Nonindigenous Crayfishes Threaten North American Freshwater Biodiversity:

Lessons from Europe

By David M. Lodge, Christopher A. Taylor, David M. Holdich, and Jostein Skurdal

ABSTRACT

North America harbors about 390 native species of crayfishes, 75% of the world's total. In this article, we highlight the threats posed by nonindigenous crayfishes to freshwater ecosystem function, fisheries, and the biodiversity of native crayfishes; draw some lessons for North American freshwater conservation from the experience with nonindigenous crayfishes in Europe; and review existing regulations that address the introduction of nonindigenous crayfishes. Most North American crayfishes have naturally small ranges in the southeastern United States, rendering them very vulnerable to environmental change. In contrast, Europe has only five, broadly distributed, native crayfishes, all of which have been greatly affected by environmental changes, especially the introduction of nonindigenous crayfishes (mostly from North America). In response, many European governments have adopted strict regulations to protect native crayfishes. The loss of thousands of populations of native European crayfishes and the political responses to it offer useful guidance to efforts to protect North American freshwater biodiversity and ecosystems. As in Europe, the most important threat to native North American crayfish biodiversity is nonindigenous crayfishes (many from within North America). In several well-documented cases, nonindigenous crayfishes have greatly altered North American lake and stream ecosystems, harmed fisheries, extirpated many populations of native crayfishes, and contributed to the global extinction of at least one native crayfish species. However, most species are still relatively unaffected, but the smaller ranges of most North American crayfishes make them more vulnerable than European crayfishes. Thus, a narrow window of opportunity exists to protect the function of North American aquatic ecosystems, their fisheries, and the unique biodiversity of crayfishes that they contain.

In most parts of the world, nonindigenous species (NIS) are the first or second (after land use change) most important threat to freshwater biodiversity and ecosystem function (Lodge in press; Sala et al. 2000). For the purposes of this article, NIS are species established outside their native range, whether on their native or another continent. While the impact of NIS alone is often great, the number and impact of NIS are usually increased by other global changes, e.g., globalization of commerce, dam and canal construction, fisheries management, land use change, and climate change (Kolar and Lodge in press). The economic costs alone of a small subset of freshwater NIS in the United States has recently been estimated at 4.1 billion dollars annually (Pimentel et al. 1999). In North America, NIS and other global changes imperil a much larger proportion of the biota in freshwater than in terrestrial ecosystems (Master 1990). This is particularly true for North American fishes (Williams et al. 1989), mussels (Williams et al. 1993), and crayfishes (Taylor et al. 1996).

Among these three freshwater groups, crayfishes have received by far the least attention from North American biologists, policy makers, and the general public, despite their extraordinary evolutionary radiation in North America. About 390 crayfish species, nearly 75% of the world's total, are endemic to North America. Therefore, our goals in this article are threefold: (1) to highlight the threats posed by nonindigenous crayfishes to freshwater ecosystem

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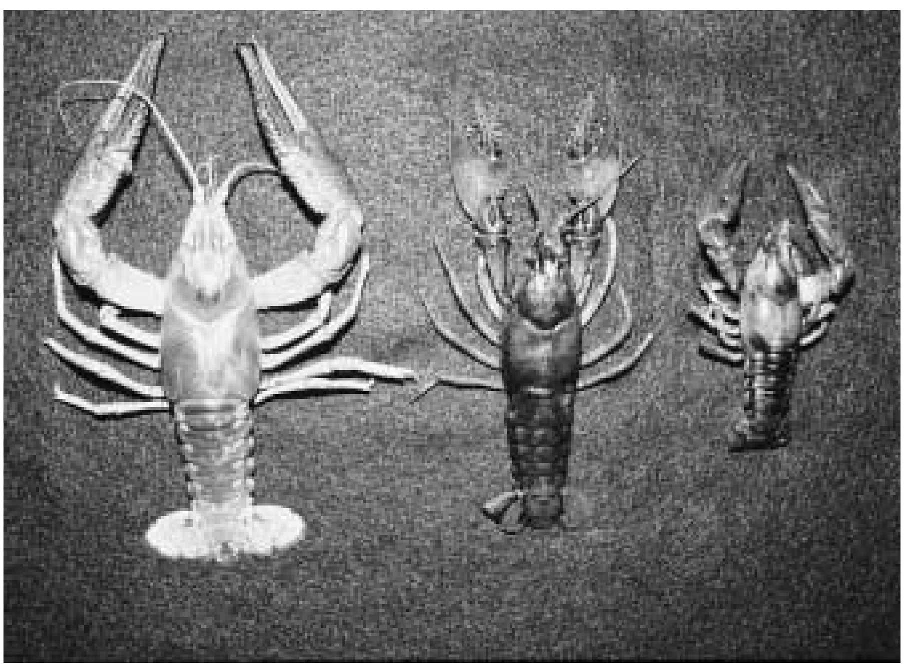
function, fisheries, and, in particular, to the biodiversity of native crayfishes; (2) to draw some lessons for North American freshwater conservation from the experience with nonindigenous crayfishes in Europe, where crayfishes have received far more ecological study and management; and (3) review existing regulations that address the introduction of nonindigenous crayfishes. In a companion essay in this issue, we recommend specific policies to reduce introductions of nonindigenous crayfishes in North America.

With more than 500 species worldwide, crayfishes are native to every continent except Antarctica and Africa (although six species are native to Madagascar) (Adegboye 1983; Hobbs 1988). In many countries, crayfishes are highly valued as food, and are therefore the basis of recreational or commercial fisheries. Wild stocks are therefore managed, catches are regulated, and some species are widely cultured. In Scandanavia and Louisiana, for example, feasting on crayfishes is a cultural icon. Crayfishes thus play an important role in many societies quite apart from their biodiversity value and role in ecosystems.

Crayfishes have the largest individual size of invertebrates in many freshwater habitats, and often exist at high densities. While passive transport and overall dispersal rates are lower than for many smaller freshwater taxa, crayfishes readily disperse along watercourses, and some species exhibit overland movements in damp conditions. Crayfishes are often a central component of freshwater foodwebs and ecosystems. They are dominant consumers of benthic invertebrates, detritus, macrophytes, and algae in streams (Huryn and Wallace 1987; Charlebois and Lamberti 1996; Whitledge and Rabeni 1997) and lakes (Chambers et al. 1990; Lodge et al. 1994; Momot 1995), and are themselves important forage for fishes (Roell and Orth 1993; Lodge and Hill 1994; Dorn and Mittelbach 1999). For example, production of populations of age-2 and older smallmouth bass, rock bass, and flathead catfish in a West Virginia river were supported primarily by crayfish (Roell and Orth 1993). Thus, additions or removals of crayfish species often lead to large ecosystem effects, in addition to changes in fish populations, and losses in biodiversity (Lodge et al. 1998a; Covich et al. 1999).



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The three crayfish species commonly found in lakes and streams of the upper midwestern United States. In many habitats, the introduced rusty crayfish (*Orconectes rusticus*, left) has extirpated the native species, the virile crayfish (*O. virilis*, middle) and the northern clearwater crayfish (*O. propinquus*, right).

Crayfishes may be extirpated (driven locally extinct) by many global changes, including acidification (Appelberg and Odelström 1986; France and Collins 1993) and climate and hydrological changes (Contreras-Balderas and de Lozano-Vilona 1996). The single greatest threat, however, to crayfish biodiversity worldwide comes from the introduction of nonindigenous crayfishes. In a summary of global crayfish introductions, Hobbs et al. (1989) listed 20 crayfish species that have been introduced into new river drainages, states, or continents, and documented a long history of deliberate and accidental introductions; that number has certainly increased since their study. In particular, when nonindigenous crayfishes are kept in outdoor ponds, the establishment of feral populations is often inevitable given the difficulty in preventing escape (Hobbs et al. 1989; Huner 1997a).

In many cases, the establishment of introduced crayfishes is enhanced by other, ongoing global changes that create environments less favorable for native species and more favorable for introduced species, e.g., organic pollution, increased rice cultivation, higher salinity from water withdrawal for irrigation (Hobbs et al. 1989; Holdich et al. 1997; Lindqvist and Huner 1999). Because of the importance of nonindigenous crayfishes in changing freshwater ecosystems and causing the extirpation of native crayfishes, we focus on the vectors and impact of nonindigenous crayfishes in the remainder of this article, first for Europe (because it offers lessons for North America) and second for North America.

The European experience

Europe has only five native crayfish species, belonging to two genera in one family (Astacidae) (Hobbs 1988; Lowery and Holdich 1988; Holdich et al. 1999a). All have naturally broad geographic distributions, and all are ecologically similar, inhabiting streams and lakes. While none of the species are near extinction, thousands of local populations have been lost, and abundance in many remaining lake and stream populations has been much reduced by nonindigenous crayfishes. Native crayfishes have suffered in competition with introduced crayfishes. Mostly, however, the native species have been decimated by a fungal plague that is carried by nonindigenous crayfishes from North America. (The North American species suffer few symptoms from the fungus.) Thus, introductions of crayfish have had a high cost by reducing native biodiversity in many freshwater habitats. In addition, there have been high economic losses in the fishery for native species, and the loss of important cultural activities surrounding human consumption of native crayfishes.

Europe has gained at least four nonindigenous crayfishes from North America and one from Australia, most deliberately introduced to meet luxury culinary demand after the native species were killed by plague following the earliest introductions of plague-carrying North American species (Holdich 1999a). Some of these introduced crayfishes have experienced substantial secondary range expansions within Europe via canals and via stocking for human food (legal and illegal) (Table 1). The culinary demand continues to drive increasing aquaculture and live food trade in crayfishes, which have great potential for causing the establishment of additional nonindigenous crayfishes. The aquarium and pond trades have also been important sources for crayfish introductions, at least in the United Kingdom (UK), and are perhaps a greater threat to southern Europe where the climate is more amenable to cultured species from North America and Australia. Finally, the use of live bait has been an important vector in some parts of Europe (especially in spreading *Pacifastacus lenuisculus* in the UK), although not nearly as important as in North America because no commercial trade in live bait exists in Europe (Table 1). The use of live crayfish as bait is now illegal in several European countries, including Britain and Norway.

Table 1. Differential importance[1] of different anthropogenic vectors of crayfish introductions in Europe and North America.

Vector of crayfish introduction	Europe	North America
1. Canals	Decreasing importance	Decreasing importance
2. Legal stocking in natural waters	Decreasing importance	Decreasing importance
3. Illegal stocking in natural waters	Remains important	Decreasing importance
4. Aquaculture	Increasing importance	Increasing importance
5. Live food trade	Increasing importance	Increasing importance?
6. Aquarium and pond trade	Remains important	Increasing importance
7. Biological supply trade	Not important	Increasing importance
8. Live bait	Decreasing importance	Increasing importance

[1]In the absence of data comparable across vectors, we relied on expert opinion. Collecting data to quantify the importance of different vectors should be a priority.

Introductions of North American crayfishes into Europe have created nuisances in rice culture, and have caused many large changes in European freshwater ecosystems, including reductions in macrophytes, macroinvertebrates, fishes, and native European crayfishes (Holdich 1999a; Table 2). Extirpation of native crayfishes, in particular, has resulted primarily from fungal plague (*Aphanomyces astaci*), which is endemic to many North American crayfishes but lethal to European crayfishes (Table 3). Plague was introduced with North American crayfish into Italy in the 1860s, and has subsequently spread throughout Europe (Alderman 1996). Other mechanisms of impact on native crayfishes include interspecific competition for shelter and food, making the native species more vulnerable to predatory fishes; and interspecific matings that lower reproductive success of the native species (Table 3).

Crayfish plague, in particular, has had, and continues to have, a devastating effect on European crayfish populations (Holdich et al. 1995; Westman 1995; Machino and Diéguez-Uribeondo 1998). Harvests of native species, particularly *Astacus astacus* and *Astacus leptodactylus*, have long been economically important in many European countries. Crayfish plague, however, reduced production of native species by up to 90% in some countries, particularly those of Scandinavia, Germany, Spain and Turkey. For example, in Sweden 90 tons were exported in 1908 (from a total catch of 200 tons), but export dropped to 30 tons by 1910 (Brinck 1975). In Finland exports declined from 16 million *A. astacus* in 1890 to less than 2 million in 1910 (Westman 1991). When the plague spread to Turkey in the 1980s, the annual catch of *A. leptodactylus* plunged from 7000 to 2000 tons (Köksal 1988; Baran and Soylu 1989), which nearly eliminated exports from Turkey to Western Europe. Western European markets resorted to other sources, including *Procambarus clarkii*, the red swamp crayfish, from Spain, China (both countries in which it had previously been introduced), and Lousiana to satisfy the demand of about 10,000 tons per year.

Hundreds of plague outbreaks still occur annually in the Nordic and Baltic countries (Skurdal et al. 1999). Although no native European crayfish has been driven extinct, the ranges and local abundances have shrunk dramatically. For example, before plague, native crayfishes were abundant in many productive lowland lakes all over central Europe. Many of these stocks are now extirpated and large lake districts are devoid of crayfish. The disease does not require its host in order to spread; the spores can be transported on damp surfaces, as is thought to have happened with the crayfish plague outbreak in central Ireland in 1986 (Reynolds 1988). The disease, of which there are several varieties (Huang et al. 1994), can spread very quickly through a native population, as evidenced by its rapid movement down some British rivers (Alderman and Polglase 1988; Alderman 1993). Because native European crayfishes

Table 2. Recent citations documenting changes (usually reductions) caused by nonindigenous crayfishes in many different freshwater taxonomic groups in both Europe and North America.

Taxa affected	Europe	North America
Algae	No studies known	Weber and Lodge 1990; Lodge et al. 1994; Charlebois and Lamberti 1996; Luttenton et al. 1998
Macrophytes	Nyström et al. 1996; Nyström and Strand 1996	Feminella and Resh 1989; Chambers et al. 1990; Lodge et al. 1994; Hill and Lodge 1995; Lodge et al. 1998b
Macroinvertebrates	Warner et al. 1995; Nyström 1999	Crowl and Covich 1990; Hanson et al. 1990; Lodge et al. 1994; Hill and Lodge 1995; Perry et al. 1997; Lodge et al. 1998a
Native crayfishes	Cukerzis 1988; Söderbäck 1991; Holdich and Rogers 1997; Arrignon et al. 1999; Stuki and Staub 1999; Holdich et al. 1999c	Lodge et al. 1986; Olsen et al. 1991; St. John 1991; Light et al. 1995; Taylor and Redmer 1996; Hill and Lodge 1999.
Amphibians	Axelsson et al. 1997	Gamradt and Kats 1996; Gamradt et al. 1997
Fishes	Guan and Wiles 1997	Horns and Magnuson 1981; Rahel and Stein 1988; Hobbs et al. 1989; Savino and Miller 1991; Miller et al. 1992
Interference with anglers	Holdich et al. 1995	No studies known
Agriculture (rice)	Anastácio and Marques 1997; Diéguez-Uribeondo et al. 1997; Fonseca et al. 1997	Chang and Lange 1967; Sommer and Goldman 1983

have shown no indication of increased resistance toward plague, their recovery is very unlikely.

The impact of plague on native European crayfishes has ironically increased subsequent intentional introductions of North American crayfishes (*Orconectes limosus*, *O. immunis*, *P. leniusculus*, *P. clarkii*) into more than 20 European countries to replace the native stocks extirpated by plague. The use in Europe of the North American signal crayfish, *P. leniusculus*, is a good example of this positive feedback, which further reduces native European crayfishes. *Pacifastacus leniusculus* was introduced from California into Sweden in the 1960s (Abrahamsson 1973; Brinck 1983; Svärdson 1995), followed by its subsequent introduction into many European countries by the 1980s (Lowery and Holdich 1988). It is now widely cultivated in Europe (Holdich 1999a). It has become a culinary substitute since the decline of the native mainland European species (*A. astacus*) from crayfish plague (Ackefors and Lindqvist 1994; Skurdal et al. 1999). However, a number of introduced species, including *P. leniusculus*, are vectors of crayfish plague (Smith and Söderhäll 1986; Alderman et al. 1990; Diéguez-Uribeondo et al. 1997). Recent genetic studies have implicated *P. leniusculus* in many recent plague outbreaks (Lilley et al. 1997).

The introduction of the red swamp crayfish, *P. clarkii*, into Europe is following a similar trajectory. It was introduced into Spain in the 1970s (Huner 1988; Diéguez-Uribeondo et al. 1997; Gutiérrez-Yurrita et al. 1999) and subsequently into Portugal (Gutiérrez-Yurrita et al. 1999), Cyprus (Hobbs et al.1989), England (Holdich et al. 1999b), France (Arrignon et al. 1999), Germany (Dehus et al. 1999), Italy (Gherardi et al. 1999), Majorca and the Netherlands (Hobbs et al. 1989), and most recently, Switzerland (Stuki 1997; Stuki and Staub 1999). Like *P. leniusculus*, it is a plague vector that has reduced some native crayfish species (Diéguez-Uribeondo and Söderhäll 1993; Bernardo et al. 1997; Diéguez-Uribeondo et al. 1997), and it provides a readily exploitable and exportable food resource (Ackefors and Lindqvist 1994; Ackefors 1998, 1999). However, it also raises the cost of rice culture by burrowing into dikes and eating rice plants. In Spain, rice farmers have used organophosphate pesticides to eliminate the crayfish from their fields, sometimes with disastrous consequences for bird life (MacKenzie 1986). Crayfish can be harvested by the public in Spain and thus additional damage is sometimes caused to the rice crop by harvesters of crayfish (Habsburgo-Lorena 1983). Hobbs et al. (1989) conclude that the majority of introductions of red swamp crayfish have had negative consequences, and little or no economic value. Exceptions include the potential use in Kenya of *P. clarkii* as a biological control agent for freshwater snails that carry human schistosomiasis (Mkoji et al. 1992).

Some authors point out that commercial, socioeconomic, and recreational benefits have resulted from some crayfish introductions in Europe because about 90% of the European harvest is now of introduced North American species (Ackefors 1999). However, the perceived need for these introductions resulted initially from the extirpation of native crayfish stocks by crayfish plague introduced via North American crayfishes. If any value is placed on protecting native biota and ecosystems (and we would place considerable value here), benefits of crayfish introductions must be weighed carefully against losses in native biodiversity and changes in ecosystem function that crayfishes frequently cause (Holdich 1999b; Table 2).

If European fisheries managers could turn the clock back to 1850, many, if not most, would surely choose to protect their native crayfish fisheries instead of replacing them with fisheries based on North American species. In the marketplace, today's Scandinavian consumers attest to the monetary value of native species: they are willing to pay substantially higher prices for the native *A. astacus* relative to the naturalized North American species *P. leniusculus* (Holdich 1999a).

In Europe, crayfish introductions have been so common that it is conceivable that in the next 50 years almost all watersheds suitable for crayfish in Europe could be inhabited by nonindigenous crayfishes, and that all native species might be endangered, surviving only in protected parks and restricted areas (Taugbøl and Skurdal 1999).

The North American situation

Compared to the European situation—where so many probably irreversible changes in the crayfish fauna and native ecosystems already exist—the North American situation offers much greater opportunities for thoughtful policies to prevent losses of native biodiversity and ecological disasters. We see this as doubly encouraging, because in North America, there is much more native crayfish biodiversity to protect.

The greatest evolutionary radiation of crayfishes on earth occurred in what is now the southeastern United States. There are about 390 species of crayfishes native to North America, with the vast majority of these species in the family Cambaridae and restricted to eastern North America (Hobbs 1988; Taylor et al. 1996). Only the five species in the family Astacidae existed west of the Rocky Mountains before anthropogenic introductions occurred.

In North America, species thrive in all aquatic and many semi-aquatic habitats, including wetlands, lakes, rivers, and streams; in very soft, acidic waters to very hard waters with moderate salinity; and in surface waters, soil porewaters (by burrowing), and groundwaters in caves (Hobbs 1991). Thus, in addition to taxonomic diversity, the North American fauna also exhibits great ecological diversity that remains to be protected.

On the other hand, the challenge of preserving crayfish biodiversity in North America is intensified because many of these species have naturally small native ranges (Taylor et al. 1996; Lodge et al. 1998a; Crandall 1998). Eleven species are known from only a single location, and another 20 species from five or fewer locations (Taylor et al. 1996). Furthermore, 43% of all crayfishes known from North America north of Mexico are distributed entirely within one U.S. state's political boundaries (Taylor et al. 1996; Lodge et al. 1998a). Numerous other species are shared by two states or provinces but are restricted to single river drainages that cross state or provincial lines. These are much smaller range sizes than those of other well known and also imperiled freshwater groups: only 16% of freshwater fishes native to North America north of Mexico are restricted to a single state or province (Page and Burr 1991; L. M. Page, Illinois Natural History Survey, pers. comm.), while only 15% of unionid mussels are endemic to a single state or province (Williams et al. 1993). Clearly, species with small ranges, like many of the North American crayfishes, are extremely vulnerable to extinction because even a small area invaded by a nonindigenous species may affect a large proportion of the individuals in a native species (Gilpin and Soulé 1986; Rabinowitz et al. 1986).

Relative to Europe, a much greater proportion of North America's crayfishes have not yet experienced nonindigenous crayfishes or other severe anthropogenic factors. However, nonindigenous crayfishes (resulting mostly from anthropogenic range expansions within North America) are increasingly important in the demise of some native crayfishes and in large changes in North American freshwater ecosystems. Anthropogenic vectors of crayfish range expansions within North America include (Table 1): (1) dispersal into new drainages via canals, most of which has probably already happened; (2) legal and (3) illegal stocking in natural waters, which is declining in importance as knowledge of the risks of nonindigenous species have become more widely known; (4) escapes from aquaculture ponds, (5) live food vendors, and

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The use of live crayfish as fish bait has been a major vector of spread of several species of crayfish in North America. Because of the large ecosystem impacts of these introduced species, the use of live crayfish is now restricted or illegal in several states.

Table 3. Recent citations for the variety of mechanisms by which nonindigenous crayfishes have reduced the abundance of native crayfishes in both Europe and North America.

Mechanism	Europe	North America
Disease vector	Vey et al. 1983; Alderman et al. 1990; Matthews and Reynolds 1992; Alderman 1993; Dieguez-Uribeondo and Söderhäll 1993	No studies known
Competition	Söderbäck 1995; Holdich and Domaniewski 1995; Vorburger and Ribi 1999	Capelli and Munjal 1982; Butler and Stein 1985; Mather and Stein 1993; Garvey et al. 1994; Hill and Lodge 1994; Hill and Lodge 1999.
Fish predator interactions	Appelberg and Odelström 1988; Holdich and Domaniewski 1995 Söderbäck 1992, 1995	DiDonato and Lodge 1993; Mather and Stein 1993; Garvey et al. 1994; Hill and Lodge 1994, 1999
Reproductive interference or hybridization	Söderbäck 1993; Cukerzis 1988	Capelli and Capelli 1980; Berrill and Arsenault 1985; Perry, Feder, and Lodge submitted

(6) the aquarium and pond trade, all of which probably are increasing as these commercial enterprises grow nationwide; (7) escapes or releases from students after studying live crayfishes obtained from biological supply houses (Hamr 1998); and (8) escapes from the live bait trade, which has probably been the most important vector in recent decades (Table 1). The importance of vectors 4–8 (Table 1) of freshwater nonindigenous species has often been treated only superficially in the past, and their importance discounted, probably because they are very difficult to quantify.

However, it is clear that the culture and subsequent escape of crayfishes indigenous to North America have led to the range expansions of those species (Hobbs et al. 1989). While there is yet no documented case of a nonindigenous crayfish introduced for aquacultural purposes displacing a native species, the potential looms large as aquaculturists in North America begin to experiment with more native species and with Australian species of the family Parastacidae that grow to large size (Rouse 1995; Semple et al. 1995). Different species of crayfishes are popular food resources in many parts of North America (Huner 1997b). In addition, crayfishes are one of the favorite live baits of recreational anglers (Dalrymple 1992). Recent rigorous analyses of the live bait trade demonstrate that it is a very important vector of nonindigenous species (Litvak and Mandrak 1993; Ludwig and Leitch 1996). In response to demands for both human food and fish bait, individuals or commercial interests often transport crayfishes across drainage and political boundaries (Taylor et al. 1996; Huner 1997a). Trade in crayfish bait has been implicated specifically in the spread of rusty crayfish (*Orconectes rusticus*) across the United States (Page 1985; Hamr 1998) and the introduction of *P. leniusculus* and *Orconectes virilis* into northern California (Eng and Daniels 1982). Among vectors of increasing importance (numbers 4-8 in Table 1), the live bait trade (including the use of live crayfishes collected by individual anglers) is unique in having as its central purpose the transportation of live crayfish to natural habitats. For all these reasons, we fear that the live bait trade will continue to be one of the most important vectors for the introduction of nonindigenous crayfishes in coming decades unless additional regulations are adopted (see our essay, this issue).

At least 10 species of crayfishes have had human assistance in expanding their North American range (Hobbs et al. 1989), and the impacts of nonindigenous crayfishes have often been large, even where native crayfishes already existed (Table 2). Impacts of several species of introduced crayfishes on a variety of taxa are thoroughly documented: crayfishes often reduce the abundance of macrophytes by $\geq$80%; reduce the abundance of algae via direct consumption and via destruction of the macrophytes on which some algae grow; reduce the abundance of some macroinvertebrates, especially snails, which are sometimes eliminated; and reduce the abundance of native crayfishes, often to the point of local extirpation (Table 2). Impacts on other taxa, e.g., amphibians, fishes, have been less studied, but existing data show reductions in these taxa also (Table 2). Nonindigenous crayfishes also interfere with recreational and commercial fisheries by consuming fishes on stringers or in gill nets (Lowery and Mendes 1977); this is particularly important in habitats with no native crayfishes. *Procambarus clarkii* is also a pest in rice culture in various parts of the world, including North America (Table 2).

The mechanisms by which native crayfishes are reduced by nonindigenous crayfishes include competition, predation, and reproductive interference (Table 3). However, no documented examples exist in North America of one crayfish species acting as a vector for disease of another crayfish, a mechanism that has been so important in Europe (Table 3). Since so little attention has been given within North America to crayfish commensals, parasites, and diseases (*e.g.*, Branchiobdellid worms, plague, *Thelohania*, *Psorospermium*), it is quite possible such interactions have gone unnoticed and could be or could become important in the same way that whirling disease has become so important in some North American salmonid fisheries. For example, only a few North American species are known to harbor plague (and that is known only because they carried it to

Europe and killed native species there) (Lilley et al. 1997). Many other native North American species may, like the European and Australian species, be susceptible to plague, or may carry other strains or species of disease organisms. Thus, the known dangers of introducing nonindigenous crayfishes are great, and it is not hard to identify other, potentially important dangers.

The serious threat to North American crayfish biodiversity posed by nonindigenous crayfishes has already contributed to a global extinction. *Pacifastacus nigrescen*s, native to the San Francisco Bay region of northern California, has disappeared as a result of urbanization, overexploitation, and interactions with the introduced signal crayfish, *P. leniusculus* (Reigel 1959; Bouchard 1977). In the same region, the federally endangered Shasta crayfish (*Pacifastacus fortis*), is now limited to small, isolated populations, having been displaced at several locations in its native watershed by habitat loss and interactions with the signal crayfish (Light et al. 1995). The estimated cost of recovery for the Shasta crayfish is $4.5 million (U.S. Fish and Wildlife Service 1998).

The best documented North American example of the ecological effects of a nonindigenous crayfish species involves the range expansion of the rusty crayfish, *O. rusticus*. From its original range centered in the streams of western Ohio and encompassing neighboring parts of Indiana and Kentucky (Taylor 2000), *O. rusticus* has expanded its range into streams, rivers, and lakes throughout much of Illinois, Michigan, Wisconsin, and Minnesota; it is also common in parts of Iowa, Tennessee, Pennsylvania, seven other northeastern states, New Mexico, and Ontario (Page 1985; Taylor et al. 1996; Hamr 1998). It now also occurs in most, if not all, the Laurentian Great Lakes (Lodge, Perry, and Feder unpublished data). Vectors of this expansion first included dispersal through canals, but in recent decades bait buckets, intentional introductions by commercial harvesters of crayfish, and subsequent dispersal through natural watercourses have been important (Capelli and Magnuson 1983). Range expansion continues in all directions from the current range boundaries. In these new habitats, the rusty crayfish often becomes extremely abundant, achieving mean summertime densities of adults of up to 15 / m^2 (Lodge and Hill 1994).

Orconectes rusticus has displaced native crayfishes, especially *Orconectes propinquus* and *O. virilis*, in lotic habitats in Ohio (Jezerinac et al. 1995) and Illinois (Taylor and Redmer 1996). The impacts of the rusty crayfish invasion have been most intensively studied in lakes of northern Wisconsin where resident crayfishes (the native species *O. virilis*, and a previous invader, *O. propinquus*) have been reduced or eliminated within a few years of establishment of the rusty crayfish (Lodge et al. 1986; Olsen et al. 1991). Of 107 lakes and 50 stream reaches surveyed in northern Wisconsin and the upper peninsula of Michigan—where *O. virilis* was the only common crayfish in the first decades of this century (Creaser 1932)—*O. virilis* now occurs in only 44% and 38% of the lakes and streams, respectively (W. Perry, D. M. Lodge, and G. L. Lamberti, unpublished data). *Orconectes rusticus* has extirpated the other crayfishes in the remainder of the habitats. Where these species replacements have been studied experimentally, the rusty crayfish is superior to the congeneric species for all of several interacting mechanisms (Hill and Lodge 1999): chemosensory responses to food and consumption rates of food (Olsen et al. 1991; Willman et al. 1994); individual growth rates (Hill et al. 1993); competition for shelter and food (Hill and Lodge 1994); differential susceptibility to fish predation (DiDonato and Lodge 1993; Garvey et al. 1994); and genetically confirmed hybridization (Perry et al. unpublished data).

Because *O. propinquus* and *O. virilis* have two of the largest natural ranges of the North American crayfishes, they are not in danger of extinction although their abundances within their ranges are being much reduced by *O. rusticus*. The situation, so far, is very similar to that experienced in Europe. However, if the expanding rusty crayfish range begins to overlap with the many other crayfishes that have small ranges, global extinction of those species seems very possible. For example, the Big South Fork crayfish (*Cambarus bouchardi*) is endemic to the Roaring Paunch Creek drainage (two counties in the Big South Fork of the Cumberland River, Tennessee), about 30 miles southeast of an introduced population of *O. rusticus* in the Laurel River (a tributary of the Cumberland River). Global extinctions caused by *O. rusticus* are especially likely in the southeastern United

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As a widely introduced species and a vector of crayfish plague, the signal crayfish (*Pacifastacus leniusculus*), native to the northwestern coast of the United States, has extirpated many local populations of native crayfishes in Scandinavia, England, and northern Europe.

States, where many native crayfishes exhibit narrow endemism.

Given the European experience with crayfishes from other continents, North American crayfishes and aquatic ecosystems are at risk from crayfishes from other continents. For example, the Australian redclaw crayfish, *Cherax quadricarinatus*, has been cultured in the United States, but so far has not established any feral populations (Warren 1997). New management policies are required to prevent further introduction of crayfishes from other continents, and to prevent further spread of North American species outside their native range. Otherwise, losses of biodiversity and changes in ecosystem function are a virtual certainty.

Even if conserving native crayfishes was not a priority, many of the other ecosystem changes wrought by the rusty crayfish and other nonindigenous crayfishes have been uniformly perceived as negative by humans. In the upper U.S. Midwest, the rusty crayfish is regarded as a nuisance because it clearcuts macrophytes (Lodge et al. 1994), thereby altering the ecosystem processes mediated by macrophytes (Carpenter and Lodge 1986). For example, habitat heterogeneity (Lodge et al. 1988) and macrophyte-associated invertebrate food for fishes (Lodge et al. 1985) are reduced. In addition, the rusty crayfish directly consumes many invertebrates, lowering their abundance (Perry et al. 1997; Lodge et al. 1998a), and possibly thereby competing with benthivorous fishes. The fishes that feed on rusty crayfish reduce, but do not eliminate these food web and ecosystem impacts (Hill and Lodge 1995; Kershner and Lodge 1995).

Existing NIS policies in Europe and North America

European policies

In many European countries, legislation now exists to protect native crayfishes and their freshwater habitats from nonindigenous crayfishes (Gherardi and Holdich 1999). In response to the Convention on Biological Diversity signed at the Earth Summit in Rio de Janeiro in 1992, the European Union (EU) issued the Habitats Directive (Directive 92/43/EEC) to conserve the EU's most endangered species and habitat types. Currently, only *Austropotamobius pallipes* is listed as warranting protection. The World Conservation Union (IUCN) also lists *A. astacus* and *Austropotamobius torrentium* as threatened (Groombridge 1993). Under the Habitats Directive, EU countries are obliged to ensure that deliberate introductions of nonindigenous species are regulated.

Details of the regulatory methods vary considerably from one European country to another (Westman and Westman 1992). Ireland and Norway ban the import of live nonindigenous crayfishes, but the General Agreement on Trade and Tariffs (GATT) and Single European Market regulations may prevent other countries from taking such stringent steps. For example, Germany (European Court of Justice 1994) and Sweden (L. Edsman, Institute of Freshwater Research, Drottningholm, pers. comm.) have not now been able to stop the importation of live crayfish by registered traders, because they had trades in live crayfish established prior to GATT (A. Scott, Centre for Environment, Fisheries, and Aquaculture Science, Weymouth, England, pers. comm.).

Such free trade restrictions do not prevent strong regulations over movements of live crayfish within a country. For example, England and other British countries now use a variety of mechanisms to protect their only species of native crayfish (*A. pallipes*) from nonindigenous crayfish (Holdich and Rogers 1997). Because *A. pallipes* is a protected species under the Wildlife and Countryside Act (WCA), it cannot be taken or sold without a licence (which is rarely granted). Nonindigenous crayfishes that have become established in the wild, including North American species (*P. leniusculus*) and those native to mainland Europe (i.e., *A. astacus*, *A. leptodactylus*) are defined as pests under the WCA. It is therefore illegal throughout Britain to keep the mainland European species without a licence, unless they are being used for culinary purposes.

Because it was introduced into England for aquaculture, *P. leniusculus* has had additional regulatory attention. Its farming has been banned over much of the island (Holdich and Rogers 1997; Holdich et al. 1999b,c), and it cannot be transported inside a series of no-go areas which cover much of central and northern England as well as Scotland and Wales (Holdich and Rogers 1997; Holdich et al. 1999b,c). Ironically, its use in aquaculture has declined as harvest from feral populations of *P. leniusculus* and *A. leptodactylus* is now probably

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The white-clawed crayfish (*Austropotamobius pallipes*), the only native crayfish species in Great Britain, many local populations of which have been extirpated by the North American signal crayfish (*Pacifastacus leniusculus*), a vector of crayfish plague. The white-clawed crayfish is the only crayfish species in Europe that receives full protection in some countries.

greater than that from cultivation (Rogers and Holdich 1992). The regulations described above for Britain and other European countries are much more stringent than those described below for the United States.

U.S. policies

In the United States, current federal legislation governing NIS is inadequate in several respects to prevent introductions of nonindigenous species, including crayfishes (U.S. Congress 1993). First, the most relevant pieces of legislation—the Federal Noxious Weed Act and the Lacey Act—are focused largely on terrestrial plants and insects that are potential pests in agriculture, giving scant attention to natural areas and aquatic species. Recent federal acts directed specifically at aquatic NIS (Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990, National Invasive Species Act of 1996) primarily address ballast water as a vector, rely on voluntary guidelines, and therefore do not address the vectors listed above that are of greatest importance for crayfishes and many other freshwater organisms (Bean and Rowland 1997).

Second, federal laws deal primarily with importation into the United States, and much less with interstate or intrastate transport or movements within states. Many harmful NIS come from within North America; neither they nor species from other continents respect political boundaries, and many watersheds (that often define natural dispersal barriers) cross political boundaries.

Third, the relevant regulations take a "black list" approach, i.e., species can be imported into the United States unless they are on a list of prohibited species. Currently, the U.S. Fish and Wildlife Service (USFWS) prohibits importation into the United States of two families of fishes; 18 genera or species of mammals, birds, reptiles, and shellfish; and two fish pathogens (U.S. Congress 1993). This leaves the door open for most species, including most potentially invasive ones, simply because few data relevant to invasiveness exist for most species (including most crayfishes) on the globe. A "white list" approach, approving only species that have been appropriately screened, would prevent many harmful introductions (Ruesink et al. 1995). From 1973 to 1977, the USFWS proposed several versions of such a white list, but in the face of strong opposition from the aquarium trade and other stakeholder industries, ultimately withdrew the proposals (U.S. Congress 1993). Given the rapidly increasing number of nuisance freshwater NIS and the increased understanding of their economic (very conservatively estimated at $4.1 billion annually by Pimentel et al. 1999) and ecological costs since that earlier attempt, a white list approach may be more viable now.

A. Barbian / ProPhoto

In many parts of the world, including areas of North America, crayfish are important not only because they are an important component of biodiversity and play a keystone role in ecosystems, but also because they are an important feature of culture and cuisine.

At the state level, general approaches and degree of regulation of NIS range widely. In Florida, a permit is required for possession of any species not native to Florida, but thousands of permits are issued annually for nonindigenous fishes and other aquatic species (Cox et al. 1997). Only a few species are prohibited; no crayfish or other invertebrates are on the Florida blacklist (Cox et al. 1997). In many other states, no general regulations apply to freshwater NIS, although some industries that bear directly on freshwater NIS are regulated. In the accompanying essay, we make several recommendations to address the lack of current federal and state regulation of nonindigenous species.

Conclusions

The establishment of nonindigenous crayfishes in Europe caused large reductions in population density and numbers of populations of native crayfishes. This, in turn, changed freshwater ecosystem function, and reduced economic viability of native crayfish fisheries over the last century (Holdich 1999b). Although many of these changes are probably irreversible, several European countries have taken very strong and successful regulatory and management steps to reduce further ecological and economic disruptions from nonindigenous crayfishes. In North America, the biodiversity and economic value of crayfishes is much greater than in Europe, and therefore worthy of substantial conservation efforts.

Ecological and economic disruptions regarding North American crayfishes have been fewer than in Europe, but North American examples of nonindigenous crayfishes (e.g., *P. leniusculus, O. rusticus*) serve as a warning of the losses in biodiversity, the changes in freshwater ecosystem function, and the economic harm that can result from moving crayfishes outside of their native range. In Europe, no crayfish species is likely to disappear completely. In North America, however, the greater number of species and small average range size suggest that more extinctions are likely if introductions of nonindigenous crayfishes are not slowed soon. A window of opportunity exists to learn from our own and Europe's experience. To prevent future changes in North American ecosystem function and losses of crayfish biodiversity, we advocate the promulgation of new regulations and management practices that carefully target the most important vectors of crayfish introductions (see our essay, this issue).

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