

Using bioenergetics and stable isotopes to assess the trophic role of rusty crayfish (*Orconectes rusticus*) in lake littoral zones

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Abstract: Crayfish often dominate freshwater ecosystems and can have strong effects on littoral habitat and biota through foraging. However, there is substantial debate regarding the trophic role of crayfish and implications of their foraging behavior on littoral ecosystems. We created a bioenergetics model for rusty crayfish (*Orconectes rusticus*) to determine how growth and prey choice constrain crayfish consumption, which affects littoral ecosystems. We simulated over 6400 potential rusty crayfish diets by varying the abundance of important prey. We judged how crayfish prey choice affects the amount and identity of prey that crayfish must consume to match observed growth. We compared our model predictions with stable isotope evidence from 10 northern Wisconsin lakes to determine energy sources and trophic position of rusty crayfish relative to other invertebrates. Our diet simulations and stable isotope analysis concurred that crayfish of all ages are primarily predators. Individuals that do not feed on zoobenthos must therefore consume large quantities of less desirable food such as macrophytes, which are an important component of littoral habitat.

Résumé : Les écrevisses dominent souvent les écosystèmes d'eau douce et peuvent, par leur recherche de nourriture, avoir de profonds effets sur l'habitat littoral et les organismes qui y vivent. Cependant, il existe un important débat sur le rôle trophique des écrevisses et les conséquences de leur comportement de recherche de nourriture sur les écosystèmes littoraux. Nous avons mis au point un modèle bioénergétique pour l'écrevisse américaine (*Orconectes rusticus*) afin de déterminer comment la croissance et le choix des proies limitent la consommation des écrevisses, ce qui affecte les écosystèmes littoraux. Nous avons fait des simulations impliquant plus de 6400 régimes alimentaires potentiels d'écrevisses en faisant varier l'abondance des proies principales. Nous avons déterminé comment le choix des proies par les écrevisses affecte le nombre et l'identité des proies que l'écrevisse doit consommer pour expliquer la croissance observée. Nous avons comparé les prédictions de notre modèle et les données d'analyse des isotopes stables provenant de 10 lacs du nord du Wisconsin afin de déterminer les sources d'énergie et la position trophique de l'écrevisse américaine par rapport aux autres invertébrés. Nos simulations de régimes alimentaires et l'analyse des isotopes stables s'accordent pour trouver que les écrevisses de tous les âges sont principalement des prédateurs. Les individus qui ne se nourrissent pas de zoobenthos doivent consommer de grandes quantités de nourriture moins désirable, telle que les macrophytes qui forment un compartiment relativement important de l'habitat littoral.

[Traduit par la Rédaction]

Introduction

Crayfish (*Orconectes* spp.) are often dominant components of freshwater ecosystems. Annual crayfish production can exceed several hundred kilograms per hectare, and biomass consumption and production by crayfish often exceeds the consumption and production of all other benthic invertebrates combined (Tanner 1960; Momot 1995; Whitley and

Rabeni 1997). Nonetheless, we are still learning how crayfish foraging affects lake littoral areas.

There is a substantial debate about the role of crayfish in lake littoral zones. Most crayfish species are undoubtedly omnivores, with detritus, periphyton, and macrophytes usually listed as the dominant elements of crayfish diets (Lorman 1975; Momot 1995; Whitley and Rabeni 1997). Further, various crayfish species have strong, negative,

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Table 1. Parameters derived from the literature for the rusty crayfish (*Orconectes rusticus*) bioenergetics model.

Parameter	Description	Value	Source
CA	Consumption intercept	0.3795	Jones and Momot 1983
CB	Consumption coefficient	-0.2419	Jones and Momot 1983
CQ	Water temperature coefficient	2.5	Estimated
CTO	Optimal temperature	27	Mundahl and Benton 1990
CTM	Maximum temperature	38	Mundahl and Benton 1990
RA	Respiration intercept	0.00135	Derived
RB	Respiration coefficient	-0.4206	Derived
RQ	Water temperature coefficient	0.0646	Whitledge and Rabeni 2002
RTM	Maximum temperature	38	Mundahl and Benton 1990
FA	Proportion egested	0.2857	Jones and Momot 1983
UA	Proportion excreted	0.003976	Villarreal 1991
SDA	Specific dynamic action	0.18	Rudstam 1989
ACT	Activity multiplier	1	Default value (Hanson et al. 1997)

ecosystem-wide effects on periphyton (Flint and Goldman 1975; Lodge et al. 1994) and macrophytes (Covich 1977; Lodge and Lorman 1987). Because their diet composition agrees with their known effect in the ecosystem, this view of crayfish diets has not been strongly challenged. However, lab studies show that crayfish that predominantly consume detritus, periphyton, or macrophytes grow slowly or not at all. This has led some to argue that crayfish rely more on protein- and energy- rich zoobenthos than demonstrated with gut content studies (Momot 1995; Charlebois and Lamberti 1996; Whitledge and Rabeni 1997). This argument appears to be especially strong for juvenile crayfish, whose rapid growth likely requires a diet of higher protein content than that of adults (Momot and Gowing 1983; Hill et al. 1993; Momot 1995).

Evidence for carnivory by crayfish is generally lacking in diet studies (but see Capelli 1980). The need for a protein-rich diet contrasted with the relative absence of animal prey in diet studies suggests that existing gut content studies may inadequately describe crayfish foraging habits. Similar assertions are made by Whitledge and Rabeni (1997), who used stable isotopes and a production-based model as evidence to argue that gut contents overestimate the contribution of plant matter to crayfish production by a factor of four or five owing to low assimilation of these items.

We studied the rusty crayfish (*Orconectes rusticus*) because it has a strong effect on littoral zones of invaded systems through foraging. Native to the Ohio River Valley, rusty crayfish were introduced into northern Wisconsin lakes about 30 years ago either as a bait-bucket release or for macrophyte control (Magnuson et al. 1975; Capelli and Magnuson 1983; Lodge et al. 1985). Since their introduction, rusty crayfish have had strong negative effects on aquatic macrophyte and gastropod communities relative to local congeners *Orconectes propinquus* and *Orconectes virilis* (Lodge and Lorman 1987; Lodge et al. 1994; Wilson 2002). Consequently, there is substantial impetus to understand how rusty crayfish foraging affects lake littoral areas.

We used multiple approaches to examine the trophic role of crayfish to assess if crayfish need to be highly predatory to match observed growth. First, we created a bioenergetics model for rusty crayfish with the Fish Bioenergetics 3.0 software (Hanson et al. 1997) to define how growth constrains the ability of crayfish to consume diets composed of

single items. Bioenergetics models provide a platform to examine energetic and food web consequences of crayfish foraging (Kitchell et al. 1977; Bartell et al. 1986). Second, we developed a unique diet simulation approach within the bioenergetics framework to describe how crayfish prey choice influences crayfish feeding rates and consumption of other prey items, which leads to their observed effects on littoral biota. Lastly, we used nitrogen and carbon stable isotopes to determine the trophic position and energy sources, respectively, of rusty crayfish and their potential prey.

Methods

Bioenergetics parameters

We used Fish Bioenergetics 3.0 software (Hanson et al. 1997) to create the rusty crayfish model. Model parameters and their sources are presented in Table 1.

Consumption

We used mass-specific crayfish consumption data from Jones and Momot (1983) for *O. virilis* to fit the following allometric function:

$$(1) \quad C = 0.3795 \cdot W^{-0.2419}$$

where C is consumption in grams dry weight of food per gram wet weight of crayfish per day, W is wet weight (g), and $R^2 = 0.5667$. The allometric mass function listed above was incorporated into a consumption equation for temperature dependence of warm-water species (consumption eq. 2 in Hanson et al. 1997). We approximated the rate at which consumption changes over low temperatures (CQ) to be 2.5 (J.F. Kitchell, 680 North Park Street, Madison, WI 53706, USA, personal communication). We used the optimal and maximum temperatures for rusty crayfish from Mundahl and Benton (1990).

Respiration

No mass-specific respiration information was available for cambarid crayfishes at the time of model formation. Therefore, we used temperature-specific information for other *Orconectes* crayfishes to guide parameter estimation of allometric terms. We defined RQ by fitting an exponential model to *O. virilis* temperature-dependent respiration (Whitledge and Rabeni 2002), forming the equation

Table 2. Energy densities and digestibility of prey used in the rusty crayfish (*Orconectes rusticus*) bioenergetics model.

Diet item	Energy density (J·g wet mass ⁻¹) (Reference)	Percent digestible
Ephemeroptera	3675 (Hanson et al. 1997)	92 (estimated from Whitledge and Rabeni 1997)
Gastropoda	1508 (Driver et al. 1974)	92 (estimated from Whitledge and Rabeni 1997)
Detritus	7000 (estimated) (~19 000 for conditioned <i>Ulmus</i> leaves; Cummins and Wuycheck 1971)	14 (Whitledge and Rabeni 1997)
Periphyton	2400 (estimated) (1381 for <i>Cladophora</i> ; Cummins and Wuycheck 1971)	39 (Whitledge and Rabeni 1997)
Macrophytes	2100 (Woolhead 1994)	41 (estimated)

$$(2) \quad R(T) = 7.1956 \cdot e^{(0.0646 \cdot T)}, R^2 = 0.98$$

where R equals respiration and T equals temperature. This equation allowed us to equate RQ to the exponent in eq. 2. We then solved the following mass-specific respiration equation:

$$(3) \quad R(W) = RA \cdot W^{RB} \cdot e^{(RQ \cdot T)}$$

(where W equals mass) for RA and RB by minimizing the sum-of-squares difference between our respiration model and the observed model. We used the allometric coefficients (RA and RB) proposed by Musgrove (1993) for juvenile *Cherax destructor* as the initial starting points for RA and RB (multiple solutions were possible). We used the same lethal temperature for respiration as for consumption, using respiration equation number 1 from the Fish Bioenergetics 3.0 manual (Hanson et al. 1997). Rudstam (1989) provided a satisfactory specific dynamic action (SDA) value for decapod crustaceans (Brylawski and Miller 2003).

Egestion/excretion

To determine the proportion of ingested food that is egested (FA), we divided the mean weight of algal diet consumed by the mean weight of *O. virilis* feces (Jones and Momot 1983). We derived the proportion of assimilated food excreted (UA) from Villarreal (1991), who indicated that 7% of food consumed by *Cherax tenuimanus* is egested. Therefore, the weight of assimilated food was calculated as follows:

$$(4) \quad (\text{mean feces weight} \cdot 0.07^{-1}) - \text{mean feces weight}$$

which was then multiplied by the mass excreted to determine UA.

Estimated parameter values: assimilation efficiencies and energy densities of diet items

We estimated the assimilation efficiencies and energy densities of diet items for the rusty crayfish bioenergetics model (Table 2). To estimate these parameters, we fit the model to laboratory growth estimates and diet information from Hill et al. (1993). Specifically, this information consists of crayfish mass and carapace growth over a 55-day period, where individuals were fed ad libitum one of four unique diet items at a constant temperature (20 °C). We created individual simulations for each of the four items, based on rough literature estimates of the energetic density and assimilation efficiency for each item. We then adjusted either the energy density or the assimilation of each prey (see details below) to fine-tune the model until each of the four prey items produced similar feeding rates.

Diet energy densities and percent of diet that is digestible

Because all crayfish foods are not equally digestible, we used the egestion model in Fish Bioenergetics 3.0 that permits part of each diet item to be indigestible. However, the literature only provides rough estimates of the energy density and assimilation efficiency for all of the diet items we used. For each prey item, we held either the energy density or the assimilation efficiency constant while adjusting the other (Table 2). We based which quanta we held constant on our confidence in the literature values we obtained. For instance, we found over a tenfold variation in detritus energy densities (Cummins and Wuycheck 1971; Ahlgren 1990; Horppila 1999), but Whitledge and Rabeni (1997) report that *O. luteus* and *O. punctimanus* assimilate about 14% of the detritus (decayed leaves) they consume. We kept the assimilation efficiency at 14% and adjusted the energy density of detritus to match the growth performance of *O. rusticus* in Hill et al. (1993). We adjusted periphyton energy density identically. For the other prey items, we found adequate information on energy density in the literature, but not on assimilation. We used a conservative energy density for Ephemeroptera found in Cummins and Wuycheck (1971) and averaged the energetic densities of Gastropoda with their shell (Driver et al. 1974). We assumed the assimilation of ephemeropterans and gastropods to equal that of chironomids (Whitledge and Rabeni 1997). We averaged the energetic densities of several macrophyte species (Woolhead 1994) and adjusted the assimilation efficiency to match growth in Hill et al. (1993).

Molting

We did not incorporate molting explicitly into this model. Molting is a complex physical process that involves changes in mass, respiration, and metabolism in crayfish (Aiken and Waddy 1992). Crayfish dry mass increases linearly throughout the growing season (Lorman 1980), so we assumed molting effects on mass are incorporated evenly throughout the growing period (Brylawski and Miller 2003). Because molting is brief relative to the growing season, we also assumed that effects on metabolism are incorporated into the respiration parameters.

Diet simulations

Simulation data

We transferred the rusty crayfish bioenergetics model into Matlab (v.7.1; The Mathworks Inc. 2004) to simulate the seasonal consumption of important rusty crayfish prey. We used daily water temperature data taken from a depth of 1 m during the 2002 growing season in Sparkling Lake, Vilas County, Wisconsin. Sparkling Lake is mesotrophic and typi-

Table 3. Rusty crayfish (*Orconectes rusticus*) masses used to fit consumption and *P* values in the bioenergetics simulations.

	Age 0	Age 1	Age 2	Age 3
Beginning mass (g)	0.05	1.0	4.7	11.1
Ending mass (g)	0.35	1.82	7.05	17.1

Note: All values are derived from crayfish growth data from Upper Sugarbush Lake in Vilas County, Wisconsin (Lorman 1975).

cal in size (64 ha) and depth (maximum 20 m) of lakes where rusty crayfish have invaded in the Northern Highland Lake District of Wisconsin (Capelli and Magnuson 1983). We limited our simulation to the period when temperatures exceeded 15 °C, using the portion of total annual growth that occurs within this period (Table 3). In Sparkling Lake, this leads to a growing season of 123 days in 2002, which corresponds with the growing seasons listed in Lorman (1980) and Lodge and Hill (1994) for this region (125 days and 108 days, respectively). Rusty crayfish exhibit some modest growth outside of this interval (Lorman 1980).

We modeled five prey items identified in previous studies as particularly important to rusty crayfish and their effect on lake ecosystems. These prey items are macrophytes, periphyton, detritus, Gastropoda, and larval Ephemeroptera. Macrophytes, periphyton, and detritus are identified as the most common items found in rusty crayfish diets (Prins 1968). Gastropods are extremely vulnerable to crayfish predation (Lodge et al. 1994), and Ephemeroptera are identified as the most common benthic invertebrate in rusty crayfish diets (Lorman 1975). We generally consider ephemeropterans to be a representative member of energy-rich benthic insects.

We modeled the consumption of an individual rusty crayfish (sensu Kitchell et al. (1977)) on a diet with constant prey proportions throughout the growing season. These simulations represent a simplified version of crayfish consumption and are meant only to address our primary research goals. We used growth rates from Upper Sugarbush Lake, Vilas County, Wisconsin (Lorman 1980). Growth was estimated from the increase in carapace length over the summer for each of four age classes, beginning with young-of-year (YOY) crayfish (Table 3). Rusty crayfish only live for 4 years in northern Wisconsin lakes (Lorman 1980). We used a length–weight regression (eq. 5) for rusty crayfish from Upper Sugarbush Lake to convert carapace length to mass for use in the model (Lorman 1980).

$$(5) \quad \text{weight} = 0.00004 \cdot \text{length}^{3.2822}$$

Simulations

We created more than 6000 unique diets for whole-summer simulations for each of the four age classes based on the five prey items listed above. To create the diets, we varied the proportion of one prey item from 0 to 1 in 0.01 increments and then created 15 unique combinations of the remaining diet items within each increment. The 15 unique combinations were created by varying the number of additional prey in the diet and then distributing the remaining diet evenly among the additional prey (Table 4). Therefore, we assumed prey equality given no prior information about crayfish preference for individual prey. In reality, energy density and digestibility varies greatly among prey groups (Table 2). This diet algorithm produces 1501 diet combina-

tions for each of five prey items, totaling 7505 combinations. Because some replicate combinations are created, we determined which diets were not original and eliminated them from further analysis. We determined both the total biomass of each prey consumed and the proportion of maximum consumption (*P* value) attained over the summer period for every diet simulation. In Bioenergetics 3.0 terminology, *P* = 1 represents the maximum foraging rate imposed by temperature and crayfish allometry (Hanson et al. 1997).

Model simulation summaries

We describe our model in two ways. First, we simulated diets composed of individual prey to determine a priori which prey produced the lowest and highest *P* values for each age class. Second, we used our simulation approach to incorporate more prey items into the diet and thus examine how crayfish diet selection influences *P* values in more detail. We summarized this output by averaging the abundance of each prey item across diets that produced *P* values within 0.01 of one another. This averaged diet (hereafter called “composite diet”) characterized the abundance of individual prey items at a given *P* value. Additionally, composite diets incorporated some characteristics of omnivory and allowed us to quantify how prey abundance varied at a given consumption rate. We also used this method to quantify biomass consumption of individual prey items within each *P* increment.

Inference for these simulations derives from the established premise that crayfish minimize activity and foraging during daytime in the presence of visual predators (Lorman 1975; Collins et al. 1983; Mather and Stein 1993). The average day length during the period we simulated is slightly longer than 16 h, indicating that crayfish have the opportunity to feed maximally for only one-third of a given day. Crayfish should therefore avoid foraging on items that cause *P* values to exceed 0.33 because daytime foraging drastically increases the chance of being consumed by predators.

Crayfish trophic position

We used ¹³C and ¹⁵N stable isotope data to determine the energy source and trophic position of rusty crayfish relative to other invertebrates. Carbon and nitrogen stable isotope ratios (δ¹³C and δ¹⁵N) are tracers of energy flow in aquatic food webs (Peterson and Fry 1987; Fry 1988; Pinnegar and Polunin 2000). There is typically a three- to four-fold increase in δ¹⁵N from prey to predator, such that δ¹⁵N can be used to estimate consumer trophic position (DeNiro and Epstein 1981; Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001). The δ¹³C of phytoplankton is isotopically depleted relative to benthic algae because of boundary-layer-driven differences in isotopic discrimination for dissolved inorganic carbon (DIC; Hecky and Hesslein 1995). These carbon isotope differences between benthic and pelagic habitats are conserved up the food chain (i.e., remain relatively constant from prey to predator) and can thus be used to estimate the contributions of littoral and pelagic resources to higher trophic levels (Hecky and Hesslein 1995; Vander Zanden et al. 1999).

Benthic macroinvertebrates were collected using dip nets and an Ekman grab sampler from littoral habitats of 10

Table 4. The algorithm used to determine prey combinations used in rusty crayfish (*Orconectes rusticus*) diet simulations. After creating diets from 1% to 100% of one diet item, the algorithm then switches columns and creates diets from 1% to 100% of another, until all five items were done. We eliminated all duplicate diets from analysis.

Prey 1 (%)	Prey 2 (%)	Prey 3 (%)	Prey 4 (%)	Prey 5 (%)
<i>i</i>	100 - <i>i</i>	0	0	0
<i>i</i>	0	100 - <i>i</i>	0	0
<i>i</i>	0	0	100 - <i>i</i>	0
<i>i</i>	0	0	0	100 - <i>i</i>
<i>i</i>	(100 - <i>i</i>)/2	(100 - <i>i</i>)/2	0	0
<i>i</i>	(100 - <i>i</i>)/2	0	(100 - <i>i</i>)/2	0
<i>i</i>	(100 - <i>i</i>)/2	0	0	(100 - <i>i</i>)/2
<i>i</i>	0	(100 - <i>i</i>)/2	(100 - <i>i</i>)/2	0
<i>i</i>	0	(100 - <i>i</i>)/2	0	(100 - <i>i</i>)/2
<i>i</i>	0	0	(100 - <i>i</i>)/2	(100 - <i>i</i>)/2
<i>i</i>	(100 - <i>i</i>)/3	(100 - <i>i</i>)/3	(100 - <i>i</i>)/3	0
<i>i</i>	(100 - <i>i</i>)/3	(100 - <i>i</i>)/3	0	(100 - <i>i</i>)/3
<i>i</i>	(100 - <i>i</i>)/3	0	(100 - <i>i</i>)/3	(100 - <i>i</i>)/3
<i>i</i>	0	(100 - <i>i</i>)/3	(100 - <i>i</i>)/3	(100 - <i>i</i>)/3
<i>i</i>	(100 - <i>i</i>)/4	(100 - <i>i</i>)/4	(100 - <i>i</i>)/4	(100 - <i>i</i>)/4

northern Wisconsin lakes during summer of 2002 as part of a larger study of food web structure. Fresh specimens were sorted, identified, and frozen. Rusty crayfish were collected by hand, in seine nets, or using crayfish traps. Approximately 0.5 g of dorsal muscle tissue was removed from each crayfish and frozen prior to isotopic analysis.

Isotopic methods and trophic model formulation

We dried samples at 60–75 °C for 24–48 h, ground them into a fine powder with mortar and pestle, and packed them into acid-washed 5 mm × 8 mm tin capsules for carbon and nitrogen isotope analysis. Stable isotope analysis was performed on a continuous flow isotope ratio mass spectrometer (dual-inlet Europa 20/20; PDZ Europa, Crewe, England) at the University of California, Davis. Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material:

$$(6) \quad \delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = ([R_{\text{sample}} \cdot R_{\text{standard}}^{-1}] - 1) \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. Approximately 20% of the samples were analyzed in duplicate. The mean standard error for sample duplicates of these samples was 0.09‰ for $\delta^{13}\text{C}$ and 0.15‰ for $\delta^{15}\text{N}$.

$\delta^{15}\text{N}$ values were converted to a continuous measure of trophic position (TP) to standardize for within- and among-system variation in $\delta^{15}\text{N}$ at the base of the food web:

$$(7) \quad \text{TP}_{\text{consumer}} = ((\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) \cdot 3.4^{-1}) + 2$$

where 3.4 is the per trophic level enrichment in $\delta^{15}\text{N}$. Primary producers are trophic level 1, primary consumers are trophic level 2, and so on. To estimate $\delta^{15}\text{N}_{\text{baseline}}$, a primary consumer $\delta^{13}\text{C} - \delta^{15}\text{N}$ relationship was established using linear regression. The baseline approximation method is similar to the nonlinear method (Vander Zanden and Rasmussen 1999), though a linear regression provided the best primary consumer $\delta^{13}\text{C} - \delta^{15}\text{N}$ curve for these lakes. The baseline $\delta^{15}\text{N}$ was calculated separately for each consumer by solving for $\delta^{15}\text{N}$ using the consumer $\delta^{13}\text{C}$ value and the lake-specific baseline equation. Trophic position (TP) was estimated for

each individual using eq. 7. Population-specific TP estimates represent the mean trophic position of the individuals sampled from a population.

$\delta^{13}\text{C}$ values of pelagic primary producers are isotopically enriched relative to benthic producers because of differences in fractionation relative to their inorganic carbon sources. Consequently, consumer $\delta^{13}\text{C}$ values are indicative of reliance on benthic versus pelagic prey. To facilitate comparisons among lakes, we used a two end-member $\delta^{13}\text{C}$ mixing model to estimate the fractional reliance of crayfish on benthic prey using the equation

$$(8) \quad \text{Percent benthic} = (\delta^{13}\text{C}_{\text{crayfish}} - \delta^{13}\text{C}_{\text{pelagic}}) / (\delta^{13}\text{C}_{\text{benthic}} - \delta^{13}\text{C}_{\text{pelagic}}) \times 100$$

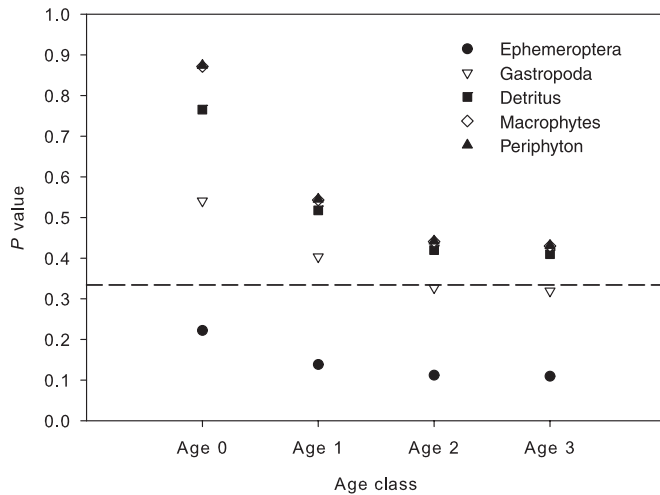
The benthic $\delta^{13}\text{C}$ end-member in this mixing model ($\delta^{13}\text{C}_{\text{benthic}}$) was calculated separately for each lake as the most $\delta^{13}\text{C}$ -enriched littoral invertebrate taxa. The pelagic end-member ($\delta^{13}\text{C}_{\text{pelagic}}$) was the mean $\delta^{13}\text{C}$ of unionid mussels. Our model assumes no trophic fractionation for $\delta^{13}\text{C}$, which is a reasonable assumption based on a recent synthesis (Vander Zanden and Rasmussen 2001). Note that “trophic position” and “percent benthic” are secondary variables that were calculated directly from stable isotope values. Use of these secondary variables allowed us to compare various food web parameters across ecosystems.

Results

Benthic invertebrate consumption

Our modeling results suggest that rusty crayfish are predators and will likely consume energy-poor food resources when more desirable prey are rare or inaccessible. In the model, growth is fixed and high P values indicate consumption of low-quality food to accomplish the observed growth. Crayfish of all ages that consumed only Ephemeroptera had the lowest P values (Fig. 1). In contrast, diets that contained only macrophytes, periphyton, or detritus had P values well over 0.33 for all age classes. Therefore, given that $P > 0.33$

Fig. 1. Bioenergetics output illustrating P values from each age class that result from diets composed entirely of one prey type. Broken line represents P value necessary to remain nocturnal ($P = 0.33$).



is by our definition accompanied by increased vulnerability to predators, the observed growth rate for all age classes cannot be accomplished on diets solely composed of macrophytes, periphyton, or detritus. Diets that contained only Gastropoda led to P values > 0.33 for age-0 and age-1 crayfish, but slightly less than 0.33 for older crayfish (Fig. 1).

The importance of Ephemeroptera to maintain reasonable feeding rates is also evident in composite diets. P values for all age classes substantially decreased as the proportion of Ephemeroptera in composite diets increased (Fig. 2). There was little variability in diet composition (see confidence intervals in Fig. 3a), indicating that Ephemeroptera had a dominant influence on the feeding rate. If Ephemeroptera were not the primary determinant of P values, variability would be relatively large because prey could be combined in many ways to produce the same P value. The 95% confidence intervals of prey proportions were larger for all other prey (Figs. 3b–3e). Periphyton and macrophytes displayed a positive relationship with composite P values, indicating increased feeding rate with increased proportion of these prey in the diet (Figs. 3b, 3c). When the feeding rate is analyzed in terms of Gastropoda or detritus (Figs. 3d, 4e), which are of intermediate energetic quality, the proportion of Ephemeroptera in the diet still drives the changes in feeding rate. This is particularly evident for Gastropoda (Fig. 3d), where the top one-third of the curve is characterized by a slow decrease in P value associated with a decreasing proportion of periphyton and macrophytes in the diet as Gastropoda increase. The bottom two-thirds shows a rapid increase in P value associated with a decreasing proportion of Ephemeroptera in the diet as Gastropoda increase.

The influence of Ephemeroptera on biomass consumption

In composite diets, individuals that consumed small proportions of Ephemeroptera had high P values, indicating increased consumption of other prey items. As the proportion of Ephemeroptera decreased, crayfish consumed at least

Fig. 2. Proportions of Ephemeroptera in composite diets relative to the composite feeding rate (P value) for all four age classes: \diamond , age 0; \blacksquare , age 1; ∇ , age 2; \bullet , age 3. Broken line represents P value necessary to remain nocturnal ($P = 0.33$).

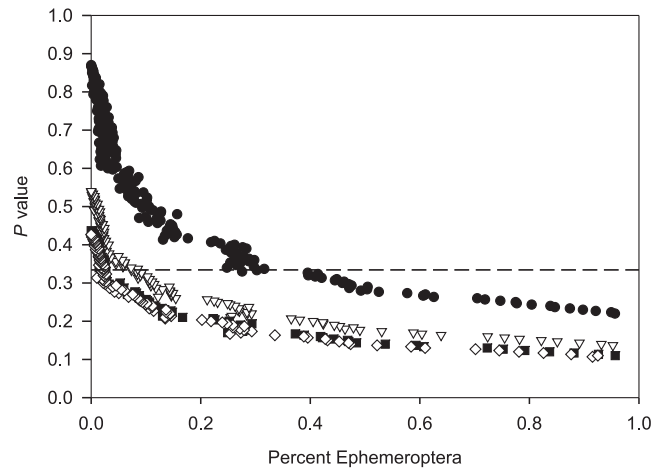
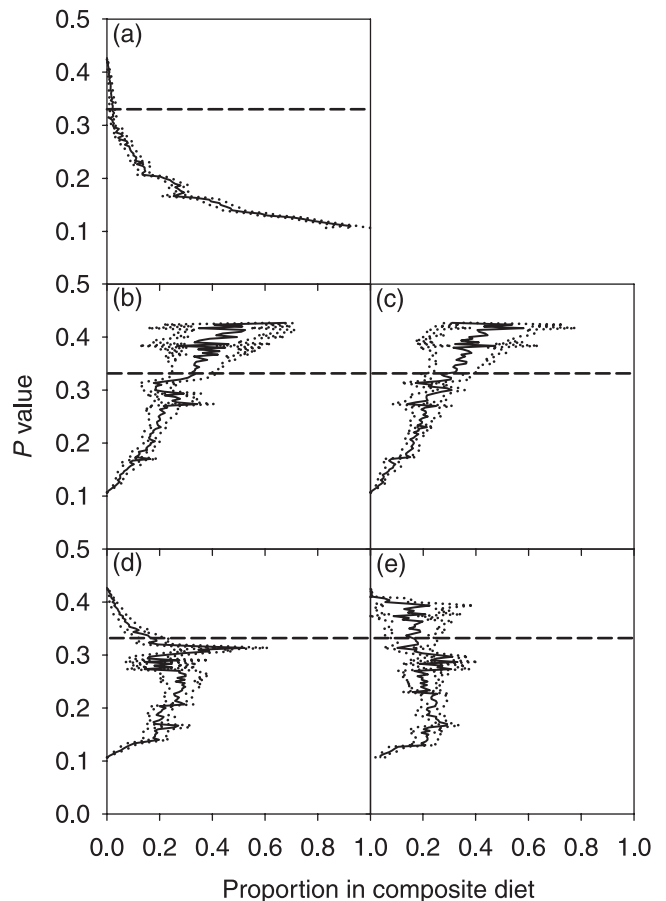


Fig. 3. The proportion of each prey ((a) Ephemeroptera, (b) macrophytes, (c) periphyton, (d) Gastropoda, and (e) detritus) within age-3 composite diets relative to the composite feeding rate (P value). The dashes represent the 95% confidence intervals for diet proportions (along the x axis), not the P value. The horizontal line represents the P value necessary to remain nocturnal ($P = 0.33$).



three times more alternative prey biomass than when Ephemeroptera was at high abundance in the diet (Fig. 4). For example, the lowest composite P value for an age-3 individual ($P = 0.11$) corresponded to the consumption of 26 g of Ephemeroptera along with 0.02 g of macrophytes and 0.02 g of periphyton. In contrast, no Ephemeroptera were consumed at the highest P value ($P = 0.43$), and an age-3 crayfish must consume 113 g of combined macrophytes and periphyton biomass to grow at the observed rate. This indicates that crayfish that do not consume energy-rich zoobenthos must instead consume large quantities of lower-quality food.

Trends in age-specific feeding rates

Rusty crayfish age 1 and older could be much less dependent on Ephemeroptera than age-0 individuals. Age-0 composite diets needed to contain at least 28% Ephemeroptera for P to remain below 0.33 (Fig. 2). In contrast, age-3 composite diets needed to contain only 2% Ephemeroptera for P to remain below 0.33 (Fig. 2). This decreased dependence on Ephemeroptera at equivalent P values allowed larger crayfish to consume more alternate prey at comparable feeding rates, notably Gastropoda and detritus. The combined contribution of Gastropoda and detritus peaked at 54% of the composite diet at P values below 0.33 for age-3 individuals, whereas these prey could only contribute at most 16% of the diet for age-0 individuals at the same feeding rate. The above evidence points to decreased dependence on energy-rich prey and increased diet flexibility at a given feeding rate as a crayfish grows.

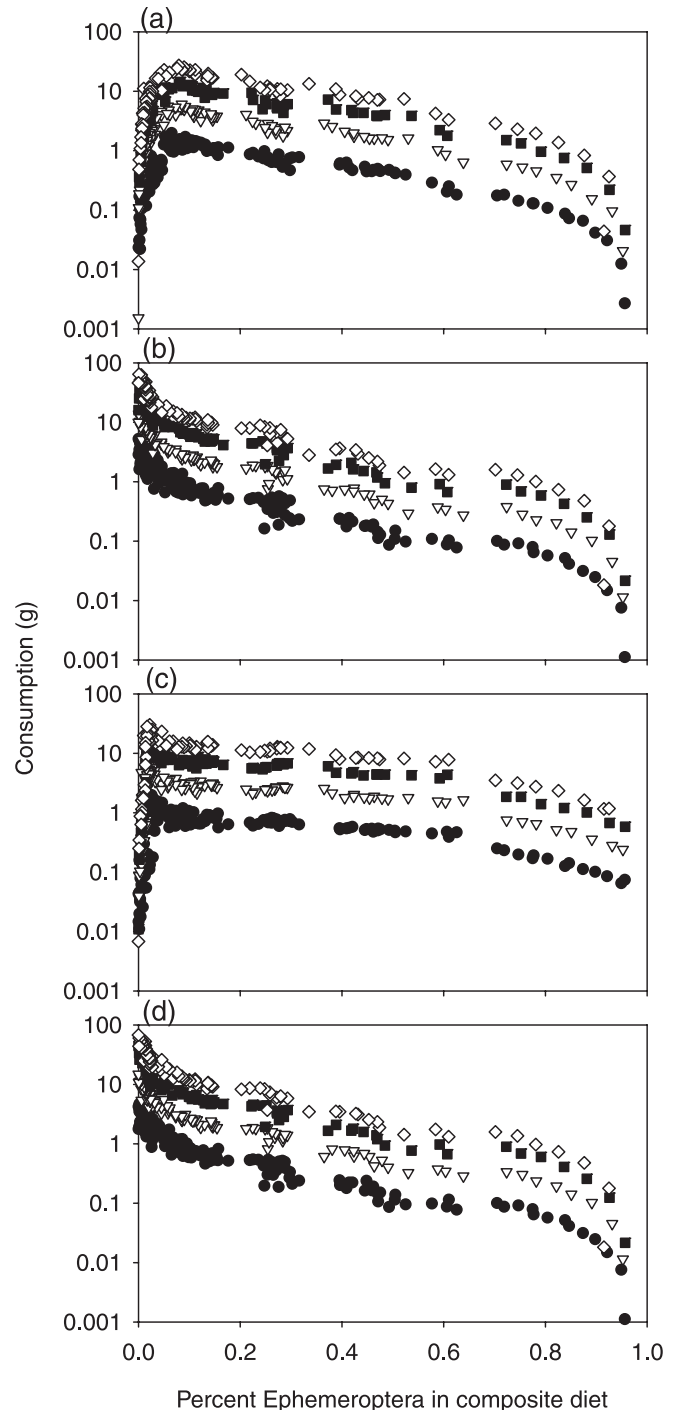
Stable isotopes

Evidence from stable isotope analysis indicated that adult and juvenile rusty crayfish prey heavily on zoobenthos. Both YOY and adults were approximately one trophic level above zoobenthos taxa, including Ephemeroptera, Amphipoda, Odonata, and Gastropoda (Fig. 5). Contrary to model results suggesting that adults have the option of feeding on lower-quality foods, adults maintained a slightly higher trophic level than juveniles. However, considerable overlap in both the trophic position and benthic reliance among lakes indicated similar diets between adult and juvenile crayfish.

Bioenergetics model performance

The model corresponds relatively well with existing studies on growth and consumption of related crayfish species. At a P value of 0.33, which corresponds to the 16 h light – 8 h dark regimen used in the Whitledge and Rabeni (2002) experiments, both consumption and respiration rates are similar to those for *O. virilis* (within 17% and 5% of *O. virilis* rates, respectively) except at 30 °C, where our model predicted 70% more consumption (Table 5) and 20% less respiration (Table 6) than *O. virilis*. Both differences can be accounted for if the optimal and lethal temperature for *O. rusticus* is only 2 °C warmer than that for *O. virilis*. Although the optimal temperature for *O. virilis* is unknown, the difference in lethal temperature between the two species supports this assertion (Mundahl and Benton 1990; Lodge and Hill 1994).

Fig. 4. Average biomass consumption (in g-individual⁻¹·simulation⁻¹) of (a) Gastropoda, (b) periphyton, (c) detritus, and (d) macrophytes corresponding to the proportion of Ephemeroptera within composite diets: ◇, age 0; ■, age 1; ▽, age 2; ●, age 3.



Discussion

Crayfish as predators

Results from modeling and stable isotope samples indicate that rusty crayfish are primarily predators and likely supplement their diet with less profitable food sources. Our

Table 5. Mean daily biomass consumption (g chironomids·g crayfish⁻¹·day⁻¹) as predicted over a 4-day simulation by the rusty crayfish (*Orconectes rusticus*) bioenergetics model, using a *P* value = 0.33, versus mean biomass consumption observed by Whitledge and Rabeni (2002) for *O. virilis* in an experiment of the same duration.

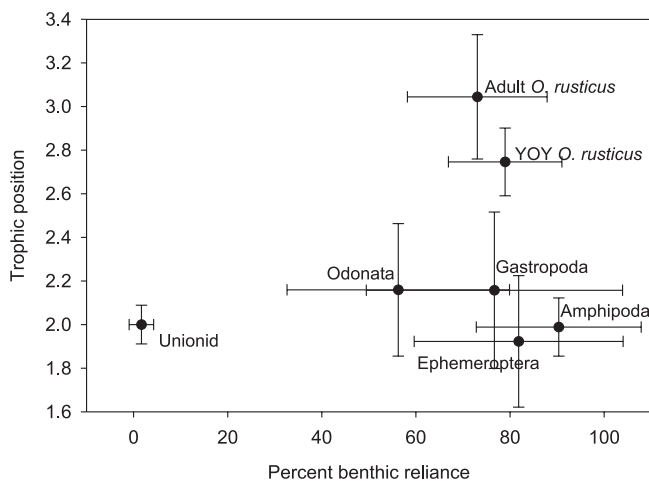
	Temperature (°C)			
	18	22	26	30
Observed consumption (<i>O. virilis</i>)	0.054	0.071	0.077	0.055
Predicted consumption (<i>O. rusticus</i>) (±1 standard deviation)	0.0534 (0.0002)	0.0748 (0.0004)	0.0898 (0.0006)	0.0813 (0.0004)

Table 6. Mean daily respiration as predicted over a 4-day simulation by the rusty crayfish (*Orconectes rusticus*) bioenergetics model versus mean respiration observed by Whitledge and Rabeni (2002) for *O. virilis* in an experiment of the same duration.

	Temperature (°C)			
	18	22	26	30
Observed respiration (<i>O. virilis</i>)	23	31	36	51
Predicted respiration (<i>O. rusticus</i>) (±1 standard deviation)	24.66 (0.16)	29.46 (0.29)	35.25 (0.42)	42.39 (0.40)

Note: All respiration values are in joules crayfish⁻¹·day⁻¹.

Fig. 5. The average trophic position and benthic reliance of benthic invertebrates from 10 northern Wisconsin lakes. Error bars represent ±2 standard errors.



modeling simulations indicate that age-0 *O. rusticus* are particularly sensitive to the diet they consume and must ingest a high proportion of energy-rich zoobenthos to sustain high growth rates and minimize daytime foraging. This result agrees with those of Momot (1995) and Whitledge and Rabeni (1997), who assert that many crayfish species are largely predators, though this has been contested by numerous studies (Prins 1968; Lorman 1975; Luttenton et al. 1998). Gastropoda and detritus hold a unique position in rusty crayfish diets. They are not likely preferred diet items when more energy-rich prey are readily available but should be an obvious choice when macrophytes or periphyton are the only other options. As evidence, Weber and Lodge (1990) illustrated that crayfish exhibit top-down control on Gastropoda, which allows periphyton to flourish where rusty crayfish attain high densities. However, other studies indicate that Gastropoda are equally preferred to macrophytes (Covich 1977). Our model results are consistent with those of Capelli (1980), who found that Ephemeroptera make up at least 50% of *O. propinquus* (a sympatric congener of *O. rusticus* in northern Wisconsin) diets in late summer and

fall months. These simulations also predict that crayfish should become less dependent on zoobenthos as they grow, but stable isotope evidence indicates otherwise (below).

Stable isotopes

Our stable isotope analysis generally corroborated our model findings. Both juvenile and adult *O. rusticus* fed approximately one trophic level above benthic invertebrate groups that included both Ephemeroptera and Gastropoda, which strongly suggests that crayfish are secondary consumers. Alternatively, individuals could feed equally on prey that are one trophic level above (e.g., a top fish predator) and one below (e.g., plant matter) to obtain a similar trophic signature. Although this is a superficially plausible hypothesis, individuals would have to feed extensively on a high trophic level fish. Animal detritus is probably rare and unlikely to substantially contribute to the stable isotope signature. Thus, rusty crayfish in northern Wisconsin lakes derive most of their nitrogen from benthic invertebrates. Macrophytes, periphyton, and plant-derived detritus are not nearly as important food resources as previously documented.

Contrary to other studies concluding that crayfish shift to macrophyte food resources as they age (Mason 1974; Lodge and Hill 1994; France 1996), our stable isotope analysis suggests that crayfish remain secondary consumers as adults. *Orconectes virilis* adults have higher trophic position than juveniles in northwestern Ontario (Hecky and Hesslein 1995). Our analysis agrees with this prospect somewhat, but a simpler explanation is that adults and juveniles consume similar foods, agreeing with the trophic relationship between juvenile and adult *O. luteus* in Jacks Fork River, Missouri (Whitledge and Rabeni 1997).

Model analysis

Our method of estimating unknown parameters may limit the broad application of this model to other situations. In particular, we were unable to identify a few parameters for the bioenergetics model from the literature, so we estimated these values based on laboratory-based growth, consumption, and respiration studies of closely related species. Unknown parameters and species borrowing are two of the most common deficiencies of bioenergetics models (Ney

1993). Although *O. virilis* and *O. rusticus* are very similar in terms of growth rates, thermal and physical habitat preferences, and diet composition (Hobbs and Jass 1988; Hill et al. 1993; Lodge and Hill 1994), we highly encourage other studies to independently validate the model parameters so that we can addend the model in the future. Nonetheless, our model performs well within the physiological bounds of congeners (Jones and Momot 1983; Hill et al. 1993; Whitley and Rabeni 2002) and produces results representative of other studies, so substantial improvement is unlikely.

Implications

The effect of rusty crayfish on littoral communities

The abundance of energy-rich zoobenthos in crayfish diets probably has a strong influence on the ability of rusty crayfish to affect littoral communities. If these prey are at low proportions in rusty crayfish diets, individuals must feed at a higher rate and consume more alternate prey. Therefore, we might predict that as a rusty crayfish population becomes more dense, it would quickly exhaust energy-rich food resources, forcing individuals to feed on large quantities of alternate prey (Lorman 1975; Lodge and Lorman 1987; Lodge et al. 1994). The initial consumption of energy-rich prey may explain short lags in macrophyte bed destruction following rusty crayfish invasions in northern Wisconsin lakes (Momot 1995; Wilson 2002). Additionally, this may explain why crayfish species in other ecosystems have strong effects on periphyton (Flint and Goldman 1975; Luttenton et al. 1998).

In conclusion, our results indicate that rusty crayfish are primarily predators. Why, then, do numerous studies list other energy-poor items as dominant components of crayfish diets? Momot (1995) suggests that mastication causes most animal matter to be misidentified as detritus. Likewise, Capelli (1980) acknowledged that he could not identify soft-bodied prey animals, as these are rapidly digested. Whitley and Rabeni (1997) suggest that poor assimilation overestimates the contribution of plant matter to crayfish diets. An alternative, food web based explanation may be that crayfish and fish deplete lakes of zoobenthos, and crayfish are forced to feed on less-desirable food items.

Although all four hypotheses are plausible, the food web based hypothesis has yet to be tested. Changes in macrophyte and benthic invertebrate communities associated with divergence in crayfish abundance or species composition (i.e., an invasion) would support the idea that crayfish resort to less profitable prey after zoobenthos are depleted. In lakes, macrophyte and gastropod communities declined in the presence of rusty crayfish, but natural assemblages of non-snail invertebrates did not (Lodge et al. 1994), perhaps because these communities have historically been difficult to accurately quantify on a large scale in lakes. Therefore, most existing studies focus on easily quantified littoral members (snails and macrophytes) or develop conclusions based on artificial assemblages of invertebrates or crayfish that may not reflect the natural abundance of either (Weber and Lodge 1990; Lodge et al. 1994; Wilson 2002). As more accurate methods to quantify benthic invertebrates develop (e.g., Wahle and Steneck 1991), future studies will likely illustrate that crayfish have a strong influence on non-snail inverte-

brate communities in addition to macrophytes and Gastropods, as predicted by our results and field studies conducted in streams (Charlebois and Lamberti 1996). The rusty crayfish bioenergetics model is a useful means to elucidate this proposition by allowing researchers to estimate the prey biomass that is necessary to satisfy a population's consumptive demand. If crayfish are keystone species, as several researchers have suggested (Lodge et al. 1994; Momot 1995), such exercises are necessary to fully understand the importance of crayfish foraging in freshwater ecosystems.

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