. KERSHNER, J. E. ALOI, AND A. P. COVICH. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater food web. *Ecology* 75:1265-1281.
- LODGE, D. M., T. K. KRATZ, AND G. M. CAPELLI. 1986. Long-term dynamics of three crayfish species in Trout Lake, Wisconsin. *Canadian Journal of Fisheries and Aquatic Sciences* 43:993-998.
- LODGE, D. M., AND J. G. LORMAN. 1987. Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. *Canadian Journal of Fisheries and Aquatic Sciences* 44:591-597.
- LORMAN, J. G. 1980. Ecology of the crayfish *Orconectes rusticus* in Northern Wisconsin. PhD Dissertation, University of Wisconsin, Madison, Wisconsin.
- MAGNUSON, J. J., AND T. K. KRATZ. 1999. LTER crayfish unpublished data set. NSF North Temperate Lakes Long Term Ecological Research Program, Center for Limnology, University of Wisconsin, Madison, Wisconsin. (Available from: (<http://www.limnology.wisc.edu>))
- MOMOT, W. T. 1995. Redefining the role of crayfish in aquatic systems. *Reviews in Fisheries Science* 3: 33-63.
- MOMOT, W. T., AND H. GOWING. 1972. Differential seasonal migration of the crayfish *Orconectes virilis* (Hagen) in marl lakes. *Ecology* 53:479-483.
- MOORE, P. A., AND J. L. GRILLS. 1999. Chemical orientation to food by the crayfish *Orconectes rusticus*: influence of hydrodynamics. *Animal Behaviour* 58:953-963.
- NYSTROM, P., AND J. A. STRAND. 1996. Grazing by a native and an exotic crayfish on aquatic macrophytes. *Freshwater Biology* 36:673-682.
- OLSEN, T. M., D. M. LODGE, G. M. CAPELLI, AND R. J. HOULIHAN. 1991. Mechanisms of impact of introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1853-1861.
- RESH, V. H., AND D. M. ROSENBERG (EDITORS). 1984. The ecology of aquatic insects. Praeger, New York.
- ROBINSON, C. A., T. J. THOM, AND M. C. LUCAS. 2000. Ranging behaviour of a large freshwater invertebrate, the white-clawed crayfish *Austropotamobius pallipes*. *Freshwater Biology* 44:509-521.
- SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. W. H. Freeman and Company, New York.
- SOMERS, K. M., AND D. P. STECHY. 1986. Variable trapability of crayfish associated with bait type, water temperature and lunar phase. *American Midland Naturalist* 116:36-44.
- STEIN, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58:1237-1253.
- THORP, J. H., AND A. P. COVICH (EDITORS). 1991. Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego.

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