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Maximum Daily Consumption and Respiration Rates at Four Temperatures for Five Species of Crayfish from Missouri, U.S.A. (Decapoda, Orconectes spp.)

# MAXIMUM DAILY CONSUMPTION AND RESPIRATION RATES AT FOUR TEMPERATURES FOR FIVE SPECIES OF CRAYFISH FROM MISSOURI, U.S.A. (DECAPODA, *ORCONECTES* SPP.)

BY

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## ABSTRACT

We tested for differences in maximum daily consumption ($C_{max}$) and respiration (R) rates at four temperatures (18, 22, 26, and 30°C) for crayfishes with varying distributions in Missouri, U.S.A. Five species of crayfish were studied: *Orconectes eupunctus* (Williams, 1952), found only in the Eleven Point River downstream of Greer Spring, *O. hylas* (Faxon, 1890), found only in the Black and St. Francis River drainages in the Ozarks, *O. luteus* (Creaser, 1933) and *O. punctimanus* (Creaser, 1933), which are widespread through the Ozarks, and *O. virilis* (Hagen, 1870), which has a broad distribution in Missouri but is most abundant in the northern agricultural region and in the transitional area along the northern and western border of the Ozarks. For species restricted to the Ozarks, $C_{max}$ increased from 18 to 22°C and stabilized or declined at the two warmest temperatures, while $C_{max}$ peaked at 26°C for *O. virilis* before declining at 30°C. Significant interspecific differences in $C_{max}$ were found at several temperatures. $C_{max}$ for *O. virilis* was significantly greater than $C_{max}$ for one or more Ozark crayfishes at 18, 22, and especially at 26°C. Respiration rates (R) increased with temperature for all species, but few differences in R were observed between species. Results suggest that *O. virilis* has a potential bioenergetic advantage over Ozark crayfishes, particularly at temperatures near 26°C. Our findings hint that warming of Ozark streams due to changes in climate or land use could yield growth conditions which are more favorable for introduced species such as *O. virilis* and possibly *O. rusticus* compared to native species, resulting in increased probability of shifts in crayfish community composition.

## RÉSUMÉ

Nous avons testé les différences de consommation journalière maximale ($C_{max}$) et de taux de respiration (R) à 4 températures différentes (18, 22, 26 et 30°C) chez des écrevisses à répartitions

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variables dans le Missouri, U.S.A. Cinq espèces d'écrevisses ont été étudiées: *Orconectes eupunctus* (Williams, 1952), trouvée uniquement en aval de la rivière Eleven Point, Greer Spring; *O. hylas* (Faxon, 1890), rencontrée seulement dans les bassins de drainage des rivières Black et St Francis dans les Ozarks, *O. luteus* (Creaser, 1933) et *O. punctimanus* (Creaser, 1933), qui sont largement répandus dans les Ozarks, enfin *O. virilis* (Hagen, 1870), qui a une large répartition dans le Missouri, mais est l'espèce la plus abondante dans la région agricole du nord et dans la zone transitoire à la limite nord et ouest des Ozarks. Chez les espèces limitées aux Ozarks, $C_{max}$ a augmenté de 18 à 22°C et s'est stabilisé ou a diminué aux deux températures les plus élevées, tandis que $C_{max}$ atteignait un pic à 26°C pour *O. virilis* avant de diminuer à 30°C. Des différences interspécifiques significatives de $C_{max}$ ont été trouvées à plusieurs températures. $C_{max}$ était significativement plus élevé chez *O. virilis* que $C_{max}$ chez une, ou plusieurs, des écrevisses des Ozarks à 18, 22 et en particulier à 26°C. Les taux de respiration (R) augmentaient avec la température chez toutes les espèces, mais peu de différences sur R ont été observées entre les espèces. Les résultats suggèrent que *O. virilis* a un avantage bioénergétique potentiel sur les écrevisses des Ozarks, en particulier aux températures voisines de 26°C. Ils laissent à penser que le réchauffement des rivières des Ozarks, en raison des changements de climat et de l'usage des sols, pourraient induire des conditions de croissance plus favorables aux espèces introduites telles que *O. virilis* et peut-être *O. rusticus* qu'aux espèces indigènes, avec pour résultat, une probabilité accrue de modification de la composition des communautés d'écrevisses.

## INTRODUCTION

Crayfishes are a prominent ecological component of many aquatic systems. In Ozark streams, crayfishes are the energetically most important food item in the diets of smallmouth bass (*Micropterus dolomieu* Lacépède, 1802) and rock bass (*Ambloplites* spp.) (cf. Rabeni, 1992), two of the most important sport fishes in the region. The annual production of crayfishes can equal or exceed annual production of the rest of the benthic invertebrate community in some streams (Rabeni et al., 1995), and crayfishes can consume as much or more terrestrial detritus, algae, and benthic invertebrates as the rest of the benthic community combined (Whitledge & Rabeni, 1997).

The Ozark plateau is located in southern Missouri and northern Arkansas, U.S.A. Mean annual air temperature in this region is 13°C and mean annual precipitation is 104 cm, most of which falls as rain during spring, summer, and early fall. The region's karst topography accounts for the large number of sinkholes, caves, and springs. Thin, stony soils contribute little fine sediment to surface runoff. Consequently, Ozark streams tend to be relatively clear and cool with sustained base flows.

Approximately 25 species of crayfish inhabit the Missouri Ozarks, sixteen of which are endemics (Pflieger, 1996). Many are restricted to a single drainage. In the U.S. and Canada, an estimated 50% of crayfishes are in need of some form of conservation recognition, and limited natural range has been implicated as the primary factor responsible for the imperilment of crayfishes that are at risk for

extirpation; other major threats include habitat alteration and the introduction of non-indigenous crayfishes (Taylor et al., 1996).

In spite of their ecological importance and conservation status as a whole, knowledge of ecological requirements for most crayfishes is fragmentary or lacking (Taylor et al., 1996), and very few bioenergetic studies in streams have included crayfishes (Momot, 1995). Published studies relating water temperature to growth of North American crayfishes are limited to just four species: *Orconectes rusticus* (Girard, 1852) (cf. Mundahl & Benton, 1990), *O. virilis* (Hagen, 1870) (cf. Momot, 1984; Wetzel & Brown, 1993), *O. immunis* (Hagen, 1870) (cf. Wetzel & Brown, 1993), and *Pacifastacus leniusculus* (Dana, 1852) (cf. Westman, 1973). Growth is an important factor in crayfish population dynamics, as fecundity (Corey, 1987; Muck, 1995) and the ability to acquire and hold shelter (Rabeni, 1985) increase with increasing crayfish size, and because fishes often prey selectively on smaller crayfish (Probst et al., 1984; Garvey et al., 1994). Higher growth rates of introduced crayfishes can also be important in the replacement of native species (Abrahamsson, 1971; Hill et al., 1993), yet our ability to predict how changes in temperature might affect crayfish production and risk to indigenous crayfishes from competitive displacement is very limited. Thus, increased knowledge of growth capacity of crayfishes at different temperatures is essential to conservation of native crayfishes facing threats from introduced species and alterations in thermal habitat.

To explore the relation of water temperature to growth for some indigenous Missouri crayfishes, maximum daily consumption ($C_{max}$) and respiration (R) rates were determined for five species of crayfish over a temperature range of 18-30°C. Maximum consumption and respiration rates are two components of Wisconsin fish bioenergetics models (Hewett & Johnson, 1992), which can provide insight into how a species' growth scope changes with temperature. Growth scope is the difference between $C_{max}$ and energy costs at a given temperature, and represents the amount of ingested energy potentially available for growth at that temperature (Warren & Davis, 1967; Jobling, 1997; Zweifel et al., 1999). Although Wisconsin bioenergetics models have not previously been applied to crayfishes, they have been used successfully with invertebrates already, i.e., in mysids (Rudstam, 1989). The five species of crayfish chosen for this study were: *Orconectes eupunctus* Williams, 1952, found only in the Eleven Point River and Spring River drainages in the Ozarks primarily below large springs (fig. 1a), *O. hylas* (Faxon, 1890), found only in the Ozarks in the Black River drainage and in the headwaters of three adjacent drainages (fig. 1a), *O. punctimanus* (Creaser, 1933), which is distributed throughout much of the eastern half of the Missouri Ozarks (fig. 1b), *O. luteus* (Creaser, 1933), whose range includes the northern and eastern Ozarks, the Current River drainage, and several Mississippi River tributaries in northeastern Missouri (fig. 1a), and *O. virilis*, which is found throughout the state except for the
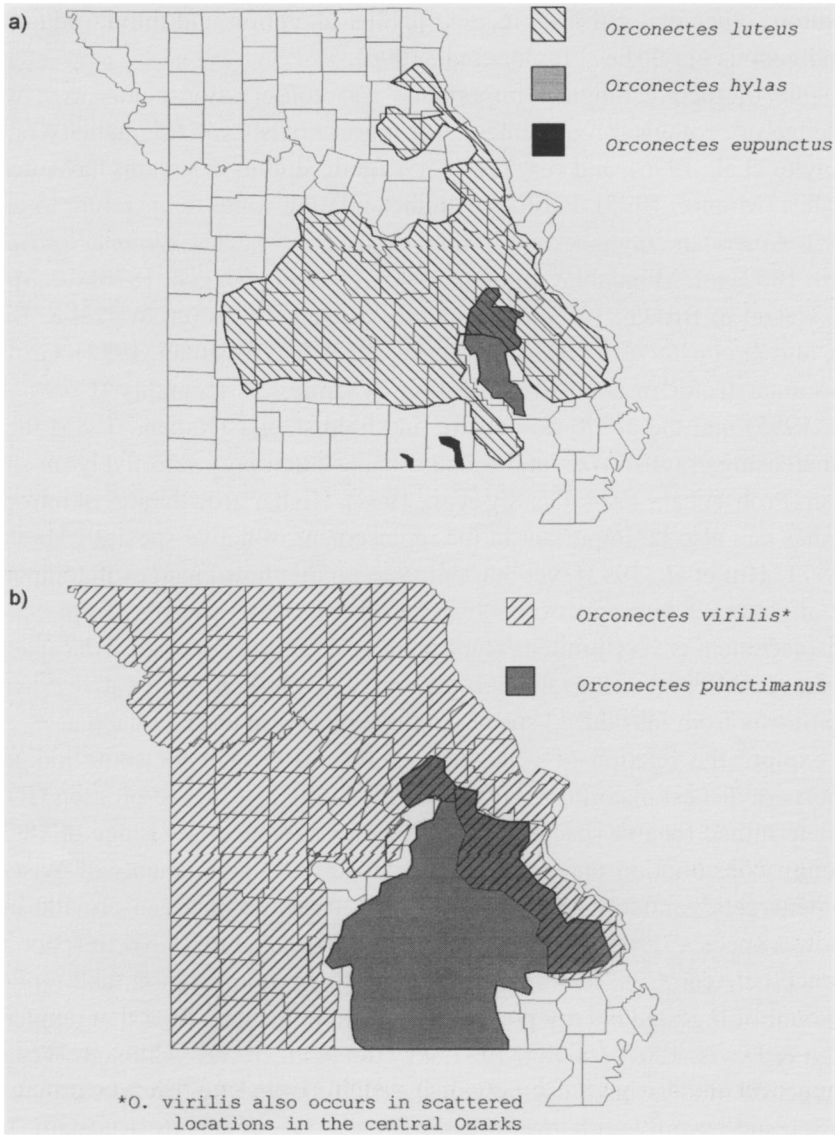
Fig. 1. Distributions of: a, the crayfishes *Orconectes luteus* (Creaser, 1933), *O. hylas* (Faxon, 1890), and *O. eupunctus* Williams, 1952; and, b, *O. virilis* (Hagen, 1870) and *O. punctimanus* (Creaser, 1933) in Missouri, according to Pflieger (1996).

southeastern lowlands and parts of the central Ozarks (fig. 1b) (Pflieger, 1996). *O. virilis* is most abundant in the prairie and prairie-margin streams in the northern and western parts of the state, and occurs in the Ozarks primarily as scattered populations thought to be the result of bait-bucket introductions (Pflieger, 1996). Maximum daily consumption and respiration rates were determined and compared

for these five species to elucidate how water temperature might influence crayfish growth scope and risk to native Ozark crayfishes from competitive replacement by introduced crayfishes.

## METHODS

Crayfishes (25 mm ± 3 mm carapace length) were collected by dip net or seine from Ozark and Ozark border streams in May, June, August, and September 1999. Crayfishes were transported to the laboratory and acclimated to laboratory conditions over 14 days. Acclimation conditions included a 16 h light : 8 h dark photoperiod, water temperature of 22°C ± 0.5°C, and daily ad libitum feedings of chironomid larvae (*Chironomus* sp.) obtained from a commercial supplier (Beldts Aquarium, Inc.). Crayfishes were held individually in 0.946 l glass canning jars with holes in the lids to allow water to circulate. Jars were submerged in a horizontal position in two adjacent 1135 l tanks equipped with water recirculation, biofiltration, and temperature control systems.

To determine maximum daily consumption ($C_{max}$) rates, five individually held crayfish of each species were provided daily ad libitum rations of chironomid larvae for four consecutive days at each of four temperatures (18, 22, 26, and 30°C, ± 0.5°C) (Zweifel et al., 1999). Prior to testing at 18, 26, and 30°C, water temperature was changed at a rate of $1\text{-}2°C \cdot d^{-1}$ until the test temperature was reached. Crayfishes were acclimated to test temperatures for 10 days before each experiment. Ad libitum feeding was continued daily throughout temperature changes and acclimation to test temperatures. During experiments, daily consumption (g) for each crayfish was determined by subtracting the total weight of chironomids remaining in each jar from the total weight provided 24 h earlier. Immediately following testing at each temperature, crayfishes were weighed to the nearest 0.1 g. $C_{max}$ ($g \cdot g^{-1} \cdot d^{-1}$) was calculated for each crayfish by dividing mean daily consumption over the 4 d period by crayfish weight. Each crayfish was tested once during experiments.

To determine respiration (R) rates, five crayfish of each species were placed in static respirometry chambers (Cech, 1990) and dissolved oxygen consumption of individual crayfish was monitored over a period of 2-3 h at each of the four temperatures tested in the $C_{max}$ experiments. Acclimation conditions were identical to those described for the $C_{max}$ experiments, except that crayfishes were starved for 24 h prior to testing at each temperature to ensure that respiration rates would not be influenced by digestion (Cech, 1990). Static respirometers consisted of 0.946 l glass canning jars identical to those used in the $C_{max}$ experiments, except that during respirometry experiments lids without holes were placed on each jar to prohibit

water exchange between the jar and the surrounding tank. Dissolved oxygen concentrations in each jar were measured to the nearest 0.1 mg·l$^{-1}$ immediately prior to placing lids on jars and after 2-3 h had elapsed using a YSI model 51B oxygen meter and a YSI model 5739 oxygen probe. Dissolved oxygen concentrations in jars were never < 5.7 mg·l$^{-1}$. Oxygen uptake (mg O$_2$·h$^{-1}$) by each crayfish was calculated as the difference between initial and final dissolved oxygen concentrations divided by the duration of the experiment at each temperature. Immediately following testing at each temperature, crayfishes were weighed to the nearest 0.1 g. Respiration rate (g O$_2$·g$^{-1}$·d$^{-1}$) was calculated for each crayfish by dividing oxygen uptake by crayfish weight and then multiplying by 24 h. Respiration rates were then converted into prey-equivalent units (g prey·g$^{-1}$·d$^{-1}$) so that respiration rate data could be compared directly to C$_{max}$ data. First, respiration rate was converted to joule-equivalent units using a multiplier of 13,724 J·g O$_2^{-1}$ (Adams & Breck, 1990). Respiration rate (R) was then converted into prey-equivalent units (g prey·g$^{-1}$·d$^{-1}$) by dividing by the energy density of chironomid larvae (2,218 J·g wet wt.$^{-1}$; Cummins & Wuycheck, 1971). Each crayfish was used only once during experiments.

Analysis of variance (ANOVA) followed by the least significant differences (LSD) procedure for separation of means was used to test for intraspecific differences in C$_{max}$ and R over the four temperatures and to test for interspecific differences in C$_{max}$ and R at each temperature. Growth scope (g·g$^{-1}$·d$^{-1}$) was calculated by subtracting mean values for R from mean values for C$_{max}$ for each species at each of the four temperatures.

## RESULTS

Maximum daily consumption rate (C$_{max}$) increased from 18° to 22°C and stabilized or declined thereafter for the three species restricted to the Ozark region (*Orconectes eupunctus*, *O. hylas*, and *O. punctimanus*; fig. 2). For *O. virilis*, C$_{max}$ increased from 18° to 26°C, peaked at 26°C, and declined at 30°C, while C$_{max}$ increased from 18° to 26°C for *O. luteus* and did not change significantly from 26° to 30°C. At 26°C, C$_{max}$ was significantly higher for *O. virilis* than for each of the other four species ($P$ < 0.05). C$_{max}$ was also significantly higher for *O. virilis* compared to *O. luteus* and *O. hylas* at 22°C and to *O. punctimanus* at 18°C ($P$ < 0.05). *O. eupunctus* had a significantly higher value for C$_{max}$ relative to *O. luteus* at 22°C ($P$ < 0.05). All other differences in C$_{max}$ between species pairs at a particular temperature were non-significant ($P$ > 0.05).

Respiration rate (R) was highest at 30°C and was significantly greater at 26° than at 18°C for all species ($P$ < 0.05; fig. 3). Although R generally increased with
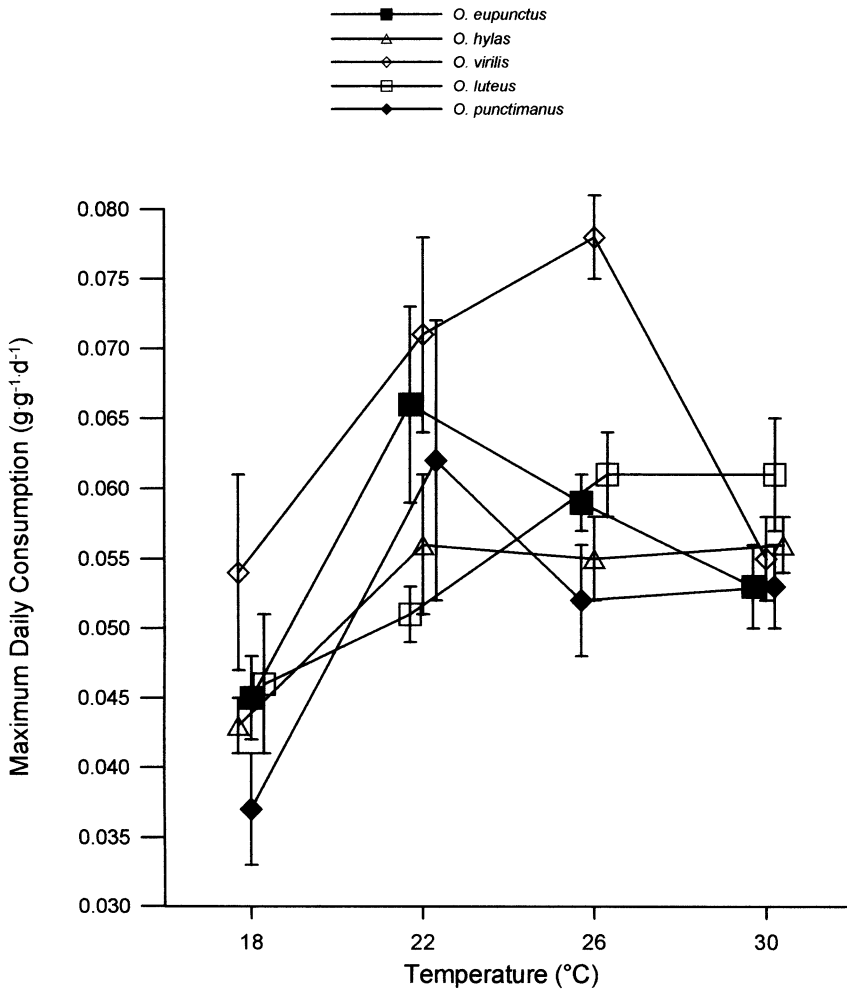
Fig. 2. Maximum daily consumption rates $(g \cdot g^{-1} \cdot d^{-1})$ for five species of crayfish from Missouri, U.S.A. at 18, 22, 26, and 30°C, respectively. Values shown are means $\pm$ 1 SE. $N = 5$ for each data point.

increasing temperature, intraspecific differences in R at 18° and 22°C were non-significant for all species ($P > 0.05$) and intraspecific differences in R at 22° and 26° were non-significant ($P > 0.05$) for all species except *O. punctimanus*. Fewer interspecific differences in R were present compared to those observed for $C_{max}$ at the four temperatures tested. *O. hylas* had a higher rate of R at 18° and at 30°C than *O. punctimanus* and a higher rate of R at 30° compared to *O. virilis* ($P < 0.05$). All other differences in R between species pairs at a particular temperature were non-significant ($P > 0.05$).
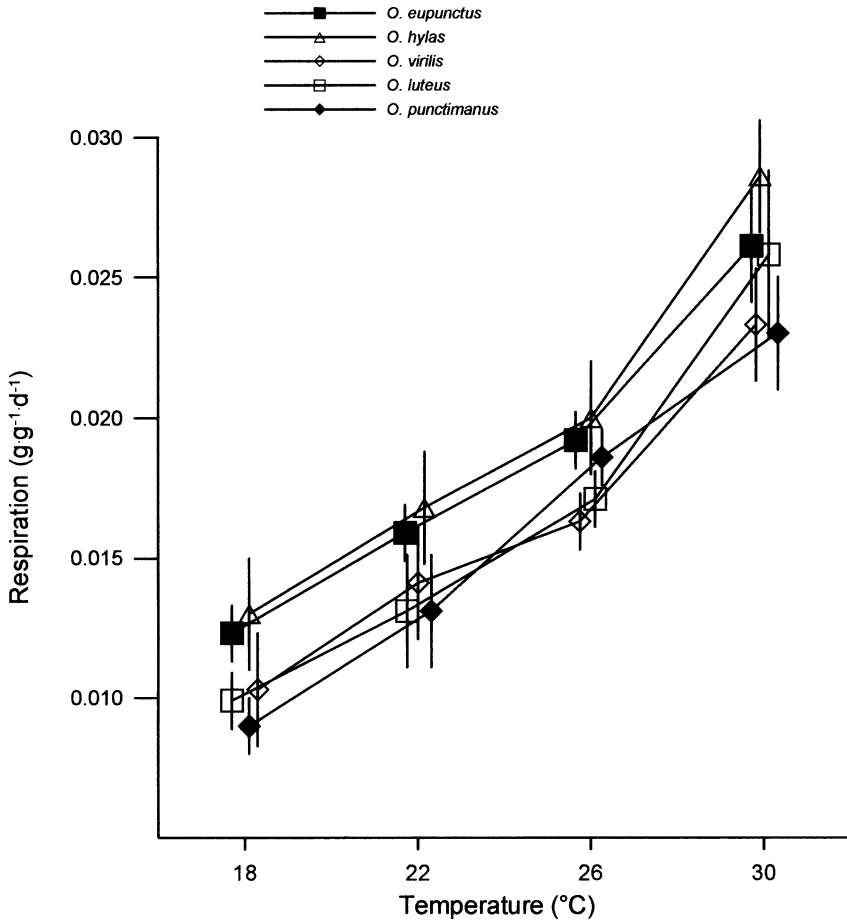
Fig. 3. Respiration rates ($g \cdot g^{-1} \cdot d^{-1}$) for five species of crayfish from Missouri, U.S.A. at 18, 22, 26, and 30°C, respectively. Values shown are means ± 1 SE. $N = 5$ for each data point.

Growth scope (the difference between $C_{max}$ and R) peaked at 26°C for *O. virilis* and *O. luteus* and peaked at 22°C for *O. eupunctus*, *O. hylas*, and *O. punctimanus*, corresponding with temperatures at which $C_{max}$ was maximized for each species (fig. 4). *O. virilis* had the highest growth scope among these species at 18, 22, and 26°C and the highest overall growth scope (0.062 $g \cdot g^{-1} \cdot d^{-1}$ at 26°C) of any species at any temperature.

## DISCUSSION

Relations between both $C_{max}$ and R and water temperature for crayfishes followed patterns typically observed for fishes and for other crustaceans. For fishes and for other crustaceans, R generally increases exponentially with increasing
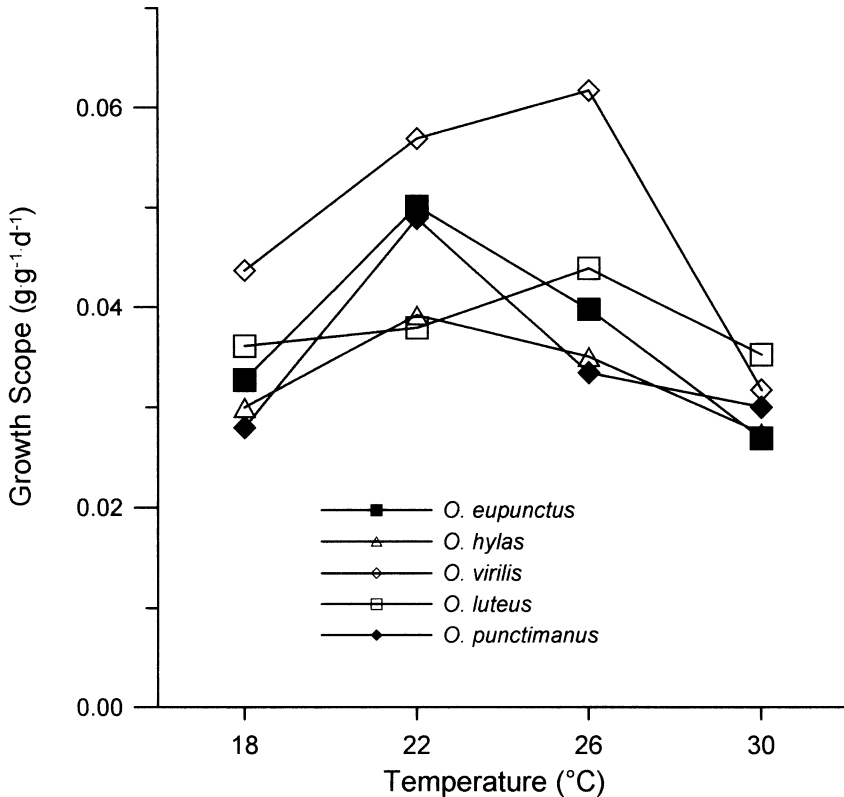
Fig. 4. Growth scope (Mean $C_{max}$ - Mean R, $g \cdot g^{-1} \cdot d^{-1}$) for five species of Missouri crayfish over the temperature range from 18 to 30°C.

temperature (Kitchell et al., 1977; Brett, 1979; Ivleva, 1980; Jobling, 1993), while among fishes $C_{max}$ initially increases with temperature, peaks or reaches a plateau at some intermediate temperature ($T_{max C}$), and then declines rapidly as temperature approaches the upper thermal tolerance limit for the species (Kitchell et al., 1977; Jobling, 1993; Elliott, 1994; Hayward & Arnold, 1996; Zweifel et al., 1999). Consequently, growth scope (the difference between $C_{max}$ and R, energy potentially available for growth, Warren & Davis, 1967; Zweifel et al., 1999) is maximized at a temperature slightly lower than $T_{max C}$, then declines precipitously at temperatures above $T_{max C}$ (Jobling, 1997). Results indicated that growth scope was maximized at 22°C for the three species restricted to the Ozarks (*Orconectes eupunctus*, *O. hylas*, and *O. punctimanus*), and at 26°C for *O. virilis* and *O. luteus*, with growth scope becoming constrained for all species at temperatures above 26°C. That *O. virilis* has higher optimum temperature for growth than the Ozark species is consistent with the fact that it is most commonly found in Missouri in streams of the Ozark border region and in the prairies of the northern and western parts of the state (Pflieger, 1996), where temperatures are typically higher during

the growing season than in the spring-fed streams of the Ozarks. At least 12 other crayfishes are endemic to spring-fed watersheds in the Ozark highlands (Pflieger, 1996), and likely have optimum temperatures for growth similar to the 22°C optimum growth temperature for the species restricted to the Ozark region that were tested in this study. Although *O. luteus* is one of the most common species found in the Ozarks, its higher thermal growth optimum compared to species restricted to the Ozarks may partly explain its occurrence in the warmer streams in northeastern Missouri (Pflieger, 1996) and in west-central Illinois (Wetzel & Poly, 2000).

That $C_{max}$ and growth scope for *O. virilis* increased from 18°C to 26°C and declined at 30°C is consistent with the results of a previous study which found that growth rates of juvenile *O. virilis* increased with increasing temperature from 10°C to 25°C, then declined at 30°C (Wetzel & Brown, 1993). Relations between water temperature and growth are known for only two other species of crayfish from the midwestern United States. Like *O. virilis*, growth of juvenile *O. immunis* increased with temperature up to 25°C, then declined at 30°C (Wetzel & Brown, 1993). Juvenile *O. rusticus*, a species that has replaced indigenous crayfishes in several locations in the central U.S. and Canada, have an optimum temperature for growth between 26 and 28°C (Mundahl & Benton, 1990).

Results indicated that *O. virilis* had significantly higher values for $C_{max}$ and a larger growth scope than each of the four Ozark crayfishes at 26°C and at least one of the other species at 18 and 22°C. Thus, *O. virilis* has a potential bioenergetic advantage over the Ozark species in several instances, but particularly at temperatures near 26°C. A larger growth scope would represent an important advantage among crayfishes given that size is positively related to fecundity (Corey, 1987; Muck, 1995) and shelter acquisition (Rabeni, 1985) and that fishes often prey selectively on smaller crayfish (Probst et al., 1984; Garvey et al., 1994). Higher growth rate has been implicated as an important factor in the replacement of *O. virilis* and *O. propinquus* in Wisconsin lakes by *O. rusticus* (cf. Hill et al., 1993) and in the replacement of *Astacus astacus* (L., 1758) by *Pacifastacus leniusculus* in Europe (Abrahamsson, 1971). Thus, factors that contribute to prolonged periods in which stream temperatures are above the optimum growth temperature for species restricted to the Ozarks (22°C) to levels more suitable for *Orconectes virilis* (25-26°C) could increase the probability of *O. virilis* displacing native Ozark crayfishes if introductions of *O. virilis* continue to occur in Ozark streams. However, growth scope becomes increasingly restricted for all five species tested at temperatures above 26°C, so conditions which result in streams warming to these levels are sub-optimal for all five species and are not expected to favor *O. virilis* over the species native to the Ozarks. Survival of crayfishes can also be reduced at temperatures above thermal optima due to increases in molt frequency and death

from molt failure at higher temperatures (Mundahl & Benton, 1990; Wetzel & Brown, 1993), making temperatures above 26°C even less suitable for the five species used in this study. Given that temperatures above 26°C would likely be sub-optimal for most Missouri crayfishes, displacement of native species by crayfishes which have higher thermal optima and are not currently known to occur in the state may be more likely to occur at these temperatures. For example, *O. rusticus* has an optimum temperature for growth between 26° and 28°C (Mundahl & Benton, 1990), so introductions of this species could have a higher probability of displacement of native Missouri crayfishes in streams where temperatures exceed 26°C. Such a scenario would be increasingly likely if the approximately 6°C mean summer air temperature increase projected for the Ozark region by the Canadian Climate Center's general circulation model after a doubling of the atmospheric $CO_2$ concentration occurs (Eaton & Scheller, 1996).

In spite of differences in $C_{max}$, R, and growth scope among these crayfishes, species replacements will not necessarily result from every introduction, even if thermal conditions are ideal for growth of invading species and poor for indigenous crayfishes. The majority of introductions do not result in displacement of native species (Simberloff, 1981). Even if a non-indigenous species becomes established in an area, differences in habitat use or other niche dimensions may lead to coexistence rather than extirpation of native species. Sympatric populations of *O. punctimanus* and *O. hylas* and of *O. virilis* and *O. luteus* currently exist in Missouri despite differences in growth scope at some temperatures between these species pairs. However, all other factors being equal, interspecific differences in growth scope do represent a potential competitive advantage for some species at some temperatures. Given that species replacements among crayfishes have frequently been observed during the last few decades (Taylor et al., 1996) and that many native Ozark crayfishes have limited ranges (Pflieger, 1996), efforts to preserve native crayfishes should consider any possible competitive advantage for non-indigenous species as a potential threat to native species. Although species replacements may occur via mechanisms other than those linked to interspecific differences in growth scope, endeavors to reduce risk of native crayfishes being displaced should be directed in part at maintaining watershed conditions (e.g., spring flow, riparian shading) which produce stream temperatures < 22°C during summer and are favorable for growth of indigenous crayfishes.

Energy losses due to activity, egestion, excretion, and specific dynamic action are potentially important energy costs to crayfishes not included in relations between growth scope and temperature described here. Values for assimilation efficiency, which would allow for estimation of energy loss due to egestion, are known for some of these crayfishes (Momot, 1995; Whitledge & Rabeni, 1997), but no information is available which would permit calculation of energy loss due

to excretion or specific dynamic action for these species. How activity affects crayfish growth scope is also difficult to predict. Measurements of $C_{max}$ and R were conducted in the laboratory using crayfishes held in enclosures that limited crayfish movement. Activity represents a potentially significant energy cost to fishes in field settings (Boisclair & Leggett, 1989), but nothing is known of crayfish movement in streams or how such factors as foraging and predator avoidance affect energy use and growth of crayfishes. Activity costs would reduce growth scope below levels presented in this study and could lead to negative growth potential for these crayfishes at temperatures above their thermal optima. At such temperatures, energy gained from feeding may not balance energy costs required for foraging, leading to declines in crayfish growth and condition.

Temperature fluctuation represents another factor which could potentially affect crayfish growth scope that was not considered in this study. Nothing is known of the effect of fluctuating temperatures on growth of crayfishes. For fishes, fluctuating temperatures may reduce growth at temperatures above optimum, have little effect on growth at temperatures near optimum, and increase growth at temperatures below optimum (Jobling, 1997). If fluctuating water temperatures have similar effects on crayfish growth, then streams which exhibit temperatures fluctuating around a mean daily temperature that is substantially greater than 22°C could be even less conducive to growth of native Ozark crayfishes than predicted from the constant temperatures used in this study. Since many aquatic environments, particularly small streams, can exhibit large daily fluctuations in temperature, studies investigating the effects of fluctuating water temperatures on crayfish energetics represent an important area for further research.

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