Freshwater Biology (2007) **52,** 1134–1146 doi:10.1111/j.1365-2427.2007.01741.x

APPLIED ISSUES

Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish

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SUMMARY

1. Invasive species frequently have adverse impacts on native communities and ecosystems. Management options are often limited. Our goal is to evaluate the effect of intensive trapping and fish predation on the population dynamics of an invasive crayfish.
2. From 2001 to 2005, we removed invasive rusty crayfish (*Orconectes rusticus*) by trapping in Sparkling Lake in northern WI. In addition, the Wisconsin Department of Natural Resources restricted harvest of fish species known to consume crayfish, thereby increasing predation on crayfish that are too small to trap.
3. After an initial increase, catch rates of rusty crayfish declined by approximately 95%, from 11 crayfish per trap per day in 2002 to 0.65 in 2004. The catch rate in 2005 remained low at 0.5 crayfish per trap. Females comprised nearly 50% of the catch from 2002 to 2004. Unlike rusty crayfish in Sparkling Lake, catch rates of *O. rusticus* and *Orconectes propinquus* in three nearby lakes increased or remained relatively constant over the 5-year removal period.
4. We also examined the influence of habitat and temperature on crayfish catch rates. Catch rates were highest at water temperatures between 20 and 25 °C and on cobble, log or macrophyte habitats that may serve as refuge from fish predation.
5. Five summers of intensive trapping and fisheries management practices reduced abundances, but did not extirpate rusty crayfish in Sparkling Lake. To determine the potential of trapping as a management option for invasive crayfishes, these methods must be tested in other systems.

Keywords: control, crayfish, invasive species, management, *Orconectes rusticus*

Introduction

Invasive species are a leading threat to aquatic ecosystems and biodiversity (Sala, Chapin & Huber-Sannwald, 2001), and there is a need to rapidly develop management strategies to reduce adverse impacts. Prevention of future invasions should be the cornerstone of management efforts (Vander Zanden *et al.*, 2004), but control and eradication are often required because many invaders already have established populations and adversely impacted native communities. Control can also be effective at curbing the spread of newly established invader populations (Myers *et al.*, 2000). Eradication or control of invasive species has been used successfully as a restoration strategy on islands (Donlan *et al.*, 2003; Cruz *et al.*, 2005), in lakes (Knapp & Matthews, 1998), in marine areas (Culver & Kuris, 2000) and other systems (Mack *et al.*, 2000; Myers *et al.*, 2000).

The rusty crayfish (*Orconectes rusticus*, [Girard]), native to the Ohio River valley, has invaded large areas of the United States and Canada (Hobbs, Jass & Huner, 1989; Taylor *et al.*, 1996; Lodge *et al.*, 2000). Rusty crayfish were introduced beyond their native range primarily as live bait, but other vectors of dispersal such as stocking for macrophyte control

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(Magnuson *et al.*, 1975), aquaculture, aquarium, live food and biological supply trades also have been responsible for crayfish introductions (Lodge *et al.*, 2000).

Adverse impacts of rusty crayfish on aquatic communities are well-documented. Rusty crayfish often reach high densities and alter aquatic systems through direct consumption of macrophytes, benthic invertebrates and fish eggs (Magnuson *et al.*, 1975; Olsen *et al.*, 1991; Wilson *et al.*, 2004; McCarthy *et al.*, 2006; Roth, Hein & Vander Zanden, 2006; Wilson & Hrabik, 2006). They also transform littoral zones by clipping macrophytes at the base of the stem (Lodge & Lorman, 1987) and displace native crayfishes through competition (Capelli & Munjal, 1982; Capelli, 1982), lower susceptibility to predation (Roth & Kitchell, 2005) and hybridisation with *Orconectes propinquus* (Girard) (Perry, Feder & Lodge, 2001).

Though prevention of species invasions is viewed widely as the most effective management approach, in many cases invasive species already have established populations, and there is a need to manage impacts. The dynamics of marine and freshwater fisheries which have collapsed because of overharvest (Hutchings & Myers, 1994; Pauly *et al.*, 2002; Allan *et al.*, 2005; Dew & McConnaughey, 2005; National Academy of Sciences, 2006) may have relevance to our efforts of intentionally over-exploiting this invasive population. In the specific case of invasive crayfish, previous studies conclude that reducing populations through trapping is not feasible (Bills & Marking, 1988; Rach & Bills, 1989) and long-term harvest of crayfish for food is sustainable (Momot & Gowing, 1977; Momot, 1991, 1993). Several authors note that crayfish traps are highly selective for large males (Momot & Gowing, 1977; Lodge, Beckel & Magnuson, 1985; Rach & Bills, 1989; Momot, 1993), thus making it difficult to efficiently trap much of the reproductive population.

We report on the first 5 years of a whole-lake experiment intended to induce a population crash of introduced rusty crayfish. Our approach combines intensive trapping of adult crayfish with fisheries management efforts aimed at increasing predation on juvenile and young adult crayfish (Rach & Bills, 1989; Dorn & Mittelbach, 1999; Hein *et al.*, 2006). The objectives of the present study are to assess the response of crayfish catch rates and sex ratios to intensive removal over 5 years (2001–05), and to assess the role of water temperature and habitat as predictors of crayfish catch rates.

Methods

Study site

Sparkling Lake is a mesotrophic seepage lake in Vilas County, WI, USA (46°00′N, 89°42′W) and is part of the North Temperate Lakes Long-Term Ecological Research Program (NTL-LTER) (Magnuson, Bowser & Kratz, 1984; Magnuson, Kratz & Benson, 2006). Sparkling Lake has a perimeter of 4.3 km, an area of 64 ha and a maximum depth of 20 m (http://lter.limnology.wisc.edu). Most of the lake's littoral zone has a sandy substrate with some cobble in the southwest. Macrophytes are sparse, but are denser in groundwater discharge areas (earlier papers address this in Sparkling Lake, Lodge, Krabbenhoft & Striegl, 1989; Hagerthey & Kerfoot, 1998). Both rainbow smelt (*Osmerus mordax* [Mitchill]) (Hrabik, Magnuson & McLain, 1998) and rusty crayfish invaded Sparkling Lake sometime during the 1970s and have become dominant members of the biota.

Lorman's (1980) research on a rusty crayfish population in nearby Upper Sugarbrush Lake provides the best life history information on WI populations, and Hein *et al.* (2006) used this information to develop a rusty crayfish population model. The mating season extends from late summer into winter. Females then lay eggs during late April or early May, and the eggs hatch in late May or early June. After the young-of-year have undergone three or four molts, they leave the protection of their mothers. Although some young-of-year become sexually mature by the first autumn, most mature after 1 year at approximately 16-mm carapace length (CL). Rusty crayfish die after 3–4 years.

Trapping

Two approaches for trapping were used in this study: 'removal trapping' and 'standardised surveys'. In both cases, catch rates are expressed as the number of crayfish per trap per 24-h period (crayfish trap^{-1} day^{-1}). Traps set for removal of rusty crayfish were concentrated in areas of the lake to maximise catch rates (Fig. 1). Removals began on 14 August 2001, and traps were emptied daily during the last 2 weeks of

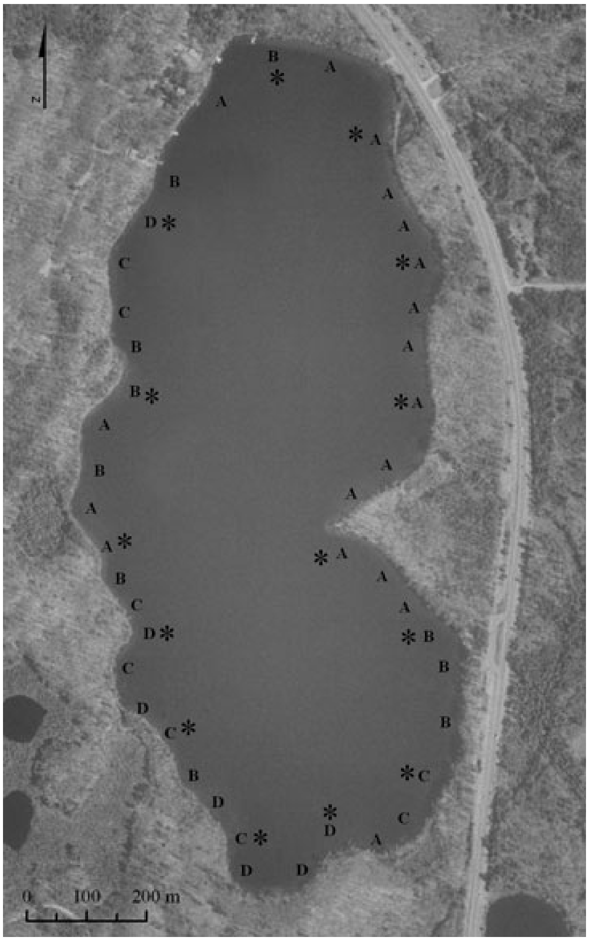

Fig. 1 Sampling locations of standardised trap surveys and areas intensively harvested during removal trapping on Sparkling Lake. Letters denote the site of a standardised perimeter trapping site and *denotes the location of standardised depth transects. The letters also indicate the intensity at which each site was trapped during the first 3 years of removal (2001–03). Trap days are the number of traps set for 24-h periods at a given site. Between 1 and 100 traps were set for 24 h at sites labelled A. Sites labelled B, C and D had 101–300, 301–600 and 601–1000 trap days, respectively.

August. From 2002 to 2005, we trapped and removed crayfish from late June to late August. We used wire mesh minnow traps with openings widened to 3.5-cm diameter. Traps were baited with 4–5 dead smelt. Traps were set in arrays of 10 at 10-m intervals along the 1-m depth contour, and were emptied daily during 2002 and 2003 and every 1–4 days during 2004 and 2005. To calculate catch rates, we divided the number of crayfish caught in a trap by the number of days the trap was in the water. During 2004, we found that crayfish catch rates (crayfish trap^{-1}) increased linearly with the number of days between emptying traps, up to 3 days. Traps were concentrated on the southern and western shorelines of the lake where catch rates were highest. The sex of each crayfish in a trap was recorded, and a randomly selected subsample of the daily crayfish catch was used to estimate mean size (CL).

Crayfish catch rates are influenced by environmental factors that may influence crayfish behaviour, such as habitat, temperature and predation risk (Somers & Stechey, 1986; Kutka *et al.*, 1992; Somers & Green, 1993; Richards *et al.*, 1996). To assess the environmental predictors of rusty crayfish catch rates, we conducted 'standardised surveys' prior to harvest in 2001 and again in 2003. Standardised surveys were comprised of perimeter trapping and depth trapping. For perimeter trapping, 43 traps were baited with 120 g of beef liver and set for 24 h at 1-m depths at 100-m intervals along the shoreline. Traps were set on 4 and 19 June, 9 and 24 July and 13 August. Three days later, 14 depth transects were set around the perimeter of the lake. Depth transects were spaced 300-m apart and along the transect, traps were set at 0.5, 3, 5, 8 and 12-m depths. Sex and CL of all crayfish in each trap were recorded. For each trap location, we characterised the habitats as sand, logs on sand, macrophytes or cobble. Each site was observed from a boat along the 1-m depth contour or by a diver using SCUBA on the depth transects. We obtained water temperature profiles from the deepest point in Sparkling Lake from NTL-LTER (http://lter.limnology.wisc.edu).

Catch rates

For each date that traps were set for removal trapping, we estimated male and female catch rate (crayfish trap^{-1} day^{-1}). This allowed assessment of the seasonal changes in crayfish catch for both males and females across the 5-year removal period (2001–05). We also used these calculations to conduct an ANOVA testing the difference in catch rates between years. We pulled traps on 23 days in 2001, 42 days in 2002, 57 days in 2003, 49 days in 2004 and 21 days in 2005. Mean annual catch rates (for males and females) were calculated as the total number of crayfish captured during a given year divided by the number of trap days for that year. To calculate the biomass removed annually, we used the annual size distribution to distribute the number removed in a summer among

1-mm CL intervals. We used a length–weight regression (weight = 0.0001 $CL^{3.2829}$) from Sparkling Lake to calculate crayfish weight for each 1-mm CL interval and then multiplied by the number of crayfish removed in each size class. The sum of these biomasses was the total biomass of crayfish removed.

Sparkling Lake is a core study lake of the NTL-LTER program (Magnuson *et al.*, 2006). Crayfish catch rates have been measured annually using widened minnow traps since 1981. This long-term data set provides a useful historical context for interpreting changes in catch rates in response to removal trapping. The LTER data archive provided annual catch rates for the three crayfish species in the region: *O. rusticus*, *Orconectes virilis* (Hagen) and *O. propinquus* (http://lter.limnology.wisc.edu). Annual catch rates were available from 1982 to 2005 for Allequash Lake and Big Muskellunge Lake and from 1981 to 2005 for Sparkling Lake and Trout Lake. Three to five crayfish traps were set at each of six standard sites on each lake for one night during the first week of August. Fishing regulations were altered only on Sparkling Lake, and other crayfish populations were not trapped intensively.

We compared the time series of four independent crayfish populations during the removal period. If the removal did cause a decline in rusty crayfish catch rates, rusty crayfish catch rates in Sparkling Lake should significantly decline through time and not necessarily decline in the other lakes. If all crayfish populations exhibit a similar decrease through time, a regional factor may be causing the decline. We examined the catch rates of four populations: *O. propinquus* in Allequash Lake, *O. propinquus* in Big Muskellunge Lake, *O. rusticus* in Trout Lake and *O. rusticus* in Sparkling Lake. Although there were populations of *O. virilis* and *O. propinquus* in Sparkling Lake, *O. virilis* in Trout Lake, and a population of *O. virilis* in Allequash Lake, none were captured by the LTER annual sampling from 2000 to 2005. Only one individual of *O. propinquus* was caught in Trout Lake in 2001 and one *O. virilis* in Big Muskellunge Lake in 2004. Therefore, these populations were not included in the analysis.

Model of catch rates

We developed a multiple regression model to examine the effects of exploitation and environmental variables on rusty crayfish catch rates. The model used standardised survey trap data from 2001 and 2003 (data from 5 and 8 June were excluded because only 30 crayfish were captured in 226 traps). Catch rates were square root transformed and fit with a multiple linear regression model using year, water temperature and habitat as predictors of catch rates. Catch rates were modelled as categorical functions of year and habitat. Year was a measure of exploitation because surveys were conducted either before (2001) or after (2003) removal trapping. The habitat variable categorised areas with (e.g. cobble, logs or macrophytes) or without (e.g. sand) structure. To better understand how habitat affects crayfish catch rates, we conducted a one-way ANOVA in S-PLUS (Mathsoft Inc., 1998). We used data from the standardised surveys for this analysis, which included 136 observations on cobble, 104 on log, 101 on macrophyte and 418 on sand habitats.

Results

Changes in catch rates during removal

Removal trapping catch rates declined by 95% over the last 4 years of removal following an initial increase in catch rates from 2001 to 2002 (Fig. 2, Table 1). The mean catch rate (crayfish $trap^{-1}$ day^{-1}) declined from 11 in 2002, to 3 in 2003, to 0.5 in 2005 (Table 1). These declines in the annual average catch rates were significant (ANOVA, $n = 192$, d.f. = 4, $P < 0.0001$, $R^2 = 0.6943$). Bonferroni pair-wise comparisons between successive years indicated significant differences ($P < 0.05$) between all years except 2001–02 and 2004–05. As catch rates declined over the 5-year removal period, we increased trapping effort by a factor of 9 from 1584 trap days in 2001 to >14 000 trap days in 2005 (Table 1). In all years, rusty crayfish catch rates showed a seasonal peak in mid-summer, corresponding with the period of highest water temperature (Fig. 2).

Catch rates for both male and female crayfish declined during the removal period (Fig. 2). Fewer females than males were caught each year (Table 1), but female catch rates exceeded male catch rates on particular days throughout the summer (Fig. 2). In the first year of trapping (2001), 68% of crayfish removed were male. From 25 July to 20 August 2001, females comprised only 25% of the catch. In subsequent years, catch rates of males and females converged, and

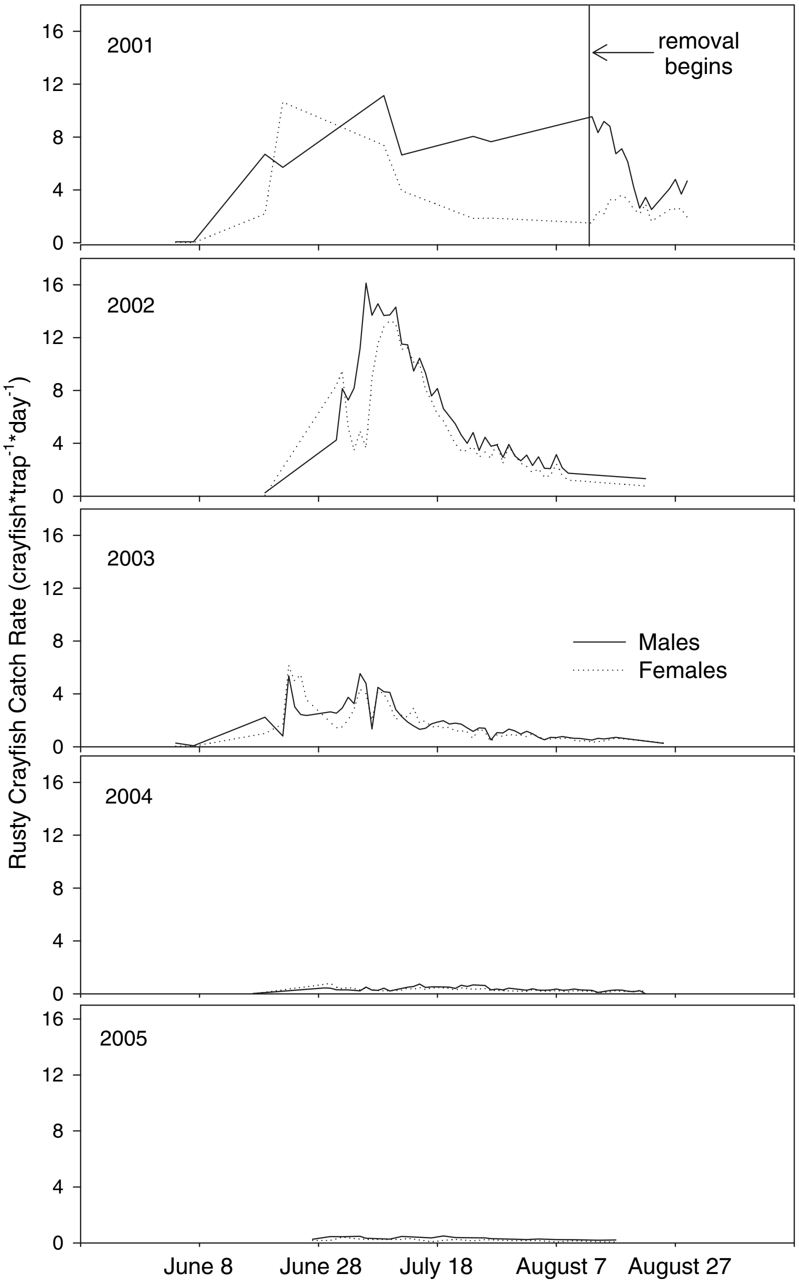

Fig. 2 Mean catch rates (crayfish trap^{-1} - day^{-1}) of male and female rusty crayfish from 2001–05. The vertical line in the 2001 panel indicates the initiation of removal. Catch rates include those from traps set both for the standardised surveys and removal trapping. Only traps from the standardised surveys that were within removal areas at 1-m depths were included in the mean catch rates to standardise for habitat and temperature effects.

males comprised 50–55% of the crayfish removed. This trend reversed in 2005, and the population reverted to a male-dominated catch: 65% of crayfish removed in 2005 were males.

In total, we removed 88 602 crayfish from Sparkling Lake, for a total biomass of 1193 kg of crayfish (Table 1). Although a large number of rusty crayfish were removed, the size distribution of crayfish did not change substantially (Fig. 3). Most crayfish caught in traps were larger than 20 mm CL. The native crayfish, *O. virilis*, were captured occasionally (and released back to the lake) throughout the 5-year removal period, though catch rates have remained comparatively low (Table 1).

Long-term catch rates

Based on LTER annual crayfish sampling data, the crayfish community of Sparkling Lake has changed dramatically over the past several decades. In 1973,

Table 1 Crayfish catch rates for each year, separated by species and by sex for *Orconectes rusticus*. Only data from 'removal trapping' is reported for 2001

Year	2001	2002	2003	2004	2005
Trap days	1584	3497	7432	13 984	14 011
Number female *O.r.*	3570	17 567	10 691	4120	2472
Number male *O.r.*	7425	20 983	11 894	4978	4562
Total number *O.r.*	10 995	38 550	22 585	9098	7034
Biomass *O.r.* (kg)	154.5	467.7	310.4	153.1	107.6
CPUE *O.r.*	6.94	11.02	3.04	0.65	0.50
Per cent male	67.5	54.4	52.7	54.7	64.8
Total number *O.v.*	24	16	23	23	132
CPUE *O.v.*	0.0152	0.0046	0.0031	0.0016	0.0094

O.r., *O. rusticus*; *O.v.*, *O. virilis*.
CPUE is expressed as crayfish trap^{-1} day^{-1}; a 'trap day' is a single trap fished for 24 h.

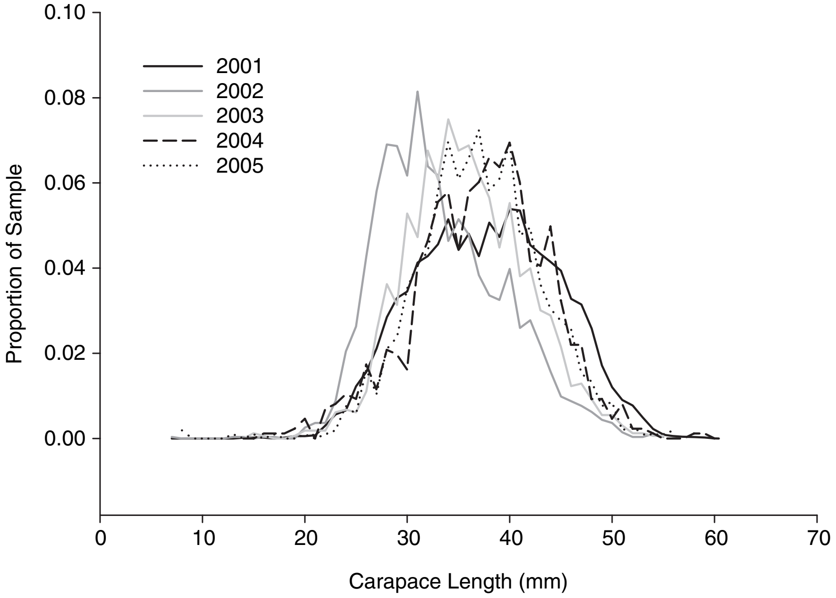

Fig. 3 The size distributions of rusty crayfish removed in traps from 2001–05.

O. propinquus dominated the catch (70%) followed by *O. virilis* (20%) and *O. rusticus* (10%) (Fig. 4, Capelli, 1982). In the early 1980s, *O. rusticus* comprised 70% of the catch, and *O. propinquus* made up the remainder (Capelli, 1982). Through the 1980s and 1990s catch rates for *O. virilis* and *O. propinquus* were generally low and fluctuated among years. The last observation of *O. virilis* from LTER annual sampling was in 1999 (Fig. 4), though we still detected low levels of *O. virilis* with our removal trapping (Table 1). The last documented observation of *O. propinquus* in Sparkling Lake was in 1998 (http://lter.limnology.wisc.edu), and none were found during our removal trapping. Since 1981, rusty crayfish catch rates have varied widely among years, and catch rates have been consistently high relative to *O. virilis* and *O. propinquus.* The removal portion of the entire time series in Sparkling Lake exhibits the only large, sustained decline in catch rates. Prior to removal, large declines in catch rates were followed by large increases within 1–2 years (Fig. 4). The rusty crayfish population in Sparkling Lake was the only population to decline from 2000 to 2005 (Fig. 5). Therefore, the decline in rusty crayfish catch rates in Sparkling Lake is not part of a broader regional trend, but rather represents the effect of our whole-lake manipulation.

Regression model

Year, water temperature and habitat explained 43% of the variation in rusty crayfish catches rates (Table 2).

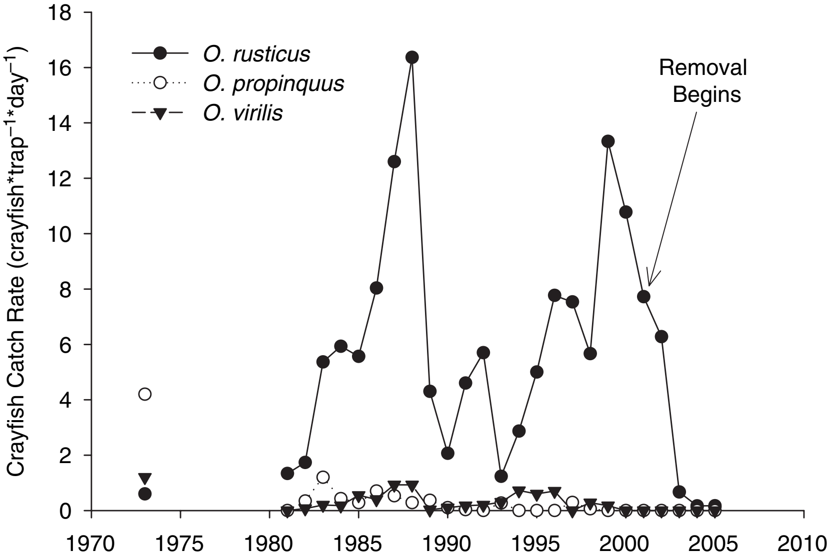

Fig. 4 Long-term changes in catch rates of *Orconectes rusticus*, *Orconectes virilis* and *Orconectes propinquus* in Sparkling Lake from 1973–2005. Data from 1973 were collected by Capelli using 18 traps (Capelli, 1982). Data from 1981–2005 were collected using 18–30 traps at six sites by NTL-LTER.

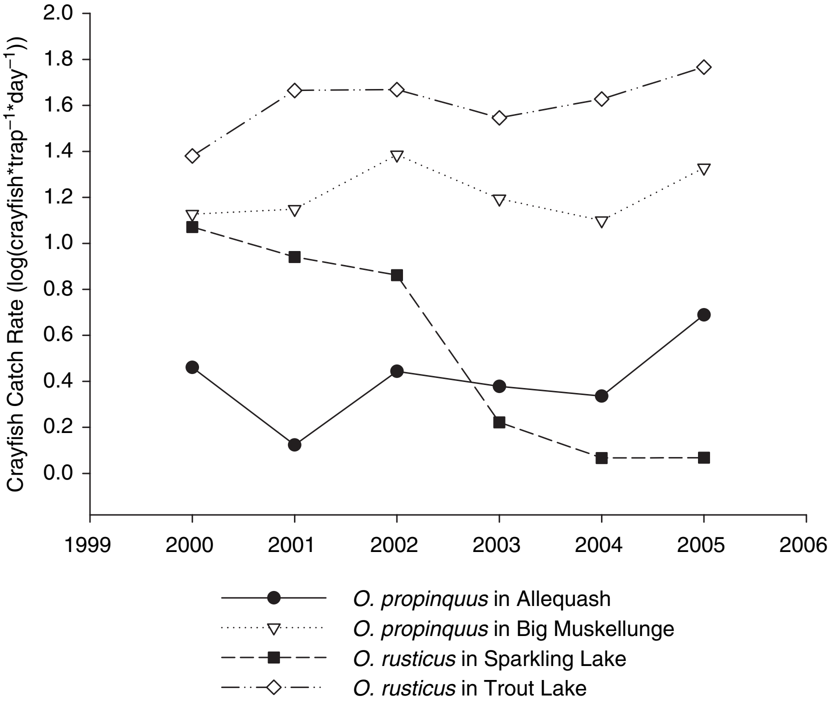

Fig. 5 Annual catch rates of *Orconectes rusticus* in Sparkling Lake and of other crayfish species in other lakes based on NTL-LTER data from 2000–05 (http://lter.limnology.wisc.edu). Other crayfish populations include *Orconectes propinquus* in Big Muskellunge Lake, *O. propinquus* in Allequash Lake and *Orconectes rusticus* in Trout Lake in Vilas County, WI. The rusty crayfish removal in Sparkling Lake began in August of 2001. There were no crayfish control efforts in the other lakes.

Catch rates were higher prior to exploitation than after. The median number of crayfish per trap per day from standardised surveys was 9 in 2001 and 1 in 2003. The highest catch rates (15–20 crayfish per trap) were between 20 and 25 °C, and catch rates reached 11 crayfish per trap above 13 °C. Catch rates were near 0 at temperatures below 13 °C. Catch rates were higher in habitats that provide refuge than on sand substrates (ANOVA, $n = 759$, d.f. $= 3$, $F = 29.05$, $P < 0.0001$). According to Tukey multiple comparisons from a one-way ANOVA ($P = 0.05$), catch rates of traps on sand substrates were significantly lower than traps in cobble, log and macrophyte habitats. The median number of rusty crayfish per trap per day in cobble, logs, macrophytes and sand was 6, 6, 5 and 1, respectively.

Table 2 Coefficients from the multiple linear regression fit to square root transformed catch rates of rusty crayfish in Sparkling Lake, WI. Data were from standardised surveys conducted prior to removal (2001) and after 2 years of exploitation (2003). Habitat categories were with (cobble, logs or macrophytes) or without (sand) structure

Coefficient	Value	SD	*t*	*P*-value
Intercept	−0.10	0.19	−0.54	0.59
Year	−0.79	0.05	−17.10	0.0000
Temperature	0.10	0.01	10.85	0.0000
Habitat	0.24	0.05	4.69	0.0000

Discussion

Removal trends

Both male and female rusty crayfish catch rates declined over the 5-year removal period. In 2001, trap effort was low and removal of rusty crayfish did not begin until mid-August when female catch rates were already seasonally low. Catch rates did not decline significantly until crayfish were removed intensively throughout the summer of 2002. By 2004, catch rates had declined to a fraction of those observed in 2001–02, and these low catch rates persisted into 2005. This initial increase followed by a large decline in catch rates with increasing effort is a standard sign of overexploitation (Allan *et al.*, 2005).

Contrary to the observations of many studies (Momot & Gowing, 1977; Bills & Marking, 1988; Rach & Bills, 1989; Momot, 1991, 1993), we found that it is possible to effectively trap the female portion of the rusty crayfish population if factors such as water temperature and life history are considered (Somers & Green, 1993; Richards *et al.*, 1996). To sustain the fishery of *O. virilis*, Richards *et al.* (1996) concluded that commercial harvest should occur only before and after the mid-summer maxima in female catch rates. Richards *et al.* (1996) concluded that female catch rates peak after releasing their young and just before or during molting. We trapped *O. rusticus* during this mid-summer period to maximise female catch rates in an effort to intentionally cause a population crash.

Female catch rates are likely influenced by inactivity during brooding, competition with males at trap entrances and avoidance of fish predation. Crayfish with larger chelae win competitive interactions for shelter (Capelli & Munjal, 1982) and are less susceptible to fish predation (Stein & Magnuson, 1976). Male cambarid crayfishes have larger chelae than females of the same body size (Bovbjerg, 1956). The proportion of females in the catch likely increased once the abundance of large males had been reduced. After 2001, when 7425 males were removed, female catch rates were similar to male catch rates for the entire summer. This agrees with assertions that large males inhibit other crayfish from entering traps (Threinen, 1958; Capelli, 1975; Momot & Gowing, 1977; Capelli, 1982; Somers & Stechey, 1986; Momot, 1993; Somers & Green, 1993; Richards *et al.*, 1996). In addition, Collins *et al.* (1983) found that female catch rates were lower than male catch rates in lakes with predatory fishes. In later years when catch rates were low and competitive interactions would be rare, avoidance of fish predation may be more important. Perhaps this is why females comprised only 35% of the catch in 2005.

The dramatic declines of rusty crayfish in Sparkling Lake likely result from the combined effect of trapping and tightening of harvest regulations for smallmouth bass. Cyclic environmental variables or density-dependent recruitment may cause large changes in population abundances of some species like the Dungeness crab (*Cancer magister* [Dana]) (Botsford, 1984; Johnson *et al.*, 1986). Our model of rusty crayfish catch rates accounted for water temperature and habitat. The variable 'year' reflected the important effect of exploitation on catch rates. Of four crayfish populations in four northern WI lakes, only rusty crayfish catch rates in Sparkling Lake declined from 2000 to 2005 (Fig. 5).

Maximising catch rates

To effectively trap rusty crayfish for removal, we found that catch rates could be maximised when water temperature and habitat are considered. Because crayfish prefer and are more active at warm water temperatures (Mundahl & Benton, 1990), catch rates were highest between 20 and 25 °C. Catch rates of *O. virilis* were also higher above 20 °C (Somers & Stechey, 1986; Somers & Green, 1993; Richards *et al.*, 1996), and water temperature has generally been cited as an important factor affecting decapod catch rates (McLeese & Wilder, 1958; Morgan, 1974).

Catch rates for both sexes were highest between late June and August, after females had released juveniles and crayfish had molted (Lorman, 1980; Somers & Green, 1993; Richards *et al.*, 1996). Females were gravid in early June and remained near shelter during this time period. Upon release of their juveniles near the end of June, females should be especially active and forage heavily (Richards *et al.*, 1996). Consistent with this idea, the contribution of females to the crayfish catch peaked between 23 June and 11 July over the 5 years of our study.

Catch rates were highest on cobble, log or macrophyte habitats. These habitats may provide shelter from fish predation (Stein & Magnuson, 1976; Smily & Dibble, 2000). Numerous studies have found lower catch rates, densities and higher rates of predation-mortality on sand substrates (Lodge & Hill, 1994; Kershner & Lodge, 1995). At our deepest sites (8 and 12 m), water temperatures were low and habitat was primarily sand or muck. Catch rates were much lower at these depths.

According to this study, trapping effort should be concentrated in mid-summer when water temperatures are high and females have released their young. In addition, removal of females may be more effective following removal of males, who may compete to enter traps. Thirdly, traps should be set in habitats that provide shelter, such as cobble, macrophytes or logs. Other studies indicate that fish bait is more effective than dog food or pellet baits (Richards *et al.*, 1996), and more females are captured on nights when the moon is not full (Somers & Stechey, 1986). These factors should be accounted for when planning to trap a rusty crayfish population for control or potential eradication.

Management implications

The primary goal of this whole-lake experiment was to decrease the rusty crayfish population growth rate to a point that would either induce a population crash or maintain low abundances of rusty crayfish. In addition to our trapping efforts, the Wisconsin Department of Natural Resources restricted the bag and size limits for the Sparkling Lake fishery to limit the harvest of fish species known to consume crayfish, thereby increasing predation on crayfish that are too small to trap (Hein *et al.*, 2006). Smallmouth bass (*Micropterus dolomieu*, [Lacepède]) and rock bass (*Ambloplites rupestris*, [Rafinesque]) are both important predators of crayfish (Vander Zanden, Cabana & Rasmussen, 1997) and are abundant in Sparkling Lake (Roth, 2005). Because we successfully trapped and removed many reproductively mature crayfish, the population growth rate of rusty crayfish should be severely reduced. Although we do not know what the current population growth rate is, a Leslie matrix population model indicated the potential for trapping to cause a substantial decline in the population growth rate of rusty crayfish in Sparkling Lake (Hein *et al.*, 2006). Because traps select large, reproductive crayfish, trapping causes a greater decline in the population growth rate than fish predation for a given portion of the population removed (Hein *et al.*, 2006). However, we estimated that fish consume a greater portion of the population and cause a greater decline in the population growth rate overall (Hein *et al.*, 2006).

As the population density declines, the population growth rate may increase, thereby impairing the success of our control efforts. These compensatory responses are often associated with reduced competition and cannibalism and indicate that the population will rebound once fishing subsides (Rose *et al.*, 2001). Many fish populations exhibit compensatory population dynamics (Myers *et al.*, 1995). Though documented less frequently, some populations exhibit depensation, or a decline in population growth rate with decreasing population density (Myers *et al.*, 1995; Liermann & Hilborn, 2001). Depensation is generally associated with predator saturation, difficulty finding a mate and impaired group dynamics (Liermann & Hilborn, 2001). If rusty crayfish exhibit depensatory dynamics, the population should collapse once it falls below a critical level. Evidence for both compensatory and depensatory life history components in other crayfish populations exists (Momot & Gowing, 1977; Momot, 1991, 1993). The fecundity of rusty crayfish in Sparkling Lake did not change from 2002 to 2003 (Hein *et al.*, 2006), but we do not know if the population dynamics are density independent.

The modelled effects of trapping and fish predation on the population growth rate do not account for interactions between control methods. Collins *et al.* (1983) found that the trapability of crayfish declines in the presence of predatory fishes. By increasing predation pressure in Sparkling Lake, might we simultaneously decrease the efficacy of trapping and therefore, the entire control effort? We believe that stimulating fish predation on rusty crayfish in Sparkling Lake did not inhibit our trapping success. The catch rates of rusty crayfish in Sparkling Lake prior to removal were similar to crayfish catch rates in lakes without predatory fishes and far above catch rates in lakes with predatory fishes. Collins *et al.* (1983) studied *O. propinquus*, *O. virilis* and *Cambarus robustus* (Girard). Because they have smaller chelae, these native crayfishes are more susceptible to fish predation than rusty crayfish (Roth & Kitchell, 2005). Furthermore, rusty crayfish larger than 35 mm CL are at a size refuge from predation (Hein *et al.*, 2006) and comprised 59% of the crayfish removed over the 5-year period. In the presence of predatory fishes, large adult crayfish alter their behaviour much less than do juvenile crayfish (Stein & Magnuson, 1976). Therefore, our two-tiered approach is operating as envisioned: trapping of adult rusty crayfish reduces the number of crayfish with high reproductive value and fish predation reduces the number of juveniles and young adults.

In the coming years, we will examine whether sustained trapping efforts are required to reduce impacts of rusty crayfish. The augmented populations of predatory fishes in Sparkling Lake may be able to maintain the currently low abundance of rusty crayfish. Ecosystem recovery in response to rusty crayfish removal may further aid in maintaining low abundances of rusty crayfish. McCarthy *et al.* (2006) report negative relationships between rusty crayfish and zoobenthos abundance in a long-term analysis of Sparkling Lake, but these results also indicate a strong potential for food web recovery in response to even short-term crayfish population decreases. Incidentally, we have witnessed major changes in the Sparkling lake food web over the period 2001–05, including increases in zoobenthos, macrophytes and fishes (*Lepomis* spp.). *Lepomis* have been shown to decline following rusty crayfish invasion (Wilson *et al.*, 2004; Willis & Magnuson, 2006; Wilson & Hrabik, 2006), but are also important predators of juvenile rusty crayfish (Roth, 2005). Recovery of macrophytes in Sparkling Lake appears to be facilitating a population rebound of *Lepomis*, which would increase predation on small crayfish and further suppress the rusty crayfish population. This macrophyte-*Lepomis*-crayfish dynamic suggests the potential for regime shifts in north-temperate lakes (Roth, 2005), and that our intensive trapping may act as a 'trigger' to induce a broader food web shift (Scheffer & Carpenter, 2003).

Catch rates of the native crayfish, *O. virilis*, varied widely among years in Sparkling Lake. Despite the massive reduction in the abundance of rusty crayfish, which are presumably the cause of the reduced population of *O. virilis*, there was no conclusive trend of population recovery over this period. Given more time and continued suppression of rusty crayfish, the *O. virilis* population may rebound. The *O. virilis* we caught were in the remaining macrophyte beds. Perhaps, like *Lepomis*, their populations will increase as macrophytes recover. Alternatively, heightened levels of fish predation associated with the more restrictive fishery regulations may suppress native crayfish populations.

In conclusion, given today's global economy and ease of travel, species invasions are inevitable. Even if we can curb future invasions through education and regulation, many invasive species already have established and continue to spread into new habitats. Our 5-year, whole-lake experiment provides one example of successful invasive species control. Unpredictable, emergent properties at the scale of the entire ecosystem will ultimately make or break a control programme like our whole-lake experiment to control rusty crayfish (Zavaleta, Hobbs & Mooney, 2001). Our understanding of the Sparkling Lake ecosystem makes us hopeful that the long-term effects of rusty crayfish control will in fact benefit aspects of the community that had been altered by rusty crayfish invasion.

Acknowledgments

Our intensive trapping was made possible by the help of many dedicated people: Laura Kessler, James Jenders, Gretchen Anderson, Ellen Feingold, Patrick Hermann, Brian Roth, Greg Sass, Adam Ray, Stacy Lischka, Andrea Fowler, Julia McCarthy and many others. We thank Dave Balsiger and Barbara Benson for their help with data management, Jeff Maxted for his help with figures and Steve Carpenter, James Kitchell and Anthony Ives for their vision and guidance in whole-lake experimentation. This work was supported by the Riparian Land, People and Lakes Biocomplexity Project (DEB-0083545), the North-Temperate Lakes Long Term Ecological Research Program (DEB-9632853) and a Research Experience for Undergraduates (REU) award to Catherine Hein.

References

Allan J.D., Abell R., Hogan Z., Revenga C., Taylor B.W., Welcomme R.L. & Winemiller K. (2005) Overfishing of inland waters. *BioScience*, **55**, 1041–1051.

Bills T.D. & Marking L.L. (1988) Control of nuisance populations of crayfish with traps and toxicants. *Progressive Fish-Culturist*, **50**, 103–106.

Botsford L.W. (1984) Effect of individual growth rates on expected behavior of the northern California Dungeness crab (*Cancer magister*) fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 337–346.

Bovbjerg R.V. (1956) Some factors affecting aggressive behavior in crayfish. *Physiological Zoology*, **29**, 127–136.

Capelli G.M. (1975) *Distribution, Life History, and Ecology of Crayfish in Northern Wisconsin, with Emphasis on Orconectes propinquus (Girard)*. PhD Thesis, University of Wisconsin-Madison, Madison, WI.

Capelli G.M. (1982) Displacement of northern Wisconsin crayfish by *O. rusticus* (Girard). *Limnology and Oceanography*, **27**, 741–745.

Capelli G.M. & Munjal B.L. (1982) Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. *Journal of Crustacean Biology*, **2**, 486–492.

Collins N.C., Harvey H.H., Tierney A.J. & Dunham D.W. (1983) Influence of predatory fish density on trapability of crayfish in Ontario lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1820–1828.

Cruz F., Donlan C.J., Campbell K. & Carrion V. (2005) Conservation action in the Galápagos: feral pig (*Sus scrofa*) eradication from Santiago Island. *Biological Conservation*, **121**, 473–478.

Culver C.S. & Kuris A.M. (2000) The apparent eradication of a locally established introduced marine pest. *Biological Invasions*, **2**, 245–253.

Dew C.B. & McConnaughey R.A. (2005) Did trawling on the brood stock contribute to the collapse of Alaska's King Crab? *Ecological Applications*, **15**, 919–941.

Donlan C.J., Tershy B.R., Campbell K. & Cruz F. (2003) Research for requiems: the need for more collaborative action in eradication of invasive species. *Conservation Biology*, **17**, 1850–1851.

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

Hagerthey S.E. & Kerfoot W.C. (1998) Groundwater flow influences the biomass and nutrient ratios of epibenthic algae in a north temperate seepage lake. *Limnology and Oceanography*, **43**, 1227–1242.

Hein C.L., Roth B.M., Ives A.R. & Vander Zanden M.J. (2006) Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: a whole-lake experiment. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 383–393.

Hobbs H.H. III, Jass J.P. & 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. & McLain A.S. (1998) Predicting the effects of rainbow smelt on native fishes in small lakes: evidence from long-term research on two lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1364–1371.

Hutchings J.A. & Myers R.A. (1994) What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2126–2146.

Johnson D.F., Botsford L.W., Methot R.D. Jr & Wainwright T.C. (1986) Wind stress and cycles in Dungeness crab (*Cancer magister*) catch off California, Oregon, and Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 838–845.

Kershner M.W. & Lodge D.M. (1995) Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. *Journal of the North American Benthological Society*, **14**, 141–422.

Knapp R.A. & Matthews K.R. (1998) Eradication of nonnative fish by gill netting from a small mountain lake in California. *Restoration Ecology*, **6**, 207–213.

Kutka F.J., Richards C., Merick G.W. & DeVore P.W. (1992) Bait preference and trapability of two common crayfishes in northern Minnesota. *The Progressive Fish-Culturist*, **54**, 250–254.

Liermann M. & Hilborn R. (2001) Depensation: evidence, models and implications. *Fish and Fisheries*, **2**, 33–58.

Lodge D.M. & Hill A.M. (1994) Factors governing species composition, population size, and productivity of cool-water crayfishes. *Nordic Journal of Freshwater Resources*, **69**, 111–136.

Lodge D.M. & Lorman J.G. (1987) Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 591–597.

Lodge D.M., Beckel A.L. & Magnuson J.J. (1985) Lake-bottom tyrant. *Natural History*, **94**, 32–37.

Lodge D.M., Krabbenhoft D.P. & Striegl R.G. (1989) A positive relationship between groundwater velocity and submersed macrophyte biomass in Sparkling Lake, Wisconsin. *Limnology and Oceanography*, **34**, 235–239.

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

Lorman J.G. (1980) *Ecology of the Crayfish Orconectes rustics in Northern Wisconsin*. PhD Thesis, University of Wisconsin-Madison, Madison, WI.

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

Magnuson J.J., Bowser C.J. & Kratz T.K. (1984) Long-term ecological research (LTER) on north temperate lakes of the United States. *Verhandlungen Internationale Vereinigung für Limnologie*, **22**, 533–535.

Magnuson J.J., Kratz T.K. & Benson B.J. (2006) *Long-Term Dynamics of Lakes in the Landscape: Long-Term Ecological Research on North Temperate Lakes*. Oxford University Press, NY.

Magnuson J.J., Capelli G.M., Lorman J.G. & Stein R.A. (1975) Consideration of crayfish for macrophyte control. In: *The Proceedings of a Symposium on Water Quality Management Through Biological Control* (Eds P.L. Brezonik & J.L. Fox), pp. 66–74. Rep. No. ENV 07-75-1, University of Florida, Gainesville, FL.

Mathsoft Inc. (1998) *S-Plus 4.5*. Mathsoft, Seattle, WA.

McCarthy J.M., Hein C.L., Olden J.D. & Vander Zanden M.J. (2006) Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biology*, **51**, 224–235.

McLeese D.W. & Wilder D.G. (1958) The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. *Journal of Fisheries Research Board of Canada*, **15**, 1345–1354.

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

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

Momot W.T. & Gowing H. (1977) Results of an experimental fishery on the crayfish *Orconectes virilis*. *Journal of the Fisheries Research Board of Canada*, **34**, 2056–2066.

Morgan G.R. (1974) Aspects of the population dynamics of the western rock lobster, *Panulirus cygnus* George. II. Seasonal changes in the catchability coefficient. *Australian Journal of Marine and Freshwater Resources*, **25**, 249–259.

Mundahl N.D. & Benton M.J. (1990) Aspects of the thermal ecology of the rusty crayfish *Orconectes rusticus* (Girard). *Oecologia*, **82**, 210–216.

Myers R.A., Barrowman N.J., Hutchings J.A. & Rosenberg A.A. (1995) Population dynamics of exploited fish stocks at low population levels. *Science*, **269**, 1106–1108.

Myers J.H., Simberloff D., Kuris A.M. & Carey J.R. (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution*, **15**, 316–320.

National Academy of Sciences (2006) *Dynamic Changes in Marine Ecosystems: Fishing, Food Webs, and Future Options*. The National Academies Press, Washington D.C.

Olsen T.M., Lodge D.M., Capelli G.M. & Houlihan R.J. (1991) Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1853–1861.

Pauly D., Christensen V., Guénette S., Pitcher T.J., Sumaila U.R., Walters C., Watson R. & Zeller D. (2002) Towards sustainability in world fisheries. *Nature*, **418**, 689–695.

Perry W.L., Feder J.L. & Lodge D.M. (2001) Implications of hybridization between introduced and resident *Orconectes* crayfishes. *Conservation Biology*, **15**, 1656–1666.

Rach J.J. & Bills T.D. (1989) Crayfish control with traps and largemouth bass. *The Progressive Fish-Culturist*, **51**, 157–160.

Richards C., Kutka F.J., McDonald M.E., Merrick G.W. & Devore P.W. (1996) Life history and temperature effects on catch of northern orconectid crayfish. *Hydrobiologia*, **319**, 111–118.

Rose K.A., Cowan J.H., Winemiller K.O., Myers R.A. & Hilborn R. (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries*, **2**, 293–327.

Roth B.M. (2005) *An Investigation of Exotic Rusty Crayfish (Orconectes rusticus) and Rainbow Smelt (Osmerus mordax) Interactions in Lake Food Webs: the Sparkling Lake Biomanipulation*. PhD Thesis, University of Wisconsin-Madison, Madison, WI.

Roth B.M. & Kitchell J.F. (2005) The role of size-selective predation in the displacement of *Orconectes* crayfishes following rusty crayfish invasion. *Crustaceana*, **78**, 297–310.

Roth B.M., Hein C.L. & Vander Zanden M.J. (2006) Using bioenergetics to determine the role of rusty crayfish (*Orconectes rusticus*) in lake littoral zones. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 335–344.

Sala O.E., Chapin F.S. III & Huber-Sannwald E. (2001) Potential biodiversity change: global patterns and biome comparisons. In: *Global Biodiversity in a Changing Environment: Scenarios for the 21st Century*. (Eds F.S. Chapin III, O.E. Sala & E. Huber-Sannwald), pp. 351–367. Springer-Verlag, NY.

Scheffer M. & Carpenter S.R. (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*, **12**, 648–656.

Smily P.C. Jr & Dibble E.D. (2000) Microhabitat use of an introduced crayfish (*Orconectes rusticus*) in Long Lake, Wisconsin. *Journal of Freshwater Ecology*, **15**, 115–122.

Somers K.M. & Green R.H. (1993) Seasonal patterns in trap catches of the crayfish *Cambarus bartoni* and *Orconectes virilis* in six south-central Ontario lakes. *Canadian Journal of Zoology*, **71**, 1136–1145.

Somers K.M. & Stechey D.M. (1986) Variable trappability of crayfish associated with bait type, water temperature and lunar phase. *American Midland Naturalist*, **116**, 36–44.

Stein R.A. & Magnuson J.J. (1976) Behavioral response of crayfish to a fish predator. *Ecology*, **57**, 751–761.

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

Threinen C.W. (1958) *A Summary of Observations of the Commercial Harvest of Crayfish in Northwestern Wisconsin, with Notes of the Life History of Orconectes virilis*. Miscellaneous Report Number 2, Wisconsin Conservation Department, Fish Management Division, Madison, WI.

Vander Zanden M.J., Cabana G. & Rasmussen J.B. (1997) Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ^{15}N) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1142–1158.

Vander Zanden M.J., Wilson K.A., Casselman J.M. & Yan N.D. (2004) Species introductions and their impacts in North American Shield lakes. In: *Boreal Shield Watersheds: Lake Trout Ecosystems in a Changing Environment*. (Eds J.M. Gunn, R.J. Steedman & R.A. Ryder), pp. 239–263. CRC Press, Boca Raton, FL.

Willis T.V. & Magnuson J.J. (2006) Response of fish communities in five north temperate lakes to exotic species and climate. *Limnology and Oceanography*, **51**, 2808–2820.

Wilson K.A. & Hrabik T.R. (2006) Ecological change and exotic invaders. In: *Long-Term Dynamics of Lakes in the Landscape: Long-Term Ecological Research on North Temperate Lakes*. (Eds J.J. Magnuson, T.K. Kratz & B.J. Benson), pp. 151–167. Oxford University Press, NY.

Wilson K.A., Magnuson J.J., Lodge D.M., Hill A.M., Kratz T.K., Perry W.L. & Willis T.V. (2004) A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 2255–2266.

Zavaleta E.S., Hobbs R.J. & Mooney H.A. (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution*, **16**, 454–459.

(Manuscript accepted 22 January 2007)