

Aspects of the thermal ecology of the rusty crayfish *Orconectes rusticus* (Girard)

Neal D. Mundahl^{1,*} and Michael J. Benton²

¹ Department of Zoology, Miami University-Middletown, 4200 East University Boulevard, Middletown, OH 45042, USA

² Department of Zoology, Miami University, Oxford, OH 45056, USA

Summary. *Orconectes rusticus* currently is undergoing an explosive range expansion in the midwestern U.S.A., but information on the potentially important effects of water temperature on the species' biology is lacking. The thermal ecology of *O. rusticus* in southwestern Ohio, U.S.A., was examined by determining 1) the effects of four water temperatures (16, 20, 25, and 29° C) on survival and growth of juveniles, 2) the responses of juveniles and adults to a thermal gradient (7–27° C), and 3) the thermal tolerances (critical thermal maximum, CTMax, and critical thermal minimum, CTMin) of free-living, field-acclimatized juveniles and adults on a biweekly basis throughout the summer. Month-long growth experiments predicted maximum growth rates of juveniles at water temperatures between 26 and 28° C, but greatest survival between 20 and 22° C. Laboratory-acclimated (22° C) adults and field-acclimatized (2.5° C) juveniles both had an acute preferred temperature of 22° C. CTMaxs and CTMins of juveniles were 0.5–2.6° C higher than those of adults throughout the summer, suggesting that juveniles were exposed to water temperatures 1.5–6.8° C warmer than those of adults. Juvenile and adult *O. rusticus* prefer habitats where water temperatures favor maximum survival, but they usually are not found together in the same habitat; adults apparently displace the juveniles into warmer habitats. Warmer temperatures can decrease survival of juveniles but improve their growth rates, leading to enhanced fecundity and competitive ability. The past and future success of *O. rusticus* in expanding its range may depend, in part, on the species ability to adjust to new thermal environments occupied by other species of crayfish.

Key words: Temperature selection – Growth – Survival – Thermal tolerances – Decapoda

Crayfish are found in many different freshwater habitats throughout North America (Hobbs 1974), where they often are the largest and most dominant members of invertebrate communities (Lorman and Magnuson 1978; Momot et al. 1978). Several species are of economic importance, generally for their roles in aquaculture (Avault 1983; Nolfi 1983), or as agricultural pests (Sommer and Goldman 1983).

* Present address and address for offprint requests: Department of Biology, Winona State University, Winona, MN 55987, USA

The rusty crayfish *Orconectes rusticus* is native to streams in Illinois, Indiana, and western Ohio, but currently is undergoing a dramatic range expansion. It has displaced endemic species adjacent to its range in Indiana and Ohio (Jezerinac 1986; St. John 1988), and is having a similar effect on native species in New England (Smith 1981), Wisconsin (Capelli 1982), and southern Ontario (Berrill 1978). The driving force behind the range expansion of *O. rusticus* is not clearly understood, although much of the expansion probably has resulted from intentional and accidental introductions of the species into new habitats by humans (Bills and Marking 1988; Butler and Stein 1985; Capelli 1982; Hobbs and Jass 1988; Momot et al. 1988). Once in a new habitat, *O. rusticus* has several attributes (e.g., higher metabolic and growth rates, aggressive behavior, greater resistance to low pH, reduced young-of-year susceptibility to predation, reproductive interference with other species) which may allow it to compete successfully with native crayfishes (Berrill et al. 1985; Butler and Stein 1985; Fielder 1972; Jezerinac 1982; Lorman 1980; Momot 1984). In some regions, control mechanisms have been devised (Bills and Marking 1988) to reduce or eliminate the negative impact of large populations of *O. rusticus* on aquatic plants and sport fisheries (Lodge et al. 1985; Lorman and Magnuson 1978).

Although the basic biology of *O. rusticus* has been examined by several investigators (e.g., Butler and Stein 1985; Lorman 1980; Prins 1968), little is known of the thermal ecology of this species. The thermal tolerances of *O. rusticus* have been well studied (Claussen 1980; Layne et al. 1985, 1987; Mundahl 1989; Spoor 1955), but the relationship between these tolerances and the success of the species in different thermal environments remains unclear (Layne et al. 1987). To understand better the thermal biology of *O. rusticus* and the potential importance of water temperature in the species' interactions with other crayfishes, we conducted growth and survival experiments at a variety of temperatures typical of those experienced by the species during the growing season. We also used temperature-selection tests to investigate the ability of *O. rusticus* to respond behaviorally to differences in ambient temperature. Finally, we employed temperature tolerance procedures to determine whether the reported segregation of juvenile and adult *O. rusticus* into separate stream habitats during summer (Butler and Stein 1985) influenced the thermal history of the age groups.

Methods

Collection sites. *Orconectes rusticus* were collected from three streams in Butler County, Ohio: Dicks Creek, Harker's Run, and Indian Creek. All are second- and third-order streams within the Great Miami River drainage, and flow through mixed woodland, agricultural, and residential areas. Substrata are similar in all three streams, with slab-bottomed pools containing fractured limestone and shale ledges. Pools in Dicks Creek generally contained more silt and organic matter than did those in the other streams.

Growth experiments. Juvenile *O. rusticus* were collected from Indian Creek during November and December 1988 (water temperature = 2.5–5.0° C) and maintained in the laboratory (22° C, fed trout chow pellets) for no longer than three weeks before experiments began. Carapace lengths (CL, anterior tip of rostrum to posterior dorsal edge of carapace) of crayfish were measured to the nearest 0.1 mm with vernier calipers. After towel-drying, live weights were measured to the nearest 1 mg on an analytical balance. Sex of each individual also was recorded.

Crayfish were placed in 40-L aquaria maintained at four different temperatures (two replicate aquaria at each temperature): 16, 20, 25, and 29° C. Eight crayfish were assigned to each aquarium to establish similar average sizes (mean \pm SE CL = 16.0 \pm 0.5 mm, live weight = 1.39 \pm 0.13 g) and size ranges (CL range = 10.0–25.5 mm, live weight range = 0.30–4.19 g) at each temperature. Water in each aquarium was aerated and filtered, and bricks were provided for shelter. Crayfish were fed trout chow pellets *ad libitum*, and were exposed to a 16 h light: 8 h dark photoperiod. Uneaten food was siphoned from the aquaria regularly, and water (dechlorinated tap) was added or changed as needed. Molted exoskeletons and dead individuals generally were removed within one day of their appearance, and frozen for later examination.

After 29 days at the experimental temperatures, crayfish again were measured, weighed, and sexed. Frozen, molted exoskeletons and dead individuals also were measured and sexed. These measurements, and the variety of sizes and sexes of crayfish in each aquarium, permitted the growth of individuals to be monitored without the need for marking or tagging.

Temperature-selection tests. Temperature selection was examined in both large juvenile and adult *O. rusticus*. Adults were collected from Dicks Creek in February 1988 and maintained in the laboratory (22° C, 14 h light: 10 h dark photoperiod, fed trout chow pellets) for eight weeks prior to testing. Large juveniles were collected from Indian Creek in October 1988 (water temperature = 2.5° C), and were tested immediately following their arrival at the laboratory.

Tests were conducted in a horizontal thermal gradient tank (see Hlohowskyj and Wissing 1987). The tank developed a stable, relatively linear, 20° C (approximately 7–27° C) gradient along its 160-cm length. Water depth in the tank was 6 cm, and the substratum consisted of fine quartz gravel. Lines on the glass top divided the tank visually into 12 sections of equal area, and water temperature in the center of each section was monitored to the nearest 0.1° C with a thermocouple and a digital thermometer (Bailey Instruments Model BAT 8).

Acute thermal preferences of *O. rusticus* were deter-

mined by placing crayfish individually into the gradient tank at a temperature nearest the acclimation or acclimatization temperature. Crayfish were left undisturbed for 10 min to habituate to the tank. Their positions within the tank then were recorded every 15 s for 10 min. A crayfish was considered to be within a particular section if at least the anterior half of its cephalothorax was located within that section. Water temperature in each section was recorded at the beginning and end of the 10-min test period and averaged to give a mean temperature for each of the 12 sections. A single temperature preference value was determined for each individual tested by averaging the temperatures of the 40 positions occupied by the crayfish during the test period. Control tests also were run to determine the distributions of crayfish in the test chamber in the absence of a thermal gradient (22° C throughout). The distribution of control *O. rusticus* (29–36 mm CL) in the test chamber was significantly non-random ($X^2 = 155.9$, $k = 12$, $P < 0.001$), and skewed toward both ends of the apparatus.

Thermal tolerance tests. Juvenile and adult *O. rusticus* were collected during June, July, and August 1988 from Harker's Run and Indian Creek. Collections were made from all areas of pools between 0900 and 1200 h on each sampling date. To avoid possible bias, no effort was made to collect the different age groups from separate habitats within the pools; collecting continued only until an adequate number of animals had been obtained for testing. Stream water temperature was measured on the substratum in mid-pool to the nearest 0.1° C with a digital thermometer (Casio Model 515 TS-1200) at the time of collection. Most crayfish were returned immediately to the laboratory where critical thermal maximum (CTMax) and critical thermal minimum (CTMin) tests were performed. However, one group of juvenile and adult *O. rusticus* was collected from Indian Creek and acclimated to laboratory conditions (22° C, 14 h light: 10 h dark cycle) for eight days before conducting thermal tolerance tests. The age groups were maintained separately in 40-L aquaria and fed trout chow pellets. Collections of field-acclimatized crayfish were discontinued in late August, when adults had virtually disappeared from Indian Creek.

CTMax tests were conducted in a 1-L, flat-bottomed glass bowl containing 900 mL of stream water at the collection-site temperature. Three to ten crayfish (depending on size) were placed in the bowl and tested simultaneously by heating the system at a rate of 0.5–0.8° C per minute with a rheostat-controlled, electric heating tape wrapped around the bowl. It was assumed that at this slow rate of heating, crayfish body temperature and water temperature were similar (Layne et al. 1985, 1987). Water in the bowl was aerated continuously to prevent thermal stratification or oxygen stress. Water temperature was monitored to the nearest 0.1° C with a thermocouple and a digital thermometer (Bailey Instruments Model BAT 8). The CTMax endpoint criterion was that temperature at which the righting response was lost (i.e., animal unable to right itself within 30 s after being placed on its back; Layne et al. 1985, 1987). The CTMax represents a temperature beyond which survival time is essentially zero (Reynolds and Casterlin 1979). At random intervals, all crayfish were placed on their backs until the first individual reached its CTMax. Thereafter, all crayfish remaining in the bowl were inverted together every 30 s. After testing, each individual was measured (mm CL), sexed, and placed in water at the starting

temperature for recovery. All animals apparently recovered, as determined by the resumption of normal activities within 30 min. The process was repeated until all crayfish collected on a given date had been tested.

CTMin tests were conducted in a 200-mL, flat-bottomed glass bowl containing 175 mL of water at the collection-site temperature. Two to five crayfish (depending on size) were cooled at a rate of 0.5° C per minute using a cold plate under the bowl (Thermoelectrics Unlimited, Inc. model TCP-2). Water was aerated, temperature was monitored, and crayfish were handled as in CTMax testing. Loss of righting response also served as the CTMin endpoint, and crayfish were measured, sexed, and transferred to water at the collection-site temperature for recovery.

Results

Growth and survival. During the 29-d experiment, a strong trend was evident toward greatest crayfish survivorship be-

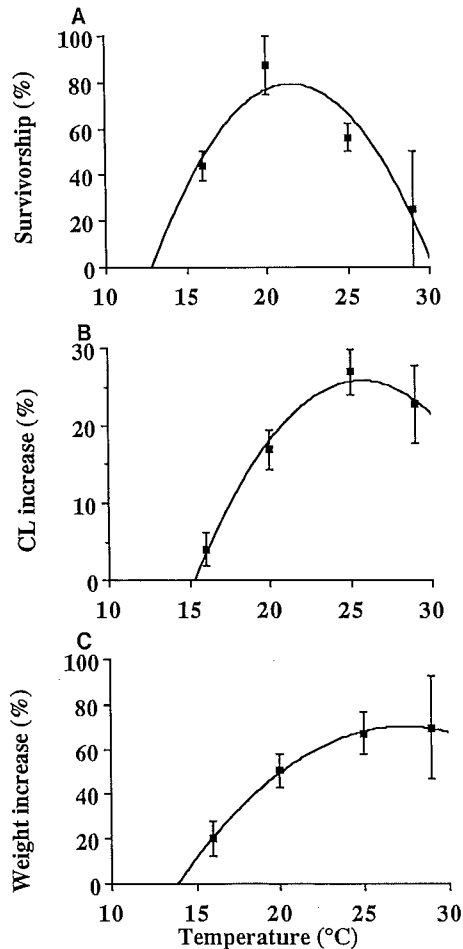


Fig. 1A–C. Survivorship (A) and growth in carapace length (CL, B) and live weight (C) of juvenile *O. rusticus* held at four water temperatures for 29 days. Values are means \pm SE of survivorship in replicate aquaria (A) or growth of individual crayfish (B and C). Equations for best-fit curvilinear regressions are as follows. A) % survivorship = $-402.56 + 44.81 \text{ temperature} - 1.04 \text{ temperature}^2$, $P=0.089$, $R^2=0.621$, $N=8$; B) % CL increase = $-124.92 + 11.57 \text{ temperature} - 0.22 \text{ temperature}^2$, $P<0.001$, $R^2=0.483$, $N=34$; C) % weight increase = $-221.33 + 21.44 \text{ temperature} - 0.39 \text{ temperature}^2$, $P=0.005$, $R^2=0.288$, $N=34$

tween 20 and 25° C (Fig. 1A). Some crayfish died in all but one of the test aquaria. Most deaths were molt-related, with crayfish dying 1–2 days after molting. One case of cannibalism also was observed. Mortality was not equal among water temperatures (G -test, $G=8.31$, $k=4$, $P<0.05$), but was highest at 29 and 16° C.

Growth in *O. rusticus* was clearly temperature-dependent. There were no significant ($P>0.10$) differences in growth rates (carapace length [CL] or live weight) between replicates at the different temperatures, so data from replicates were combined for further analyses. Kruskal-Wallis tests (on arcsine-transformed percentage increases in CL and weight of individual organisms, heterogeneous variances among temperatures) revealed significant differences among test temperatures in the changes in CL ($H=14.41$, $P<0.002$, $N=34$; Fig. 1B) and live weights ($H=9.84$, $P=0.020$, $N=34$; Fig. 1C). Curvilinear regressions predicted maximum CL increases at 26.3° C (Fig. 1B) and maximum weight increases at 27.5° C (Fig. 1C). Across all temperatures, there was a significant linear relationship between CL increases and weight gains (weight increase (%) = $7.06 + 2.49 \text{ CL increase (%)}$, $r^2=0.77$).

Temperature selection. The mean (\pm SE) acute preferred temperatures of laboratory-acclimated and field-acclimated *O. rusticus* were $22.1 \pm 1.2^\circ \text{C}$ and $22.3 \pm 0.3^\circ \text{C}$, respectively. When the thermal gradient was established, the distribution of laboratory-acclimated (20–35 mm CL) and field-acclimated (18–22 mm CL) crayfish within the chamber were significantly different (laboratory-acclimated: $X^2=95.7$, $k=12$, $P<0.001$; field-acclimated: $X^2=29.4$, $k=12$, $P<0.005$) from that of controls, indicating that crayfish responded to the presence of the thermal gradient. Both test groups avoided the cold end of the chamber (Fig. 2).

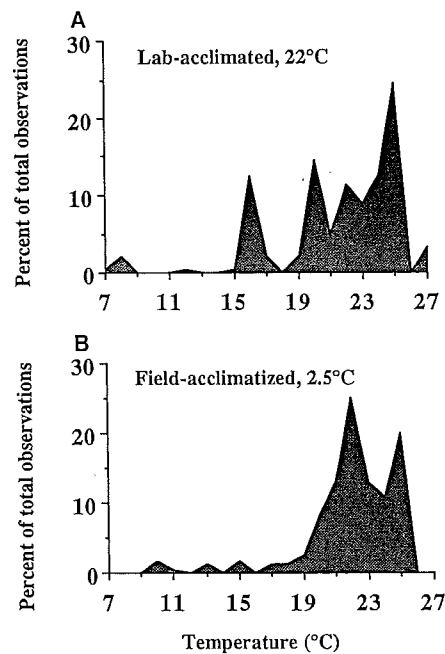


Fig. 2A, B. Temperatures selected by laboratory-acclimated adult and field-acclimated juvenile *O. rusticus* within a thermal gradient. Total number of observations in each test group was 240 (40 observations on each of six individuals)

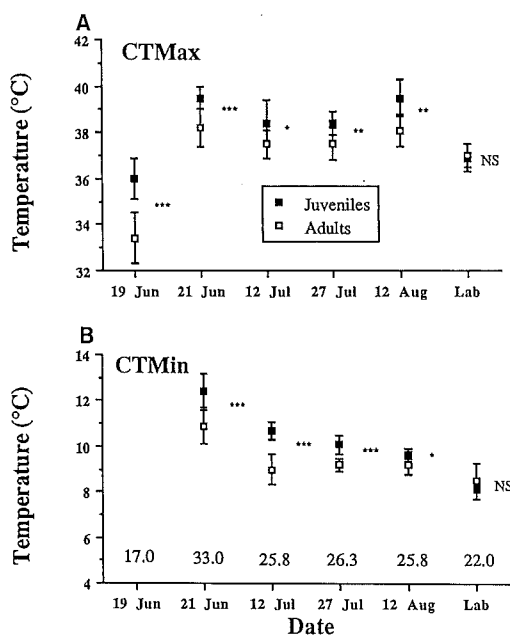


Fig. 3A, B. Thermal tolerances (CTMax and CTMin) of field-acclimatized and laboratory-acclimated juvenile and adult *O. rusticus* measured during summer 1988. Values are means \pm SE. Sample sizes are listed in Table 2. Asterisks indicate significant differences (*t*-tests, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$) in tolerances between age groups; NS indicates no significant difference. Numbers above lower horizontal axis are water temperatures ($^{\circ}$ C) at time of field collections or during laboratory acclimation

Thermal tolerance tests. On all dates the thermal tolerances of free-living, field-acclimatized, juvenile *O. rusticus* were significantly higher than those of adults (Fig. 3). Mean CTMax values for juveniles were 0.9 to 2.6 $^{\circ}$ C higher than for adults, whereas mean CTMin values for juveniles were 0.5 to 1.5 $^{\circ}$ C higher than for adults. The CTMax and the CTMin both were affected by water temperature at the time of collection (Fig. 3). The ranges of temperature between thermal tolerance limits (difference between CTMax and CTMin) were similar for juvenile (27.1–29.8 $^{\circ}$ C) and adult (27.3–28.9 $^{\circ}$ C) crayfish, and both age groups showed an increase in this range during the study period (Fig. 3). In contrast to field-acclimatized crayfish, juvenile and adult *O. rusticus* acclimated in the laboratory for eight days displayed no significant differences in their mean CTMax values, or in their mean CTMin values (Fig. 3). Sex of the crayfish had no apparent effect on their thermal tolerances.

The average size (CL) of juvenile crayfish collected from Indian Creek nearly doubled from June to August, but the sizes of adults remained similar throughout this period (Table 1). The mean CL of juveniles increased by 29% during the 30-d period from 12 July to 12 August. This increase is comparable to CL growth rates observed at 25 and 29 $^{\circ}$ C during the 29-d laboratory growth experiments (Fig. 1B).

Discussion

In natural habitats in Ohio, *O. rusticus* may be exposed to seasonal water temperatures ranging from near 0 $^{\circ}$ C in winter to 39 $^{\circ}$ C in summer (e.g., Layne et al. 1987; Mundahl 1989). Survival is enhanced by the species' ability to adjust its physiological tolerance limits as temperatures change

(Claussen 1980; Layne et al. 1985, 1987; Mundahl 1989). However, our results suggest that physiological adjustments may not insure optimum survivorship at different temperatures. Post-molting mortality (the apparent cause of most deaths in our experiments) was lowest at 20 $^{\circ}$ C but increased at cooler and warmer temperatures, indicating that some optimal temperature (between 20 and 25 $^{\circ}$ C) may exist for molting. Prins (1968) observed that *O. rusticus* avoided spring-fed stream sections with constant 12–14 $^{\circ}$ C temperatures, presumably because these temperatures were suboptimal and inhibited molting. Temperatures \geq 25 $^{\circ}$ C likewise may interfere with post-molting processes and result in decreased survivorship. Although we have no data on crayfish survival below 16 $^{\circ}$ C, long-term exposure of *O. rusticus* to water temperatures $<$ 15 $^{\circ}$ C (e.g., during winter) probably has little effect on molt-related survival, as molting likely does not occur at these temperatures.

Growth rates of *O. rusticus* increased from minimum levels at 16 $^{\circ}$ C to maximum levels at 25–29 $^{\circ}$ C. Westman (1973) reported that growth rates of the American crayfish *Pacifastacus leniusculus* increased throughout the temperature range 7–21 $^{\circ}$ C. Comparable data on other North American species are lacking. The increased growth rates of *O. rusticus* apparently resulted from increased caloric consumption at the higher temperatures (Jones and Momot 1983). Although crayfish at all temperatures were fed to excess, those at higher temperatures fed more actively and consumed greater quantities of food. Growth experiments at or above 30 $^{\circ}$ C were not conducted, but our results suggest that growth may decrease at these higher temperatures. Such a decrease likely would result from increased energetic demands for maintenance at higher temperatures approaching and/or exceeding caloric intake. The temperature at which this might occur is unknown, but Mundahl (1989) observed that juvenile *O. rusticus* altered their habitat use at water temperatures \geq 33 $^{\circ}$ C, possibly implying a change in feeding by these individuals as well. Jones and Momot (1983) observed that *Orconectes virilis* normally expends three times as much energy for maintenance as for growth at 19 $^{\circ}$ C. If *O. rusticus* is similar (its metabolic rate is typically higher than that of *O. virilis*; Momot 1984), increased metabolic demands at temperatures \geq 30 $^{\circ}$ C would leave relatively little energy for growth.

The growth rates of juvenile *O. rusticus* observed in the laboratory likely are indicative of those of animals growing under field conditions within the species' natural range. The mean growth rate of *O. rusticus* juveniles in Indian Creek during summer virtually was identical to growth rates of juveniles at 25 and 29 $^{\circ}$ C in the laboratory. Juveniles in the stream were living at water temperatures \geq 25 $^{\circ}$ C (see water temperatures in Fig. 3), and were growing at near-maximum rates.

Temperature selection has not been examined previously in *O. rusticus*. Our study indicates that the species is capable of behavioral thermoregulation, preferring water temperatures at or near 22 $^{\circ}$ C. These temperatures are similar to those preferred by *Cambarus bartoni* (22.1 \pm 0.5 $^{\circ}$ C; Casterlin and Reynolds 1977), *Orconectes immunis* (18.0–22.5 $^{\circ}$ C; Crawshaw 1974), *Orconectes causeyi* (22 $^{\circ}$ C; Loring and Hill 1976), and *Orconectes virilis* (20–26 $^{\circ}$ C; Peck 1985), but are lower than those preferred by *Orconectes obscurus* (29–30 $^{\circ}$ C; Hall et al. 1978; Mathur et al. 1982). It is not known, however, whether such factors as light intensity, shelter availability, or intra- or interspecific competition

may modify the species' temperature selection (Momot 1967; Roberts 1944).

In general, the acute thermal preference of an organism is affected by its previous thermal history (Reynolds and Casterlin 1979). For example, crayfish acclimated to cooler temperatures usually exhibit lower thermal preferences than those acclimated to warmer temperatures (e.g., Loring and Hill 1976; Hall et al. 1978; Mathur et al. 1982). Despite the wide variation (19.5° C) in acclimation/acclimatization temperature between the age groups of crayfish used in temperature selection tests, both groups had the same mean acute thermal preference. This may indicate that the age groups differ in their thermal preferences (juveniles preferring slightly warmer temperatures), or that thermal acclimation has little influence on temperature selection in this species of crayfish. The overlap in size ranges between the test groups suggests that any size-specific differences in temperature selection probably were slight; however, differences in temperature preferences may exist between adults and smaller juveniles. It is also possible that thermal history may not be as important in the temperature selection process in this crayfish as it is in other species. More investigation is needed to better understand this aspect of the ecology of *O. rusticus*.

Juvenile *O. rusticus* typically occupy shallow (<15 cm) areas bordering stream edges, whereas adults prefer relatively deeper (>20 cm) pool areas (Butler and Stein 1985). Juveniles and adults in Harker's Run and Indian Creek exhibited similar distributions (N. Mundahl, personal observation). The reason for this segregation between age groups is unknown, although it may result from aggressive encounters between small juveniles and adults (Butler and Stein 1985), or from differences in thermal preference. Because *O. rusticus* has an extremely rapid rate of thermal acclimation (Claussen 1980; Layne et al. 1985), the differences in thermal tolerances observed between juveniles and adults suggest that the habitats occupied by the age groups also differed thermally. The magnitude of the range between thermal tolerance limits (difference between CTMax and CTMin) was similar for both age groups, but the entire range of juveniles generally was shifted 1–2° C higher than that of adults on each sampling date, indicating that juveniles were acclimated to warmer temperatures than were the adults. The 0.5–2.6° C differences in mean thermal tolerances between juveniles and adults translate to 1.5–6.8° C differences in acclimatization water temperatures (Layne et al. 1987; Mundahl 1989). Temperature differences of this magnitude were common in stream pools of Indian Creek during afternoons in summer 1988 (Mundahl 1989, unpublished data), being highest in sunlit pool shallows and lowest in deeper, shaded areas and beneath submerged slab rocks and ledges.

It is possible that the observed differences in both CTMaxs and CTMins between juvenile and adult *O. rusticus* were simply the result of ontogenetic differences in heat tolerance. Such differences have been reported in other crustaceans (Sprague 1963; Craig 1974). However, Claussen (1980) found no effect of size on the CTMax of *O. rusticus*. In the present study, juveniles and adults acclimated to the same temperature did not differ in their thermal tolerances (CTMax and CTMin). This indicates that the differences in thermal tolerance observed between the age groups were indeed the result of differences in acclimatization water temperature.

Our results indicate that *O. rusticus* selected water temperatures (20–25° C) where short-term survival apparently is maximized. These temperatures generally were slightly cooler than those where growth rates were highest. In contrast, fish usually select water temperatures 1–3° C warmer than those at which their growth is highest (see review by McCauley and Casselman 1981). The reason for this difference is unknown, but it likely is related to the post-molting problems encountered by crayfish at higher temperatures.

Small juvenile *O. rusticus* occupied warmer habitats than adults in the stream environment. Laboratory experiments suggest that these warmer temperatures (>25° C) may decrease survivorship among juveniles, but also may increase growth rates of survivors. Because crayfish do most of their growing during their first summer of life (Butler and Stein 1985), higher growth rates eventually should lead to higher fecundity among surviving females (Fielder 1972; Lorman 1980) and enhanced competitiveness of both males and females toward coexisting species of crayfish (Butler and Stein 1985). This could have important ramifications in habitats where *O. rusticus* comes in contact with potential competitors.

The range expansion of *O. rusticus* has brought the species into direct competition with several congeners, including *Orconectes sanbornii*, *Orconectes sloanii*, and *O. virilis* (Berrill 1978; Butler and Stein 1985; Capelli 1982; Jezerinac 1986; St. John 1988; Smith 1981). Because of its high growth rate, aggressive behavior, reproductive interference with other species, and several other attributes, *O. rusticus* has been able to displace the native crayfishes from many habitats (e.g., Berrill 1978; Butler and Stein 1985; Jezerinac 1986). However, in some waters *O. rusticus* has been unsuccessful at dominating other crayfish species (Butler 1988; Capelli 1982; St. John 1988). This differential success of *O. rusticus* suggests that some additional factor(s), such as the thermal ecology of the competing species, may be important in determining the outcome of the competitive interactions.

Few data are available concerning the thermal ecology of the crayfish species that, at present, are interacting with *O. rusticus* (Claussen 1980; Momot 1984; see temperature selection discussion above). The influence of water temperature on growth and survival of most crayfish species is unknown. Because larger size is a key element in many of the attributes (e.g., aggressive dominance, shelter acquisition to avoid predators, reproductive interference) that allow *O. rusticus* to compete successfully with other species, the influence of temperature on its growth may be of primary importance to its success.

Our data indicate that growth of *O. rusticus* is most rapid at water temperatures between 26 and 28° C, so populations should be most successful in waters with average summer temperatures near this range. In Ohio, *O. rusticus* populations appear most successful (as judged by highest densities, largest average sizes, absence of competitors) in larger, warmer (>20° C throughout summer) streams and rivers (N. Mundahl, personal observation), whereas other species (*Orconectes obscurus*, *O. sanbornii*, *O. sloanii*) maintain population strongholds in the cooler, upper reaches of many streams (Butler 1988; Jezerinac 1986; St. John 1988; N. Mundahl, personal observation). Butler (1988) reported that the average size of female *O. rusticus* adults in an Ohio stream decreased in an upstream direction, whereas the size of competing *O. sanbornii* females in-

Table 1. Mean (\pm SE) carapace lengths (mm) of juvenile and adult *O. rusticus* used in thermal tolerance tests (CTMax and CTMin). Sample sizes are in parentheses

Site/date	Test	Age group	
		Juvenile	Adult
Harker's Run			
19 June	CTMax	9 \pm 0 (19)	30 \pm 2 (8)
Indian Creek			
21 June	CTMax	12 \pm 1 (10)	28 \pm 2 (10)
	CTMin	13 \pm 0 (10)	27 \pm 2 (10)
12 July	CTMax	16 \pm 0 (10)	25 \pm 1 (10)
	CTMin	15 \pm 0 (10)	25 \pm 1 (10)
27 July	CTMax	18 \pm 0 (10)	29 \pm 1 (10)
	CTMin	19 \pm 0 (10)	26 \pm 1 (10)
12 August	CTMax	20 \pm 1 (10)	30 \pm 2 (5)
	CTMin	20 \pm 0 (10)	28 \pm 2 (3)
Laboratory			
21 August	CTMax	21 \pm 1 (10)	31 \pm 2 (4)
	CTMin	21 \pm 0 (10)	28 \pm 2 (4)

creased, suggesting a possible differential effect of water temperature on the growth rates of the two species. In our study, *O. rusticus* juveniles collected from the cooler, spring-fed Harker's Run (where *O. sloanii* also is present) in mid-June were significantly smaller than those collected from the warmer Indian Creek (where no other crayfish species are present) during the same period (see Table 1). Apparently, the cooler water temperatures in headwater areas slow the growth rate of *O. rusticus* and reduce or eliminate any size-related advantage it may have over its competitors. If human disturbances (e.g., cutting riparian vegetation, channelization) alter the thermal regime of the upper stream reaches, *O. rusticus* may be able to invade these habitats and displace the native species.

In more northern habitats (in Wisconsin, Minnesota, New England, southern Ontario), introduced *O. rusticus* have displaced native species (e.g., *O. virilis*) in some systems, but not in others (Berrill 1978; Capelli 1982). Momot (1984) hypothesized that the higher metabolic rate of *O. rusticus* can make the species a formidable competitor in habitats with abundant nutrients and optimum temperatures, allowing individuals to incorporate more energy per unit time, grow rapidly, and reach a larger overall size. However, in habitats with low temperatures and/or low nutrients, *O. rusticus* may be at a bioenergetic disadvantage when compared to species such as *O. virilis* that normally occupy such systems (Momot et al. 1988). Both thermal regime and food supply may be important in determining the competitive success of *O. rusticus* in northern waters.

In conclusion, water temperature plays an important role in the ecology of *O. rusticus*. Temperature affects survival and growth of juveniles, and the species apparently is able to select water temperatures that enhance survival. In the stream environment, juveniles occupy warmer habitats than adults, which generally should result in enhanced growth rates for juveniles. These higher growth rates, and the accompanying improvements in fecundity and competitive ability, may explain, in part, the recent success of *O. rusticus* in displacing other crayfish species. Comparative studies of the effect of water temperature on growth rates

of *O. rusticus* and its potential competitors are needed to help understand the possible role of temperature as a mediator of competition among crayfishes.

Acknowledgments. We thank T.E. Wissing, D.L. Claussen, and S.I. Guttman for use of equipment and laboratory space. E.D. Mundahl assisted with field collections and tolerance testing, B. Hoppes helped with temperature selection experiments, and R.L. Kopp provided aid during growth experiments. J. Costanzo, W. Clements, and J. Oris provided critical reviews of an earlier version of the manuscript. Funding for this research was provided by a grant from the Rod & Reel Club, Centerville, Ohio, and a Miami University Undergraduate Research Award to C.T. Hockett.

References

- Avault JW Jr (1983) Crayfish species plan for the United States: aquaculture. In: Goldman CR (ed) Freshwater crayfish V. AVI Publishing Company, Incorporated, Westport, Connecticut, pp 528-533
- Berrill M (1978) Distribution and ecology of crayfish in the Kawartha Lakes region of southern Ontario. *Can J Zool* 56:166-177
- Berrill M, Hollett L, Margosian A, Hudson J (1985) Variation in tolerance to low environmental pH by the crayfish *Orconectes rusticus*, *O. propinquus*, and *Cambarus robustus*. *Can J Zool* 63:2586-2589
- Bills TD, Marking LL (1988) Control of nuisance populations of crayfish with traps and toxicants. *Progr Fish-Cult* 50:103-106
- Butler MJ IV (1988) Evaluation of possible reproductively mediated character displacement in the crayfishes, *Orconectes rusticus* and *O. sanbornii*. *Ohio J Sci* 88:87-91
- Butler MJ IV, Stein RA (1985) An analysis of the mechanisms governing species replacements in crayfish. *Oecologia* 66:168-177
- Capelli GM (1982) Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). *Limnol Oceanogr* 27:741-745
- Casterlin ME, Reynolds WW (1977) Behavioral fever in crayfish. *Hydrobiologia* 56:99-101
- Claussen DL (1980) Thermal acclimation in the crayfish *Orconectes rusticus* and *O. virilis*. *Comp Biochem Physiol* 66A:377-384
- Craig WJ Jr (1974) Physiological ecology of the commensal crabs, *Polyonyx gibbesi* Haig and *Pinnixa chaetoptera* Stimpson. *Oecologia* 15:235-244
- Crawshaw LI (1974) Temperature selection and activity in the crayfish, *Orconectes immunis*. *J Comp Physiol* 95:315-322
- Fielder DD (1972) Some aspects of the life histories of three closely related crayfish species *Orconectes obscurus*, *O. sanbornii*, and *O. propinquus*. *Ohio J Sci* 72:129-145
- Hall LW Jr, Cincotta DA, Stauffer JR Jr, Hocutt CH (1978) Temperature preference of the crayfish *Orconectes immunis*. *Arch Environ Contam Tox* 7:379-383
- Hlohowskyj I, Wissing TE (1987) Seasonal changes in the thermal preferences of fantail (*Etheostoma flabellare*), rainbow (*E. caeruleum*), and greenside (*E. bennioides*) darters. In: Matthews WS, Heins DC (eds) Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, pp 105-110
- Hobbs HH Jr (1974) A checklist of the North and Middle American crayfishes (Decapoda: Astacidae and Cambaridae). *Smiths Contrib Zool* No 166
- Hobbs HH III, Jass JP (1988) The crayfishes and shrimp of Wisconsin (Cambaridae, Palaemonidae). Milwaukee Public Museum
- Jezerinac RF (1982) Life-history notes and distribution of crayfishes (Decapoda: Cambaridae) from the Chagrin River basin, northeastern Ohio. *Ohio J Sci* 82:181-192
- Jezerinac RF (1986) Endangered and threatened crayfishes (Decapoda: Cambaridae) of Ohio. *Ohio J Sci* 86:177-180
- Jones PD, Momot WT (1983) The bioenergetics of *Orconectes virilis* in two pothole lakes. In: Goldman CR (ed) Freshwater cray-

- fish V. AVI Publishing Company, Incorporated, Westport, Connecticut, pp 192-209
- Layne JR Jr, Manis ML, Claussen DL (1985) Seasonal variation in the time course of thermal acclimation in the crayfish *Orconectes rusticus*. *Freshw Invert Biol* 4:98-104
- Layne JR Jr, Claussen DL, Manis ML (1987) Effects of acclimation temperature, season, and time of day on the critical thermal maxima and minima of the crayfish *Orconectes rusticus*. *J Therm Biol* 12:183-187
- Lodge DM, Beckel AL, Magnuson JJ (1985) Lake-bottom tyrant. *Nat Hist* 94:33-37
- Loring MW, Hill LG (1976) Temperature selection and shelter utilization of the crayfish, *Orconectes causeyi*. *Southwest Nat* 21:219-226
- Lorman G (1980) Ecology of the crayfish *Orconectes rusticus* in northern Wisconsin. Doctoral dissertation, University of Wisconsin, Madison
- Lorman JG, Magnuson JJ (1978) The role of crayfishes in aquatic systems. *Fisheries* 3:8-11
- Mathur D, Schutsky RM, Purdy EJ Jr (1982) Temperature preference and avoidance responses of the crayfish, *Orconectes obscurus*, and associated statistical problems. *Can J Fish Aquat Sci* 39:548-553
- McCaughey RW, Casselman JM (1981) The final preferendum as an index of the temperature for optimum growth in fish. In: Proceedings of the world symposium on aquaculture in heated effluents and recirculation systems, volume 2. Student Aquaculture Association of the United Nations, Berlin, pp 81-93
- Momot WT (1967) Population dynamics and productivity of the crayfish, *Orconectes virilis*, in a marl lake. *Am Midl Nat* 78:55-81
- Momot WT (1984) Crayfish production: a reflection of community energetics. *J Crust Biol* 4:35-54
- Momot WT, Gowing H, Jones P (1978) The dynamics of crayfish and their role in ecosystems. *Am Midl Nat* 99:10-35
- Momot WT, Hartviksen C, Morgan G (1988) A range extension for the crayfish *Orconectes rusticus*: Sibley Provincial Park, northwestern Ontario. *Can Field-Nat* 102:547-548
- Mundahl ND (1989) Seasonal and diel changes in thermal tolerance of the crayfish *Orconectes rusticus*, with evidence for behavioral thermoregulation. *J N Am Benthol Soc* 8:173-179
- Nolfi JR (1983) Commercialization of Vermont crayfish species (*Orconectes immunis* and *Orconectes virilis*): putting theory into practice. In: Goldman CR (ed) *Freshwater crayfish V*. AVI Publishing Company, Incorporated, Westport, Connecticut, pp 429-441
- Peck SK (1985) Effects of aggressive interaction on temperature selection by the crayfish, *Orconectes virilis*. *Am Midl Nat* 114:159-167
- Prins R (1968) Comparative ecology of the crayfishes *Orconectes rusticus* and *Cambarus tenebrosus* in Doe Run, Meade County, Kentucky. *Int Rev Ges Hydrobiol* 53:667-714
- Reynolds WW, Casterlin ME (1979) Behavioral thermoregulation and the "final preferendum" paradigm. *Am Zool* 19:211-224
- Roberts TW (1944) Light, eyestalk, chemical and certain other factors as regulators of community activity for the crayfish *Cambarus virilis* Hagen. *Ecol Monogr* 14:359-392
- Smith DG (1981) Evidence for hybridization between two crayfish species (Decapoda: Cambaridae: *Orconectes*) with a comment on the phenomenon in Cambarid crayfish. *Am Midl Nat* 120:405-407
- Sommer TR, Goldman C (1983) The crayfish *Procambarus clarkii* from California ricefields: ecology, problems, and potential for harvest. In: Goldman CR (ed) *Freshwater crayfish V*. AVI Publishing Company, Incorporated, Westport, Connecticut, pp 418-428
- Spoor WA (1955) Loss and gain of heat-tolerance by the crayfish. *Biol Bull* 108:77-87
- Sprague JB (1963) Resistance of four freshwater crustaceans to lethal high temperatures and low oxygen. *J Fish Res Board Can* 20:387-415
- St John FL (1988) Distribution and status of *Orconectes (Rhoadesius) sloanii* (Bundy) (Crustacea: Decapoda: Cambaridae). *Ohio J Sci* 88:202-204
- Westman K (1973) Cultivation of the American crayfish *Pacifastacus leniusculus*. Abrahamsson S (ed) *Freshwater crayfish*. Studentlitteratur, Lund, Sweden, pp 211-220

Received March 5, 1989 / Received in revised form
September 11, 1989 / Accepted October 16, 1989