

Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates

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Abstract. Crayfish are common inhabitants of North American streams and many species are undergoing human-assisted range expansions. We studied the effects of an introduced crayfish (*Orconectes rusticus*) on benthic macroinvertebrates and periphyton in a northern Michigan (USA) stream by 1) conducting a 46-d enclosure–exclosure experiment and 2) sampling benthic communities along a longitudinal gradient in crayfish density. In stream enclosures, crayfish reduced total macroinvertebrate densities by 47–58% and herbivore densities by 55–72% relative to exclosures. Over the course of the experiment, periphyton chlorophyll *a* increased by 48–70% in enclosures compared to an increase of only 8% in exclosures. Periphyton biomass, however, did not vary across treatments. Periphyton primary productivity increased 4–7 times in the presence of crayfish, probably because crayfish reduced grazer densities (indirect effect) and removed non-autotrophic components of the periphyton matrix (direct effect). The longitudinal survey supported experimental results. At sites along a crayfish density gradient occurring over 3 km of stream, periphyton chlorophyll *a* on rocks increased and macroinvertebrate density decreased with increasing crayfish density. These studies show that crayfish directly and indirectly affected the stream benthos, thereby producing responses at more than 1 trophic level. Some responses were consistent with a trophic cascade, but crayfish increased food web connectance by consuming periphyton. Therefore, crayfish can have complex, multi-trophic-level effects on the food webs of invaded streams.

Key words: *Orconectes rusticus*, crayfish, macroinvertebrates, periphyton, food webs, exotic species, stream, enclosure-exclosure, trophic cascade.