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Food web consequences of long-term invasive crayfish control

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Abstract: Controlling invasive species can restore ecosystems while also quantifying species interaction strengths. We experimentally removed invasive rusty crayfish (*Orconectes rusticus*) from a Wisconsin lake. Rusty crayfish abundance declined by 99% in 8 years and did not significantly increase 4 years postharvest, with no compensatory recruitment response observed. Native crayfish (*Orconectes virilis*) and sunfish (*Lepomis* spp.) abundances increased by two orders of magnitude as rusty crayfish abundance declined, and macrophyte cover increased significantly in 2–4 m waters. We expected benthic macroinvertebrate densities to increase as rusty crayfish were removed; however, fish consumption of invertebrates increased as rusty crayfish density declined, and macroinvertebrate responses varied among families and habitats. Total Gastropoda density increased 300-fold in cobble, while the density of one gastropod family declined in macrophytes. Ephemeroptera, Odonata, and Amphipoda densities also declined in certain habitats as rusty crayfish were removed, suggesting that they are indirectly facilitated by rusty crayfish. This study highlights the importance of considering indirect effects when assessing the impacts of invasive species and demonstrates that these impacts may be reversed over relatively short time scales.

Résumé : Le contrôle des espèces envahissantes peut mener au rétablissement d'écosystèmes tout en permettant de quantifier la force des interactions entre espèces. Nous avons retiré expérimentalement l'écrevisse américaine (*Orconectes rusticus*), une espèce envahissante, d'un lac du Wisconsin. L'abondance de l'espèce a diminué de 99 % en huit ans, n'avait pas significativement augmenté quatre ans après la récolte, et aucune réponse de recrutement compensatoire n'a été observée. L'abondance des écrevisses indigènes (*Orconectes virilis*) et des crapets (*Lepomis* spp.) a augmenté de deux ordres de grandeur parallèlement à la diminution de l'abondance des écrevisses américaines, et la couverture de macrophytes a augmenté significativement dans les eaux de 2 m à 4 m de profondeur. Nous nous attendions à une augmentation de la densité de macroinvertébrés benthiques avec le retrait de l'écrevisse américaine, mais la consommation d'invertébrés par les poissons a augmenté parallèlement à la baisse de densité des écrevisses américaines, de sorte que la réponse des macroinvertébrés variait selon la famille et l'habitat. La densité totale des gastéropodes a été multipliée par 300 dans les galets, alors que la densité d'une famille de gastéropodes a diminué dans les macrophytes. Les densités des éphéméroptères, des odonates et des amphipodes ont également diminué dans certains habitats parallèlement au retrait de l'écrevisse américaine, ce qui suggère que leur présence est indirectement facilitée par cette dernière. Cette étude fait ressortir l'importance de tenir compte des effets indirects dans l'évaluation des impacts d'espèces envahissantes et démontre que ces impacts peuvent être renversés à relativement court terme. [Traduit par la Rédaction]

Introduction

Invasive species threaten biodiversity worldwide, particularly in aquatic ecosystems (Sala et al. 2000; Carpenter et al. 2011). While prevention is the first line of defense in any invasive species management program (Lodge et al. 2006), eradication or maintenance of low densities of invasive species can reduce their impacts when prevention fails (Myers et al. 2000). Additionally, species eradications can be used to evaluate the strength of food web interactions (Yodzis 1988) and to identify indirect effects, where species interact through an intermediary (Wootton 1994). Indirect effects of invasive species can lead to unexpected outcomes of control efforts (Zavaleta et al. 2001; Bergstrom et al. 2009), but are often only apparent in studies spanning large spatial and temporal scales (e.g., White et al. 2006; Brown et al. 2011). Whole-ecosystem manipulations allow evaluation of ecosystem responses to perturbations at meaningful scales even in the absence of replication (Carpenter 1998; Schindler 1998), and in this sense, species invasions and subsequent control efforts are manipulations that can provide insights into food web structure (Sax

et al. 2007). Control of established invasive species can thus serve two purposes: restoring native biodiversity and ecosystem function, and quantifying the effects of food web interactions on ecosystem dynamics (Hulme 2006; Vander Zanden et al. 2006).

Successful control of an invasive species and restoration of ecosystem function does not necessarily require that 100% of the invasive population be eliminated (Simberloff 2009), although the long-term effectiveness of control is determined by the stock–recruitment relationship of the exploited species. If reproduction or juvenile survival increases at low adult densities (i.e., a compensatory recruitment response), then attempts to control invasive species can backfire, resulting in greater abundance of the target species (Zipkin et al. 2008; Zipkin et al. 2009; Ruiz-Navarro et al. 2013). On the other hand, control strategies such as predator augmentation can reduce invasive species population growth rates at low densities, thereby increasing the chances of long-term maintenance of low abundance (Tobin et al. 2011). Thus, an invasive species' population dynamics, in particular how they are influenced by control efforts, are critical in determining whether they can be controlled.

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One example of an invasive species control effort is the experimental removal of rusty crayfish (*Orconectes rusticus*) from a northern temperate lake (Hein et al. 2007). Rusty crayfish are notorious invaders with many well-documented impacts (Lodge et al. 2000). Rusty crayfish displace native crayfish from shelter, increasing the native species' vulnerability to fish predators (Mather and Stein 1993). They act as ecosystem engineers (Crooks 2002) by altering sediment dynamics (Nogaro et al. 2006) and destroying aquatic macrophytes, which causes declines in Gastropoda densities (Lodge et al. 1994) and in recruitment of bluegill (*Lepomis macrochirus*) and pumpkinseed (*Lepomis gibbosus*) (collectively hereafter referred to as *Lepomis*; Wilson et al. 2004; Roth et al. 2007). *Lepomis* and Gastropoda densities have also declined as a result of direct predation by crayfish (Brown 1998; Dorn and Mittelbach 2004), but the effects of rusty crayfish on other benthic macroinvertebrates have been mixed (e.g., Wilson et al. 2004; McCarthy et al. 2006; Rosenthal et al. 2006). Meanwhile, rusty crayfish are important prey for littoral fishes including *Lepomis*, smallmouth bass (*Micropterus dolomieu*), and rock bass (*Ambloplites rupestris*; Garvey et al. 2003; Tetzlaff et al. 2010).

Predicting the community response to rusty crayfish control is difficult at the whole-ecosystem scale owing to the myriad interactions between rusty crayfish and other littoral species. Rusty crayfish may in some cases simultaneously exert both positive and negative pressures on native species via direct and indirect interactions. For instance, rusty crayfish exert strong negative effects on benthic macroinvertebrates associated with macrophytes directly via predation and indirectly through the destruction of macrophyte habitat (Wilson and Hrabik 2006). At the same time, rusty crayfish may indirectly benefit benthic invertebrate taxa by negatively affecting recruitment of invertivorous fishes such as *Lepomis*, or by providing an alternative prey source to generalist littoral predators such as smallmouth bass and rock bass (Abrams 1987). The relative strength of these opposing interactions determines the response of native species to control of rusty crayfish and is best quantified on the whole-ecosystem scale.

We experimentally removed rusty crayfish from a northern Wisconsin lake via intensive harvest from 2001 to 2008 and protection of fish predators from 2001–2012. The objectives of this paper are (*i*) to document changes in rusty crayfish abundance and population dynamics over the entire experiment, including 4 postharvest years; (*ii*) to quantify changes in the native littoral community, including native crayfish, aquatic macrophytes, benthic macroinvertebrates, and littoral fishes, as rusty crayfish abundance declined; and (*iii*) to use the community responses to infer the relative strength of rusty crayfish predation, habitat, and fish predation in shaping benthic macroinvertebrate densities. We predicted that macrophyte cover, native crayfish abundance, and *Lepomis* abundance would increase as rusty crayfish were controlled. We further hypothesized that benthic macroinvertebrate taxa subject to strong direct predation from rusty crayfish and those that rely on macrophyte habitat for refuge would increase in abundance (e.g., Gastropoda), while those that were important diet items to littoral fishes would decline or remain constant.

Methods

Study site

Sparkling Lake is a 64 ha mesotrophic seepage lake in Vilas County, Wisconsin, USA (46.008°N, 89.701°W) with a maximum depth of 20 m. The North Temperate Lakes Long Term Ecological Research (NTL-LTER) program has monitored physical, chemical, and biological variables in the lake since 1981 (http://lter.limnology.wisc.edu; Magnuson et al. 2006). Rusty crayfish invaded Sparkling Lake in the 1970s (Capelli 1975) and reached relatively high densities by the late 1980s (Hein et al. 2007). A whole-lake manipulation was initiated in Sparkling Lake in 2001 to control rusty crayfish via trapping and fish predation, reducing rusty crayfish catch rates by

95% from 2001 to 2005 (Hein et al. 2007). Rusty crayfish harvest continued through 2008, and monitoring trapping continued through 2012. Fishing regulations were changed in 2001 with the intent of reducing angler harvest and increasing fish predation on juvenile rusty crayfish (Hein et al. 2006); the length limits of smallmouth bass and walleye (*Sander vitreus*) were increased to 457 and 711 mm, respectively, and bag limits were decreased to one for both species (compared with a statewide bag limit of five and length limits of 356 and 381 mm, respectively). These regulations were in effect for the duration of this study.

Crayfish

Abundance

Adult rusty crayfish were trapped using Gee minnow traps; traps were modified by widening the openings and baited with beef liver or frozen fish following the methods of Capelli and Magnuson (1983). Between 30 and 313 (mean = 149) traps were set at 43 transects around the perimeter of the lake at the 1 m depth contour, with higher concentrations of traps in locations of higher rusty crayfish abundance (Hein et al. 2007). Rusty crayfish were harvested via trapping in August 2001 and from June to August 2002–2008; during this period all trapped rusty crayfish were removed from the lake, while all native virile crayfish (*Orconectes virilis*) were released. Traps were deployed continuously during the removal period; traps were emptied every day from 2002 to 2003, and every 1–3 days from 2004 to 2008 as catch rates declined (daily catch rates were unaffected by duration of trap deployment when rusty crayfish density was low; M.J. Vander Zanden, unpublished data). From 2009 to 2012, trapping continued for monitoring purposes, during which time traps were deployed one or two times per week and emptied after 1–3 days, with all captured crayfish of both species released. Catch per unit effort (CPUE) of each crayfish species was used as an index of adult abundance, calculated for each day that traps were emptied (total crayfish caught per total number of traps per number of days traps were deployed) and presented as mean annual CPUE. Trap days prior to 18 June in any year were excluded from CPUE analysis to eliminate variability in annual catch rates due to differences in start dates of trapping. Statistical differences among annual catch rates were assessed using one-way analysis of variance (ANOVA) on natural log transformed data, and Tukey post hoc tests were used to assess differences among individual pairs of years (family-wise confidence level = 0.95, reported *p* values adjusted for multiple comparisons, $\alpha = 0.05$).

For several analyses described below, rusty crayfish density was categorized as "high", representing the early years of the experiment (2001–2003) and "low", representing the later years of the experiment plus the 4 years after rusty crayfish harvest ceased (2004–2012). A threshold of 9 rusty crayfish·trap^{-1}·day^{-1} has been previously used as a breakpoint for high versus low abundance (Wilson et al. 2004). Daily catch rates greater than 9 rusty crayfish·trap^{-1}·day^{-1} were observed from 2001 to 2003, but not in subsequent years.

Independent estimates of rusty crayfish densities (number·m^{-2}) were obtained in mid-July 2002–2004 and 2007–2010 shortly following the release of juveniles from brooding females. Adult (age-1+) and juvenile (age-0) rusty crayfish were sampled with SCUBA in cobble habitat using hand collections and an airlift suction sampler, respectively, following methods described by Hein et al. (2007). Additionally, adult population sizes of both rusty and virile crayfish were estimated using the Chapman modification of the Schnabel mark–recapture method (Ricker 1975) in 2009 and 2010 for comparison to the rusty crayfish population estimate from 2003 (Hein et al. 2006), which was recalculated to include only adults and to exclude those consumed by fishes (C.L. Hein, unpublished data). Crayfish for mark–recapture were trapped and collected by hand while snorkeling to increase numbers of small (<25 mm carapace

length) individuals. All captured crayfish of both species were individually marked using visual implant elastomer tags (Northwest Marine Technologies) embedded in abdominal flexor muscles.

Stock–recruitment

We examined the stock–recruitment relationship of rusty crayfish to assess the evidence for a compensatory recruitment response to control efforts; that is, increased juvenile production as a function of decreased adult density. We analyzed adult female density and juvenile density in Sparkling Lake over time and in 10 nearby lakes sampled in 2002–2004 that represented a range of rusty crayfish densities (Appendix A). Adult and juvenile crayfish were sampled concurrently in cobble using SCUBA (see Hein et al. 2007) and were identified to species and sex. Three common stock–recruitment models allowing for differing levels of density dependence in recruitment were fit to the data (see Appendix A for model forms). The linear model includes no density dependence and predicts that juvenile density decreases linearly as adult density declines. The Beverton–Holt model (Beverton and Holt 1957) predicts density-dependent recruitment where juvenile density remains constant and then declines as adult density decreases. The Ricker model (Ricker 1954) also predicts density-dependent recruitment where juvenile density increases before eventually declining as adult density decreases. The Ricker model is the only model where increased adult mortality could result in a compensatory increase in juvenile densities, thereby undermining control efforts (Zipkin et al. 2009). The best-fit model was selected using Akaike's information criterion (AIC) (Akaike 1973) with extra parameters included if they reduced the AIC value by more than 2 (Burnham and Anderson 2002).

Macrophytes

Macrophyte cover was assessed in Sparkling Lake in the third or fourth week of July from 2002 to 2004 and from 2007 to 2010. Eight transects were selected that collectively represent the range of macrophyte communities in the lake. These transects stretched from the waterline to a depth of 4 m, running perpendicular to shore. Circular quadrats (0.25 m²) were placed along each transect at 1 m longitudinal intervals, and SCUBA divers visually estimated percent cover of each macrophyte species within the quadrat. The sum of percent cover of all species within a quadrat does not necessarily add to 100; rather, this sum reflects the percentage of bottom substrate covered by all species. For statistical analysis, percent cover in each quadrat (+0.5, half of the minimum nonzero observed value) was natural log transformed to correct for heteroscedasticity of residuals and modeled as the dependent variable. Macrophyte data were grouped into years of high (2002–2003) and low (2004; 2007–2010) rusty crayfish abundance. Differences in total macrophyte percent cover in these year groups were assessed using a multilevel general linear model, with rusty crayfish abundance index (high or low), depth range (0–1, 1–2, 2–3, and 3–4 m), and their interactions as fixed effects and transect and year as random effects. See the section Data analysis: multilevel modeling (below) for more information on statistical analysis of macrophyte data and assessment of statistical significance. We also visually examined species-specific frequencies of occurrence (the proportion of quadrats containing a given species) across years and depths.

Benthic macroinvertebrates

Benthic macroinvertebrates were sampled in Sparkling Lake from 2002 to 2003 and from 2008 to 2010 along five transects that correspond to crayfish survey sites. Together these sites represented a range of habitat types and rusty crayfish abundance in 2002 when sampling began. Samples were collected at 1, 3, and 5 m depths, although not all depths were sampled for all transects in all years. Three replicate samples delimited by 0.09 m² circular quadrats were collected at each site–depth combination in each year using an underwater vacuum air-lift sampler (Butkas et al. 2011). The sampler consists of a SCUBA tank connected to a length of PVC with a 500 μm mesh bag attached to the top. All surfaces potentially available as macroinvertebrate habitat were sampled within a quadrat. For example, macrophytes were placed inside the PVC tube prior to opening the SCUBA tank, and soft substrates surrounding macrophytes were also sampled. In cobble habitat, the upper surfaces of the rocks were suctioned, and then all rocks contained inside the quadrat were picked up, suctioned on all surfaces, and placed outside of the quadrat. Substrate exposed when cobble was moved was also suctioned. Samples were sealed in plastic bags with lake water, placed on ice, and separated live within 48 h. Macroinvertebrates were separated from substrate, preserved in 95% ethanol, and later identified to the lowest practical taxonomic level (genus in most cases).

Habitat for each benthic macroinvertebrate sample was classified as soft substrate (mainly sand), cobble, or macrophyte. All sites classified as soft substrate in 2002–2003 were subsequently covered with macrophytes in 2008–2010; therefore, for analysis we grouped data into only two habitat types: macrophyte–soft habitat and cobble. The effect of rusty crayfish relative abundance and habitat on benthic macroinvertebrate taxa was evaluated using multilevel models similar to those used to evaluate macrophyte percent cover. Rusty crayfish abundance was classified as high (2002–2003) or low (2008–2009), and this crayfish abundance factor, habitat, and their interaction were evaluated as fixed effects. Sample site (transect × depth combination) nested within year were included as random effects to account for non-independence of samples from the same location and year. Macroinvertebrate density (+5, one-half of the minimum nonzero observed value) was natural log transformed to resolve heteroscedasticity of residuals and modeled as the dependent variable. Analyses were conducted on the density of all benthic macroinvertebrates combined (total density), mollusk classes and insect orders, and individual families appearing in at least 10% of samples. See the section Data analysis: multilevel modeling (below) for more information on statistical analysis of macroinvertebrate data and assessment of statistical significance.

Fish

Relative abundance of *Lepomis* was indexed from 1981 to 2012 using catch rates from LTER sampling (methods and data available online at http://lter.limnology.wisc.edu). CPUE was calculated for each gear type (beach seine, electrofishing, fyke net, trammel net) in each year and summed across all gear types to avoid bias introduced by any single gear type (Weaver et al. 1993).

We also sampled the Sparkling Lake littoral fish community bimonthly during the summer months from 2001 to 2004 using electrofishing, and from 2009 to 2010 using electrofishing and fyke nets. All fish were measured (total length, mm), weighed (g), and tagged with Floy tags or fin clips. Adult population sizes of smallmouth bass, rock bass, bluegill, and pumpkinseed were estimated in each year using the Chapman modification of the Schnabel mark–recapture method (Ricker 1975). Diets were collected from each species at each electrofishing sampling event using gastric lavage (Seaburg 1957) and preserved in 95% ethanol. Diet items were identified to order for non-crayfish invertebrates and to species (when possible) for fish and crayfish, enumerated, dried at 57 °C for 48 h, and weighed.

Data analysis

Multilevel modeling

For statistical analysis of macrophyte percent cover and benthic macroinvertebrate densities, we used a multilevel modeling approach (Gelman and Hill 2006). We estimated fixed effects and their confidence intervals from the full model (all potential fixed effects, interactions, and random effects included), which results in higher variance within groups but avoids problems of "data

snooping", and is thus a conservative test (Bolker et al. 2009). Full models included a small number (two or three) of fixed effects expected to influence results based on biological knowledge of the system and random effects to account for nonindependence of samples from the same sites or years, similar to classical blocked experimental designs. Effects are reported as restricted maximum likelihood estimates of fixed effects from the lme4 package (Bates and Sarkar 2007) in R version 2.14 (R Development Core Team 2011). Confidence intervals were calculated as Bayesian highest posterior density confidence intervals of parameter estimates generated from Markov chain Monte Carlo simulations using the languageR package, which incorporates variation from random effects (Baayen et al. 2008). Statistically significant differences are based on nonoverlapping 95% highest posterior density intervals of fixed effect estimates (Gelman and Hill 2006; Qian and Shen 2007). Adjusted R^2 values for mixed-effects models were calculated as the likelihood ratio test R^2 (Magee 1990; Kramer 2005).

Fish diet similarity

To assess change in fish diet composition over time, the similarity of smallmouth bass and rock bass diets between each pair of sampled years was quantified using Morisita's index of diet overlap (Smith and Zaret 1982). We used nonparametric bootstrapping to assess whether diets of a given species differed significantly among any 2 study years (Chipps and Garvey 2007). For each year, we sampled with replacement the number of fish contained in the original sample from the entire population of individuals from all years. We recalculated Morisita's index for each pair of years using the resampled data and repeated 1000 times to generate a distribution of similarities between any 2 years. We calculated the proportion of times that the actual index was lower (more dissimilar) than the bootstrapped index for each pair of years; actual values more dissimilar than 95% of the resampled values were considered statistically significant.

Bioenergetics modeling of fish consumption

To assess the effects of fish consumption on prey populations, total annual consumption (kg) of major prey items by bluegill, pumpkinseed, rock bass, and smallmouth bass was estimated using Bioenergetics 3.0 (Hanson et al. 1997) modified to run in R version 2.14.1 (R Development Core Team 2011). Bioenergetic parameters for rock bass and smallmouth bass were obtained from Roell and Orth (1993) and Whitledge and colleagues (2003), respectively. Bioenergetics analysis requires data on water temperature, fish growth, and diet composition. Mean daily surface water temperatures of Sparkling Lake were obtained from NTL-LTER (http://lter.limnology.wisc.edu). Year- and age-specific growth rates were estimated from scales using the Fraser–Lee back-calculation model (Appendix B; Ricker 1975). Age–length keys with semirandom age assignment were used to estimate age-specific population sizes in each year; this approach explicitly assigns an age to each individual in a sample based on a subsample of aged fish (Isermann and Knight 2005). Separate age samples were used for 2001–2003 and 2009–2010, as preliminary analysis showed differences in growth rates in these year groups. Diet proportions (% by mass) specific to each sampling date were used for each species, subdivided into length classes (<150, 151–250, >250 mm total length) to reflect ontogenetic diet changes. Diet items were grouped for analysis according to diet item descriptions in Appendix Table B1. The "Fish" category consisted mostly of mimic shiners (*Notropis volucellus*) but also included rainbow smelt (*Osmerus mordax*), bluntnose minnow (*Pimephales notatus*), *Lepomis* spp., and rock bass. Energy densities (J·(g wet mass)$^{-1}$) of prey items were obtained from various sources (Appendix Table B1; Cummins and Wuycheck 1971; Roell and Orth 1993; Hanson et al. 1997; Gray 2005). When reported energy density values were in J·(g dry mass)$^{-1}$, they were converted to wet mass using percent water (when available; Cummins and Wuycheck 1971). Bioenergetics models estimate

Fig. 1. (A) Catch per unit effort (CPUE, number per trap per day) of rusty crayfish (filled circles) and virile crayfish (open triangles) in Sparkling Lake. Harvest trapping took place from 2001 to 2008 (dashed lines); all trapped crayfish were released from 2009 to 2012. (B) Densities (no.·m^{-2}) of age-0 (open circles) and older (filled circles) rusty crayfish from Sparkling Lake. Densities are from cobble (preferred) habitat only. Error bars are standard error for all series. Note log scale of *y* axis of both panels.
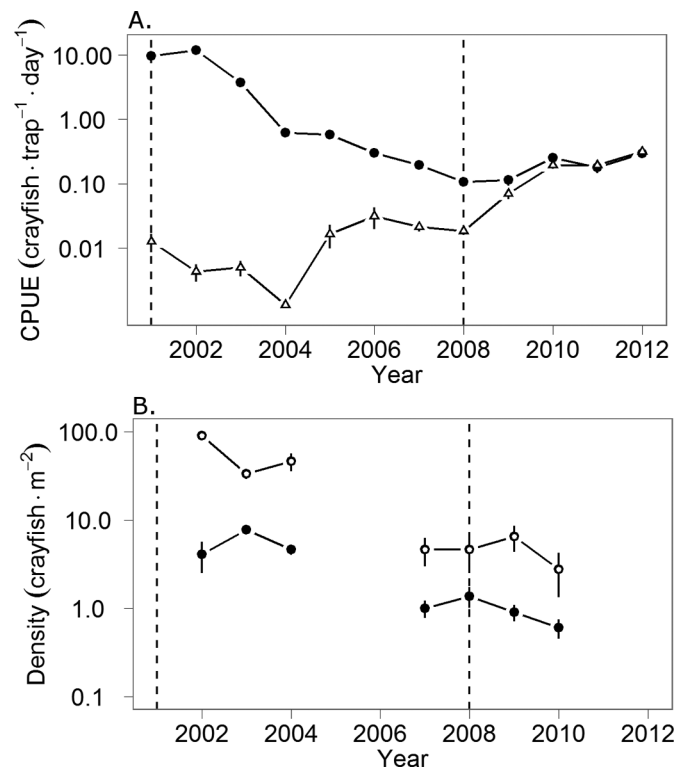
daily consumption of all prey groups for each fish predator and age class — these consumption totals were summed to generate annual consumption estimates of each prey group by each of the four littoral fish species.
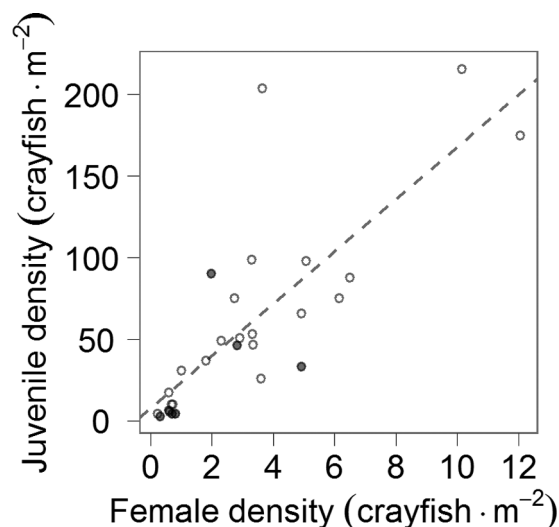
Results

Crayfish

Abundance

We removed a total of 91 930 rusty crayfish with traps from 2001 to 2008. Rusty crayfish CPUE decreased by two orders of magnitude from its peak of 11.8·trap^{-1} in 2002 to 0.11·trap^{-1} in the final year of harvest in 2008, and remained low through 2012 (Fig. 1A). Rusty crayfish catch rates differed significantly among years (ANOVA, $F_{[11, 284]} = 145.9$, $p < 0.001$), although from 2007 to 2012 annual catch rates were statistically indistinguishable (Tukey HSD, all pairwise comparisons, $p > 0.12$), with the exception of 2008 and 2010 (Tukey HSD, $p = 0.01$). Adult and juvenile rusty crayfish densities decreased by approximately 1.5 orders of magnitude from the early years of the experiment to the final year of sampling (Fig. 1B). Native virile crayfish CPUE increased by two orders of magnitude from a low of 0.001·trap^{-1} in 2004 to a peak of 0.315·trap^{-1} in 2012 (Fig. 1A). Virile catch rates also differed significantly among years (ANOVA, $F_{[11, 284]} = 45.01$, $p < 0.001$), and were higher in 2010–2012 compared with rates in all other years (Tukey HSD, all pairwise comparisons, $p < 0.001$).

Mark–recapture population estimates of adult rusty crayfish also decreased by two orders of magnitude over the course of the experiment. The total number of marked (recaptured) rusty crayfish in 2009 and 2010 was 767 (85) and 1258 (227), and for virile

Fig. 2. Juvenile (age-0) density as a function of adult female density of rusty crayfish. Solid grey circles are from Sparkling Lake; open circles are from cross-lakes surveys. Including a separate model for Sparkling Lake did not improve model fit based on AIC values. The dashed line represents the best-fit linear stock–recruitment relationship fit to all data combined ($y = 7.99 + 15.98x$, adjusted $R^2 = 0.616$, $p < 0.001$).

Fig. 3. Total percent cover of all macrophyte species (restricted maximum likelihood estimate ± 95% confidence intervals from multilevel model) in various depth ranges: (A) 0–1 m; (B) 1–2 m; (C) 2–3 m; (D) 3–4 m (adjusted $R^2 = 0.50$). Percent cover is represented by the restricted maximum likelihood estimate in high crayfish years and in low crayfish years in each depth category; nonoverlapping confidence intervals indicate statistically significant differences.

crayfish was 124 (4) and 656 (165), respectively. The adjusted population estimate of adult rusty crayfish was 120 143 in 2003 (Hein et al. 2006) and declined to 4032 (95% CI 3229–5367) in 2009 and 4420 (95% CI 3876–5142) in 2010. The virile crayfish population estimate was 1397 (95% CI 621–3343) in 2009 and 1904 (95% CI 1636–2277) in 2010. No comparable estimates for virile crayfish exist from 2003 owing to low catches (only 21 individuals were captured over 6403 trap days).

Stock–recruitment

The relationship between female rusty crayfish density and juvenile density was linear (Fig. 2). Although differences in AIC values of all potential stock–recruitment models were ≤2, indicating equal probability of each model fitting the observed data, the best-fit parameter estimates included zero for both nonlinear stock–recruitment models, reducing these models to the linear (density-independent) form (Appendix A).
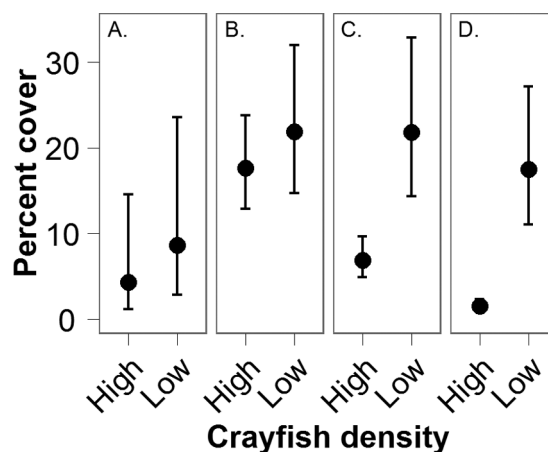
Macrophytes

Macrophyte percent cover was significantly higher in years of low compared with those of high rusty crayfish CPUE; percent cover increased by a factor of 4 in the 2–3 m depth range and by a factor of 11 in the 3–4 m depth range (Figs. 3C, 3D). Macrophyte cover also doubled in the 0–1 m depth range and increased 23% in the 1–2 m range but these changes were not statistically significant (Figs. 3A, 3B). Change in macrophyte cover was driven primarily by an increase in the frequency of occurrence of *Najas flexilis*, *Potomogeton gramineus*, *Eleocharis acicularis*, and the macroalga *Chara* spp. (Fig. 4). In 2001, *N. flexilis* occurred in only 3.5% of sites; by 2010 it occurred in nearly 75% of sites. The frequency of occurrence of *P. gramineus*, *Chara* spp., and *E. acicularlis* also more than doubled during the study period.

Benthic macroinvertebrates

Benthic macroinvertebrate densities changed during the experimental period, and the direction, magnitude, and statistical significance of change differed among taxonomic groups and habitat types (Fig. 5). In cobble habitat, the density of each gastropod family was <1·m⁻² in years of high rusty crayfish abundance. Total Gastropoda density increased approximately 300-fold in cobble,

from around 0.25·m⁻² when rusty crayfish were abundant to over 76·m⁻² when rusty crayfish densities were low (Fig. 5A). Densities of two gastropod families (Lymnaeidae and Planorbidae) significantly increased in cobble habitat as rusty crayfish densities declined, and densities of the remaining three gastropod families did not change significantly in cobble. When rusty crayfish density was high, total Gastropoda density and Physidae density were each significantly higher in macrophyte–soft habitat than in cobble habitat. Physidae densities decreased by approximately 80% from 2.9 to 0.58·m⁻² in macrophyte–soft habitat following the reduction in rusty crayfish. Other gastropod families exhibited variable and nonstatistically significant changes in macrophyte–soft substrates (Fig. 5B).

Total Ephemeroptera density was 11 times greater in cobble than in macrophyte–soft habitat when rusty crayfish density was high. Total Ephemeroptera density declined by nearly 90% in cobble as rusty crayfish density declined; densities of two families (Heptageniidae and Ephemeridae) decreased by over 95%, while one family (Caenidae) increased by a similar magnitude (Fig. 5A). Densities of total Ephemeroptera and each Ephemeroptera family also declined in macrophyte–soft substrate, but changes were not statistically significant. Amphipoda and total Odonata densities were also significantly lower in the years following rusty crayfish removal in macrophyte–soft habitats (Fig. 5B). Total benthic invertebrate density as well as that of most macroinvertebrate groups (6 of 10 classes–orders and 9 of 15 families) did not change significantly between years with high or low rusty crayfish abundance in either habitat.

Fish

Lepomis abundance increased during the experimental period. The seven highest CPUE values from the 32-year NTL-LTER record (1981–2012) were observed in 2006–2012 (Fig. 6A). Mark–recapture population estimates of *Lepomis* were not possible in 2001–2004 owing to low sample sizes (a total of 23 pumpkinseed and 0 bluegill collected in these 4 years combined), but the population was estimated at 2042 (95% CI 1096–4125) and 2841 (95% CI 1415–6212) in 2009 and 2010, respectively (Fig. 6B). Rock bass and smallmouth bass populations fluctuated but did not show a directional trend during the experimental period (Figs. 6C, 6D).

Diet composition of littoral fishes differed from early in the experiment (2001–2003) to post-crayfish harvest (2009–2010) as

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Fig. 4. Frequency of occurrence (proportion of quadrats containing at least one stem) of each macrophyte species as a function of depth range (fill colors, shown in legend). Species are (A) Chara spp., (B) *Eleocharis acicularis*, (C) *Elodea canadensis*, (D) *Gratiola aurea*, (E) *Isoetes* spp., (F) *Juncus pelocarpus*, (G) *Lobelia dortmanna*, (H) *Najas flexilis*, (I) *Potamogeton gramineus*, (J) *Potamogeton* spp. (includes *P. ampifolius*, *P. diversifolius*, *P. epihydrus*, *P. praelongus*, *P. pusilis*, and *P. spirillus*), (K) *Vallisneria americana*, and (L) Other (includes *Elatine minima*, emergent *Eleocharis* spp., *Ericocaulon aquaticum, Nitella* spp., *Ranunculus flammula*, *Sagittaria* spp., and *Scirpus* spp.).
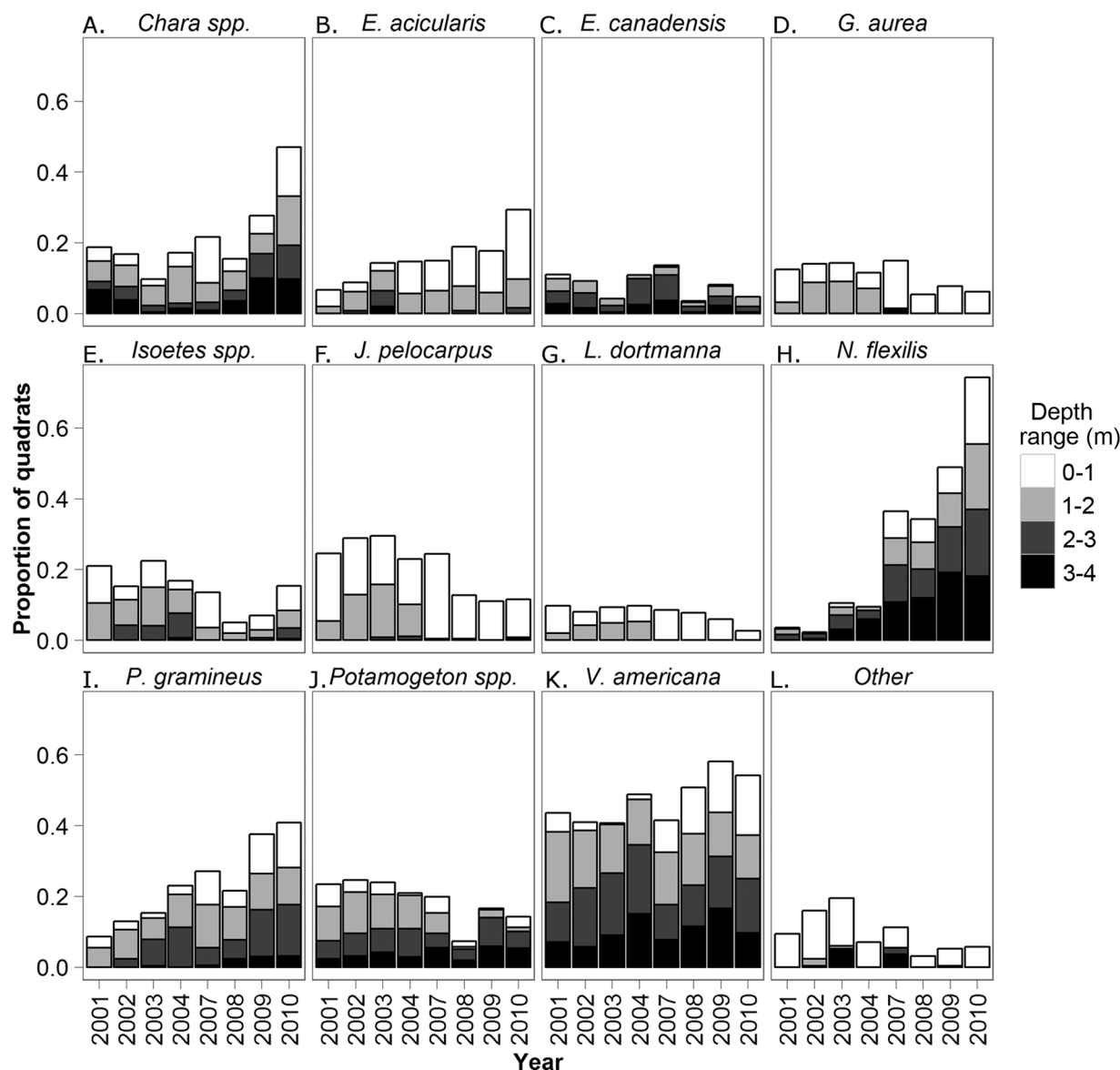
demonstrated by decreasing within-species diet similarity over time for rock bass and smallmouth bass (Table 1). In particular, during the first year of study, crayfish constituted approximately 25% and 20% by number of rock bass and smallmouth bass diets, respectively (Fig. 7A). At the end of the experiment (2009 and 2010), crayfish made up less than 1% of rock bass diets and just over 1% of smallmouth bass diets. The proportion of Ephemeroptera in diets of both rock bass and smallmouth bass also decreased as rusty crayfish density declined (Fig. 7D), while the proportion of Diptera (Fig. 7C) and fish (Fig. 7G) increased over the same time period.

Annual consumption of most prey by fishes increased over time (Fig. 8). Crayfish and Ephemeroptera were notable exceptions; total annual consumption of these groups declined owing to reductions in consumption by rock bass and smallmouth bass. Increased consumption of most macroinvertebrate taxa in later years (e.g., Amphipoda, Bivalva, Diptera, Isopoda) was due to the appearance of

substantial pumpkinseed and bluegill populations that previously had exerted negligible predation pressure, although diet shifts in rock bass and smallmouth bass contributed to increases in consumption of some groups (e.g., Gastropoda, Trichoptera).

Discussion

Control of invasive rusty crayfish

Our results demonstrate that it is possible to alleviate the negative effects of invasive rusty crayfish even in the absence of complete eradication. The experimental removal of rusty crayfish from Sparkling Lake was successful in reducing the population by 99%, and this low density state was maintained for 4 years following the cessation of removal trapping (Fig. 1). We observed declines of similar magnitude in trapping CPUE, density surveys of juveniles and adults, and in mark–recapture population estimates, indicating that the reduction in rusty crayfish numbers

Fig. 5. Macroinvertebrate density (restricted maximum likelihood estimates from multi-level models, ± 95% confidence intervals) as a function of relative crayfish abundance (open circles, high; triangles, low) in (A) cobble and (B) macrophyte–soft substrates. Asterisks indicate statistically significant differences between years of high and low rusty crayfish abundance based on nonoverlapping 95% confidence intervals; black symbols indicate entire macroinvertebrate orders or classes; grey symbols indicate family-specific densities. Only families that appeared in ≥10% of samples were included in family-specific analyses.
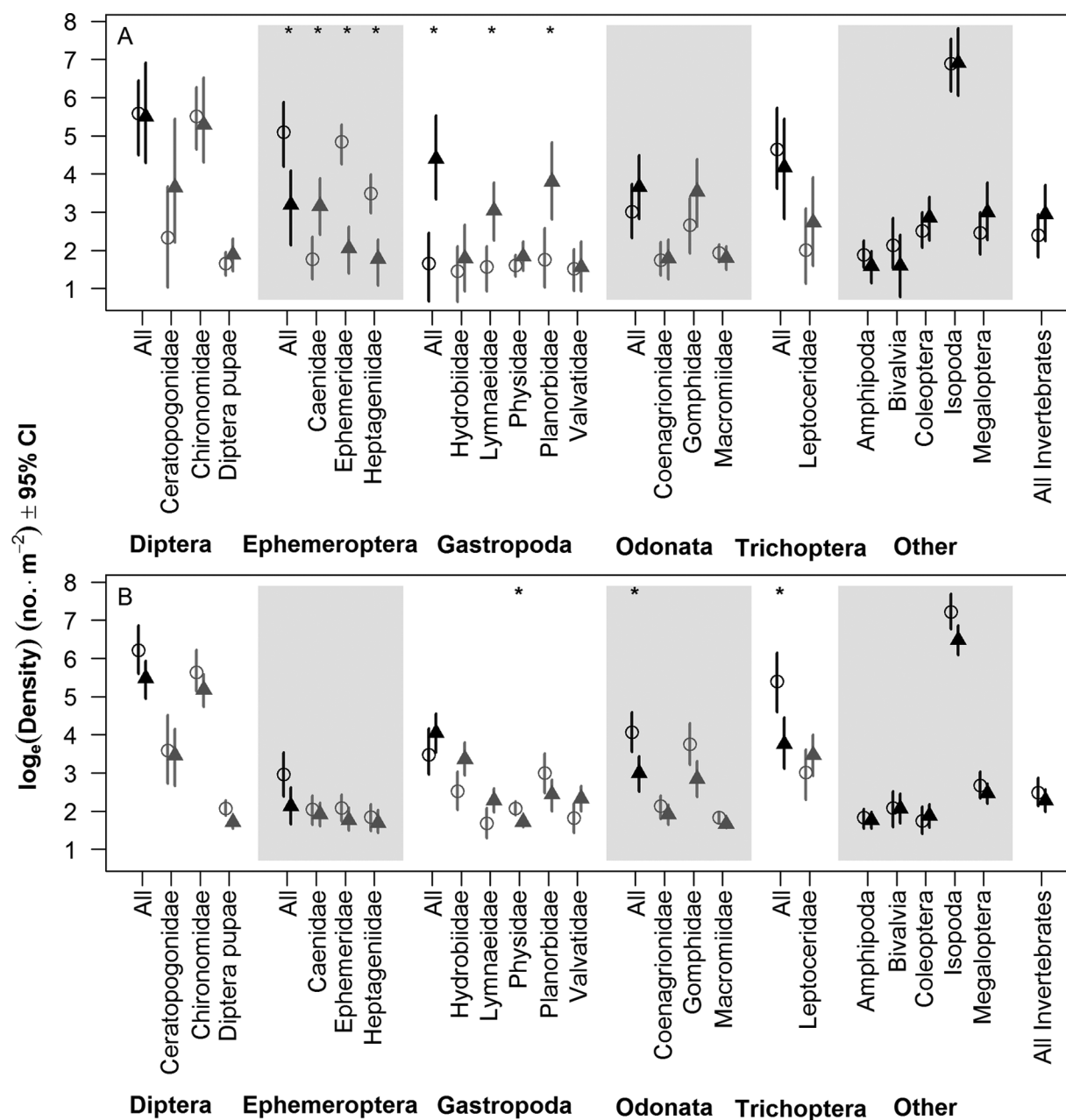
occurred across age classes and sexes and was not constrained by known biases of traps towards larger male crayfish (Stuecheli 1991). The stock–recruitment relationship of rusty crayfish exhibited no density dependence (Fig. 2); per capita recruitment appeared constant regardless of adult density, consistent with predictions that species with low per capita fecundity are good candidates for control via harvest (Zipkin et al. 2009). This density-independent relationship between adult and juvenile density is common among exploited species, and possibly indicates that even at their highest abundance, rusty crayfish did not fully saturate available habitat (Hilborn and Walters 1992). Owing to the linear relationship between adult and juvenile rusty crayfish, it is possible that rusty crayfish densities will increase in subsequent years, but the maintenance of the response

for several years post-trapping indicates that control of established invasive rusty crayfish populations is possible without annual trapping.

Community response to control of invasive rusty crayfish

Aquatic macrophytes

The macrophyte community responded strongly to reduced rusty crayfish density, especially at 2–4 m depths (Fig. 3). In contrast with previous research indicating limited reversibility of the adverse effects of rusty crayfish on macrophytes (Rosenthal et al. 2006), macrophyte cover increased within less than a decade in Sparkling Lake in the absence of other restor-

Fig. 6. (A) Catch per unit effort (summed for beach seines, electrofishing, fyke nets, and trammel nets) of *Lepomis* spp. in Sparkling Lake from 1981 to 2012. Rusty crayfish were harvested from 2001 to 2008 (dashed lines). (B–D) Population estimates (±95% confidence intervals) estimated using the modified Schnabel mark–recapture method for (B) *Lepomis* spp. (estimates not available for 2001–2004 owing to low sample sizes), (C) rock bass, and (D) smallmouth bass.
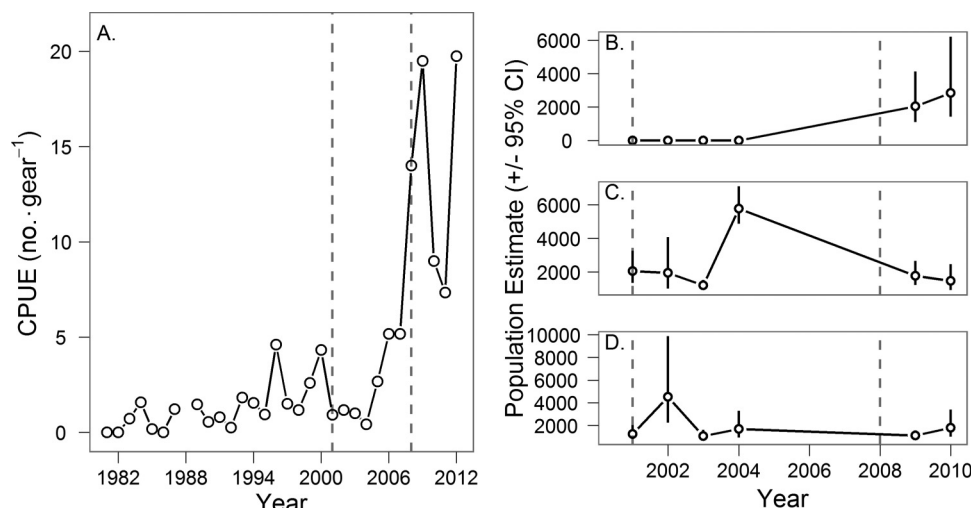
Table 1. Morisita's similarity index of diets for rock bass (above diagonal) and smallmouth bass (below diagonal) between all pairs of years in which diets were sampled.

	2001	2002	2003	2004	2009	2010
2001	—	0.539	**0.321**	0.404	**0.144**	**0.145**
2002	0.353	—	0.338	0.481	**0.098**	**0.126**
2003	0.373	0.351	—	0.428	0.430	0.392
2004	0.231	0.406	0.306	—	0.370	0.340
2009	**0.245**	**0.130**	0.183	0.194	—	0.596
2010	**0.174**	**0.196**	0.187	0.277	0.265	—

Note: Smaller values indicate more dissimilar diets. Bold values represent statistically significant (α = 0.05) differences based on bootstrapped data.

ative measures. The greatest change in percent macrophyte cover occurred in *N. flexilis* and *Chara* spp. (Fig. 4), consistent with the observations of Rosenthal et al. (2006) that viable seeds of these two species remain in the sediments of lakes with high rusty crayfish abundance. However, we also documented increases in caulescent or long-leaved species such as *Potomogeton gramineus* and *Vallisneria americana*, indicating that even species that generally reproduce clonally and rarely set seed (Sculthorpe 1967) are able to rapidly increase in abundance from small remnant populations following reductions in rusty crayfish herbivory. The species-specific changes in the macrophyte community can also explain the greater increase in macrophyte cover at 2–4 m depths compared with that at 0–2 m depths; shallow waters of Sparkling Lake are dominated by rosulate, short-statured species (e.g., *Isoetes* spp., *Juncus pelocarpus*), while deeper waters contain more single-stemmed or long-leaved species that are likely targets of destructive rusty crayfish activities (Lodge and Lorman 1987; Olsen et al. 1991).

Benthic macroinvertebrates

Following the decline in rusty crayfish abundance, changes in densities of benthic macroinvertebrates were highly variable and differed among habitat types (Fig. 5). As expected from previous studies (e.g., Lodge and Hill 1994; Wilson et al. 2004; Kreps et al. 2012), total gastropod density increased approximately 300-fold in cobble habitat (Fig. 5A). Initial densities were quite low (<1·m⁻²) in cobble habitat, an order of magnitude lower than the gastropod densities in other lakes that have been highly impacted by rusty crayfish (Wilson et al. 2004; Kreps et al. 2012). Total gastropod density increased primarily as a result of significant changes in the abundance of *Planorbidae* and *Lymnaeidae*, both thin-shelled

families that are preferentially consumed by crayfish (Stein et al. 1984; Brown 1998). Unlike other lakes where recovery of snail populations following rusty crayfish reduction was limited (Kreps et al. 2012), our results demonstrate that snail populations can respond within a decade to decreases in rusty crayfish abundance even if rusty crayfish are not extirpated completely.

Total gastropod density did not change significantly in macrophyte–soft substrates as rusty crayfish were removed (Fig. 5B). Total gastropod density in macrophyte–soft substrates was 27·m⁻² when rusty crayfish were abundant, significantly higher than initial density in cobble, although several orders of magnitude lower than density on soft substrates prior to rusty crayfish invasion in a nearby lake (Wilson et al. 2004). Initial density in macrophyte–soft habitats was driven primarily by Hydrobiidae and Planorbidae densities. Hydrobiid snails migrate to macrophyte habitats to avoid predation and are relatively thick-shelled (Lewis 2001), and thus were able to maintain a relatively large population in non-cobble habitats even when rusty crayfish were abundant. Similarly, physid snails were significantly more abundant in macrophyte–soft habitats than in cobble when rusty crayfish were abundant, suggesting that physid snails also used macrophyte–soft habitats for refuge. As rusty crayfish were removed, *Physidae* density remained low in cobble habitat and significantly decreased in macrophyte–soft habitat. Declines in *Physidae* densities and the lack of positive response of other gastropod taxa in macrophyte–soft habitat can perhaps be attributed to fish predation. Gastropoda consumption by fishes increased by an order of magnitude in the years following the experimental rusty crayfish harvest (Fig. 8), driven primarily by pumpkinseed that prefer gastropods and forage primarily in macrophytes (Mittelbach 1988; Osenberg and Mittelbach 1989).

Total Ephemeroptera density in cobble habitat was approximately 90% lower in years of low versus high rusty crayfish abundance, suggesting that predation by rusty crayfish is not a major determinant of Ephemeroptera density. In fact, rusty crayfish may have indirectly facilitated high densities of Ephemeroptera in cobble. Two families, Ephemeridae (Hexagenia spp. and *Ephemera* spp.) and Heptageniidae (mainly *Stenonema* spp.), decreased following rusty crayfish removal. Mayflies from these families may have benefited from sediment excavation activities of rusty crayfish increasing aeration and interstitial spaces in sediments and between cobbles where these taxa live (Pringle et al. 1993; Usio and Townsend 2004). Furthermore, heptageniids compete with

Fig. 7. Diet composition (percent by number) over time for rock bass (solid bars) and smallmouth bass (open bars). Note discontinuous *x* axis. Panels correspond to prey taxa. "Other" includes Annelida, Arachnida, Bivalvia, Hemiptera, Hydracarina, Hymenoptera, Isopoda, Megaloptera, Oligochaeta, Trichoptera, zooplankton, and unidentified items. Numbers of diets analyzed for each species in each year are in Appendix Table C1.
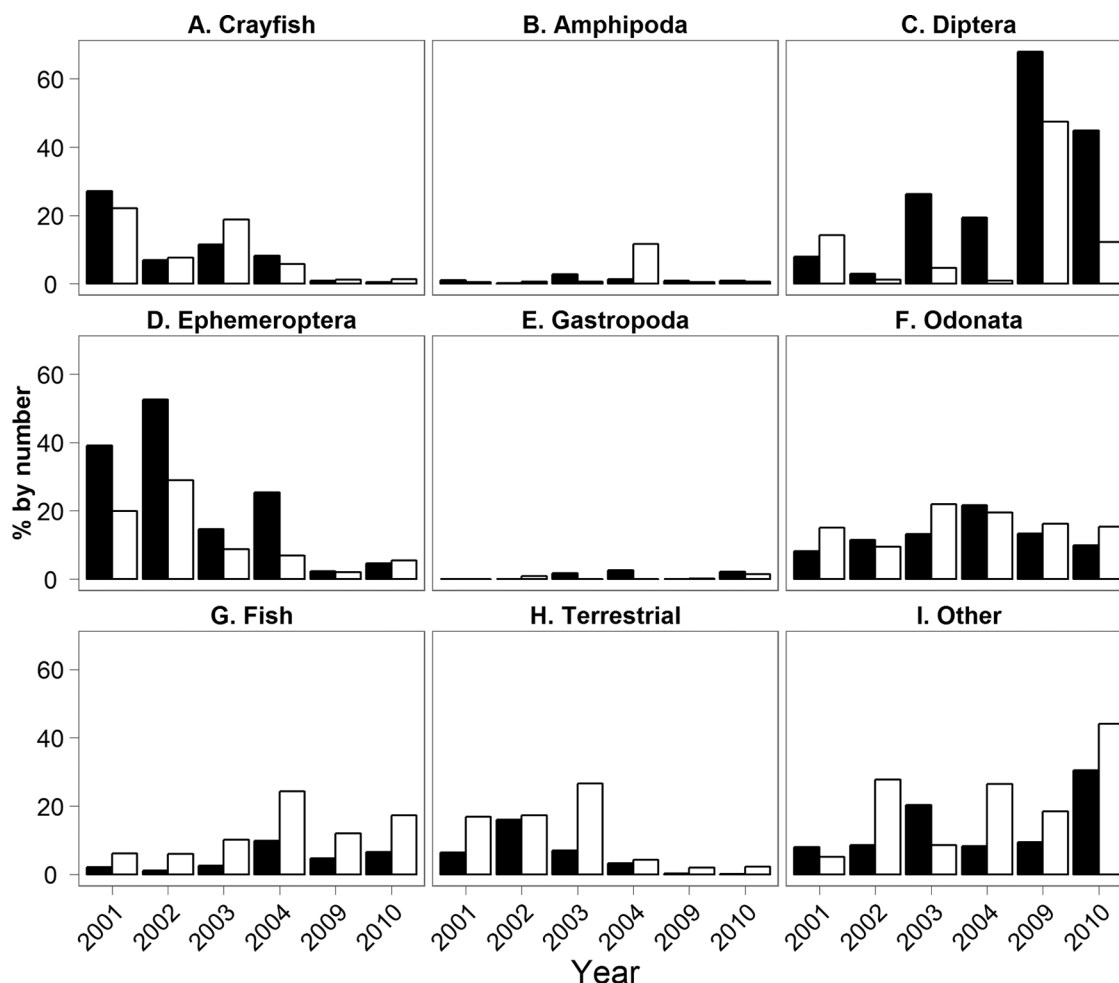
gastropods for periphyton resources on cobbles and could respond positively to the suppression of gastropods by rusty crayfish (Hertonsson et al. 2007). Finally, heptageniids crawl quickly to evade predation by invertebrate predators (Peckarsky 1980), perhaps making them more vulnerable to visual predators such as fish as fish switched from consuming crayfish to other invertebrate prey. In contrast with the decline in abundance of ephemerid and heptageiid mayflies, *Caenidae* densities increased 20-fold as rusty crayfish were removed. Caenids are small, cryptic, and slow moving and are often covered in sediment (Edmunds et al. 1976). These attributes make them relatively invulnerable to fish predation but potentially more vulnerable to invertebrate predators such as crayfish (Matthews et al. 1993).

Densities of most other macroinvertebrate groups increased in cobble and decreased in macrophytes as rusty crayfish density declined, although the majority of these changes were not statistically significant (Fig. 5). In macrophyte–soft substrates, increased macrophyte cover and habitat heterogeneity would be expected to result in increased macroinvertebrate densities as rusty crayfish declined (Crowder and Cooper 1982; Beckett et al. 1992). In fact, only three benthic macroinvertebrate taxa exhibited statistically significant changes in density in macrophyte–soft substrates as rusty crayfish were removed; densities of all three groups declined (Fig. 5B). The decline or lack of significant response of many macroinvertebrate groups reflects the complexity of direct and indirect effects of rusty crayfish on the littoral

food web, and in some cases could be explained by changes in fish consumption.

Fish

Fish consumption of crayfish was critical to successfully controlling rusty crayfish (Hein et al. 2006), but fish consumption also likely contributed to the variable responses of non-crayfish benthic macroinvertebrate groups to reduced rusty crayfish density. Fish consumption of most macroinvertebrate taxa increased as rusty crayfish were removed via two primary mechanisms (Fig. 8): increased abundance of two nearly extirpated invertivorous fishes (bluegill and pumpkinseed) and shifts in diet composition of smallmouth bass and rock bass as they decreased consumption of rusty crayfish and increased consumption of fishes and some macroinvertebrate prey items.

Relative abundance of *Lepomis* increased nearly 50-fold from a CPUE of less than 0.5 in 2004 to the highest observed value (19.75) in 2012 (Fig. 6A). *Lepomis* responded quickly to reductions in the rusty crayfish population; the upward trend in *Lepomis* abundance began in 2005, just 1 year after rusty crayfish relative abundance was first classified as "low" (see Methods), and has remained orders of magnitude higher than preexperiment abundance for the 4 years since rusty crayfish harvest ended. The negative relationship between rusty crayfish and *Lepomis* has been previously documented and implicated as a driver of alternative states of rusty crayfish abundance, where each

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Fig. 8. Total annual consumption (kg) of prey groups by littoral fishes estimated from bioenergetics simulations for each year of analysis. Note that x axis is not continuous and y axes differ by prey item. "Other" includes Annelida, Arachnida, Hemiptera, Hydracarina, Hymenoptera, Isopoda, Megaloptera, Oligochaeta, terrestrial items, and unidentified items. Fish predator species are shown in the legend.
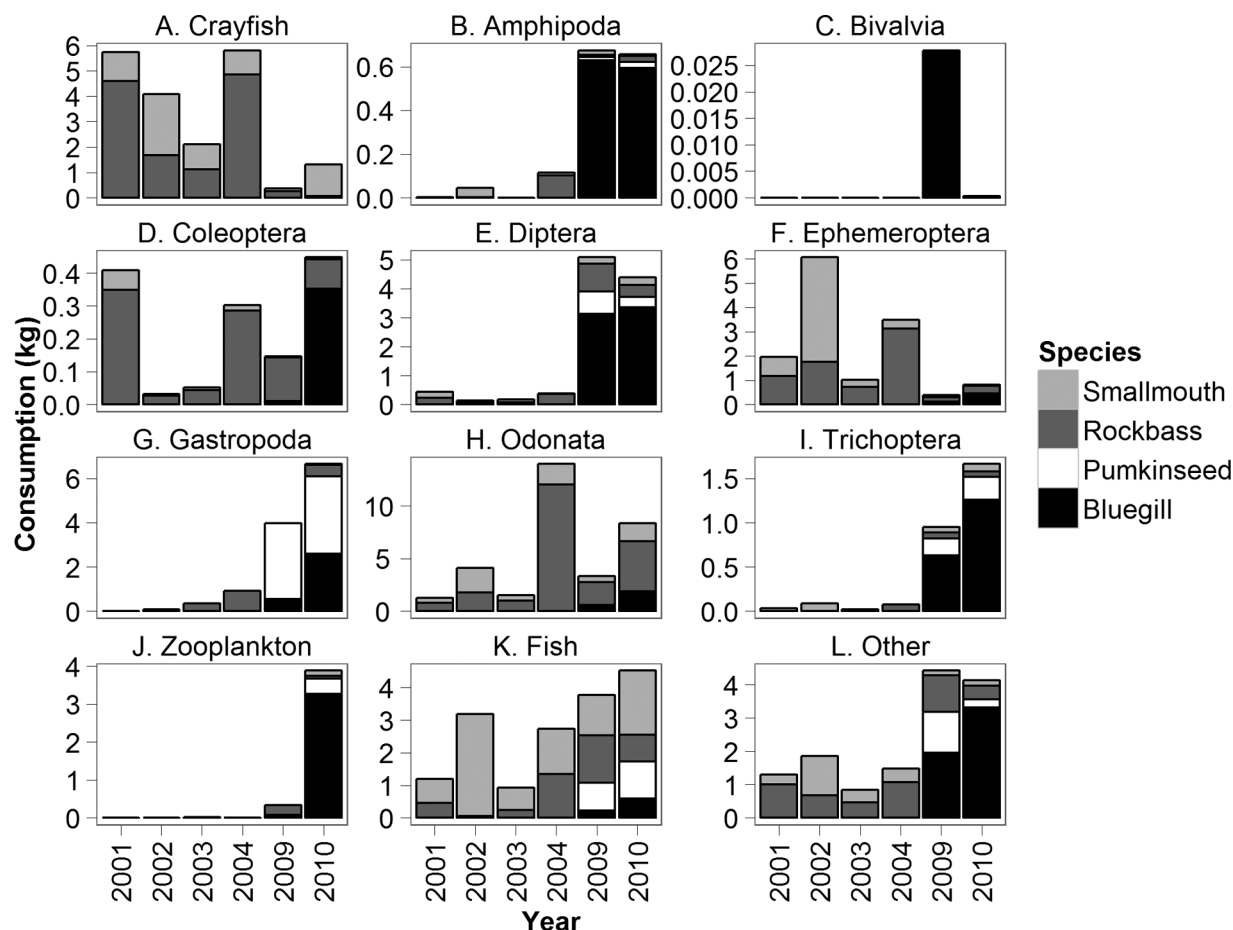
group can suppress the other's densities via negative effects on recruitment (Wilson et al. 2004; Roth et al. 2007). Our study demonstrates that nearly extirpated *Lepomis* populations are able to increase rapidly when rusty crayfish densities are reduced, and provides support for alternative community states (see also Hansen et al. in press).

We observed no directional change in the abundance of either smallmouth bass or rock bass (Figs. 6C, 6D), despite altered fishing regulations and major changes in prey resources and diets (Fig. 7; Table 1). Restrictive fishing regulations implemented at the beginning of the study protected smallmouth bass with the goal of increasing their population and thereby the efficacy of control measures (cf., Tobin et al. 2011). The lack of response in smallmouth bass abundance could be a reflection that angler harvest of this species is low even in the absence of restrictive regulations (Isermann et al. 2013). Although prey availability and diet composition of both smallmouth bass and rock bass changed dramatically throughout the experimental period, both species switched their diets to include more fish and non-crayfish benthic macroinvertebrates without apparent population-level consequences for the fish predators.

Rusty crayfish control as a management and experimental tool

Eradication or control of established invasive species is often viewed pessimistically by managers and scientists (Simberloff 2009), and control via harvesting has been discounted as impossible for most species owing to the low probability of removing all

individuals (Dahlsten et al. 1989). Furthermore, others have argued that controlling invasive species will require ongoing management to prevent recovery by the invader (Norton 2009). In this study, however, rusty crayfish densities remained low 4 years after cessation of harvest. While prevention should remain the top priority for invasive species management, it is important to document successful remediation efforts to optimize future control of rusty crayfish and other invasive pests (Simberloff 2009; Epanchin-Niell and Hastings 2010). The trapping effort employed in this study may exceed the resources available to most management agencies; however, the dynamics of rusty crayfish populations at low densities and the maintenance of the community response after trapping ended indicate that a pulse of trapping could sustain positive effects for many years.

This study provides a unique example of successful control of an established aquatic invasive species leading to sustained changes in the native community of an inland lake. Native virile crayfish, macrophyte, Gastropod (in cobble), and *Lepomis* densities all increased as rusty crayfish were controlled, and these increases continued in the 4 years following the termination of rusty crayfish harvest. Although these four groups are frequently observed at high densities in the absence of rusty crayfish or in lakes with low rusty crayfish densities (Wilson et al. 2004; Rosenthal et al. 2006; Wilson and Hrabik 2006; Roth et al. 2007), we cannot determine whether Sparkling Lake has been restored to preinvasion conditions because data collection began after rusty crayfish were established. However, the changes we observed are qualitatively

consistent with preinvasion conditions. The present macrophyte community is similar to that documented in the early 1930s, when *V. americana*, *P. gramineus*, and *N. flexilis* were the most abundant submerged macrophytes and *N. flexilis* was the most widely distributed species in the lake (Wilson 1935). Intensive littoral fish community surveys in the early 1980s classified pumpkinseed as "abundant" (Lyons 1984), and virile crayfish were the only crayfish captured in Sparkling Lake in 1972 (Capelli 1975). Still, virile crayfish catch rates in 2012 were an order of magnitude below preinvasion catch rates, indicating that native crayfish have not recovered completely and likely currently play a relatively minor role in food web dynamics. Although our study spans more than a decade, some observed community responses may be transitory, and future monitoring will be necessary to determine the stability of the new community configuration.

The effects of rusty crayfish on the benthic macroinvertebrate community are less straightforward than might be expected based on direct effects alone. Similar to other invasive species, the full extent of impacts of rusty crayfish were only apparent following their removal (Hulme 2006). The variable responses of benthic macroinvertebrates to the rusty crayfish removal likely result from the potentially conflicting effects of decreased rusty crayfish predation, increased habitat heterogeneity due to increased macrophyte cover, increased fish predation, and changes in interactions among macroinvertebrate taxa. Alternatively, if rusty crayfish act as "keystone species" (Power et al. 1996), whereby they exert disproportionately large effects at low abundances, some taxa may experience high mortality even during "low crayfish" conditions, and these populations may only increase following complete eradication of rusty crayfish. Although further experiments are needed to test potential mechanisms underlying the observed changes in benthic macroinvertebrate densities, our results can be used to generate hypotheses regarding the relative importance of direct and indirect effects of rusty crayfish in this littoral food web, providing a fruitful area of future research. In sum, the whole-lake response to experimental rusty crayfish control highlights the importance of considering the broader food web on management-relevant scales when assessing the impacts of invasive species and demonstrates that these impacts may be reversed over relatively short time scales.

Acknowledgements

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Appendix A. Rusty crayfish stock–recruitment analysis

The relationship between female density (stock) and juvenile density (recruitment) for rusty crayfish was evaluated by fitting three common stock–recruitment models (Hilborn and Walters 1992) to data collected from Sparkling Lake and 10 other northern Wisconsin lakes (Appendix Table A1). The models included the following:

(1)   the linear model:

$$R = \alpha S$$

(2)   the Beverton–Holt model (Beverton and Holt 1957):

$$R = \frac{\alpha S}{1 + \beta S}$$

(3)   the Ricker model (Ricker 1954):

$$R = \alpha S e^{-\beta S}$$

where R is juvenile density, S is adult female density, α is the maximum number of offspring produced by each female in the absence of density dependence, and β represents the strength of density dependence. Note that both the Beverton–Holt and the Ricker model reduce to the linear form when $\beta = 0$. All models were fit on the natural log scale using R version 2.14.2 (R Development Core Team 2011). Best-fit parameter estimates and AIC values for each model are shown in Appendix Table A2; both the Beverton–Holt and the Ricker models reduced to the linear form (maximum likelihood estimates of $\beta = 0$).

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Table A1. Lakes included in stock–recruitment analyses.

Lake	S–R survey years	Latitude (°N)	Longitude (°W)	Max. depth (m)	Perimeter (km)	Area (ha)
Arrowhead Lake	2002–2004	45.90634	−89.69024	13.11	3.50	40.05
Big Lake	2002, 2004	46.15474	−89.76970	18.59	15.17	343.64
Birch Lake	2002–2004	46.21767	−89.83838	13.72	10.50	212.03
Big Portage Lake	2002	46.12560	−89.28492	12.19	10.84	240.47
Little Star Lake	2002	46.11529	−89.86147	20.42	6.36	107.12
Round Lake	2002–2004	46.17186	−89.71024	7.62	3.66	71.52
Sparkling Lake	2002–2004, 2007–2010	46.00865	−89.69971	19.51	3.75	65.50
White Sand Lake	2002	46.08872	−89.59413	21.64	9.32	304.57
Plum Lake	2002	46.00328	−89.51930	17.37	23.33	427.75
Trout Lake	2002–2004	46.02900	−89.66500	35.70	25.90	1607.90
Wild Rice Lake	2002–2004	46.06481	−89.79323	7.90	5.90	153.00

Note: All lakes are in Vilas County, Wisconsin, USA.

Table A2. Best-fit parameter estimates for three candidate stock–recruitment models for rusty crayfish, where R is recruitment (juvenile crayfish density) and S is stock size (adult female crayfish density).

Model	Equation	α	β	AIC
Linear	$\log_e (R) = \log_e (\alpha \times S)$	15.99	NA	50.5
Beverton–Holt	$\log_e (R) = \log_e [(\alpha \times S)/(1 + \beta \times S)]$	15.99	0	52.5
Ricker	$\log_e (R) = \log_e (\alpha Se^{-\beta S})$	15.55	−0.01	52.4

Note: AIC, Akaike information criterion; NA, not applicable.

Appendix B. Inputs for bioenergetics simulations

Energy densities of prey items are listed in Appendix Table B1.

Age-specific individual growth rates were determined by back-calculating length at age from scales. Smallmouth bass, rock bass, and *Lepomis* were sampled via electrofishing on 4 nights in mid-summer 2000, and biweekly from late May to early September from 2001 to 2004 and from 2009 to 2010. A few smaller sampling efforts by the Wisconsin Department of Natural Resources and researchers from the University of Wisconsin-Madison added to the sample size for 2005 and 2006. Additional rock bass data were collected by LTER from 1981 to 2010 using Trammel and Fyke nets. Total length (TL; mm), mass (g), and scales were collected during all fish sampling efforts. Scale annuli were used to determine annual growth increments for individual fish (see below). Otoliths were collected from a small subsample ($n_r = 16$, $n_s = 24$ for rock bass and smallmouth bass, respectively) at the end of 2010.

Scales were aged by two independent readers. Length-at-age for each individual was calculated using the Fraser–Lee back-calculation model (Fraser 1916; Lee 1920):

$$L_i = \frac{S_i}{S_c}(L_c - c_{Sp}) + c_{Sp}$$

where L_i is the fish TL at time i, S_i is the scale length at time i, S_c is the scale length at time of capture, L_c is the fish TL at time of capture, and c_{Sp} represents the length (in mm) of fish when scale growth begins for a particular species. For this analysis published estimates of c were used ($c_{bluegill} = 20$, $c_{pumpkinseed} = 25$, $c_{rock\ bass} = 25$, $c_{smallmouth\ bass} = 35$; Carlander 1982). Mean age-specific lengths at the beginning and end of each growing season were calculated for each year of analysis and converted to masses (g) using empirical length–mass relationships for each species:

Bluegill: $\log_e (mass) = \log_e (length)$
$$\times\ 3.41-12.9\ (Adj.\ R^2 = 0.967)$$

Pumpkinseed: $\log_e (mass) = \log_e (length)$
$$\times\ 3.51-13.2\ (Adj.\ R^2 = 0.885)$$

Rock bass: $\log_e (mass) = \log_e (length)$
$$\times\ 2.96699-10.66337\ (Adj.\ R^2 = 0.908)$$

Smallmouth bass: $\log_e (mass) = \log_e (length)$
$$\times\ 2.9773-11.1293\ (Adj.\ R^2 = 0.934)$$

If size at age data were not available for a given year, mean values from other years within the same qualitative crayfish density category (high or low; see main text) were used. Because scales were last collected in 2010, the annulus for that year had not formed, and 2009 size-at-age data were used for the 2010 analysis.

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Table B1. Prey items found in fish diets, energy density values for bioenergetics modeling, and sources.

Prey item description	Energy density ($J \cdot (g\ wet\ mass)^{-1}$)	Source
Amphipoda	4429	Hanson et al. 1997
Annelida	2699	Cummins and Wuycheck 1971
Arachnid	5320	Gray 2005
Bivalva	2008	Cummins and Wuycheck 1971
Coleoptera	7970	Gray 2005
Crayfish	3766	Roell and Orth 1993
Zooplankton	2653	Hanson et al. 1997
Diptera adult	6317	Gray 2005
Diptera larvae	1763	Hanson et al. 1997
Ephemeroptera adult	9686[a]	Cummins and Wuycheck 1971
Ephemeroptera larvae	4703[b]	Cummins and Wuycheck 1971
Gastropoda	1799	Cummins and Wuycheck 1971
Hemiptera	9686[a]	Cummins and Wuycheck 1971
Hydracarina	4099	Cummins and Wuycheck 1971
Hymenoptera	5710[c]	Cummins and Wuycheck 1971
Isopoda	3142	Cummins and Wuycheck 1971
Megaloptera	4360	Cummins and Wuycheck 1971
Odonata adult	9686[a]	Cummins and Wuycheck 1971
Odonata larvae	3139[d]	Cummins and Wuycheck 1971
Oligochaeta	2699[e]	Cummins and Wuycheck 1971
Plant matter	1331[f]	Cummins and Wuycheck 1971
Terrestrial items	9686[a]	Cummins and Wuycheck 1971
Trichoptera adult	7760	Gray 2005
Trichoptera larvae	3848	Cummins and Wuycheck 1971
Unidentified	4903[g]	Cummins and Wuycheck 1971
Unidentified invertebrate	3314[h]	Cummins and Wuycheck 1971
Fish	5328[i]	Cummins and Wuycheck 1971

Note: If multiple energy densities were available for a prey group (e.g., multiple species within an order), the mean value of all taxa was used (exceptions noted). When energy densities were presented on a per dry mass basis, they were converted to wet mass using percent water values for similar taxa from Cummins and Wuycheck (1971).
[a]All terrestrial insects.
[b]Baetidae larvae.
[c]Honey bee (*Apis mellifera*) excluded.
[d]Gomphidae and Libellulidae larvae.
[e]Aquatic Annelida.
[f]*Najas* spp. and *Chara* spp.
[g]All other prey groups.
[h]Aquatic arthropods.
[i]Cyprinidae.

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Appendix C. Diet sample sizes

Table C1. Diet sample sizes (number of fish) for each species and year used in this analysis.

	2001	2002	2003	2004	2009	2010	Total
BGS	0	0	0	0	28	44	72
PKS	0	0	0	0	22	33	56
RKB	101	98	59	80	90	75	517
SMB	121	107	84	87	132	101	661
Total	222	205	143	167	272	253	1306

Note: BGS, bluegill; PKS, pumpkinseed; RKB, rock bass; SMB, smallmouth bass. One pumpkinseed diet was collected in 2001 but not used in this analysis.