Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: a whole-lake experiment

Catherine L. Hein, Brian M. Roth, Anthony R. Ives, and M. Jake Vander Zanden

Abstract: Improved methods are needed for the prevention and control of invasive species. We investigated the potential to control a rusty crayfish (*Orconectes rusticus*) population in an isolated lake in northern Wisconsin by trapping adult crayfish and restricting fishing, thereby increasing fish populations and predation on small crayfish. Over a 3 year period, traps and predatory fishes removed substantial portions of the rusty crayfish population. We used an age-structured population model to determine which removal method had the largest effect on crayfish population growth rates. Because more crayfish were vulnerable to and removed by fish predation than by trapping, fish predation caused a larger decline in the population growth rate. However, trapping removed crayfish with the highest reproductive value and caused the largest decline in population growth rate per individual crayfish removed. Consideration of density-dependent responses to removal is necessary to predict long-term effects on rusty crayfish population dynamics. Nonetheless, our results suggest that the combination of trapping and fish predation can control established rusty crayfish populations and deserves further consideration for management.

Résumé : Il est nécessaire d'améliorer les méthodes de prévention et de contrôle des invasions d'espèces. Nous avons évalué le potentiel d'une méthode de contrôle d'une population de l'écrevisse américaine (*Orconectes rusticus*) dans un lac isolé du nord du Wisconsin en piégeant les écrevisses adultes et en limitant la pêche, augmentant ainsi les populations de poissons et la prédation sur les petites écrevisses. Sur une période de 3 ans, le piégeage et la prédation par les poissons ont éliminé un pourcentage important de la population d'écrevisses américaines. Un modèle démographique structuré en fonction de l'âge a servi à déterminer quelle méthode de retrait a le plus d'effet sur les taux de croissance de la population d'écrevisses. Parce que les écrevisses sont plus vulnérables à la prédation par les poissons qu'au piégeage et que plus d'écrevisses sont éliminées par les poissons prédateurs, la prédation cause un déclin plus important du taux de croissance de la population. Cependant, le piégeage retire les écrevisses qui ont la valeur reproductive la plus élevée et cause donc le déclin le plus important du taux de croissance de la population par écrevisse individuelle retirée. Il faut tenir compte des réactions dépendantes de la densité aux retraits afin de prédire les effets à long terme sur la population d'écrevisses américaines. Néanmoins, nos résultats indiquent qu'une combinaison de piégeage et de prédation par les poissons peut contrôler une population établie d'écrevisses américaines; on devrait en tenir compte en gestion.

[Traduit par la Rédaction]

Introduction

Invasive species are regarded as the most significant threat to biodiversity in aquatic ecosystems (Sala et al. 2001). In the Great Lakes region, aquatic invaders such as zebra mussels (*Dreissena polymorpha*) and rainbow smelt (*Osmerus mordax*) have altered food webs and extirpated native species, causing significant economic costs (Nalepa and Schloesser 1993; Hrabik et al. 1998; Pimental et al. 2000). Negative eco-logical and economic impacts of aquatic invasive species are best minimized through targeted prevention of future invasions (Mack et al. 2000; Kolar and Lodge 2001; Vander Zanden et al. 2004). In many areas, invasive species are already established, necessitating methods to manage exotic populations. In addition, eradication may suppress future spread from new source populations (Myers et al. 2000).

Opportunities for remediation of established exotic populations do exist, and the literature is rich with examples of

C.L. Hein,[1,2] B.M. Roth,[3] and M.J. Vander Zanden. Center for Limnology, 680 N. Park Street, University of Wisconsin, Madison, WI 53706, USA.
A.R. Ives. Department of Zoology, 459 Birge Hall, 430 Lincoln Drive, University of Wisconsin, Madison, WI 53706, USA.

[1]Corresponding author (e-mail: clhein@cc.usu.edu).
[2]Present address: Department of Aquatic, Watershed and Earth Resources, 5210 Old Main Hill, Utah State University, Logan, UT 84322-5210, USA.
[3]Present address: Coastal Fisheries Institute, School of the Coast and Environment, Energy, Coast, and Environment Building No. 2255, Louisiana State University, Baton Rouge, LA 70803, USA.

384

Can. J. Fish. Aquat. Sci. Vol. 63, 2006

successful and unsuccessful attempts to control or eradicate exotics (Smith and Tibbles 1980; Knapp and Matthews 1998; Myers et al. 2000). Many management strategies use toxicants or introduce other exotic species to control target invaders (Ray and Stevens 1970; Bills and Marking 1988; Simberloff and Stiling 1996), which may create new problems with or without alleviating the original ones. Additionally, restoration goals may not be accomplished if the outcome of removal is not placed in a whole-ecosystem context (Zavaleta et al. 2001). Thus, targeted control efforts that enhance the natural control of exotic species and consider the ecosystem-level result are of high value.

The rusty crayfish (*Orconectes rusticus*) is an invader that has significantly impacted aquatic ecosystems. Rusty crayfish expanded beyond their native range in the Ohio River Valley in the 1970s and are well studied as invaders (Hobbs et al. 1989; Taylor et al. 1996; Lodge et al. 2000). In the lakes of northern Wisconsin, rusty crayfish were probably introduced by fishermen as live bait and then dispersed naturally through connected systems (Capelli and Magnuson 1983; Hobbs et al. 1989). Rusty crayfish populations are established in many bodies of water, often leading to rapid ecological change in invaded lakes. Rusty crayfish displace native species of crayfish (Capelli 1982; Capelli and Munjal 1982), destroy macrophyte beds (Olsen et al. 1991; Wilson 2002), compete with fishes for invertebrate prey, and decrease recruitment rates of sport fishes by eating eggs and removing macrophyte habitat (Magnuson et al. 1975; Capelli and Magnuson 1983; Lodge and Lorman 1987).

Given these impacts on aquatic ecosystems, there are substantial benefits to reducing the effects of rusty crayfish in invaded lakes. We initiated a whole-lake experiment to determine whether it is practical to remove enough rusty crayfish to control or reduce their impact on the lake ecosystem. Success depends on the logistic feasibility of rusty crayfish population reduction, the potential for rusty crayfish reinvasion, and the susceptibility of rusty crayfish to control measures (Myers et al. 2000). Sparkling Lake in Vilas County, Wisconsin (46.00°N, 89.70°W), was ideal for this rusty crayfish eradication experiment because the lake is relatively small (64 ha) and already contains two crayfish predators, smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*). The probability of reinvasion is low owing to the lack of surface inlets or outlets and a ban on the use of crayfish as live bait (Capelli and Magnuson 1983; Lodge et al. 1985). The efficacy of crayfish removal remains unclear: several studies conclude that trapping alone is ineffective for crayfish control (Momot and Gowing 1977; Momot 1991, 1993), whereas other studies conclude that fish can effectively control crayfish (Svärdson 1972; Rach and Bills 1989).

We designed a whole-lake experiment to overexploit a rusty crayfish population by trapping and simultaneously protecting the population of smallmouth bass from fishing pressure. We used an age-structured population model to determine which age classes to remove for the most effective rusty crayfish control. Specifically, which results in a greater reduction in population growth rate, selective trapping or fish predation? Traps select large, adult crayfish (Capelli 1975), whereas fish select small crayfish (Stein 1977; Roth 2001). We compared the number of crayfish removed by trapping and the number consumed by fish each year with a population estimate. By using an age-structured population model to calculate population growth rates after trap or predator-induced mortality, we were able to account for the size and reproductive value of individuals removed.

Methods

Study site

Sparkling Lake is a mesotrophic seepage lake and is part of the North Temperate Lakes Long-Term Ecological Research Program (http://lter.limnology.wisc.edu). Sparkling Lake has a perimeter of 4.3 km and a maximum depth of 20 m (http://lter.limnology.wisc.edu). Most of the lake's littoral zone has a sandy substrate, although there are some cobble areas in the southwest. Macrophytes are sparse but densest in groundwater discharge areas (Hagerthey and Kerfoot 1998). Both rainbow smelt (*Osmerus mordax*) (Hrabik et al. 1998) and rusty crayfish invaded Sparkling Lake in the 1970s (Capelli 1982). In 1973, *Orconectes propinquus* dominated the catch (70%) followed by *O. virilis* (20%) and *O. rusticus* (10%) (Capelli 1982). *Orconectes virilis* is now only present at low levels, and the last documented observation of *O. propinquus* in Sparkling Lake was in 1998 (http://lter.limnology.wisc.edu). The density of *O. rusticus* in Sparkling Lake, at 60 crayfish·m^{-2}, is intermediate compared with densities of *O. rusticus* in surrounding lakes, which range from 0 to over 200 crayfish·m^{-2} (Roth 2005).

Trapping

We trapped and removed crayfish daily from 14 to 30 August 2001, from 2 July to 10 August 2002, and from 23 June to 26 August 2003. Preliminary trap surveys indicated that catch rates were highest on cobble substrates and extremely low on sand substrates (Hein 2004). Therefore, we concentrated traps on the southern and western shorelines of the lake, where cobble was prevalent and catch rates were highest. Wire minnow traps with an enlarged (3.5 cm diameter) opening were baited with 4 to 5 frozen smelt (8–13 g each) and set 1–2 m deep at ~10 m intervals. Effort increased in successive years. The number of trap-days increased from 1584 in 2001 to 3497 in 2002 to 7432 in 2003, where a trap-day is one trap fished for 24 h. At the highest level of effort, we set and pulled 184 traps per day. We counted every male and female crayfish captured in each trap and determined length–weight relationships by weighing and measuring carapace lengths of subsamples. Estimates of the biomass removed by traps and fish used this length–weight regression.

Fish predation

To protect and enhance populations of crayfish predators, the Wisconsin Department of Natural Resources instated strict regulations on smallmouth bass. As part of this project, the minimum length was increased from 356 mm to 457 mm total length, and the daily bag limit was decreased from 5 to 1 fish. Using electrofishing, we sampled fish bimonthly from late May through August in 2001, 2002, and 2003. Fish were also sampled once in mid-September and once in late October each year. We tagged all fish with Floy tags, fin clips, or both to estimate population sizes of smallmouth bass and rock bass each year using the modified Schnabel

mark and recapture method (Ricker 1975). Diets of both fish species were sampled using gastric lavage (Seaburg 1957). Carapace and chelae lengths of crayfish in diets were measured with vernier calipers.

We determined the total number and biomass of crayfish consumed by fish each year using Bioenergetics 3.0 (Hanson et al. 1997), using parameters developed by Whitledge et al. (2003) and Roell and Orth (1993) for adult smallmouth bass and rock bass, respectively. Analysis of fish scales provided age-specific growth estimates (Ricker 1975). Predator size–frequency data and population estimates were combined to approximate the number of fish at each age consuming crayfish. Simulations used average daily water temperatures of Sparkling Lake throughout the sampling period (http://lter.limnology.wisc.edu). We based diet information on that obtained from bimonthly sampling, as described above, and categorized the prey species. "Other fishes" included any fish species other than rainbow smelt (*Osmerus mordax*) found in diets, but was dominated by mimic shiners (*Notropis volucellus*). Adult Ephemeroptera and Odonata, Hirudinea, Oligocheata, and Anura composed the "Other" prey category. The energy densities (J·g^{-1} wet mass) used in the model are 3766 for crayfish (Roell and Orth 1993), 4850 for rainbow smelt (Lantry and Stewart 1993), 5328 for fish (modeled as a Cyprinid; Cummins and Wuycheck 1971), and 4705 for all invertebrate categories (modeled as the mean energy density for larval Ephemeropterans; Hanson et al. 1997). The bioenergetics model incorporated the changing proportions of prey items throughout the summer.
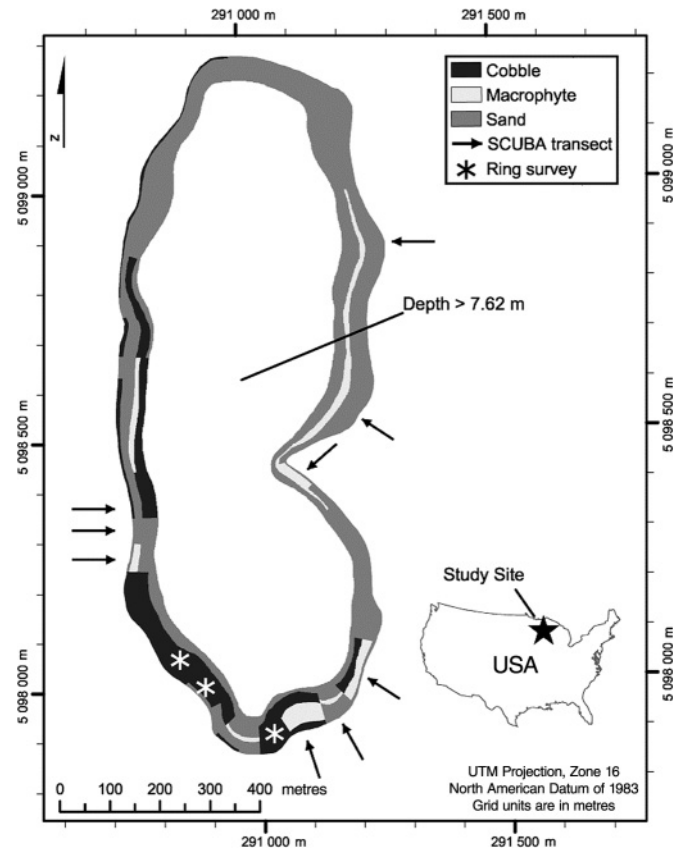
Population estimates

We estimated the total crayfish population size in August 2003 to gauge the portion of the population removed by trapping and fish predation. We summed the products of average crayfish densities and areas derived from a variety of habitat and depth zones according to

$$(1) \qquad \Sigma C_{h,d} \cdot A_{h,d}$$

where $C_{h,d}$ is the average crayfish density in habitat h and depth zone d, and $A_{h,d}$ is the corresponding area. Habitats were characterized as sand, macrophytes, or cobble; depth zones were 0–0.5, 0.5–3, 3–5, 5–6.5, and 6.5–8 m. At depths greater than 8 m, the substrate is muck, which is unsuitable habitat for crayfish (Capelli and Magnuson 1983). Because no simple method to calculate confidence intervals for this type of population estimate exists (because of the uncertainty in both crayfish densities within areas and the size of the areas), we present the point estimate.

We first estimated the area of the littoral zone. We swam 23 depth transects using SCUBA and recorded the habitat type within each depth zone. In addition, we observed the substrate around the perimeter of the lake at the 1 m depth contour from a boat using a global positioning system (GPS). We divided the lake into polygons of the same habitat for each depth range, called habitat–depth hereafter (Fig. 1). We assumed that areas between two transects with the same habitat were characterized by that habitat. If the habitats at adjacent transects were different, we assumed the transition was midway between transects. We interpolated the contour of the lake bottom using a digitized bathymetric map. We then used a geographic information system (GIS)

Fig. 1. Habitat characterization of cobble, macrophytes, and sand in five depth zones of Sparkling Lake, Wisconsin, USA. At depths greater than 7.62 m, the substrate was muck. Arrows represent transects surveyed for crayfish densities, and asterisks represent sites where netted rings were sampled using SCUBA.

to calculate the area of each habitat within each of the five depth zones.

We used three methods to estimate densities of adult and juvenile crayfish on different habitat types during the day. To accurately sample dense aggregations of small crayfish on cobble substrates, SCUBA divers collected all crayfish above and beneath the cobble within an area bounded by a ring set at 1–2 m depths. The ring consisted of a circular net 30 cm tall with 4 mm mesh suspended by a buoyant plastic ring and anchored with light chain. The netting prevented crayfish from escaping the ring during collection. Thus, we were able to obtain more accurate density estimates of small individuals and measure crayfish carapace lengths (CL). We sampled three 10 m^2 rings at each of three sites in July and August of 2002 and ten 1 m^2 rings at three sites in July and August of 2003 (Fig. 1). Because juvenile crayfish are often at high densities and difficult to collect, we sampled juvenile crayfish within a 0.09 m^2 ring using an underwater vacuum powered by air from a SCUBA tank, similar to the method employed by Wahle and Steneck (1991) to sample juvenile American lobsters (*Homarus americanus*). We completed three replicates at each site in 2002 and four replicates at each site in 2003. For the population estimate, we multiplied the average crayfish densities in August of 2003 by the area of cobble substrate.

386

Can. J. Fish. Aquat. Sci. Vol. 63, 2006

The quadrat method was not effective on sand and mud substrates because crayfish left the area before the quadrat landed on the bottom. Therefore, we swam transects to count the number of crayfish on open substrates. On 22 and 23 August 2003, we surveyed crayfish densities along nine transects perpendicular to shore using SCUBA. Transect sites that crossed sand or macrophyte habitats were selected randomly from trapping locations routinely sampled in 2001 and 2003 (Hein 2004). A pair of divers swam from the 0.5 m to the 8 m depth contours. We assumed that crayfish densities from 0 to 0.5 m depths were the same as those from 0.5 to 3 m depths on each habitat type. One diver held a 3 m long polyvinyl chloride (PVC) pipe to delineate the sample area and used a compass to maintain a heading perpendicular to shore. The other diver counted the number of crayfish within each depth zone used to estimate habitat area. The diver turned over logs and rocks to count hidden individuals and avoided recounting the same individuals. The average densities obtained from SCUBA transects were multiplied by the areas of sand and macrophyte habitats for the population estimate.

Modeling

Following the methods of Lin and Ives (2003), we built an age-structured Leslie matrix model for rusty crayfish to assess how age-selective mortality by traps and fish affect population growth rates (Table 1). These models use matrix algebra to calculate both the number of offspring born into each age class and the probability of surviving through a time step to enter the next age class (Caswell 2001). Refer to Crouse et al. (1987) for a detailed summary of matrix population models. Often, the population growth rates obtained from matrix models are used to project the population size and structure (Crouse et al. 1987). However, our goal was simply to compare population growth rates given different removal strategies.

We modified the Leslie matrix model to account for the additional mortality of crayfish removal by multiplying the age-specific survivorship (s_i) by survivorship from either trapping or fish predation (k_i). Because baseline survivorships were obtained from a lake with fishes subject to standard management practices (size and bag limits), the survivorship term for fish predation represents the effect of an enhanced predator population caused by changes in fishery management. The age-specific survivals from trapping and fish predation (k_i) were calculated as

$$(2) \qquad k_i = e^{(-mP_i)}$$

where P_i is the selectivity of traps and fish for crayfish of age i, and m scales the total population mortality resulting from trapping or fish predation: the larger the value of m is, the greater the mortality is from either trapping or enhanced predation pressure.

To calculate the impact of trapping or fish predation on the rusty crayfish population, we assumed that populations were initially at their stable-age distribution given by the Leslie matrix without additional mortality (i.e., $m = 0$). We then added age-selective removal (by either trapping or fish predation) by calculating the value of m that would remove a target proportion p of the total crayfish population. Age-specific removal of crayfish changes the stable-age distribu-

Table 1. Population projection matrix of the age-structured Leslie matrix model for an *Orconectes rusticus* population including age-specific survivorships (s_i), fertilities (f_i), and survivorships owing to additional mortality of trapping or fish predation (k_i).

	Age 0	Age 1	Age 2	Age 3
Fecundities	$(f_0 \cdot s_0)k_0$	$(f_1 \cdot s_0)k_0$	$(f_2 \cdot s_0)k_0$	$(f_3 \cdot s_0)k_0$
Age 1	$s_1 \cdot k_1$	0	0	0
Age 2	0	$s_2 \cdot k_2$	0	0
Age 3	0	0	$s_3 \cdot k_3$	0

tion and hence the proportion of the total population removed. For the new stable-age distribution, we recomputed m to again remove the target proportion of the population. We iterated this procedure until it converged on a value of m such that, at the stable-age distribution, the target proportion p of the crayfish population was removed by trapping or fish predation. This results in the hypothetical population growth rate of rusty crayfish after experiencing the same trapping or fishing pressure for many years.

To obtain age-class selectivity (P_i), we divided the proportion of crayfish in each age class in traps or fish diets by the proportion of that age class in the environment and standardized these numbers to add to 1 (Fig. 2b). The higher P_i is, the more selective the removal method is for that age class. We defined age classes according to sizes at age determined by Lorman (1980) in July and August (Fig. 2a). Crayfish in age class 0 are not yet reproductively mature, but those in age class I are (the smallest gravid female in Sparkling Lake had a carapace length of 15.8 mm). Data collected from the SCUBA quadrat surveys provided the sizes of crayfish in the environment. We measured 9671 crayfish in traps, 250 crayfish in fish diets, and 606 crayfish from hand collections and partitioned these individuals into the four age classes defined by Lorman (1980).
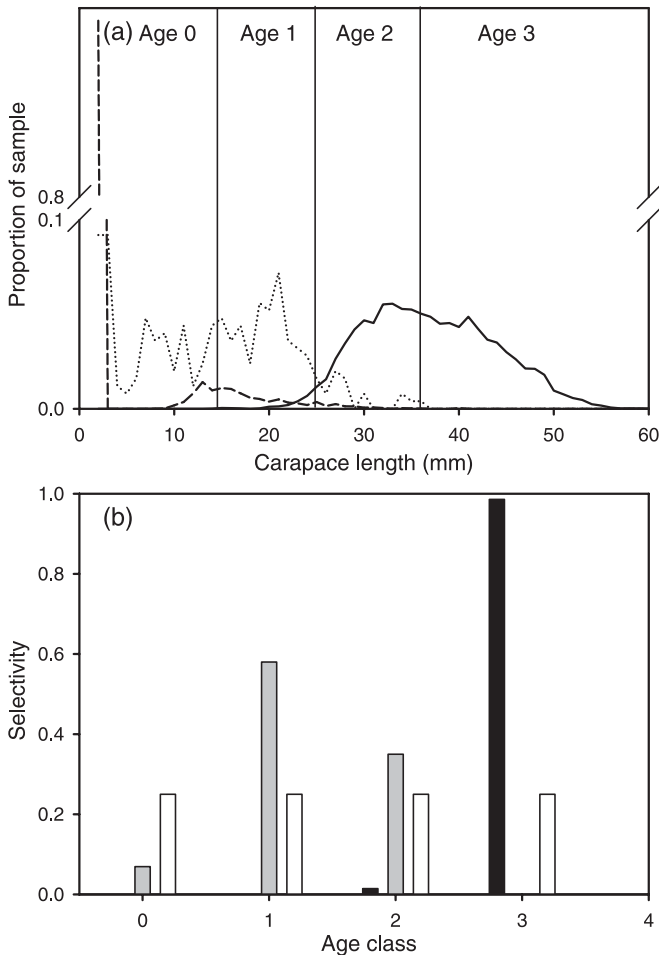
Because the population in Sparkling Lake was being manipulated, we parameterized the age-structured model using fertility and survivorship data from a rusty crayfish population in Upper Sugarbush Lake, Wisconsin, collected in the late 1970s by Lorman (1980). The age-specific fecundity (F_i) is the product of fertility (the number of juveniles per female) and juvenile survivorship ($f_i \cdot s_0$) (Caswell 2001). We approximated fertility using Lorman's regression between female carapace length and number of attached juveniles. Lorman observed a 50:50 sex ratio, so we halved the number of juveniles per female to obtain the fertility of each individual in the population (Caswell 2001). From Lorman's data, we used two methods to compute survivorships (s_i) because they both give plausible yet different Leslie matrices. First, we divided September age-specific population estimates by those in May (Lorman 1980) to obtain survivorships for age classes I to III (Table 2). Juvenile survivorship (s_0) was estimated using population estimates from June to September (Lorman 1980). These survivorships do not include winter, but most mortality occurs during summer owing to molting and increased predation by fishes (Lorman 1980; Momot 1991). This method computes survivorships directly, but only for the single year of Lorman's study. For the second method, we computed survivorships from the stable-age dis-

Table 2. Survivorship (s_0–s_3) and fertility (f_1–f_3) for the Leslie matrix model based on an *Orconectes rusticus* population in northern Wisconsin (Lorman 1980).

Parameter	s_0	s_1	s_2	s_3	f_1	f_2	f_3
Method 1	0.0316	0.652	0.3633	0.1283	44.5	62.5	81.5
Method 2	0.0157	0.708	0.607	0.091	44.5	62.5	81.5

Note: In method 1, survivorships were calculated from censuses in May and September, and in method 2, survivorships were computed to give a stable-age distribution corresponding to the observed age distribution in May.

Fig. 2. (*a*) Sizes of crayfish (*Orconectes rusticus*) in traps, fish diets, and the environment as determined by hand collections. Lines in (*a*) show the percentage of crayfish in traps (solid), fish diets (dotted), and SCUBA collections (broken) in each 1 mm carapace length interval. Vertical lines denote the size ranges of each age class. Crayfish measured over all three years are included in the figure. Bars in (*b*) show age selectivities (P_i) of trapping (solid bars), fish predation (shaded bars), and nonselective removal (open bars).

tribution observed in May under the assumption that the population was at stationarity with an average population growth rate of 0. Because the rusty crayfish population was well established in Upper Sugarbush Lake at the time of Lorman's study, assuming stationarity is reasonable.

We performed a sensitivity analysis to determine the robustness of our conclusions about the relative impacts of trapping and fish predation on rusty crayfish population growth rates. We began with the Leslie matrix parameterized using method 1 and randomly varied the parameters by selecting values from independent uniform distributions ranging from 50% below to 50% above the estimated values. We generated 2000 Leslie matrices by randomly selecting parameter values and then calculated the crayfish population growth rates with trapping, fish predation, or nonselective removal.

Results

Removal and population estimates

In combination, traps and fish removed a substantial portion of the population. We estimated that traps and fish removed a total of 1 212 148 individuals and 1212 kg of crayfish over three years of removal. Together they removed approximately 55% of the population in 2003. Fish predation removed a greater portion of the entire rusty crayfish population than trapping in terms of biomass and numbers of crayfish (Fig. 3). Our surveys gave an estimated population size of 365 960 crayfish in August of 2003. However, this estimate does not account for mortality that occurred over the summer owing to removal. A more accurate population estimate for the summer of 2003 is 578 790, which is the sum of the August 2003 population estimate and the number of crayfish consumed by fishes and removed by traps prior to the population estimate in August 2003. Fish consumed an estimated 298 600 crayfish in 2003, or 51% of the entire crayfish population. Traps removed 22 585 crayfish in 2003, or 4% of the total population. Over the three years of removal, fish consumed ~247 kg more crayfish than traps captured. A larger proportion of the crayfish population was susceptible to fish predation relative to trapping (Fig. 2*a*). Approximately 91% of crayfish collected in 1 m² rings were juveniles and less than 1% of crayfish were age class II or III. The size distributions of crayfish in traps and fish diets overlapped between 20 mm and 35 mm CL, but most crayfish consumed by fishes had CL less than 25 mm. Conversely, most trapped crayfish had CL greater than 25 mm (Fig. 2*a*).

Although trapping removed fewer crayfish than fish predation, traps effectively removed crayfish biomass and nearly all crayfish vulnerable to trapping. Crayfish biomass caught in traps was nearly as high as that removed by predators each year (Fig. 3*b*). Crayfish most vulnerable to trapping, those in age classes II and III, composed only 3% of the population, and we removed approximately 4% of the total population in 2003. This slight discrepancy is largely the result of error in the population estimate and suggests that trapping removed most crayfish vulnerable to trapping in

Fig. 3. (*a*) Number and (*b*) biomass (kg) of crayfish (*Orconectes rusticus*) removed each year by trapping (solid bars) and fish predation (shaded bars). The open bar in (*a*) shows the 2003 rusty crayfish population estimate adjusted for mortality that occurred over the summer as the result of removal.
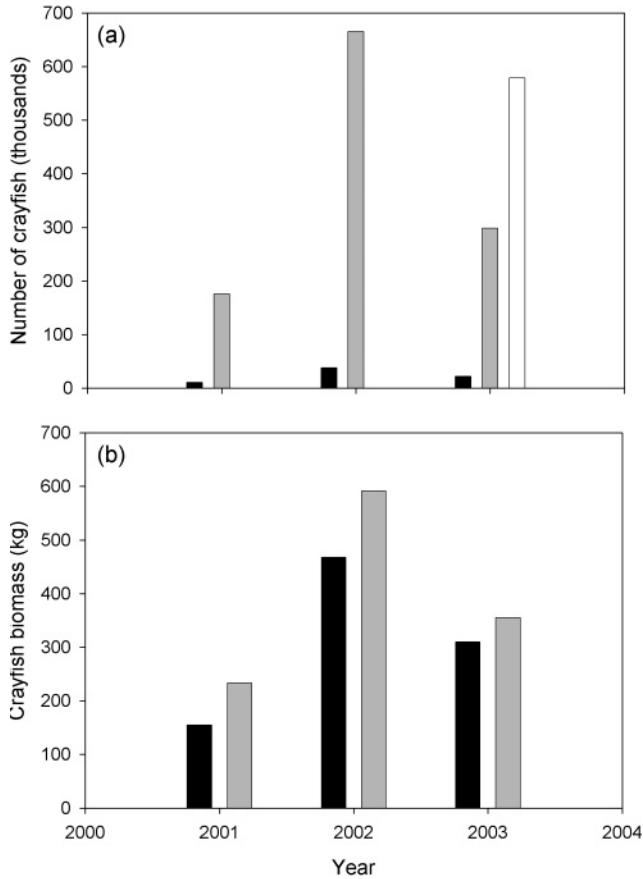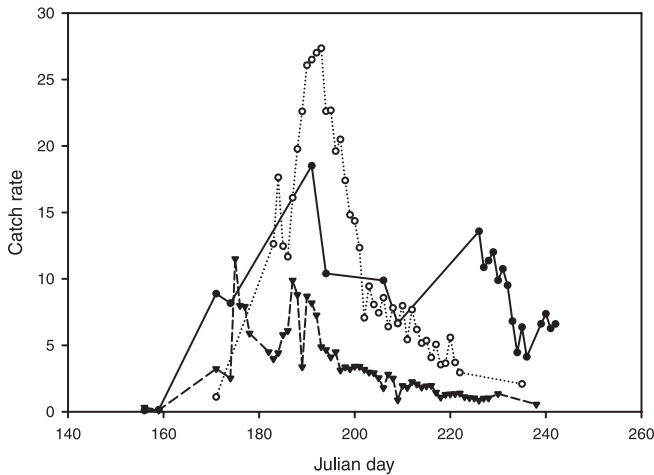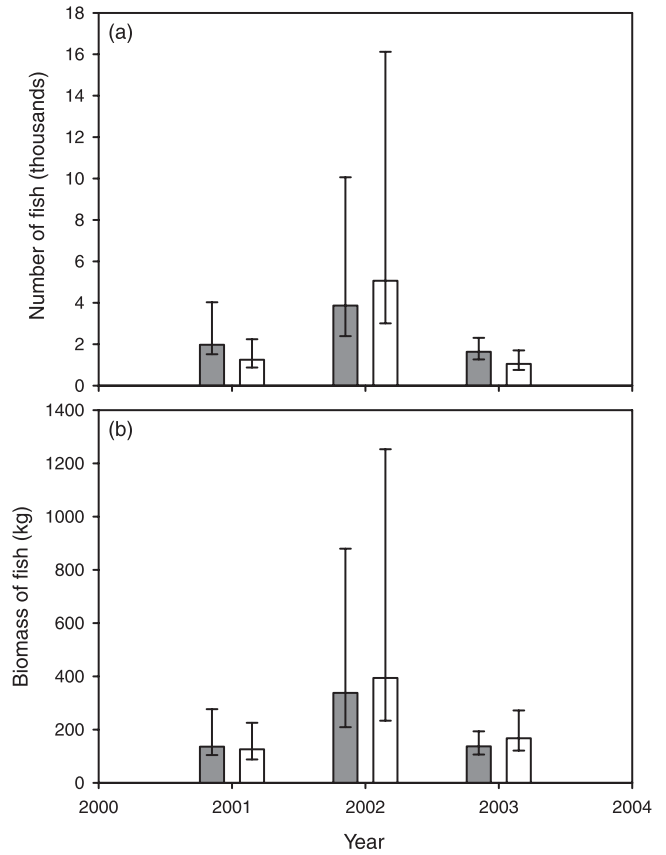

Fig. 4. Mean daily catch rates of rusty crayfish (*Orconectes rusticus*) in 2001 (●), 2002 (○), and 2003 (▼). The removal began on 14 August 2001 (Julian day 226).

2003. Substantial declines in catch rates each year of the removal provide further evidence for the strong impact of trapping on large crayfish. After one year of removal, catch

Fig. 5. (*a*) Schnabel population estimates and (*b*) estimated biomass of rock bass (*Ambloplites rupestris*) (shaded bars) and smallmouth bass (*Micropterus dolomieu*) (open bars) each year. Error bars give the 95% confidence intervals.

rates in August declined from 6.6 to 2.1 crayfish per trap. After two years of removal, catch rates fell to 0.56 crayfish per trap (Fig. 4).

The abundance of smallmouth bass and rock bass did not steadily increase each year (Fig. 5). The population estimates and estimated biomass of both species were highest in 2002. Because there were few recaptures in 2002, the error bars of these population estimates were also large (Fig. 5). Crayfish composed the largest portion of bass diets each year, except in 2002 when smallmouth bass consumed a greater proportion of fishes (Table 3). Rock bass diets contained a smaller proportion of crayfish in 2002 and 2003 than in 2001, and an individual ate fewer crayfish per day (Fig. 6*a*). Similarly, smallmouth bass consumed fewer crayfish per day in 2002 and 2003 than in 2001 (Fig. 6*b*). Fishes became a more dominant prey item in smallmouth bass diets over time (Table 3). These changing consumption rates and diet compositions were incorporated into the bioenergetics models used to estimate the number and biomass of crayfish consumed by bass each year.
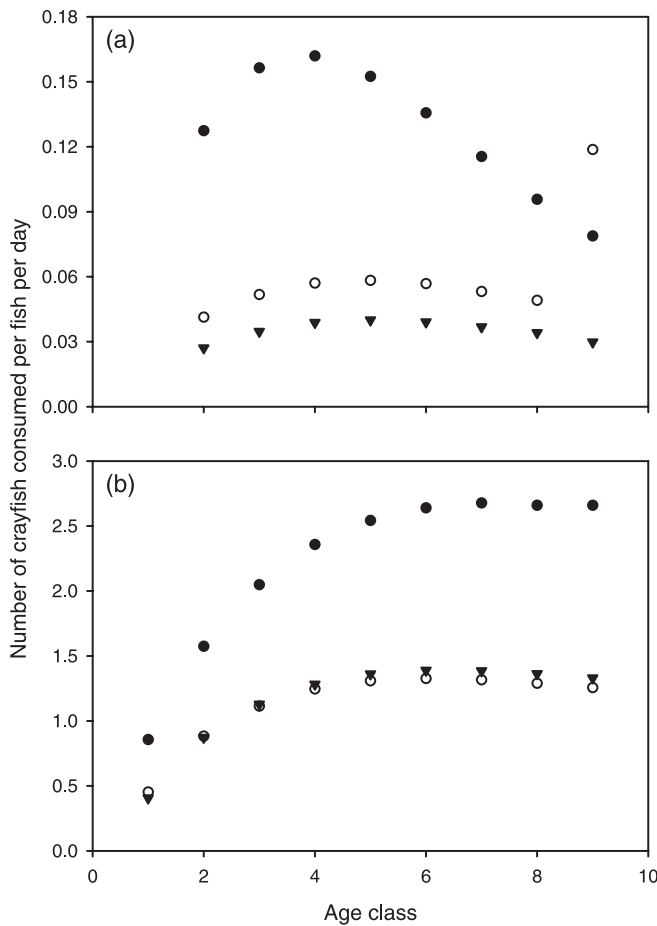
Catch rates of native crayfishes in Sparkling Lake did not change. We caught 17, 16, and 20 *O. virilis* in 2001, 2002, and 2003, respectively. Because effort increased each year, the catch rate of *O. virilis* slightly decreased from 0.008 crayfish per trap in 2001 to 0.003 crayfish per trap in 2003. We did not catch any *O. propinquus*.

Table 3. Average (standard deviation in parentheses) proportion of each prey item in the diets of smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) between May and October each year.

	Rock bass			Smallmouth bass		
	2001	2002	2003	2001	2002	2003
Crayfish	0.6776 (0.2116)	0.4035 (0.3296)	0.4579 (0.2377)	0.5663 (0.2555)	0.1523 (0.1379)	0.3677 (0.2461)
Osmerus mordax	0 (0)	0 (0)	0 (0)	0.0805 (0.0756)	0.1540 (0.3059)	0.0906 (0.1849)
Other fish	0.0623 (0.1759)	0.0705 (0.1334)	0.1390 (0.0957)	0.0966 (0.0907)	0.3394 (0.2157)	0.2828 (0.2483)
Ephemeroptera	0.1065 (0.1158)	0.0977 (0.1377)	0.0737 (0.0653)	0.0581 (0.0974)	0.0370 (0.0452)	0.0343 (0.0731)
Odonata	0.0537 (0.0739)	0.0987 (0.1065)	0.1551 (0.1016)	0.0868 (0.1565)	0.0717 (0.1071)	0.0684 (0.0463)
Other	0.0998 (0.1513)	0.3295 (0.3555)	0.1743 (0.0439)	0.1116 (0.1639)	0.2457 (0.2198)	0.1563 (0.2197)

Note: Refer to the text for descriptions of prey categories.

Fig. 6. Average daily consumption rate of crayfish by individual (*a*) rock bass (*Ambloplites rupestris*) and (*b*) smallmouth bass (*Micropterus dolomieu*) in 2001 (●), 2002 (○), and 2003 (▼).

Fig. 7. Crayfish (*Orconectes rusticus*) population growth rates as functions of the proportion (*p*) of the total population removed by trapping (r_{trap}), fish predation, (r_{fish}), or nonselective removal (r_{even}) with Leslie matrix model parameterization by (*a*) method 1 or (*b*) method 2.
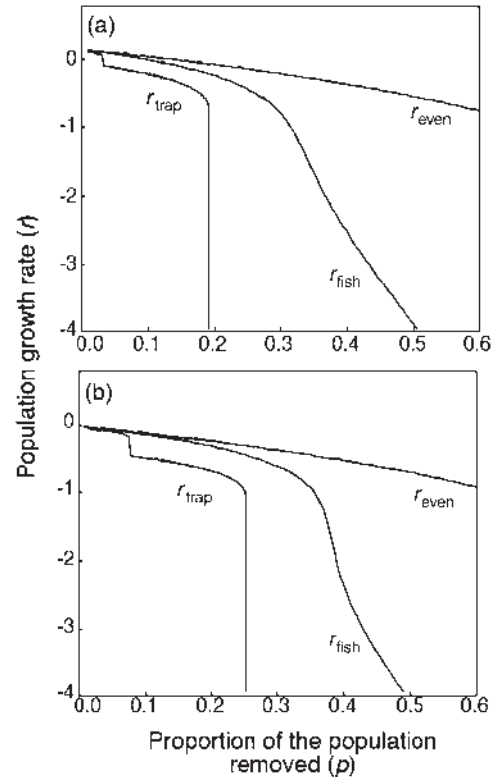

Modeling

The effect of removal on the population growth rate depends on the number and reproductive value of individuals removed. Trapping removes large crayfish with a high reproductive value, whereas fish consume a greater quantity of crayfish with low reproductive value. Overall, fish predation decreased the population growth rate most because a greater number of crayfish were removed.

Because trapping removes individuals of greater reproductive value, trapping leads to lower crayfish population growth rates than fish predation when standardized so that the same proportion of the total crayfish population is removed (Fig. 7). Although not as extreme as trapping, fish also remove larger crayfish than the average size in the population (Fig. 2*a*). Therefore, fish predation leads to lower population growth rates than nonselective crayfish removal when standardized to the same proportion of the total population removed (Fig. 7). The impact of trapping on larger age classes is apparent in the step-like changes in the population growth rate when the proportion of the total population removed by trapping reaches 0.04 (Fig. 7*a*) or 0.08 (Fig. 7*b*). At these levels, the population growth rate drops as the most fecund component of the population (age class III) essentially be-

Table 4. Sensitivity analysis for parameter values in the Leslie matrix model parameterized using method 1.

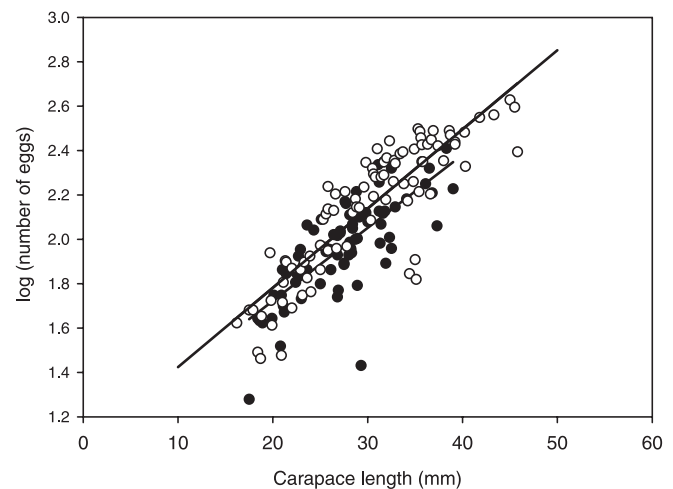| Measure	Minimum	5% quantile	Mean	95% quantile	Maximum
$r_{trap}(0.04) - r_{fish}(0.04)$	–0.41	–0.29	–0.15	–0.04	–0.013
$r_{trap}(0.04) - r_{even}(0.04)$	–0.43	–0.31	–0.16	–0.05	–0.018
$r_{fish}(0.04) - r_{even}(0.04)$	–0.030	–0.024	–0.014	–0.0066	–0.0032
$r_{trap}(0.04) - r_{fish}(0.51)$	3.81	3.88	3.99	4.20	4.33
$r_{fish}(0.51) - r_{even}(0.51)$	–3.75	–3.63	–3.48	–3.37	–3.31
$r_{trap}(0.04)$	–0.75	–0.42	–0.078	0.21	0.30
$r_{fish}(0.04)$	–0.46	–0.21	0.072	0.33	0.46
$r_{fish}(0.51)$	–4.66	–4.44	–4.06	–3.74	–3.64

Note: Two-thousand Leslie matrices were constructed by randomly selecting survivorship (s_0–s_3) and fertility (f_1–f_3) values from uniform distributions ranging from 50% below to 50% above the estimated parameter values. The first four rows of the table give the differences in population growth rates between removal methods; the last three rows give the range of population growth rates of each removal method. The proportions of the population removed by each method are given in parentheses.

comes 0. The population growth rate drops precipitously when age class II is eliminated by trapping.

Although trapping leads to the lowest population growth rates, this is only true if each of the selective agents removes the same proportion (p) of the population. In Sparkling Lake, trapping removed roughly 4% of the total population, whereas fish predation removed 51% of the total population. The population growth rate is –0.0972 or –0.0657 after 4% of the population was removed by trapping and –4.0258 or –4.2451 after 51% of the population was consumed by fishes (for the Leslie matrix parameterized by method 1 or method 2, respectively). Therefore, fish predation caused a greater reduction in the population growth rate than trapping.

Although these values cannot be used to project the crayfish population size into the future, the relative impacts of trapping and fish predation on the population growth rate are robust to parameter uncertainty in the Leslie matrix. We subtracted the population growth rates of one removal method from another removal method for all 2000 randomly constructed Leslie matrices. Because all of the differences had the same sign, our conclusions about the relative effects of each removal method withstand model uncertainty. The differences in crayfish population growth rates between the three age-selective removal methods are given (Table 4): trapping, $r_{trap}(p)$, fish predation, $r_{fish}(p)$, and nonselective removal, $r_{even}(p)$, when the proportion of crayfish removed (p) equals either that achieved by traps ($p = 0.04$) or that achieved by fish predation ($p = 0.51$). For example, negative values obtained when $r_{fish}(0.04)$ is subtracted from $r_{trap}(0.04)$ show that the population growth rate given trapping is always lower than that given fish predation. When $p = 0.04$, trapping always led to the lowest crayfish population growth rates ($r_{trap}(0.04) - r_{fish}(0.04) < 0$), and nonselective removal always led to the highest crayfish population growth rate ($r_{fish}(0.04) - r_{even}(0.04) < 0$). Using those levels of removal observed during the experiment, fish predation always led to the lowest population growth rate ($r_{trap}(0.04) - r_{fish}(0.51) > 0$). The robustness of our conclusions is emphasized by the wide range of values of crayfish population growth rates ($r_{trap}(0.04)$, $r_{fish}(0.04)$, and $r_{fish}(0.51)$) that were calculated from the 2000 randomly constructed Leslie matrices used for the sensitivity analysis (Table 4).

Fig. 8. Fecundity of rusty crayfish (*Orconectes rusticus*) in 2002 (●) and 2003 (○). The lower line shows the regression from 2002 ($y = 0.0329x + 1.0636$, $R^2 = 0.5813$), and the upper line shows the regression from 2003 ($y = 0.0357x + 1.0672$, $R^2 = 0.7458$).

No evidence of a compensatory response in rusty crayfish fecundity to the removal exists. The fecundity of rusty crayfish did not increase from 2002 to 2003 (Fig. 8). Fecundity data from 2001 and prior years are not available. Therefore, the assumption that the rusty crayfish population in Sparkling Lake exhibits stable, age-specific fecundities is valid. Further investigation is necessary to determine whether other aspects of the rusty crayfish population (e.g., survivorship) exhibit a density-dependent response.

Discussion

The combination of trapping and fishing regulations that protect predatory fishes effectively reduced the catch and abundance of rusty crayfish. Our age-structured population model showed that fish predation caused the largest decline in the crayfish population growth rate because a large number of crayfish were consumed. Although a small portion of the population was vulnerable to trapping, the population growth

rate at low levels of removal decreased most with trapping, which removed crayfish of the highest reproductive value.

Other studies support the conclusion that smallmouth bass and rock bass could feasibly control rusty crayfish populations. Centrarchids commonly consume crayfish (Stein 1977; Vander Zanden et al. 1997) and depend on crayfish energetically (Rabeni 1992). In many bodies of water, fish consume as much as 40% of the annual crayfish production (Dorn and Mittelbach 1999). Largemouth bass (*Micropterus salmoides*) removed 98% of *O. immunis* from a small pond (Rach and Bills 1989), and eels (*Anguilla anguilla*) have extirpated crayfish populations (*Astacus astacus* and *Pacifastacus leniusculus*) in Sweden (Svärdson 1972).

Knowledge of baseline levels of crayfish mortality in Sparkling Lake resulting from fish predation is necessary to determine how much additional mortality occurred after the change in fishing regulations. Fish may have consumed a substantial proportion of the crayfish population prior to the manipulation, as well as in 2003. Although the survivorship parameters of the matrix model were based on a system with predators, which assumed crayfish and fish populations were at equilibrium, increased predation will only decrease population growth rates further.

Traps substantially reduced growth rates and may effectively control rusty crayfish. Many studies claimed that crayfish control or eradication by trapping is infeasible, but these studies were on small lakes with low populations of predatory fishes (Momot and Gowing 1977; Momot 1991, 1993). Traps have also been widely cited as selective for large males (Momot and Gowing 1977; Lodge et al. 1985; Momot 1993), leaving behind females with whom remaining males may breed. However, Hein (2004) showed that 47% of crayfish removed were females in 2003. These females are the largest, most fecund members of the population, and their removal is critical to the success of the eradication effort. Accordingly, the model led to large declines in the population growth rate when crayfish in age classes vulnerable to trapping were removed.

The goal of the model was to contrast the relative rather than absolute effects of trapping and fish predation on population growth rates. Just as other studies have observed (Momot 1967; Momot and Gowing 1977), survivorship is extremely low for age-0 individuals, higher for age-1 individuals, and low for age-2 and age-3 individuals. As seen from the sensitivity analysis, the predicted relative effects of trapping vs. fish predation were robust to high levels of uncertainty in the model parameter values. Nonetheless, survivorship estimates are not exact (e.g., method 1 does not include overwinter mortality), and the absolute crayfish population growth rates obtained during the sensitivity analysis fluctuated widely, giving both positive and negative estimates. Therefore, to accurately predict the actual change in population growth rates resulting from trapping and fish predation, parameterization of the Leslie matrix model must be more precise.

Age- or size-based population models have been used to determine which age classes to protect for conservation of endangered populations (Crouse et al. 1987), to protect for sustainable forestry (Freckleton et al. 2003) and fishery practices (Frisk et al. 2002), or to exploit for control of pests or invaders (Shea and Kelly 1998; Parker 2000). Many of these studies use elasticity analysis, which is the proportional change in population growth rate caused by a proportional change in a life history parameter (Crouse et al. 1987; Shea and Kelly 1998; and Frisk et al. 2002). These studies recommend that management strategies focus on life history parameters with the highest elasticity, but Norris and McCulloch (2003) show that the scope for management must also be considered because management practices may not be able to significantly affect the vital rate targeted by the analysis. Our model did not directly measure changes in vital rates given management strategies, but it did recognize that trapping and fish predation remove different quantities of crayfish from a range of age classes.

In addition, Freckleton et al. (2003) conclude that management recommendations may be erroneous when population models do not include density dependence. Our exponential growth model does not consider density-dependent responses of the crayfish population to removal, which is necessary to predict the long-term effects of rusty crayfish removal. If population growth increased at low adult densities, rusty crayfish extirpation would be more difficult. Alternatively, decreased growth, fecundity, or juvenile survivorship in response to removal would indicate depensation (Hilborn and Walters 1992). Momot and Gowing (1977) found decreased fecundity with harvest in an *O. virilis* population, but fecundity in the Sparkling Lake *O. rusticus* population has not changed in response to removal. Crayfish production and juvenile survivorship respond variably to trapping in different lakes (Momot and Gowing 1977; Momot 1991, 1993). A greater understanding of density dependence in crayfish populations is required before including density dependence in our crayfish population model.

Even if rusty crayfish are not eradicated, we may be able to manage invader populations for reduced impacts. Our results illustrate that the combination of trapping and fishing regulations that protect native crayfish predators effectively control rusty crayfish. Continued removal may minimize negative effects on the aquatic community. Abundance and diversity of macrophytes and benthic invertebrates decline with rusty crayfish invasions (Wilson 2002). We expect an increase in the biomass of macrophytes and benthic invertebrates because of the decline in rusty crayfish since removal began. Preliminary analyses indicate that the percent cover of *Eleocharis* spp. and *Najas* spp. has increased, suggesting increased macrophyte abundance.

These large-scale changes in the lake ecosystem may interact to either benefit or hinder rusty crayfish control efforts. Predation rates on crayfish appear to be decreasing, perhaps because fewer crayfish and more macrophytes, which provide cover for crayfish, lead to lower encounter rates. Bass may switch to prey that are more abundant, such as mimic shiners. Therefore, the efficacy of removal may decline as the removal proceeds, and population growth rates may begin to increase. Alternatively, more macrophytes may aid in the recovery of sunfish populations (*Lepomis* sp.), which are important predators of juvenile crayfish (Roth 2005). In the latter case, population growth rates might decrease even further to the point where rusty crayfish are ac-

tually extirpated. These lakewide interactions will continue to be monitored and analyzed as the removal proceeds.

This type of whole-ecosystem experiment is crucial to understanding the ecology of rusty crayfish and to outlining pathways for successful management of this nuisance species. Small-scale experiments are useful for describing effects that occur over short temporal and small spatial scales but may fail to scale up to the proper management unit (a whole lake), which limits their application (Diamond 1986). Our eradication effort occurs on a scale that is relevant to both managers and ecologists. Scientists and managers should continue to develop invasive species control programs in contained systems that target the exotic species and enhance native predator populations. Removal of rusty crayfish on Sparkling Lake provides one example of invasive species control that may be effective, but studies on other lakes are necessary to determine the generality of our results. By taking an active approach, we may learn more about the ecology of invaders and minimize negative impacts on the ecosystems they invade.

Acknowledgments

References

Bills, T.D., and Marking, L.L. 1988. Control of nuisance populations of crayfish with traps and toxicants. Prog. Fish-Cult. **50**: 103–106.

Capelli, G.M. 1975. Distribution, life history and ecology of crayfish in northern Wisconsin with emphasis on *Orconectes propinquus* (Girard). Ph.D. thesis, University of Wisconsin, Madison, Wisc.

Capelli, G.M. 1982. Displacement of northern Wisconsin crayfish by *O. rusticus* (Girard). Limnol. Oceanogr. **27**: 741–745.

Capelli, G.M., and Magnuson, J.J. 1983. Morphoedaphic and biogeographic analysis of crayfish distribution in northern Wisconsin. J. Crustac. Biol. **3**: 548–564.

Capelli, G.M., and Munjal, B.L. 1982. Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. J. Crustac. Biol. **2**: 486–492.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. 2nd ed. Sinauer Associates, Sunderland, Mass.

Crouse, D.T., Crowder, L.B., and Caswell, H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology, **68**: 1412–1423.

Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Int. Assoc. Theor. Appl. Limnol. **18**: 1–158.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. *In* Community ecology. *Edited by* J. Diamond and T.J. Case. Harper & Row, New York. pp. 3–22.

Dorn, N.J., and Mittelbach, G.G. 1999. More than predator and prey: a review of interactions between fish and crayfish. Vie Milieu, **49**: 229–237.

Freckleton, R.P., Silva Matos, D.M., Bovi, M.L.A., and Watkinson, A.R. 2003. Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest for a tropical palm tree. J. Appl. Ecol. **40**: 846–858.

Frisk, M.G., Miller, T.J., and Fogarty, M.J. 2002. The population dynamics of little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*: predicting exploitation limits using matrix analyses. ICES J. Mar. Sci. **59**: 576–586.

Hagerthey, S.E., and Kerfoot, W.C. 1998. Groundwater flow influences the biomass and nutrient ratios of epibenthic algae in a north temperate seepage lake. Limnol. Oceanogr. **43**: 1227–1242.

Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish Bioenergetics 3.0 for Windows. University of Wisconsin Sea Grant Institute, Madison, Wisc.

Hein, C.L. 2004. Rusty crayfish (*Orconectes rusticus*) population dynamics during three years of intensive removal in Sparkling Lake, Wisconsin. M.Sc. thesis, University of Wisconsin, Madison, Wisc.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman & Hall, New York.

Hobbs, H.H., III, Jass, J.P., and Huner, J.V. 1989. A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). Crustaceana, **56**: 299–316.

Hrabik, T.R., Magnuson, J.J., and McLain, A.S. 1998. Predicting the effects of rainbow smelt on native fishes in small lakes: evidence from long-term research on two lakes. Can. J. Fish. Aquat. Sci. **55**: 1364–1371.

Knapp, R.A., and Matthews, K.R. 1998. Eradication of nonnative fish by gill netting from a small mountain lake in California. Restor. Ecol. **6**: 207–213.

Kolar, C.S., and Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. Trends Ecol. Evol. **16**: 199–204.

Lantry, B.F., and Stewart, D.J. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes — an interlake comparison. Trans. Am. Fish. Soc. **122**: 951–976.

Lin, L.A., and Ives, A.R. 2003. The effect of parasitoid host-size preference on host population growth rates: an example of *Aphidius colemani* and *Aphis glycines*. Ecol. Entomol. **28**: 542–550.

Lodge, D.M., and Lorman, J.G. 1987. Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. Can. J. Fish. Aquat. Sci. **44**: 591–597.

Lodge, D.M., Beckel, A.L., and Magnuson, J.J. 1985. Lake-bottom tyrant. Nat. Hist. **94**: 32–37.

Lodge, D.M., Taylor, C.A., Holdich, D.M., and Skurdal, J. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. Fisheries, **25**(8): 7–20.

Lorman, J.G. 1980. Ecology of the crayfish *Orconectes rustics* in northern Wisconsin. Ph.D. thesis, University of Wisconsin, Madison, Wisc.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. **10**: 689–710.

Magnuson, J.J., Capelli, G.M., Lorman, J.G., and Stein, R.A. 1975. Consideration of crayfish for macrophyte control. *In* Sympo-

sium on Water Quality Management Through Biological Control. Rep. No. ENV07-75-1. *Edited by* P.L. Brezonik and J.L. Fox. University of Florida, Gainesville, Fla. pp. 66–74.

Momot, W.T. 1967. Population dynamics and productivity of the crayfish, *Orconectes virilis*, in a marl lake. Am. Midl. Nat. **78**: 55–81.

Momot, W.T. 1991. Potential for exploitation of freshwater crayfish in coolwater systems: management guidelines and issues. Fisheries, **16**(5): 14–21.

Momot, W.T. 1993. The role of exploitation in altering the processes regulating crayfish populations. Freshw. Crayfish, **9**: 101–117.

Momot, W.T., and Gowing, H. 1977. Results of an experimental fishery on the crayfish *Orconectes virilis*. J. Fish. Res. Board Can. **34**: 2056–2066.

Myers, J.H., Simberloff, D., Kuris, A.M., and Carey, J.R. 2000. Eradication revisited: dealing with exotic species. Trends Ecol. Evol. **15**: 316–320.

Nalepa, T.F., and Schloesser, D.W. 1993. Zebra mussels: biology, impacts, and control. Lewis Publishers, Boca Raton, Fla.

Norris, K., and McCulloch, N. 2003. Demographic models and the management of endangered species: a case study of the critically endangered Seychelles magpie robin. J. Appl. Ecol. **40**: 890–899.

Olsen, T.M., Lodge, D.M., Capelli, G.M., and Houlihan, R.J. 1991. Mechanisms of impact of introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. Can. J. Fish. Aquat. Sci. **48**: 1853–1861.

Parker, I.M. 2000. Invasion dynamics of *Cytisus scoparius*: a matrix model approach. Ecol. Appl. **10**: 726–743.

Pimental, D., Lach, L., Zuniga, R., and Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. Bioscience, **50**: 53–65.

Rabeni, C.F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. Can. J. Fish. Aquat. Sci. **49**: 1714–1721.

Rach, J.J., and Bills, T.D. 1989. Crayfish control with traps and largemouth bass. Prog. Fish-Cult. **51**: 157–160.

Ray, J., and Stevens, V. 1970. Using Baytex to control crayfish in ponds. Prog. Fish-Cult. **32**: 58–60.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Department of Fisheries and Oceans, Ottawa, Canada.

Roell, M.J., and Orth, D.J. 1993. Trophic basis of production of stream-dwelling smallmouth bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. Trans. Am. Fish. Soc. **122**: 46–62.

Roth, B.M. 2001. The role of competition, predation, and their interaction in invasion dynamics: predator accelerated replacement. M.Sc. thesis, University of Wisconsin, Madison, Wisc.

Roth, B.M. 2005. An investigation of exotic rusty crayfish (*Orconectes rusticus*) and rainbow smelt (*Osmerus mordax*) interac-

tions in lake food webs: the Sparkling Lake biomanipulation. Ph.D. thesis, University of Wisconsin, Madison, Wisc.

Sala, O.E., Chapin, F.S., III, and Huber-Sannwald, E. (*Editors*). 2001. Potential biodiversity change: global patterns and biome comparisons. *In* Global biodiversity in a changing environment: scenarios for the 21st century. Springer-Verlag, New York. pp. 351–367.

Seaburg, K.G. 1957. A stomach sampler for live fish. Prog. Fish-Cult. **19**: 137–139.

Shea, K., and Kelly, D. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. Ecol. Appl. **8**: 824–832.

Simberloff, D., and Stiling, P. 1996. Risks of species introduced for biological control. Biol. Conserv. **78**: 185–192.

Smith, B.R., and Tibbles, J.J. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. **37**: 1780–1801.

Stein, R.L. 1977. Selective predation, optimal foraging, and the predator–prey interaction between fish and crayfish. Ecology, **58**: 1237–1253.

Svärdson, G. 1972. The predatory impact of eel (*Anguilla anguilla* L.) on populations of crayfish (*Astacus astacus* L.). Fishery Board of Sweden, Institute of Freshwater Research, Drottningholm, Norway. Rep. No. 52.

Taylor, C.A., Warren, M.L., Jr., Fitzpatrick, J.F., Jr., Hobbs, H.H., III, Jezerinac, R.F., Pflieger, W.L., and Robison, H.W. 1996. Conservation status of crayfishes of the United States and Canada. Fisheries, **21**(4): 25–38.

Vander Zanden, M.J., Cabana, G., and Rasmussen, J.B. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}N$) and literature dietary data. Can. J. Fish. Aquat. Sci. **54**: 1142–1158.

Vander Zanden, M.J., Olden, J.D., Thorne, J.H., and Mandrak, N.E. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecol. Appl. **14**: 132–148.

Wahle, R.A., and Steneck, R.S. 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus* — a demographic bottleneck. Mar. Ecol-Prog. Ser. **69**: 231–243.

Whitledge, G.W., Hayward, R.S., and Zweifel, R.D. 2003. Development and laboratory evaluation of a bioenergetics model for subadult and adult smallmouth bass. Trans. Am. Fish. Soc. **132**: 316–325.

Wilson, K.A. 2002. Impacts of the invasive rusty crayfish (*Orconectes rusticus*) in northern Wisconsin lakes. Ph.D. thesis, University of Wisconsin, Madison, Wisc.

Zavaleta, E.S., Hobbs, R.J., and Mooney, H.A. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends Ecol. Evol. **16**: 454–459.