Predation on and Distribution of *Orconectes* Crayfish Species in Tenderfoot Lake, Wisconsin/Michigan

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Abstract

Two surveys and one experiment were conducted on Tenderfoot Lake in northern Wisconsin and Michigan in relation to the ongoing invasion of two exotic crayfish - *Orconectes rusticus* and *O. propinquus*. A lakewide survey of crayfish species in rocky habitats was used to determine if *O. rusticus* was present in the lake, and estimate the relative proportions of species in rocky habitats. In the second survey, crayfish were trapped in three different substrate types – rocky, marshy, and mucky – to determine whether crayfish species distribution differed by substrate type. The predation experiment was conducted using tethered crayfish in the rocky and mucky substrates to determine if fish predation on crayfish differed between the species by substrate.

No *O. rusticus* were trapped in Tenderfoot Lake, confining the study to the other two species. Species distribution was found to differ by substrate type: most *O. virilis* were found in mucky habitats while most *O. propinquus* were found in rocky habitats. The predation experiment indicated that in the rocky area the species experienced similar rates of predation. In the mucky area only *O. propinquus* was removed at a significantly greater rate than in the rocky area. This study suggests that predation by fish may be a key determinant in the location of *O. propinquus* within the lake, while interspecific competition may more strongly determine the location of *O. virilis*. Additional studies on crayfish species' and predatory fish's tolerance ranges of abiotic factors, as well as additional research on intraspecific and intersex competition between crayfish would be useful to more clearly determine the mechanisms affecting crayfish distribution and replacements.

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Introduction

The ongoing invasion of exotic species is a worldwide concern of ecological and commercial importance. Some 50 years ago, northern Wisconsin lakes experienced the invasion of the exotic crayfish *Orconectes propinquus*, which is now found in conjunction with the native *O. virilis* in virtually all lakes in the region. A second and more recently arrived crayfish, *O. rusticus*, is spreading rapidly via introduction from its native range in Indiana and Kentucky, USA (Lodge et al. 1998), to increasing numbers of lakes in the upper Midwest and Canada (Hill and Lodge 1999). Where found, *O. rusticus* unquestionably dominates the ecosystem, reducing *O. propinquus* and *O. virilis* numbers, and decreasing macrophyte growth and benthic invertebrate populations (Hill and Lodge 1999). Studies of the mechanisms governing the successful invasion of *O. rusticus* suggest that many variables, including competition and predation, determine the relative abundances of each species (Lodge et al. 1986, DiDonato and Lodge 1993, and Olsen et al. 1991). DiDonato and Lodge (1993) suggested that predation by fish is an important mechanism in species replacements, and that the replacement rate of congeners by *O. rusticus* should be positively related to rates of fish predation. However, the effect of *O. rusticus* on relative abundances of species does not exactly parallel the observed population arrangements.

Lakes without *O. rusticus* are less well studied. While *O. propinquus* is well established, it does not have the dominating effect of *O. rusticus*. Reversals in abundance of *O. propinquus* and *O. virilis* have been found, indicating that multiple factors are at work – predation, competition, local fish assemblages, and others. In particular it is interesting to note that species and size-selective predation tests produce opposite predictions for the replacement of *O. virilis* by *O. propinquus*: size-selection favors the success of *O. virilis* as it is the larger of the two species, while species-selection favors *O. propinquus*, presumably due to its more aggressive behavior (Lodge and Hill 1994).

To the best of my knowledge, all previous experiments on predation on crayfish have been conducted in habitats favorable or ideal for crayfish (cobble substrates), or in open sandy habitats that expose crayfish to predation (DiDonato and Lodge 1993). Lodge and Hill (1994) noted that while both crayfish species primarily prefer rocky habitats, and secondarily prefer vegetated habitats, *O. virilis* was shown to next choose soft lentic substrates, while no third preference was listed for *O. propinquus*. This suggested that *O. virilis* could tolerate habitats that *O. propinquus* could not, thereby raising questions regarding the effect of habitat tolerance on distribution, selective predation, competition, and resulting species abundances.

In this study we first sought to establish if *O. rusticus* had been introduced into Tenderfoot Lake; surveys in previous years had not revealed its presence. The next goal was to survey crayfish populations in varying substrate types within Tenderfoot Lake to characterize crayfish species distribution between habitats. In the predation experiments, same-sex, -size, and –species crayfish pairs were tethered in the lake, one of each pair in rocky substrate, the other in the spongy, organic "mucky" substrate, in order to test whether predation rates by fish differed in different substrate types.

Materials and Methods

The *Orconectes* crayfish species were surveyed in rocky substrates in Tenderfoot Lake using standard trapping techniques for large crayfish (Olsen et al. 1991). Olsen et al. (1991) and Lodge et al. (1986) found that *O. rusticus* tends to replace *O. propinquus* and *O. virilis* where occurring together. Lodge and Hill (1994) indicate that crayfish prefer dense cobble substrates. Thus, it was predicted that *O. rusticus*, if present in significant numbers, would be found in the rocky habitats of Tenderfoot Lake. Twenty-three traps containing approximately 110g beef liver bait were set in rocky habitats at 0.5-1.0m depth in the late afternoon on June 19, 2000, and collected the next day at mid-morning. (Figure 1). Crayfish caught were identified, sexed, and measured for carapace length. In addition, the form of each male was determined. All captured crayfish were then maintained in a 2m diameter flow-through tank with well water and were fed once daily with flaked fish food. Rocks were provided as shelters within the tank.

Species distribution between habitat types was surveyed by the same method of trapping on June 20-21, 2000, in three different locations, each having a distinctly different substrate - rocky, marshy, and mucky. A rocky substrate was defined as having a bottom completely covered in small to large-sized rocks and lacking macrophyte growth; marshy substrates were characterized by reeds (*Scirups*) extending out of the water, a firm sandy or gravelly bottom, and a few small rocks scattered about infrequently; mucky was characterized by a deep organic layer with various submerged macrophytes and lacked rocks completely. Four traps (five in the marshy area) at 12-15 meters apart were placed in each location. (Figure 1).

Predation on crayfish in different substrates was tested during the week of July 3-7, 2000 by tethering pairs crayfish that were alike in species, sex, and size; one of each pair was placed in the rocky or mucky environments. (Figure 1). Eight pairs of *O. virilis* and eight pairs of *O. propinquus* were used; half of the *O. virilis* were female, while all *O. propinquus* were male. Carapace length was measured from the tip of the rostrum to the end of the carapace in millimeters. *O. propinquus* ranged in size from 23-35mm; *O. virilis* ranged from 37-46mm. Placement order of crayfish at each location was randomized but checked for even distribution of size, sex, and species. (Table 1).

The tether anchor was constructed of 8-lb fishing line with a swivel tied securely around a rock (for the rocky area) or around a 18x18cm clay tile (for the mucky area). Rocks had been obtained from the test area three days beforehand and were stored in lakewater to retain algal growth and other features. Another swivel was superglued to the center of the carapace of each crayfish, and the two swivels were connected using a loop of 2-lb fishing line, for a total rock/tile-to-crayfish length of approximately 20cm. A fishing bobber on another line was tied to 8-lb line around the rock or tile, serving as a marker for each crayfish. On July 3rd, the crayfish were placed 2-5 meters apart in 0.5-1.0m of water in each location and left for 5 days and nights. The crayfish were checked every 24-48 hours; missing or dead crayfish were replaced when possible with similar-sized and same-sex crayfish of the same species.

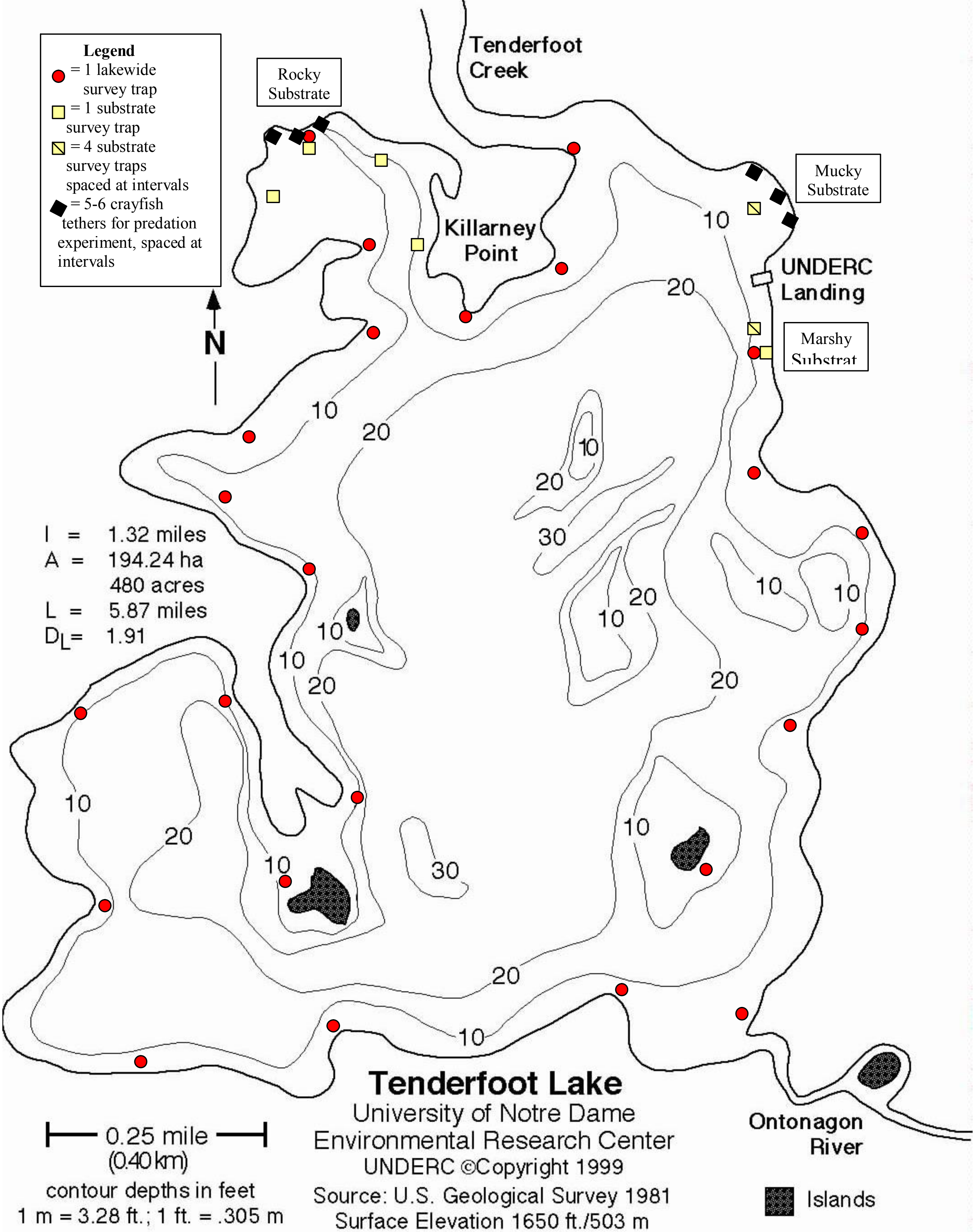

Figure 1: Map of Tenderfoot Lake showing the placement of traps in the lakewide species survey and the substrate survey. This also shows the locations of the crayfish in the predation experiment. The bay to the northwest of Killarney Point was the experimental rocky substrate, while the bay to the northeast of the UNDERC landing was the experimental mucky substrate.

Table 1: Matching crayfish pairs used in the predation experiment are shown horizontally by line. Order of placement, from south to north, of each crayfish in the two substrate locations is given in parentheses at the right of each column. See also Figure 1 for experimental locations.

Rocky Substrate		Mucky Substrate	
Crayfish description	S→N order of placement at location	Crayfish description	S→ N order of placement at location
38.6 male *virilis*	(1)	38.2 male *virilis*	(8)
46.5 female *virilis*	(2)	46.5 female *virilis*	(16)
32.5 *propinquus*	(3)	32.5 *propinquus*	(7)
26.4 *propinquus*	(4)	26.4 *propinquus*	(14)
24.4 *propinquus*	(5)	24.4 *propinquus*	(5)
44.5 male *virilis*	(6)	44.2 male *virilis*	(13)
35.5 *propinquus*	(7)	35.5 *propinquus*	(9)
40.0 male *virilis*	(8)	40.1 male *virilis*	(6)
39.4 female *virilis*	(9)	39.4 female *virilis*	(1)
23.2 *propinquus*	(10)	23.2 *propinquus*	(12)
34.0 *propinquus*	(11)	34.0 *propinquus*	(15)
46.0 female *virilis*	(12)	46.0 female *virilis*	(10)
29.4 *propinquus*	(13)	29.4 *propinquus*	(2)
34.8 male *virilis*	(14)	34.9 male *virilis*	(4)
41.2 male *virilis*	(15)	41.2 male *virilis*	(3)
30.5 *propinquus*	(16)	30.5 *propinquus*	(11)

Results

In surveying crayfish species distribution in Tenderfoot Lake, one male type I *O. virilis*, five female *O. virilis*, 21 male type II *O. propinquus*, and six female *O. propinquus* were trapped. (Figure 2). No *O. rusticus* was found in this survey of rocky habitats.

In the survey of crayfish species variation by substrate type in Tenderfoot Lake, we found differential distribution of the two species between the rocky and mucky habitats. In the rocky area, 11 male *O. propinquus* were caught, as compared to 1 male *O. virilis* and 2 female *O. virilis.* In the mucky area, 1 female *O. propinquus*, 9 male *O. virilis* and 16 female *O. virilis* were trapped. In the marshy area, we captured 2 male *O. propinquus*, 1 male *O. virilis*, and 2 female *O. virilis.* (Figure 3)

The *O. virilis* males and females were found approximately eight times more frequently in the mucky location than in the rocky and marshy areas. The *O. propinquus* males were found at least five times as frequently in the rocky location as the others, while the single *O. propinquus* female was found in the mucky area. Error and statistical variation were not calculated due to no trap-specific recordings. (Figure 4).

In the predation experiment, the two species did not experience significantly different predation rates in the rocky habitat (Figure 5). However, removal of *O. virilis* was confined to the rocky area, while *O. propinquus* was consumed significantly more often in the mucky area than in the rocky area. Overall, *O. propinquus* experienced more frequent consumption. (Figure 5).

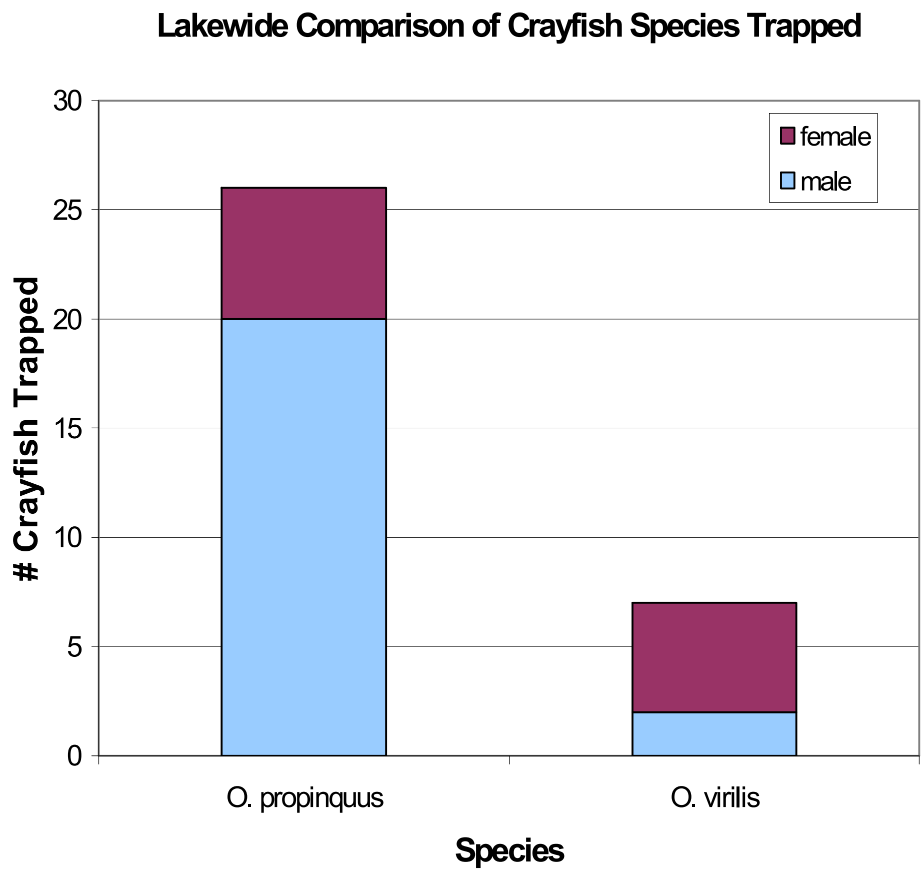

Figure 2: Number and sex of crayfish species caught in 23 traps in rocky habitats of Tenderfoot Lake.

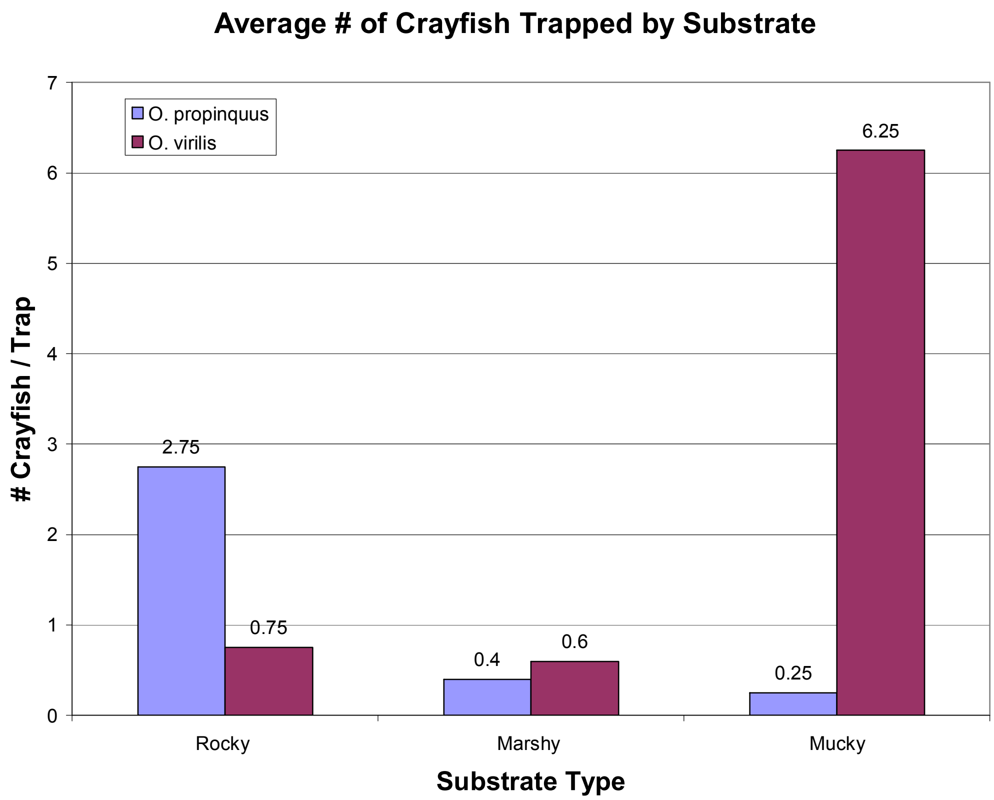

Figure 3: Average number of species caught per trap at each substrate type.

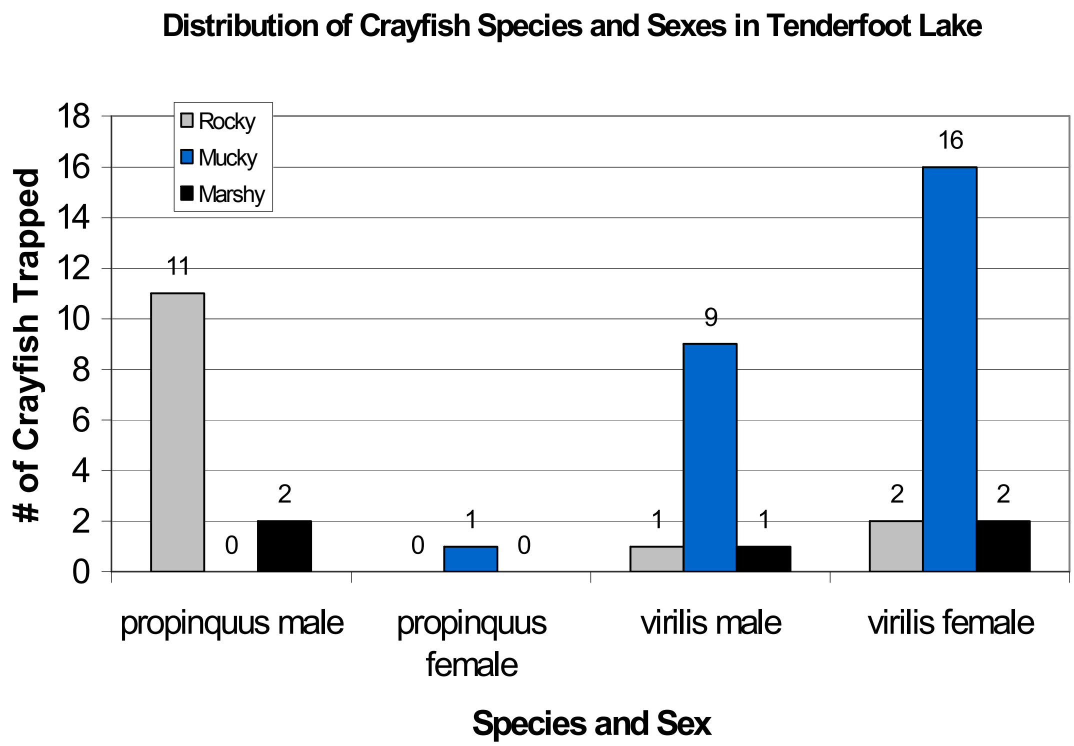

Figure 4: Distribution of species' sexes by substrate type.

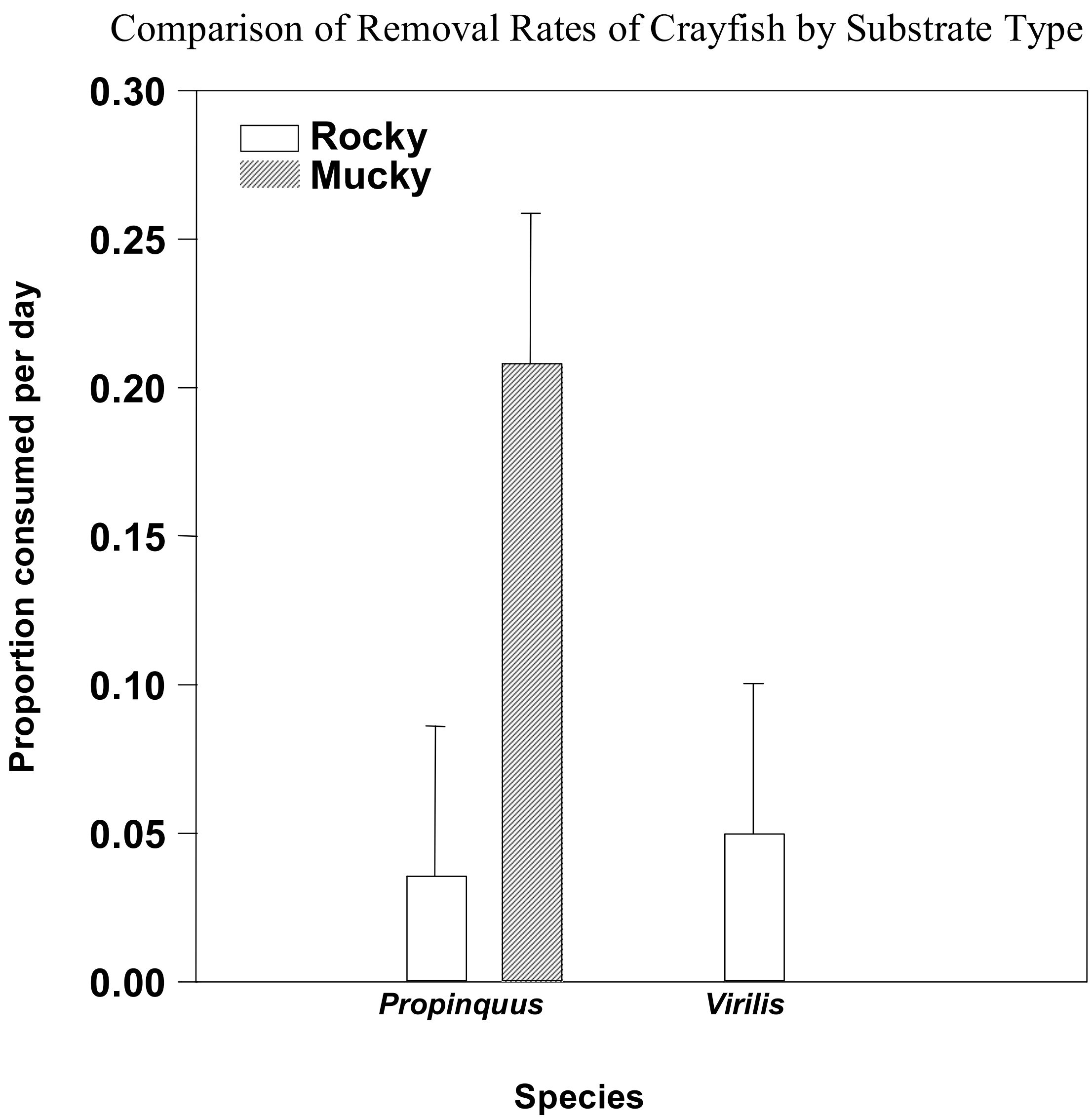

Figure 5: Comparison of removal rates between *Orconectes* species and substrate types.

Discussion

Since the initial survey of Tenderfoot Lake did not find any *O. rusticus*, research was conducted exclusively on *O. propinquus* and *virilis*. *O. propinquus* outnumbered *O. virilis* nearly 4:1 in the initial lake-wide survey of rocky habitats. Male *O. propinquus* were much more common than females as was expected (Lodge and Hill 1994). That female *O. virilis* outnumbered males may be explained by low numbers (i.e. chance), or that males may have been molting, given that the one male found was a Type I. It has been shown previously that females in general are more active when males molt, but are otherwise difficult to capture since males tend to be more active and aggressive (Lodge and Hill 1994). At this point it seems that while *O. rusticus* has not invaded the lake, *O. propinquus* is well established and *O. virilis* is still fairly common.

In the survey trapping by substrate type, the ratio in the rocky substrate was again almost 4:1 in favor of *O. propinquus*, comparing similarly to the lake-wide survey. Interestingly, the greatest overall number of crayfish were trapped in the spongy, organic "mucky" area, with all but one being *O. virilis*. Naturally we expected to find the greatest numbers in the traditionally favored rocky habitat. Additionally, well over half (16 of 25) of these were female. However, this was again attributed to *O. virilis* males molting (Lodge, *pers. comm.* July 2000).

The presence of *O. virilis* in the mucky area supports the observation of Lodge and Hill (1994) that *O. virilis* will tolerate soft substrates despite their preference for firm, cobbled substrates. It seems possible that *O. propinquus* is infrequent in the mucky area due to its avoidance of soft substrates as indicated by Lodge and Hill (1994), although the macrophyte growth probably provided sufficient shelter for crayfish in this area. Also, it seems likely that *O. propinquus* has, at that point, out-competed *O. virilis* for the more desirable rocky habitats, relegating many *O. virilis* to areas not populated by *O. propinquus*, but where *O. virilis* can still survive. That the only *O. propinquus* found in the mucky area was a female supports the idea of competitive exclusion as females are known to be out-competed by males. *O. virilis* may be more suitable to survival in mucky areas, though in what ways it is not known. Lodge and Hill (1994) indicated that *O. virilis* has greater tolerance than *O. propinquus* of lower pH, but species' survival ranges of dissolved oxygen concentrations are not known. While pH and dissolved oxygen were not recorded in this study, the slow, nearly stagnate waters and spongy, boggy bottom of the mucky area suggest that dissolved oxygen and pH, respectively, may be lower in this environment than in the more wave-swept rocky areas.

Trappings in the sandy, more marshy area were the lowest overall, despite the additional trap. This suggests disadvantage (or lack of advantage) for both species at this site. The most obvious cause seems to be inadequate shelter; the cobbles and slender reeds were probably too small and infrequent to provide shelter. The area also may not have supported sufficient invertebrate populations or had enough detritus or other plant material to support a larger crayfish populations' energy requirements (Lodge and Hill 1994).

From these results we wondered if females of both species occurred more frequently in the mucky areas since crayfish females are at a competitive disadvantage and are thus forced from the more favorable areas by the more active and aggressive males. While the data for *O. virilis* is skewed by the males molting, it is interesting that *O. propinquus* males were found only in the rocky and marshy areas, while the only female was found in the mucky area. The occurrence and effects of intersex and interspecies competition needs further study.

In the predation experiment, *O. propinquus* experienced significantly higher removal rates in the mucky area than in the rocky area, and indeed experienced the highest overall rate of predation. This may help explain why *O. propinquus* is not found with regularity or noted to inhabit soft substrates. The high rate of removal suggests that predation, rather than *O. propinquus'* inherent biology or behavior, may be determining its viability in soft substrates. Further study on substrate tolerance in the absence of predators would help determine for both species the factors governing *O. propinquus's* apparent non-viability in soft substrates.

That *O. virilis* did not experience any removal by predation in the mucky area supports the idea that *O. virilis* is at an advantage there over *O. propinquus*. Again, the factors influencing this advantage are not clear. It is possible that predatory fish frequent the mucky area less often as compared to the rocky area, which would be advantageous for both species. Temperature, depth, oxygen concentrations, dissolved nutrients, or other abiotic factors that differ from the rocky area are likely considerations that may affect fish predation and require additional study. However, the scarcity of *O. propinquus* in the mucky environment suggests that *O. virilis* has been out-competed in more desirable habitats, or that it has some adaptation – physiological or behavioral – that makes the mucky environment a suitable habitat for *O. virilis*. Removal of *O. propinquus* and *O. virilis* did not differ significantly in the rocky area, suggesting that predation is not a significant determining factor in the distribution of species in this case. Competition may be a stronger ruling factor here, as the interspecific competitive advantage of *O. propinquus* has been noted before (Lodge and Hill 1994).

This study thus suggests that predation may be a key determinant in the distribution of *O. propinquus* within the lake, while competition may more strongly determine the location of *O. virilis* within the lake. These observations are consistent with previous findings that *O. propinquus* is exposed to higher predation presumably due to its smaller size (DiDonato and Lodge 1993), while the disadvantage of *O. virilis* lies in its behavior (Lodge and Hill 1994). Other variables conferring advantage or disadvantage are each species' inherent biology, including tolerance ranges of abiotic factors. Further study of the distribution by sex and species between the different substrates would also be illustrative of the mechanisms determining the distribution of *O. propinquus* and *O. virilis* in Wisconsin lakes.

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