Review of effects of variation in crayfish abundance on macrophyte and macroinvertebrate communities of lakes

John Mark Hanson and Patricia A. Chambers

This study examined the effects of variation in crayfish abundance on the structure of the plant and animal communities in lakes. Field and laboratory studies indicated that relatively low biomasses of crayfish can have marked direct and indirect effects on the littoral zone habitat. In small pools, male crayfish (Orconectes virilis) stocked at biomasses of 5 to 10 g m$^{-2}$ significantly reduced the abundance of Myriophyllum exalbescens, Nuphar variegatum, Potamogeton richardsonii, and Sparganium eurycarpum. In the laboratory, male and female crayfish showed a strong preference for Chara sp. and Lemna trisulca, ate smaller amounts of M. exalbescens and Utricularia vulgaris, and consumed very small amounts of S. eurycarpum, N. variegatum, Hippuris vulgaris, P. richardsonii, Ceratophyllum demersum, and P. vulgaris. These feeding preferences were not correlated with measures of plant fiber content or crude alkaloid extract and were negatively correlated with phosphorus levels, available nitrogen levels, and organic content. In small pools, the abundance of snails (Physa gyrina and Stagnicola elodes) was greatly reduced by biomasses of male and female crayfish of 5 to 10 g m$^{-2}$. Indirect effects of crayfish foraging on macroinvertebrate communities could be much stronger than direct effects if crayfish foraging results in changes in the species composition of aquatic weedbeds. Replacement of Chara by rooted plants in lakes could result in reduced total biomass of macroinvertebrates, reduced abundance of large organisms (e.g., Anisoptera and Gastropoda), and marked changes in the taxonomic composition of the macroinvertebrate community, independent from direct effects of crayfish predation. The consequences of these crayfish mediated changes in the littoral zone on the populations of fish and waterfowl dependent on this zone for food and cover are unknown.

Introduction

Crayfish are one of the key components of the littoral zone community of lakes (Moom et al., 1978; Lorman and Magnuson, 1978; Lodge et al., 1985) yet their role in structuring this community is poorly understood. Most research on crayfish has focused on the harvest of wild crayfish for food or bait (e.g., Momot and Gowing, 1977; Nielson and Orth, 1988), the establishment of efficient aquaculture operations (Eversole and Pomeroy, 1989; Huner, 1989; Romaine and Lutz, 1989), or assessing the impact of introduced species on native crayfishes (Unestam, 1975; Butler and Stein, 1985; Lodge et al., 1986). Moreover, there is surprisingly little information on the consequences of introducing crayfish into waterbodies previously devoid of them, even though this is a widespread practice (Lowery and Mendes, 1977; Hepworth and Duffield, 1987; Hobbs et al., 1989). Similarly, little is known of the effects of variation in crayfish abundance, or the loss of crayfish, on the community structure of waterbodies currently supporting them. For example, crayfish of the genus Orconectes appear to be particularly sensitive to acidification of watersheds; their populations collapse when pH drops below 5.5 (Berrill et al., 1985; France, 1987; Davies, 1989). When pH levels improve in acidified watersheds (e.g., Kelso et al., 1990), the littoral zone community may be greatly different from that which
Table 1. Selected studies that report consumption of submersed macrophytes by crayfish in lakes and ponds. The lakes and ponds surveyed were not used for commercial culture of crayfish.

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<tr>
<th>Crayfish species</th>
<th>Plant species</th>
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Effects of crayfish on aquatic plant communities

It is generally accepted that adult crayfish feed on plants. A number of crayfish species have been shown to decrease the biomass of a variety of plant species (Table 1). However, feeding selectivity and the biomass of crayfish needed to effect these changes are less well established. Flint and Goldman (1975) found that crayfish (Pacifastacus leniusculus) biomasses >69 g m⁻² reduced the density of Myriophyllum exalbescens in Lake Tahoe. The rusty crayfish (Orconectes rusticus) appeared to have a much greater impact on the abundance and diversity of macrophyte communities after this crayfish was introduced into three Wisconsin lakes (Lodge and Lorman, 1987). In one experiment, crayfish biomasses >19 g m⁻² reduced the biomass of Potamogeton robinsii and Megalodonta beckii, totally eliminating these plant species at crayfish biomasses >140 g m⁻². In a second experiment, crayfish biomasses of 24 to 223 g m⁻² resulted in significantly reduced biomass of Vallisneria americana. In three other experiments, however, different plant species (as well as V. americana) were not affected by crayfish foraging, partly due to problems related to duration of the experiments, the inability to maintain the desired crayfish abundances in the enclosures, and possible differences in palatability among the plant species.

In order to minimize some of these problems, Chambers et al. (1990) conducted field experiments in small pools (4.7 m² by 0.4 m deep) to examine the impact of female and male crayfish (O. virilis) stocked at four levels (0, 5, 10, and 18 g m⁻²) on the biomass, density, and shoot morphology of four commonly occurring aquatic plant species in Alberta lakes (P. richardsonii, M. exalbescens, Nuphar variegatum, and Sparganium eurycarpum). Plant species, crayfish sex and activity, and the abundance of alternate food affected the impact of crayfish foraging on macrophyte growth. The effects of foraging by female crayfish on macrophyte growth, especially that of P. richardsonii and M. exalbescens, were generally positive (Table 2). This positive effect may have been due to reduction in the abundance of snails (as a consequence of crayfish predation) or a stimulatory effect similar to that reported by Flint and Goldman (1975) for low biomasses (<60 g m⁻²) of Pacifastacus leniusculus feeding on M. exalbescens. How-
ever, in the study by Chambers et al. (1990), the female crayfish were carrying eggs or hatchlings for most of the 5-week study and spent most of their time in hiding. In contrast, male crayfish were very active, even during the day, in the second trial of the same study. Here there were significant reductions in the biomass of crayfish were carrying eggs or hatchlings for most of the study by Chambers et al. (1990), where C. demersum = E. canadensis = P. richardsonii > Isoetes spp., which falsified the hypothesis that crayfish preferred single-stemmed species over plants of branched or rosulate growth form. In addition, feeding rates were different between crayfish species. Although the crayfish were all of the same size, O. rusticus and O. virilis consumed or destroyed more macrophytes on a daily basis than O. propinquus. The rate of macrophyte consumption by crayfish was low during this study – the maximum consumption of any plant species was only 30% after 6 days. These low consumption rates were consistent with results of Chambers et al. (1991), where C. demersum and P. richardsonii were among the least preferred plant species of O. virilis (Isoetes spp. and E. canadensis were not tested in the latter study).
Chambers et al. (1991) conducted laboratory experiments to quantify directly feeding selectivity of crayfish (*O. virilis*) for 10 species of aquatic plants commonly found in Alberta lakes and to correlate this selectivity with morphological and chemical characteristics of the plant species. The consumption of fresh macrophytes by female crayfish did not differ from that of the males in this study. The crayfish showed clear feeding preferences as follows: *Chara* > *Lemma trisulca* > *Myriophyllum exalbescens* = *Utricularia vulgaris* > *Sparganium eurycarpum* = *Nuphar variegatum* > *Hippuris vulgaris* > *Potamogeton richardsonii* > *Ceratophyllum demersum* > *P. vaginatus*. *Isoetes* sp. is present in Alberta lakes but was not included in this study; however, the study by Olsen et al. (1991) indicates that *Isoetes* would be one of the least preferred plant species in Alberta lakes. Chambers et al. (1991) also reported significant differences in the amount of the various plant species eaten by *O. virilis*. In a 48-h period, the crayfish consumed 53 to 72% of the biomass of the first four plant species tested in the study but never more than 24% of the biomass of the last six species. These feeding preferences were not significantly correlated with plant fiber content (*p* > 0.05) nor with crude "alkaloid" extract (*p* > 0.05) and were negatively correlated with total phosphorus concentration (*p* < 0.01), available nitrogen concentration (*p* < 0.001), and plant organic content (*p* < 0.025). Identifiable alkaloids were only found in *N. variegatum* and *C. demersum* and they were not the least preferred species. Although crayfish showed strong feeding preferences among the 10 plant species tested, the functional basis for this selection is not clear, although Lodge (1991) has suggested that the presence of phenolic compounds may affect plant feeding preferences for a variety of aquatic grazers. With regard to plant morphology, Chambers et al. (1991) suggested that the strong preference of crayfish for *Chara* and *Lemma trisulca* over the other eight plant species examined was due to the ease in handling small, short, bottom-dwelling species as compared with large erect, rosetate, or floating leaved forms.

The strong feeding preference of crayfish for *Chara* reported by Brown et al. (1990) and Chambers et al. (1991) is consistent with field observations that *Chara* is usually absent from areas of moderate to high crayfish abundance (Abrahamsson and Goldman, 1970; Rickett, 1974; Coffey and Clayton, 1988). Because *Chara* is abundant in many Alberta lakes, the establishment of large populations of crayfish in these lakes could greatly alter the abundance and species composition of aquatic macrophyte beds and, in so doing, affect the composition of the macroinvertebrate community.

Direct effects of crayfish on macroinvertebrate communities

Crayfish are generally considered to be carnivores as juveniles, consuming more plant material and detritus as adults (Abrahamsson, 1966; Lorman and Magnuson, 1978; Momot et al., 1978). Nevertheless, macroinvertebrates can comprise a significant proportion of the diet of adult crayfish (Abrahamsson, 1966; Covich, 1977; Capelli, 1980), but the impact of this predation on macroinvertebrate communities is not clear.

Laboratory studies show that adult crayfish will readily consume snails and small bivalves (Covich, 1977; Covich et al., 1981; Crowl and Covich, 1990). In one field study, Lodge and Lorman (1987) observed differences in snail abundance between enclosures containing crayfish (*O. rusticus* and *O. virilis* at biomasses of 24–223 g m⁻²) and those without. However, they noted that the differences could also have been due to snail migration into and out of the enclosures. Hanson et al. (1990) conducted field experiments in small pools to examine the impact of predation by female and male *O. virilis* stocked at four densities (0, 5, 10, and 18 g m⁻²) on the abundance of a variety of macroinvertebrates commonly found in Alberta lakes. The pools were stocked with known numbers of amphipods, trichopteran larvae, and adult snails. The abundance of snails (*Physa gyrina* and *Stagnicola elodes*) was greatly reduced by biomasses of crayfish between 5 and 10 g m⁻². This is much lower than the biomass of crayfish associated with reduced snail densities in Lodge and Lorman's (1987) study. Because snails are efficient grazers on epiphytes, one consequence of reduced snail densities in lakes could be to release these resources to other grazers, such as chironomids and oligochaetes (Cattaneo, 1983; Cuker, 1983; Kairesalo and Koskimies, 1987) or crayfish themselves (Abrahamsson, 1966; Flint and Goldman, 1975; Capelli, 1980). In addition, recent laboratory experiments indicated that crayfish predation affected the life history characteristics of the snail *Physella virgata virgata* by increasing the size and age at first reproduction (Crowl and Covich, 1990). Furthermore, a recent laboratory study (Olsen et al., 1991) showed that *O. rusticus* consumed more snails (*Amyicola* sp.) than either *O. virilis* or *O. propinquus*, indicating that simple replacement of one crayfish species by another in a waterbody could have a strong adverse effect on existing snail populations. Clearly, variation in crayfish abundance can strongly affect snail populations.

In contrast, the effects of crayfish predation on the abundance of non-molluscan invertebrates are less well known. Rickett (1974) found that experimental ponds that had been invaded by crayfish (*Orconectes nais*) had greatly reduced total macroinvertebrate biomass, more oligochaetes, and fewer chironomids and ephemerop-
terans than ponds containing few or no crayfish. Hanson et al. (1990) found that female and male crayfish stocked in separate trials at densities of 0, 5, 10, or 20 g m\(^{-2}\) (each treatment in triplicate) had different effects on non-molluscan invertebrate abundances in their study conducted in small pools. This was thought to be due to the high densities of age-0 crayfish (6-116 g m\(^{-2}\)) present in all pools in the trial conducted with males. In the female crayfish trial, age-0 crayfish were not present until the last week of the trial and even then were too small to eat macroinvertebrate prey. Thus the strong inverse correlation of amphipod density with crayfish biomass (p < 0.001) and weak inverse correlations of oligochaete density (p < 0.02) and total invertebrate density (p < 0.05) with crayfish biomass were attributable to direct predation by female crayfish. In addition, there were proportionately more large organisms (>8 mg) in pools containing female crayfish than in pools devoid of them, which indicates that female crayfish were consuming small-sized invertebrates. The results were less clear in the trial that used male crayfish. In that trial, the density of amphipods and the total biomass of non-molluscan invertebrates were lower in the 5 and 10 g m\(^{-2}\) treatments than in the 0 and 18 g m\(^{-2}\) treatments. Unfortunately, unlike the trial with female crayfish, the age-0 crayfish were large enough to eat macroinvertebrates (but not snails) in this trial, which may have masked any direct predation effects by male crayfish. One interesting finding was that the benthic fauna at the end of the trial with male crayfish was dominated by oligochaetes. This is similar to the findings of Rickett (1974) and suggests that the more carnivorous age-0 crayfish were responsible for the species composition of the non-molluscan invertebrate community at the end of both studies.

Indirect effects of crayfish predation on macroinvertebrates

Indirect effects of crayfish on macroinvertebrate communities have rarely been studied. Abrahamsson (1966) reported that large populations of leeches and molluscs appeared when Chara became abundant after extinction of crayfish from small ponds in Sweden. Rickett (1974) found higher abundances of snails, dipteran larvae, and ephemeropteran larvae in ponds that contained few or no crayfish but did contain abundant vegetation (Chara and Potamogeton foliosus). Feminella and Resh (1986) found that Procambarus clarkii reduced the density of Potamogeton pectinatus in a marsh, which eliminated the predation refuge for the mosquito Anopheles occidentalis, and mosquito densities were reduced almost 150-fold. These studies represent the extreme case where plants were present or absent. However, less dramatic changes in the species composition of aquatic weedbeds caused by crayfish selective foraging could also affect the structure of the macroinvertebrate community.

The macroalga Chara is very abundant in many Alberta lakes and, should crayfish become established in these lakes, it is expected that Chara would be replaced by plant species less preferred by crayfish. This could alter the macroinvertebrate community structure of the littoral zone because different plant species appear to support different abundances and species of invertebrates (Keast, 1984; Talbot and Ward, 1987; Cyr and Downing, 1988). Because crayfish feed directly on macroinvertebrates, the question of indirect effects of crayfish foraging on macroinvertebrate communities due to selective foraging on plant species is best addressed using a comparative approach in lakes devoid of crayfish.

Hanson (1990) compared the macroinvertebrate communities of weedbeds dominated by Chara and those dominated by rooted plants (various Potamogeton spp., Myriophyllum exalbescens, Nuphar variegatum, and Isoetes spp.) in a small Alberta lake that is devoid of crayfish. The two weedbed types were sampled at 2-week intervals for 18 weeks and the total macroinvertebrate biomass (excluding unionid clams), taxonomic composition, and size structure (using biomass size spectra, Schwinghamer, 1981; Strayer, 1986; Hanson et al., 1989) of the two communities were compared. The seasonal mean total biomass of the macroinvertebrate community in the Chara beds was 3.5 times higher than that of the rooted plant weedbeds (Table 3). Amphipods and chironomids dominated the rooted plant community, whereas anisopterans, gastropods, sphaerid clams, and chironomids dominated the Chara community. The distributions of amphipods and gastropods appeared to represent true preferences of these taxa for the particular weedbed type. The comparatively low abundance of gastropods in the rooted plant community is noteworthy because crayfish prey directly on snails, especially Physa spp., when they are available (Rickett, 1990). This is similar to the findings of Rickett (1974) and reported that large populations of leeches and molluscs appeared when Chara became abundant after extinction of crayfish from small ponds in Sweden. Rickett (1974) found higher abundances of snails, dipteran larvae, and ephemeropteran larvae in ponds that contained few or no crayfish but did contain abundant vegetation (Chara and Potamogeton foliosus). Feminella and Resh (1986) found that Procambarus clarkii reduced the density of Potamogeton pectinatus in a marsh, which eliminated the predation refuge for the mosquito Anopheles occidentalis, and mosquito densities were reduced almost 150-fold. These studies represent the extreme case where plants were present or absent. However, less dramatic changes in the species composition of aquatic weedbeds caused by crayfish selective foraging could also affect the structure of the macroinvertebrate community.

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1974; Covich, 1977; Hanson et al., 1990) and the data in Hanson (1990) suggest that crayfish can also affect snail abundance indirectly by altering the species composition of the weedbeds.

The average size structure of the macroinvertebrate communities inhabiting the two plant communities described by Hanson (1990) differed markedly. There were no clear peaks in the biomass distribution of the macroinvertebrate community associated with the Chara beds but that of the rooted plant weedbeds showed a strong peak in the 4 to 8 mg size class and a weak peak in the 32 to 64 mg size class. Further, there were proportionately more large (>64 mg) organisms in the Chara beds (30% total biomass) than in the rooted plant weedbeds (11% total biomass). In areal terms, there were 8 g m$^{-2}$ of large organisms in the Chara beds compared with 0.8 g m$^{-2}$ in the rooted plant weedbeds. Because fish depend on prey of increasingly greater size in order to grow (Kerr, 1971; Wankowski, 1979; Diana, 1987), this latter result suggests that crayfish induced changes in the species composition of aquatic weedbeds could affect not only the structure of the macroinvertebrate community but also the total biomass and growth of the fish species dependent upon macroinvertebrate prey by reducing total prey abundance or by reducing the abundance of large prey needed for good fish growth.

Effects of crayfish on fish

The preceding sections have indicated that relatively low abundances of crayfish can greatly affect the structure of the plant and invertebrate communities of the littoral zones of lakes. In so doing, crayfish affect the food resources and habitats of economically valuable fish. Unfortunately, studies of ecological interactions between fish and crayfish are uncommon, despite the fact that many fish species prey upon crayfish, and one reason for introducing crayfish into waters previously devoid of them has been to provide food for fish (e.g., Dean, 1969; Saiki and Tash, 1979; Hepworth and Duffield, 1987). The few studies available show that only one fish species, largemouth bass (Micropterus salmoides), can control crayfish abundance in small waterbodies (Saiki and Tash, 1979; Rach and Bills, 1989). For some other fish species, growth has been found to decline when the fish population could not effectively exploit the introduced crayfish (e.g., Rickett, 1974; Gowing and Momot, 1979; Hepworth and Duffield, 1987). The mechanisms responsible for these decreases in fish growth are unknown.

Crayfish can have direct negative effects on fish populations by preying on eggs and young, interfering with fish harvest in hatcheries, and by evicting forage fish from shelters (Horns and Magnuson, 1981; Rahel and Stein, 1988; Rach and Bills, 1989). Furthermore, many fish species depend on aquatic macrophytes for cover from predation (Werner et al., 1983; Keast, 1984; Rozas and Odum, 1988) and, in extreme cases, introduced crayfish can completely remove the macrophyte cover needed by these fish (Lodge et al., 1985). In general, indirect effects of variation in crayfish abundance on fish populations are very difficult to predict. It is clear, however, that crayfish can reduce the abundance of such invertebrate prey as snails either by direct predation or by selective predation on plants preferred by snails. Therefore, crayfish are potential competitors with snail-eating fish (e.g., pumpkinseed Lepomis gibbosus). Further, many fish species prey on macroinvertebrates (Wissmar and Wetzel, 1978; Boisclair and Leggett, 1985; McQueen et al., 1986) and any changes in the abundance or structure of the macroinvertebrate community are likely to affect these fish. Unfortunately, the responses of fish to changes in the macroinvertebrate prey community are poorly understood, in part because studies that compare the availability and profitability of prey to fish between weedbeds comprising different plant species are lacking.

In summary, there is insufficient information currently available to predict how variation in crayfish abundance will affect the structure of the littoral zone plant and invertebrate communities. However, the studies summarized here indicate that crayfish biomass as low as 5 to 10 g m$^{-2}$ could greatly affect the structure of the plant and invertebrate communities of lakes, with unknown consequences for the fish dependent upon these resources. Thus, crayfish may be a keystone species in freshwater waterbodies.

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References


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