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Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*

MARK W. KERSHNER¹ AND DAVID M. LODGE

Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556 USA

Abstract. In northern Wisconsin lakes, patterns of spatial distribution of an exotic crayfish, *Orconectes rusticus* (Girard), were related to differences in four littoral zone habitats: cobble, sand, macrophyte/firm (vegetated firm sediments), and macrophyte/muck (vegetated soft sediments) in northern Wisconsin lakes. Field surveys of crayfish abundance and mortality rates of tethered crayfish were used to determine the relationship of habitat-specific predation risk to cross-habitat patterns of crayfish distribution. Predation risk differed significantly across habitat types; crayfish on sand (particularly small crayfish, 15–18 mm carapace length) experienced significantly higher predation than crayfish in either cobble or macrophyte habitats, which were not significantly different. Crayfish use of cobble and sand habitats was inversely related to habitat-specific predation risk, whereas use of macrophyte/firm and macrophyte/muck habitats was not related to predation risk. Crayfish use of these latter habitats may be related to physical attributes of substrate (e.g., physical impediment to crayfish movement). An additional survey of crayfish habitat use and fish predator density in seven lakes was consistent with these results. Crayfish were overrepresented in cobble relative to its availability, used sand in proportion to its availability, and were underrepresented in macrophytes. Among the seven lakes, crayfish use of cobble was significantly and positively correlated with lakewide predator density, suggesting the potential importance of predation risk in structuring patterns of crayfish distribution. The combination of the crayfish's association with cobble habitat and the low predation risk associated with cobble suggests that cobble availability may significantly influence the success of *O. rusticus* invasions.

Key words: *Orconectes rusticus*, crayfish, predation, littoral zone habitats.

Approximately 30 years ago, the rusty crayfish, *Orconectes rusticus*, was introduced into northern Wisconsin lakes by anglers from Indiana and Illinois (Capelli and Magnuson 1983). Since that time, *O. rusticus* has displaced congeneric crayfish species in several lakes (Capelli 1982, Lodge et al. 1986, Olsen et al. 1991) and probably reduced abundance of submersed macrophytes and benthic macroinvertebrates (Lodge and Lorman 1987, Lodge et al. 1994). Thus, *O. rusticus* may significantly affect biotic characteristics of littoral zones.

Conversely, littoral zone habitat types may influence patterns of *O. rusticus* distribution. To identify factors structuring crayfish distributions among lakes, Capelli and Magnuson (1983) examined patterns of crayfish abundance among 67 northern Wisconsin lakes. Among-lake variation of crayfish abundance and species composition was related to human activity, calcium level, dominant lake substrate type, and surface connections between lakes. In this paper, we

address what factors may affect the spatial distribution of *O. rusticus* within lakes.

Cross-habitat patterns of crayfish distribution may reflect habitat-specific impacts of 1) direct and indirect effects of predation (Stein and Magnuson 1976, Stein 1977, Saiki and Tash 1979), 2) physical attributes of substrate types (e.g., substrate firmness), 3) food abundance (Crowl and Schnell 1990), 4) intra- or inter-specific competition among crayfish (Bovbjerg 1959, 1970, Hill and Lodge 1994), and 5) ontogenetic shifts in habitat use (Lorman 1980). We postulated that habitat-specific predation risk and physical attributes of substrate type are of primary importance, given that predator density and effectiveness may depend on habitat type (Huffaker 1958, Stein and Magnuson 1976, Werner et al. 1983).

Previous laboratory experiments demonstrated that both cobble (Stein and Magnuson 1976, Garvey et al. 1994) and macrophyte (Saiki and Tash 1979) habitats provide refuge for orconectid crayfish from fish predation. Correspondingly, field and laboratory studies have found that crayfish abundance is generally related to that of cobble (Stein 1977, Lorman 1980, Hill

¹ Present address: Aquatic Ecology Laboratory, Department of Zoology, Ohio State University, 1314 Kinnear Road, Columbus, Ohio 43212 USA

TABLE 1. Lakes used in the cross-habitat survey and the among-lake survey. Abbreviations under crayfish species composition are: OR = *Orconectes rusticus*, OP = *O. propinquus*, and OV = *O. virilis*.

Lake	Township, Range	Latitude	Longitude	Crayfish species composition
Little Star	T42N, R5E	46°25'N	89°50'W	OR
Papoose	T43N, R5E	46°30'N	89°50'W	OR
Plum	T41N, R8E	46°20'N	89°30'W	OR, OP, OV
Presque Isle	T43N, R6E	46°30'N	89°50'W	OR
Spider	T42N, R5E	46°25'N	89°50'W	OR
Squirrel	T39N, R5E	45°55'N	89°50'W	OR, OV
Trout	T41N, R7E	46°2'N	89°40'W	OR, OP, OV
Van Vliet	T43N, R6E	46°30'N	89°50'W	OR, OV

and Lodge 1994) and/or macrophyte (Saiki and Tash 1979) habitats, but not sand habitat. In fact, Stein (1977) found that *O. propinquus* density decreased as predator density increased on sand transects in northern Wisconsin lakes. Further, DiDonato and Lodge (1993) demonstrated that crayfish mortality on sand was size-specific, with higher mortality for small crayfish. Beyond this, few field studies have investigated the influence of habitat-specific predation on crayfish habitat use in lentic communities. The only direct test of habitat-specific predation was in Ohio streams; Mather and Stein (1993a) found that *O. sanborni* mortality was higher in pools than in riffles and attributed this to higher fish predation in the pools. However, crayfish densities were higher in pools than in riffles, indicating that factors other than fish predation may be influencing crayfish distribution in Ohio streams.

Given these previous studies, we predicted that 1) *O. rusticus* would be more abundant in cobble than in sand or macrophyte habitats, 2) predation risk would be highest on sand, and 3) increased predator density would lead to increased use of cobble and macrophyte habitats and reduced use of sand. Therefore, we used field censuses of habitat-specific crayfish abundance and habitat-specific predation assays to describe local (cross-habitat) and regional (among-lake) patterns of crayfish habitat use.

Methods

Three field studies were designed to examine effects of habitat type and predation risk on patterns of the distribution of *Orconectes rusticus*. First, cross-habitat visual censuses of *O. rusticus* abundance examined crayfish-habitat as-

sociations. Second, we used field predation assays to measure habitat-specific predation risk for three size classes of *O. rusticus*. Finally, we conducted an among-lake survey of the habitat-specific abundance of *O. rusticus* and fish predators to examine the relationship between predator density and crayfish habitat use.

Study sites and habitat categorization

We categorized littoral zone substrates in north-central Wisconsin lakes into four major habitats: cobble, sand, macrophytes on firm substrate (e.g., sand), and macrophytes on muck substrate (i.e., fine organic sediments). Study sites used in the cross-habitat surveys and field predation assays were composed of two large habitat patches (300 to 600 m across) with a distinct border between them. Large habitat patches were required because previous studies found that crayfish may move distances of 400 to 600 m in 24 h (Fürst 1977, H. H. Harvey, D. A. Jackson, and K. M. Somers, University of Toronto, personal communication). Study sites consisted of the following habitat pairings: 1) cobble-sand (Site A, Trout Lake—Southeast Bay; Site B, Trout Lake—South Shore), 2) cobble-macrophyte/firm (Site C, Plum Lake), 3) cobble-macrophyte/muck (Site D, Squirrel Lake—East Shore), and 4) sand-macrophyte/muck (Site E, Squirrel Lake—West Shore) (Table 1). We characterized habitat types by three variables, 1) presence of cobble (100% cover by cobble with diameter ≥ 7 cm at cobble sites), 2) macrophyte density (shoot density $> 70/m^2$ at macrophyte sites; this density estimate represents pooled counts of all macrophyte species, and macrophytes would be considered abundant at these sites), and 3) substrate firmness: sand (0

to 1 cm of organic sediment) or muck (>4 cm of organic sediment on lake bottom). Habitat pairs were unreplicated except for cobble-sand ($n = 2$). Although the lack of replication limits confidence in the generality of interpretations, our goal of documenting patterns of crayfish distribution at broad spatial scales meant that we had to trade replication for multiple habitat combinations. This design was necessary given that no one lake contained all pairings of large habitat patches separated by distinct boundaries. Therefore, for the cross-habitat survey and field predation assay, study sites were in different lakes, limiting inferences regarding the importance of predation risk or food availability (which likely differed among lakes) to observed patterns of habitat-specific crayfish distribution. A more rigorous analysis of the importance of predation risk to habitat-specific crayfish distribution was provided by the among-lake survey.

Cross-habitat survey

At each study site, we sampled the area within five 1-m² quadrats made of PVC pipe at the border between the two habitats. Within each habitat patch, we sampled five quadrats along each of five transects located at the following distances from the border: 10 m, 40 m, 100 m, 150 m, and 200 m (for a total of 55 quadrats per site). Multiple distances were sampled in each habitat patch to generate a more accurate estimate of patch-specific crayfish density, acknowledging that crayfish are likely patchily distributed within a habitat patch. Quadrats were positioned in water depths of 1.3–1.5 m. On the day following quadrat placement, we counted (while snorkeling) crayfish present in the quadrats that had an approximate carapace length (CL) >12 mm. As described by Lamontagne and Rasmussen (1993), quadrat counts provide a good estimate of crayfish density. Because crayfish are less visible in cobble and macrophyte habitats than in sand, counts in these habitats required careful movement of individual rocks and macrophyte shoots. Crayfish did not use quadrats as shelter (Kershner and Lodge, personal observations). At Sites A and B (cobble-sand sites), we conducted separate visual censuses on two successive nights. For Sites C, D, and E, the visual census was conducted on only one night. All visual censuses were run

during intermolt periods (27 July–22 August 1990). For each of the five sites, the difference in crayfish abundance in neighboring habitats was compared graphically. To facilitate comparisons across all sites, total crayfish abundance (summed across the two habitats within a site) was normalized to 100 crayfish for each of the five sites. We normalized the data because the total number of crayfish counted at each of the five sites ranged from 67 to 183.

Field predation assay

Predation assays examined habitat-specific predation on tethered crayfish. Crayfish were collected from Trout Lake. Tethers consisted of a 15-cm piece of 4-lb test monofilament line glued to the carapace, which was attached to a 15 × 15 cm clay tile. The tile was buried in the given substrate, leaving only the tethered crayfish above the substrate surface. Tethers restricted access to shelter, to keep crayfish available to predators. Tethering methods limited habitat effects on crayfish removal rates to the color, texture, and visual and physical obstruction (macrophyte habitat) provided by different habitat types. Thus, we view crayfish removal rates as an index of the risk of predation faced by an active crayfish (out of shelter) in different habitats. We also ran three control experiments to determine whether crayfish could escape tethers in the absence of predation. Twenty-four crayfish were tethered in a 1.8-m diameter tank for 6–10 d. During this time, a few crayfish molted but no other crayfish escaped, a result confirming tethering studies by DiDonato and Lodge (1993) and Mather and Stein (1993a).

Predation assays were run 26 June–25 August 1990 at the same sites used in the cross-habitat survey. At a given site, the survey and assay did not overlap in time but were done within one week of each other. Either all Form I (sexually active molt stage) or all Form II (sexually inactive molt stage) *O. rusticus* males were used in a given run. Three size classes were used in these assays: small—15–18-mm CL (S), medium—23–28-mm CL (M), and large—33–35-mm CL (L). Assays were conducted for 24 h (8:30 AM–8:30 AM the next day) at three positions within a habitat pair: at the border, and 50 m into each of the two habitat patches. At each position, there were three tiles/sample (3 size classes), with 15 samples (45 tiles). Tiles were

systematically arranged by size class of crayfish (S, M, L, S, M, L, S, . . .) along a single transect parallel to shore (depth = 1.3–1.5 m), and were spaced 0.5 m apart. The following morning, remaining crayfish were counted.

Results of the field predation assay were graphically compared with results of the cross-habitat survey. A two-way ANOVA was run comparing % crayfish mortality across habitats and crayfish sizes, using the sites as replicates: cobble $n = 4$; macrophyte $n = 3$ (macrophyte/firm and macrophyte/muck were pooled to provide replicates); and sand $n = 3$. Tukey's test (at $\alpha = 0.05$) was used to determine significant differences between treatments. The data met the assumptions of ANOVA, and therefore were not transformed.

Among-lake survey

In summer 1987, the abundance and species composition of fish and crayfish were surveyed in 21 lakes in north-central Wisconsin. Although these data were collected for a separate set of objectives, we used data from a seven-lake subset to examine the effects of habitat type and predation risk on patterns of habitat use by *O. rusticus*. These seven lakes were chosen because they had three major habitat types (i.e., cobble, macrophyte, sand), and had densities of *O. rusticus* adequate for analysis (between 5 and 33 male *O. rusticus*/trap). Lakes used in these analyses were Papoose Lake, Presque Isle Lake, Spider Lake, Squirrel Lake, Little Star Lake, Plum Lake, and Van Vliet Lake (Table 1).

In each lake, nighttime electrofishing (5.5-m, dual-boom shock boat) was used to survey the fish community along 50-m transects in all three habitat types (7–11 transects per lake; 1–5 transects per habitat; 16 July–10 August 1987). Known crayfish predators collected were largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), yellow perch (*Perca flavescens*), and rock bass (*Ambloplites rupestris*); numbers of those >90 mm long were pooled for each transect in each habitat type. Mean predator capture (per 50-m transect) was then calculated for each habitat type in each lake. Habitat-specific estimates of male *O. rusticus* abundance (size data were not collected) were determined by placing a single baited minnow trap along electrofishing transects (with 3.5–4.5-cm entry holes) overnight in each of 24 or

36 sectors (sector number differed between lakes). As described by Olsen et al. (1991), these trapping methods provide a good index of large male crayfish abundance, and our analyses were limited to male crayfish. The shoreline of each lake sampled was divided into 24 or 36 equal shoreline-length sampling units. Habitat type in each sector was characterized as cobble, sand, or macrophyte (macrophyte/firm and macrophyte/muck were not distinguished), allowing estimation of the proportion of lake littoral zone composed of different habitat types. To generate a lakewide estimate of predator abundance, we weighted habitat-specific estimates of predator abundance by habitat occurrence within a lake.

To determine the potential effect of habitat type and predator density on patterns of habitat use by *O. rusticus*, we calculated Chesson's α (Chesson 1983) to determine crayfish habitat association for each habitat in each lake:

$$\alpha = \frac{\frac{r_i}{p_i}}{\sum \left(\frac{r_i}{p_i} \right)}$$

where r_i is the proportion of lakewide male *O. rusticus* trapped in habitat i , and p_i is the proportion of lakewide substrate composed of habitat i . For each habitat in each lake, we graphically compared our calculated α to the α expected if crayfish used habitats in proportion to habitat abundance. Therefore, Chesson's α values >0.33 indicate positive association and values <0.33 indicate negative association for a given habitat type. Habitat-specific Chesson's α values were compared (across all seven lakes) using the nonparametric Kruskal-Wallis test. Parametric regressions were used to test the relationship between both lakewide and habitat-specific predator number (per 50-m transect) and habitat-specific Chesson's α values for each lake.

Results

Cross-habitat survey and field predation assay

In the cross-habitat survey at Sites A and B, results were very repeatable, indicating little temporal variability (Fig. 1). Crayfish abundance differed among habitats, with normalized crayfish densities at cobble-sand sites (Sites

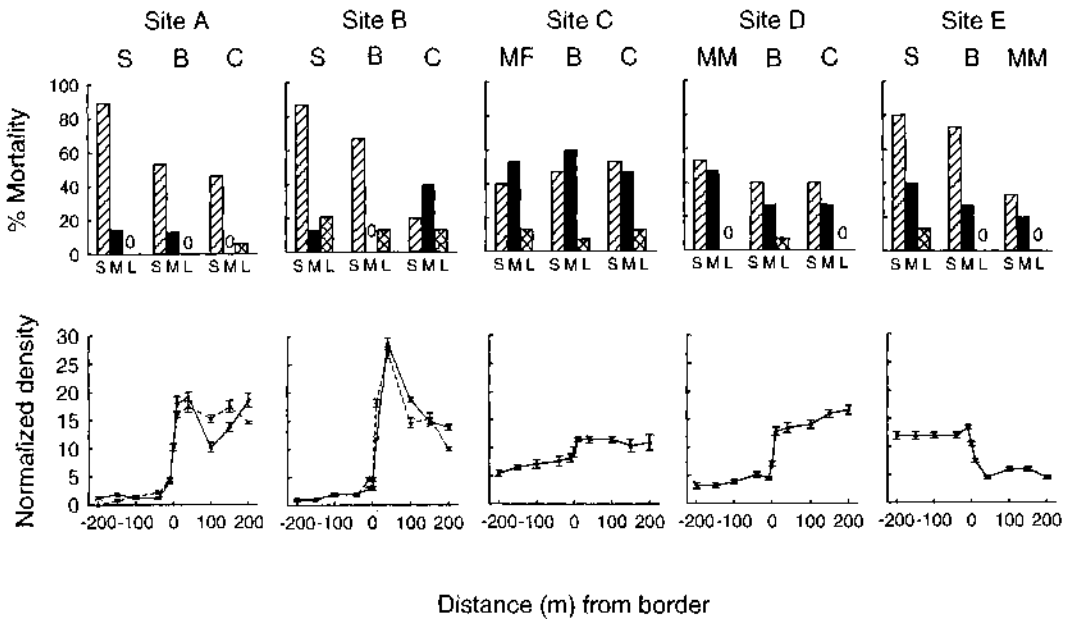


FIG. 1. Field results for sites A, B, C, D, and E. Habitats at each site are noted above each pair of panels as S = sand, C = cobble, MF = macrophyte/firm, MM = macrophyte/muck, and B = border between habitats. The top panel for each site represent results of the size-specific field predation assay for each habitat pairing; S = small crayfish (15–18-mm CL), M = medium crayfish (23–25-mm CL), L = large crayfish (33–35-mm CL). The bottom panels represent results of the cross-habitat survey: distance from border vs. normalized crayfish density. For sites A and B, the solid line represents survey results from the first night and the dashed line represents survey results from the second night. Total number of crayfish caught at each site were: Site A = 166 (first night), Site A = 137 (second night), Site B = 101 (first night), Site B = 110 (second night), Site C = 183, Site D = 156, Site E = 67 (see Methods for normalization procedure). Mean site-specific crayfish densities (per m², calculated from the 40, 100, 150, and 200 m locations within each habitat) were: Site A (first night): sand = 0.45/m², cobble = 5.15/m²; Site A (second night): sand = 0.30/m², cobble = 4.45/m²; Site B (first night): sand = 0.30/m², cobble = 3.85/m²; Site B (second night): sand = 0.30/m², cobble = 3.70/m²; Site C: macrophyte/firm = 2.45/m², cobble = 4.05/m²; Site D: macrophyte/muck = 1.20/m², cobble = 4.70/m²; Site E: sand = 1.60/m², macrophyte/muck = 0.70/m². Error bars represent ± 1 SE ($n = 5$ quadrats).

A and B) being 7–10 × higher in cobble than in sand (Fig. 1). Cobble patches at both the cobble-macrophyte/firm (Site C) and cobble-macrophyte/muck (Site D) field sites had crayfish densities 2–3 × higher than at either type of macrophyte habitat (Fig. 1). The sand-macrophyte/muck field site (Site E) had crayfish densities 2 × higher in sand than in macrophyte/muck (Fig. 1).

From a comparison of crayfish abundance across all field sites, the following rank order of crayfish habitat association emerges: cobble > macrophyte/firm > sand > macrophyte/muck. Because we did not have replication or multiple site-specific sample dates (except for Sites A and B), this ranking may be affected by between-site differences in predation regime

and food availability over which we had no control.

Crayfish densities were inversely related to predation risk at two sites (Sites A and B), positively related at one site (Site E), and showed no relationship at two sites (Sites C and D). Clearly, predation risk does not always adequately explain patterns of crayfish distribution.

Small crayfish experienced significantly higher mortality than either medium or large crayfish, and medium crayfish had significantly higher mortality than large crayfish in the field predation assay (Fig. 2; Tukey's HSD $p < 0.05$). Small crayfish in cobble and macrophyte habitats experienced significantly lower mortality than small crayfish in sand habitats, whereas

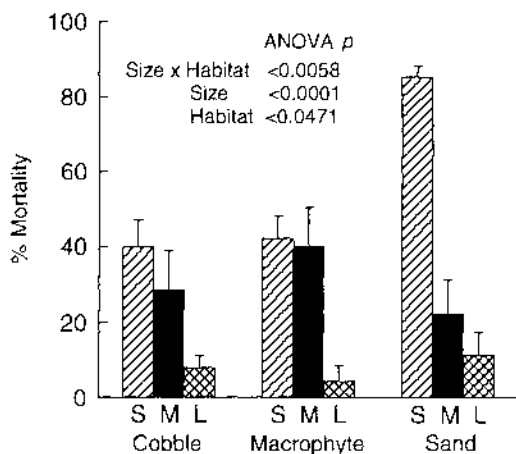


FIG. 2. Results of the field predation assay, regarding size-specific predation risk in different habitats; S = small crayfish (15–18-mm CL), M = medium crayfish (23–25-mm CL), and L = large crayfish (33–35-mm CL).

mortality in macrophyte habitats did not differ significantly from that in cobble habitats (Fig. 2; Tukey's HSD $p < 0.05$). The significant habitat \times size interaction in the field predation assay appears primarily to reflect the fact that predation on small crayfish was higher in sand than in cobble or macrophyte (Fig. 2). Although the significant interaction effect makes it difficult to make general statements about significance of the main effects, it appears that both size-specific and habitat-specific predation were observed for *O. rusticus* in the field predation assays (Fig. 2).

Among-lake survey

Crayfish use of cobble in the among-lake survey was consistent with results of the cross-habitat survey. In the seven lakes surveyed, Chesson's α values indicate that male *O. rusticus* were overrepresented in cobble habitat, used sand habitat in proportion to its abundance (indicating neither preference nor avoidance), and were underrepresented in macrophyte habitat (Fig. 3; Kruskal-Wallis test, $p < 0.025$).

Regressions of the relationship between habitat-specific predator density and habitat-specific Chesson's α values were statistically significant for cobble ($n = 7$, $p = 0.049$, $R^2 = 0.57$), but not for sand ($n = 7$, $p = 0.919$, $R^2 = 0.002$) or macrophyte ($n = 7$, $p = 0.139$, $R^2 = 0.382$)

habitats. Similarly, regressions between lake-wide predator density and habitat-specific Chesson's α values were statistically significant for cobble ($n = 7$, $p = 0.024$, $R^2 = 0.67$), but not for sand ($n = 7$, $p = 0.131$, $R^2 = 0.394$) or macrophyte ($n = 7$, $p = 0.089$, $R^2 = 0.47$) habitats (Fig. 4). At higher predator densities, male crayfish use of cobble habitat was greater, while use of sand and macrophyte habitats did not differ significantly.

Discussion

Overall, the predicted importance of habitat type in structuring patterns of crayfish distribution was supported by the cross-habitat survey and field predation assay. Strong support for the predicted inverse relationship between predation risk and crayfish distribution was found in both lower-risk cobble and higher-risk sand habitats in these two field studies, particularly for small crayfish. In contrast, crayfish densities in macrophyte/muck (and possibly macrophyte/firm) habitat were unrelated to predation and may be limited by physical attributes of substrate type (e.g., fine sediments may impede crayfish movement). While the consistent pattern in these results (Fig. 1) is that crayfish abundance is strongly associated with cobble habitats, results also suggest that pre-

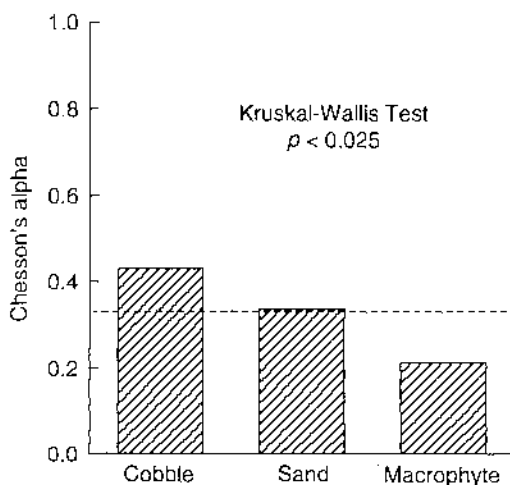


FIG. 3. Effect of habitat type on patterns of crayfish habitat use as measured by Chesson's α ($n = 7$ lakes). The dashed line indicates neutral association ($\alpha = 0.33$).

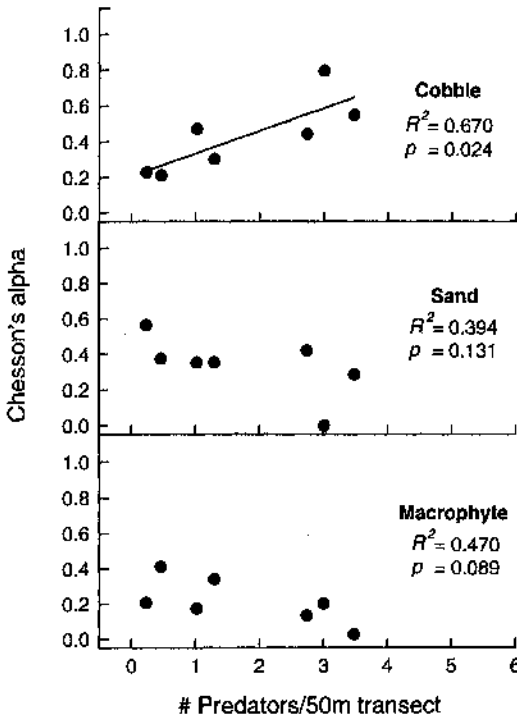


FIG. 4. Relationship between lakewide predator density (number of predators/50 m transect) and crayfish habitat use as measured by Chesson's α . Each value represents a single lake.

dation risk has differential importance in different habitat types.

The field predation assay demonstrated that size-specific predation risk differs between habitat types, which might result in habitat-specific patterns of size-structured crayfish distribution; however, we did not test these patterns directly. Another explanation for observed crayfish mortality may be cannibalism. However, cannibalism occurs exclusively or at least primarily during crayfish molting periods (Lodge and Hill 1994), which we avoided in our experiments.

In the among-lake survey, male crayfish were more abundant in cobble than in either sand or macrophyte habitats (Fig. 3), which is largely consistent with the rank order of habitat association derived from the cross-habitat survey (Fig. 1). Male crayfish use of cobble increased significantly with both increased lakewide and habitat-specific predator density (Fig. 4). While not statistically significant, crayfish use of sand and macrophyte habitats appeared to decline with increased lakewide predator density (Fig.

4). Garvey et al. (1994) found that *O. rusticus* mortality was slightly lower in cobble than in macrophytes. Although our data come from a limited number of sample dates, we feel that observed patterns are representative, given that crayfish distributions in this region are relatively constant during summer months (Lorman 1980). Overall, these results provide further support for the potential importance of predation in structuring patterns of male *O. rusticus* distribution.

The lack of statistical significance in the among-lake survey for the relationship between crayfish use of sand habitat and predator density was puzzling, given high predation risk for small crayfish on sand and our expectation that avoidance of sand would increase as predator density increased. These contradictory results are likely due to differences in sampling methods used in the cross-habitat and among-lake surveys. Trapping (used in the among-lake survey) probably provided a poorer index of abundance of small crayfish than did the visual surveys used in the cross-habitat survey. Thus, we would probably not have detected any inverse relationship existing between small crayfish abundance and abundance of fish predators.

Our results are consistent with studies demonstrating that the presence of predators may cause organisms to seek low-predation-risk habitats and/or reduce activity levels. Crayfish in both lentic habitats (Stein and Magnuson 1976, Saiki and Tash 1979, Collins et al. 1983, Garvey et al. 1994, Hill 1994) and lotic ones (Mather and Stein 1993a, 1993b) reduce their activity and increase their use of sheltering habitats when under predation pressure. Our finding that crayfish use of cobble increased with increased predator density is certainly consistent with Collins et al. (1983), who found that crayfish from lakes with high predator density were more shelter-bound than those from systems with low predator density. Marine studies demonstrate that size-related differences in habitat use by American lobsters (Wahle and Steneck 1992) and Caribbean spiny lobsters (Smith and Herrnkind 1992) can also be explained by habitat-specific predation risk. The second factor of interest, physical attributes of substrate type, has not been tested, despite the fact that it may be important in influencing crayfish distributions.

Observed patterns of crayfish distribution may also be affected by intraspecific interactions. For example, segregated habitat usage by conspecific juvenile and adult crayfish resulted from agonistic interactions (Mather and Stein 1993a, 1993b). Interspecific interactions may also influence crayfish distribution, as less-competitive crayfish species are often forced into unfavorable habitat types (Capelli 1982, Capelli and Munjal 1982, Mather and Stein 1993a, 1993b, Hill and Lodge 1994). However, effects of interspecific competition on the distribution and dispersal of *O. rusticus*, the competitive-dominant in northern Wisconsin lakes (Garvey et al. 1994, Hill and Lodge 1994), are probably negligible.

Our results suggest that the relative abundance of different habitat types would influence the success of ongoing *O. rusticus* invasions in northern Wisconsin lakes (Lodge et al. 1986, Olsen et al. 1991) and Ohio rivers and streams (Butler and Stein 1985, Mather and Stein 1993a, 1993b). Low predation risk in cobble and the strong positive association of crayfish with cobble suggest that the success of *O. rusticus* establishment may be sensitive to cobble abundance. Therefore, systems composed mainly of cobble habitat may be more susceptible to crayfish invasions than systems where cobble is rare or absent. Preliminary results of simulation modeling that examined the influence of habitat type on crayfish invasion rate supported this prediction (Kershner 1992).

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