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## Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard)<sup>1</sup>

**Abstract**—*Orconectes rusticus*, an introduced species in northern Wisconsin, is confirmed as displacing other species of crayfish. Displacement rates are extremely rapid in some cases but are highly variable among lakes. Displacement mechanisms and ecological implications are not well known; however, significant reductions in macrophyte populations are an apparent result.

Crayfish are common in lake and stream communities throughout most of the United States; in some lakes standing

crops may be several times that of all other benthic fauna combined (Momot 1967). Creaser (1932) reported six species of crayfish in Wisconsin: *Orconectes virilis* (Hagen), *Orconectes propinquus* (Girard), *Orconectes immunis* (Hagen), *Cambarus diogenes* (Girard), *Procamburus acutus* (Girard), and *Procamburus gracilis* (Bundy). Although his survey data are meager for much of northern Wisconsin, his published records and the collections in various museums strongly suggest that *O. virilis* and possibly the semiterrestrial *C. diogenes* were the only species present in the extensive lake district of the Vilas County area. By 1970, however, *O. propinquus* and *Orconectes*

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*rusticus* (the latter formerly known only as far northward as southern Michigan and northern Illinois) were also abundant throughout the area, and *O. immunis* and *P. acutus* were present in small numbers (Capelli 1975). Colonization mechanisms are unknown, but the use of crayfish as bait by fishermen is suspected. Distribution patterns and other circumstantial evidence suggest that *O. propinquus* was introduced sometime before *O. rusticus*, that *O. propinquus* is able to displace *O. virilis*, and that *O. rusticus* is able to displace both the other species.

I present here data which confirm such displacements, but indicate high variation in displacement rate.

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All nine lakes discussed below, except Sparkling, are relatively large (90–340 ha), moderately productive drainage lakes; Sparkling is a 50-ha oligotrophic seepage lake. The location and various physical-chemical characteristics of each are described by Capelli (1975). Sparkling Lake was originally sampled during mid-July 1973 and the others during July–August 1975. Collecting gear consisted of 18 wire-mesh minnow traps baited with 120 g of beef liver placed at about 100-m intervals in a selected area of each lake. Traps are strongly selective for adult males, which usually comprise 80–100% of the catch; however, other collecting methods including direct capture by use of SCUBA verified that traps reliably determined both species composition and relative abundance (Capelli 1975). All data reported here are based on numbers of adult males. Papoose Lake was resampled with 12 traps in mid-July 1979 and 1980 in the same general area as the original sample; other lakes were similarly resampled with 10–12 traps during mid-July 1980 only. All lakes chosen for resampling contained *O. rusticus* at the time of the original sample and one or both of *O. virilis* and *O. propinquus*. In most cases *O. rusticus* was numerically subordinate in the original sample. Be-

cause I thought that reproductive interference, possibly involving hybridization between *O. rusticus* and *O. propinquus*, might be a mechanism for changes in distribution, I examined all individuals collected from South Turtle Lake and Papoose Lake in detail for evidence of hybridization, using the characteristics described by Capelli and Capelli (1980).

In the 5–7 years between samples, seven of the nine lakes changed significantly in species composition (Fig. 1). Changes generally involved reductions in *O. propinquus* in relation to *O. rusticus*, and reductions in *O. virilis* in relation to both the others. However, the degree of change was highly variable. The most dramatic change was in Papoose Lake. In 1975 the lake was dominated by *O. propinquus* (81%), with small numbers of *O. rusticus* (11%) and *O. virilis* (8%). In 1979 (data not shown), no *O. virilis* was found, and *O. propinquus* comprised only 17% by number. One year later, only *O. rusticus* was found. A similar rapid shift occurred in Birch Lake, although both *O. propinquus* and *O. virilis* were still present in small numbers in 1980. In Sparkling Lake, *O. virilis* was apparently eliminated and *O. propinquus* reduced significantly. Van Vliet Lake shifted from dominance by *O. virilis* with a few *O. rusticus* to the reverse. Clear Lake was already dominated by *O. rusticus* in 1975, but by 1980 a continued significant shift at the expense of *O. virilis* had occurred.

Changes favoring *O. rusticus* were less dramatic or absent in other lakes. In both Big Lake and South Turtle Lake *O. rusticus* increased significantly, with a significant reduction in *O. virilis* but little change in *O. propinquus*. In Island Lake, *O. rusticus* retained its large numerical advantage over *O. propinquus* but no significant change occurred. In Boulder Lake, *O. rusticus* showed no change from its very low original density, and all three species remained in similar proportions.

For the data in Fig. 1, all individuals which exhibited any evidence of hybridization were referred to the species they most closely resembled. However, among

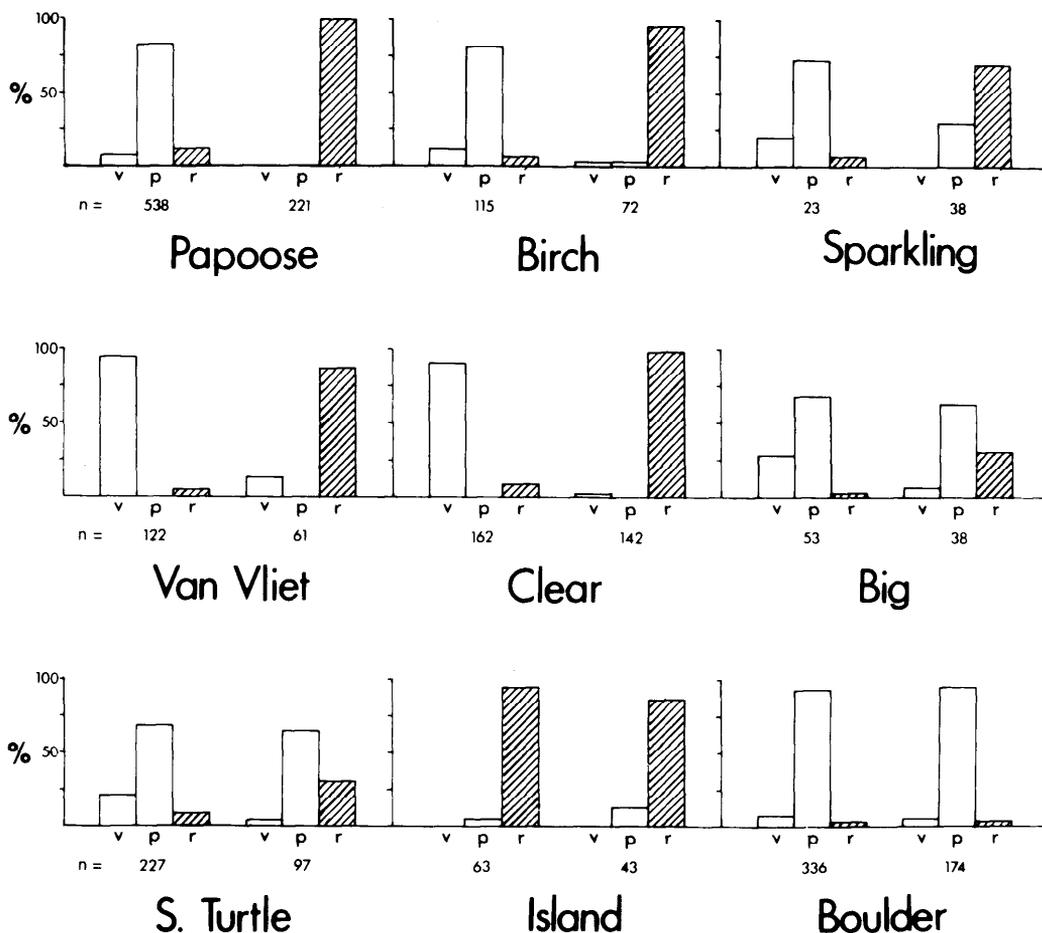


Fig. 1. Percent composition by number of adult male crayfish for nine northern Wisconsin lakes; *O. rusticus* results are hatched. For all lakes, data to left are from original sample (see text), those to right are from 1980. Sample size given below each year's data. Differences were not significant for Island Lake ( $\chi^2$ ,  $P = 0.35$ ); in all other lakes differences were significant ( $\chi^2$ ,  $P < 0.01$ ); v—*O. virilis*, p—*O. propinquus*, r—*O. rusticus*.

the total number referred to *O. rusticus* and *O. propinquus* from South Turtle Lake, 25% showed some evidence of hybridization, about the same proportion found by Capelli and Capelli (1980) earlier in the same lake. There was no evidence of hybridization in Papoose Lake.

Neither the mechanisms by which *O. rusticus* displaces other species nor the ecological implications of such displacement are known with much certainty. All three species are apparently ecologically similar, preferring firm substrates in clear, well-oxygenated waters. Although all possible species combinations occur

in lakes of the region, 30 of the 50 crayfish-containing lakes for which data are available contain only one species, and in most of the others the numerically dominant species is at least several times more abundant than the next species. Many lakes of differing species composition occur in close proximity, with no strong correlations between species composition and any known physical, chemical, or biological variables (Capelli 1975). Thus competitive exclusion of some kind seems to be important to crayfish distribution patterns.

In laboratory studies of adults, *O. rus-*

*ticus* was clearly dominant over *O. virilis* in direct aggressive interactions and out-competed *O. virilis* for shelter in simplified environments (Capelli and Munjal 1983). *Orconectes propinquus* was intermediate, outcompeting *O. virilis* but not *O. rusticus*. A similar hierarchy was found among young-of-year of the same species (P. Medvick pers. comm.). Although these results are consistent with the displacements which are occurring, little is known of the extent to which shelter or other resources are actually limiting in the field or the extent to which direct competitive interactions are important.

Although traps are generally reliable indicators of both species composition and relative abundance (Capelli 1975), the greater aggressive tendencies of *O. rusticus* may exaggerate to some extent the apparent displacement. Aggressive *O. rusticus* individuals aggregating near a trap before entering it may inhibit other species from entering. The data clearly confirm significant increases in *O. rusticus* populations; the exact extent of concurrent decreases in other populations is less certain. However, direct collection of 30 crayfish during 1980 by divers in the sample area of Papoose Lake produced no *O. propinquus*, which had been common in the area in 1975. Therefore significant displacement, as suggested by the trap data, seems to be real.

Male crayfish of all three species molt twice during summer. Inactivity associated with molting lasts about 2 days for an individual; the molt period for a population as a whole in a given lake lasts about 7–10 days (Capelli 1975). Although there is some variation among populations from species to species and lake to lake, animals generally molt in mid-to-late June and late July–early August. All sampling was done during expected intermolt periods, and variation in the data due to differing molt conditions of populations is believed to be minimal.

The rapid reduction of *O. virilis* and *O. propinquus* in lakes such as Papoose and Birch implies a nearly complete cessation of successful reproduction in the

presence of *O. rusticus*. In laboratory studies, *O. rusticus* males mated interspecifically much more often than did males of the other species, which suggests possible differential mating interference favoring *O. rusticus* (Capelli unpubl.). However, nothing is known of the extent to which interspecific mating occurs under natural conditions, or more important, the extent to which females of the various species lack correct sperm plugs when eggs are produced and fertilized. The relatively slow displacement accompanied by hybridization in South Turtle Lake, in contrast to the rapid displacement without hybridization in Papoose Lake, only adds further confusion; indeed, the exact taxonomic relationship of *O. rusticus*, *O. propinquus*, and apparent hybrids must be considered very uncertain at present (Capelli and Capelli 1980).

The introduction of *O. rusticus* is strongly implicated as the major factor in substantial reductions in macrophytes in many northern Wisconsin lakes; in some cases such reductions, possibly combined with crayfish predation on fish eggs, have probably caused significant declines in fish populations (primarily Centrarchidae: Lorman and Magnuson 1978; Lorman 1980). Some species such as walleye (*Stizostedion vitreum*), however, seem to be unaffected and exploit *O. rusticus* significantly as food. Few data on effects on other community components or processes are available. Thus the overall implications of the invasion by *O. rusticus* may be significant and complex but are as yet not well known.

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## Reversal of cadmium toxicity in a diatom: An interaction between cadmium activity and iron<sup>1</sup>

**Abstract**—In batch cultures of *Thalassiosira weissflogii* subjected to high Cd<sup>2+</sup> activities, normal growth rates are resumed when the cadmium ion activity is lowered by either dilution of the medium or addition of a chelating agent (EDTA). Toxicity reversal is possible after up to several days of high (Cd<sup>2+</sup>) exposure, depending on the initial Cd<sup>2+</sup> activity. A sufficiently high ferric ion activity is critical for toxicity reversal; Fe must be added when the Cd<sup>2+</sup> activity is decreased by addition of EDTA. The order of Fe and EDTA addition is unimportant for the reversal process. An antagonism between Cd and Fe is clearly indicated, implying that the mechanism of Cd toxicity involves in some way an impairment of iron nutrition.

It has become widely accepted that for most, if not all, trace metals, availability and toxicity to phytoplankton are determined by the metal's ionic activity. For example, the toxicity of copper and cadmium (Davey et al. 1973; Sunda and Guillard 1976; Anderson and Morel 1978; Sunda and Gillespie 1979) and the nutritional efficacy of copper, zinc, and iron (Manahan and Smith 1973; Anderson et al. 1978; Anderson and Morel 1982) are functions of the free metal concentrations. The ranges of phytoplankton

sensitivities in culture bracket the calculated ranges of free copper, zinc, and cadmium activities in seawater (Hughes 1981), so that trace metals may well be controlling factors for primary productivity and the distribution of algal species in the sea. The way in which trace metals could play such a role depends not only on their mode of toxicity and limitation to algae, but also on the modulation of these effects with changes in water chemistry. The toxicity of a metal can be influenced by the concentrations of other metals (Braek et al. 1976, 1980) and algal nutrients (Lewin 1954; Morel et al. 1978; Rueter and Morel 1981). In a few instances, the reversal of metal toxicity to a phytoplankton has been reported (Steeemann Nielsen and Kamp-Nielsen 1970; Anderson and Morel 1978; Canterford 1980; Hughes 1981). To date there have been no published studies quantifying the conditions of reversal.

We report here the response of a common diatom, *Thalassiosira weissflogii*, to a changing regime of trace metals. This organism was chosen because it has been the object of many trace metal studies and thus provides a convenient physiological model for our purpose. We investigate the reversal of cadmium toxicity as a function of free metal activity, time of exposure, and iron nutrition.

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