

Importance of Hybridization Between Indigenous and Nonindigenous Freshwater Species: An Overlooked Threat to North American Biodiversity

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Abstract.—Biodiversity of North American freshwaters is among the greatest in the world. However, due to extensive habitat degradation, pollution, and introductions of nonindigenous species, this biodiversity is also among the most endangered. Unlike habitat degradation and pollution, nonindigenous species represent a permanent loss of biodiversity because their removal or control is often impossible. Most species introduced into nonnative North American ranges, however, are not from Eurasia but have been introduced from geographically isolated regions within North America. Although the ecological effects of introduced species have been widely documented, the effects of hybridization, especially between closely related species, represents an equally serious mechanism of extinction but is much less studied. Identification of which species are likely to hybridize after contact is of critical importance to prevent the further loss of native species. Molecular phylogenetics serves as a powerful tool to identify freshwater species at risk of introgression, if we can assume that genetic distance is a good predictor of the potential for hybridization. Although not a thorough review of all cases of hybridization, this article documents the extent and effects of hybridization in fishes, crayfishes, mussels, and other invertebrates in light of the currently accepted phylogenetic relationships. We suggest this approach may be the first step in addressing the potential threat of hybridization between many of the closely related species in North American fresh waters. [Aquatic biodiversity; invasion; hybridization; systematics.]

Proper classification and phylogenetic reconstruction provide a blueprint for life's relationships and history. Without this information, building a solid understanding of the evolutionary processes generating biological diversity would be impossible. Equally important is that systematists also write biodiversity's obituary. Extinction is the natural flip side of speciation. Both processes tell life's story, together determining patterns and trends seen in the historical record and on earth today. Until recently, the study of extinction has primarily been the domain of paleontologists. However, heightened interest in conservation stemming from the anthropogenic homogenization and destruction of Earth's biota has changed this (Rahel, 2000). Humans are currently causing the extinction of taxa at a very high rate. Without reversals of these trends, "modern" times will rival the periods of mass extinction recorded at the end of the Permian and Cretaceous eras (Sala et al., 2000, 2001).

Many factors currently contribute to the decline of global biodiversity, including global climate change, pollution, habitat alteration, overharvesting, and interactions with invading species (Sala et al., 2000).

Here, the negative consequences of human-mediated species introductions on biodiversity will be emphasized. We focus on freshwater streams and lakes in North America because aquatic ecosystems appear to be the most vulnerable to nonindigenous species introductions (Miller, 1989; Williams et al., 1993, 1996; Taylor et al., 1996; Kolar and Lodge, 2000; Lodge, 2001). Indeed, one of the greatest threats to freshwater fauna may be the enemy within: Threats posed by the movement of regional endemics within the continent of North America may equal or exceed that of nonindigenous species introduced from outside North America.

Most studies of species invasions emphasize the ecological effects of nonindigenous taxa on natives, especially effects related to competition, predation, and parasitism. But hybridization associated with invasions of nonindigenous species also poses a serious threat to the integrity of endemic gene pools (Rhymer and Simberloff, 1996). Unfortunately, the magnitude of this danger to the conservation and management of biodiversity is only now being recognized (Rhymer and Simberloff, 1996; Haig, 1998). This review examines invasions in

which ecological interactions and hybridization between nonindigenous species and resident species threaten resident biodiversity for North American fishes (Leary et al., 1984; Allendorf and Leary, 1988; Echelle and Connor, 1989; Miller et al., 1989; Dowling and Childs, 1992), crayfishes (Lodge et al., 2000a,b; Perry et al., 2001a,b), and mollusks (Lydeard and Roe, 1998). These studies confirm that hybridization may be especially relevant to freshwater taxa that exist as numerous locally differentiated populations and to species now in contact that were previously isolated (Lodge et al., 2000b). This review will stress the point that without detailed taxonomic and genetic information, threats posed by hybridization may be underestimated or overlooked altogether (Rhymer and Simberloff, 1996).

A detailed review of the invasion of the rusty crayfish, *Orconectes rusticus*, in northern Wisconsin and Michigan will provide an example of the combined role of hybridization and ecological mechanisms, competition, predation sensitivity, and demographics. Only after an extensive genetic analysis of this invasion in northern Wisconsin was the importance of hybridization in the extirpation of resident species, *O. propinquus*, realized. Similarly, many cryptic taxa of closely related freshwater mussels may disappear before they are even described (Lydeard and Roe, 1998). Consequently, hybridization not only eliminates biodiversity in the present but also, because of the fusion of incipient evolutionary lineages, destroys the source of biodiversity for the future. Understanding and forecasting this impact cannot be accomplished without a thorough understanding of the systematics of the affected taxa. The degree of relatedness estimated from systematic relationships may be the most reliable index for predicting the probability of hybridization and introgression.

NORTH AMERICAN BIODIVERSITY AND NONINDIGENOUS SPECIES

North America is a particularly bountiful continent with respect to freshwater ecosystems. The biodiversity of crayfishes (333 species), mussels (296 species), and fishes (822 species) is among the greatest in the world (Table 1). This extensive diversity probably results from a combination of vicariance and dispersal during

the Pleistocene era, leading to a combination of isolation and reradiation of fauna from glacial refugia as evidenced by the crayfishes (Fitzpatrick, 1986; Crandall and Templeton, 1999), fishes (Mayden, 1988), and salamanders (Mayden, 1988). The likely centers of glacial refugia were in the Central Highlands, Ozarks, Ouchitas, and the Eastern Highlands (Fitzpatrick, 1986; Murdoch and Hebert, 1997; Rempel and Smith, 1998; Crandall and Templeton, 1999). These areas have the greatest endemism and biodiversity of fishes, mussels, and crayfishes. The glacial history and reradiation of the aquatic taxa in North America has led to a diverse assemblage of closely related freshwater taxa occupying ranges that are often limited to one or few stream systems.

These unique assemblages of taxa are now imperiled by a variety of abiotic and biotic factors. Fishes, crayfishes, and mussels rank among the most threatened and endangered taxonomic categories in North America. Approximately 11–20% of terrestrial vertebrates in North America are at risk of extinction (Naiman et al., 1995; Master et al., 1998), whereas 32.7% of fishes, 50.5% of crayfishes, and 56.4% of mussels are in need of immediate conservation attention (Master et al., 1998) (Table 1). These often-small populations are particularly susceptible to habitat degradation, pollution, overharvesting, and especially introductions of nonindigenous species (Master et al., 1998; Claudi and Leach, 1999; Lodge et al., 2000b; Sala et al., 2000).

Increased trade with other continents is one of the major pathways of introductions of nonindigenous species from other continents, and the number of species introduced is steadily increasing (Fuller et al., 1999). The economic and ecological effects of these introductions are well illustrated by the invasion of zebra mussels (*Dreissena polymorpha*) (Strayer and Smith, 1996; Strayer et al., 1996). Filter-feeding by zebra mussels in the Great Lakes has increased water clarity and shifted primary production from the open water zone to the benthic zone, decreasing food for other filter feeders (Lowe and Pillsbury, 1995). In the Hudson River, zebra mussels are thought to have outcompeted unionids for food, causing the decline of resident unionids (Strayer and Smith, 1996). Zebra mussels represent a unique growth form in North American freshwaters because

TABLE 1. Status of biodiversity in the USA: Comparing federally threatened and endangered species and those listed as vulnerable to extinction.^a

Taxa	Total North American species	Federally listed as threatened and endangered, %	Nongovernmental views of percent in need of conservation	US ranking of the number of species worldwide
Terrestrial				
Mammals	419	16.7	16.2	6
Reptiles	285	12.6	20	14
Birds	772	10.1	10.9	27
Freshwater				
Fish	822	13.6	32.7	7
Amphibians	240	8.3	38.3	12
Crayfish	333	1.5	50.5	1
Mussels	296	24.3	56.4	1
Snails	658	4.9	57.3	1

^aSource: Association for Biodiversity Information. 2001. Downloadable data sets. http://www.natureserve.org/datasets_zoo/overview.htm. Natural Heritage Central Databases. Association for Biodiversity Information, Arlington, VA. Copyright © 2001 NatureServe. All rights reserved.

they attach to hard substrata, especially shells of unionids, thereby causing direct mortality of unionids. Similar examples exist for invasions of other Eurasian species— invasions that have resulted in substantial economic costs and in reductions of resident biodiversity from competition, predation, parasitism, and other ecological mechanisms (Benson and Boydstun, 1999). Consequently, much attention has been focused on curbing the introduction of nonindigenous species from Eurasia and other continents.

Somewhat surprisingly, however, the greatest threats to crayfish, mussels, and fish may come from introductions within North America. With the increased recreational and commercial use of lakes and rivers, the number of species introduced from within North America is also on the rise (Miller et al., 1989; Benson and Boydstun, 1999; Fuller et al., 1999; Lodge et al., 2000a,b; Rahel, 2000). Estimates of the number and origin of nonindigenous aquatic species established in North America suggest that at least 50% of all taxa originate from within North America; >65% of fishes, 50% of crustaceans, and 20% of mussels are spread from one isolated geographic region to another within North America (Mills et al., 1993; Benson and Boydstun, 1999; Fuller et al., 1999; Rahel, 2000).

Nonindigenous species introduced from within North America pose a two-pronged threat to resident species. The ecological impacts may be similar to those of Eurasian species introduced, but the potential to hybridize with closely related species and genetically swamp the often smaller, highly

endemic, resident populations is greater for North American intruders (Rhymer and Simberloff, 1996). Human-assisted transfer from one watershed to another can easily introduce species into watersheds previously outside the species' natural range (Rahel, 2000). The risk of hybridization is not minor: The use of molecular tools is only now beginning to uncover the full extent of hybridization and introgression between introduced and native populations. The combination of increased commerce, recreational uses, land use change, global climate change, fisheries management, and construction of dams, canals, and irrigation systems will probably continue to accelerate the homogenization of aquatic fauna within North America (Rahel, 2000).

Hybridization associated with invasions has been demonstrated in several taxa, including fishes and crayfishes, and is a potentially serious threat to unionids as well. Examples illustrating a few well-documented studies reviewed below are indicative of a potentially pervasive and serious threat to North America's rich and often unrecognized freshwater biodiversity. In the remainder of the review, the status of nonindigenous species introduced from one region to another in North America for fish, crayfish, mollusks, and other invertebrates will be discussed. This review highlights specific invasions where studies of the combined effects of hybridization and ecological mechanisms have been examined. This review also highlights the current understanding of the phylogenetic relationships of the species involved and how this may help in predicting

the risks of hybridization between invading and resident species; it may also help in understanding and preventing future introductions.

FISHES

The number, origins, methods of introduction, and impacts of nonindigenous fishes have been among the most extensively documented of all aquatic taxa (Crossman and Cudmore, 1999; Dextrase and Coscarelli, 1999; Fuller et al., 1999). The total number of nonindigenous fishes in the USA exceeds 800 species, with >500 species having translocated from one region to another since 1951 (Fuller et al., 1999). Of those species introduced after 1951, >60% originated from within North America (Fuller et al., 1999). Many of these introductions are unintentional introductions of species as contaminants in fish stocking programs, traveling through canals, and fish bait; moreover, the extent of these introductions is probably an underestimate because many introductions go unnoticed (Litvak and Mandrak, 1993, 1999; Ludwig and Leitch, 1996; Benson and Boydsun, 1999; Goodchild, 1999). Thus, the common impression that most species are introduced from other continents is not true for fishes. Also unlike introductions from other continents, many of these introductions consist of species that are closely related to the species of the receiving community and thus may affect resident biodiversity through a combination of ecological mechanisms and hybridization (Dextrase and Coscarelli, 1999).

Hybridization has been a contributing factor in 38% of the documented cases of fish extinctions in the USA (Miller et al., 1989). This number too is probably an underestimate because morphology alone is often a poor indicator of hybridization, and the use of molecular tools in studies of natural populations is just beginning (Leary et al., 1985; Ferguson and Danzmann, 1987; Ferguson et al., 1988). Even species separated for >2.5 million years are still able to produce fertile offspring (Gyllensten et al., 1985; Smith, 1992). Examples of extensive hybridization and introgression between fish species, subspecies, or even genetically distinct populations occurring either naturally or as the result of anthropogenic introductions have been documented since Hubbs (1955). Hybridization

between fishes as a result of introductions is increasingly common and threatens species (Awise et al., 1984; Awise and Saunders, 1984; Echelle and Connor, 1989; Kruger and May, 1991; Philipp, 1991; Smith, 1992, and references therein; Echelle and Echelle, 1997).

One of the most extensively documented cases of hybridization associated with the decline and extirpation of fishes was conducted for the subspecies of cutthroat trout, *Oncorhynchus clarki* spp., of the western USA (Gyllensten et al., 1985; Allendorf and Leary, 1988; Forbes and Allendorf, 1991; Dowling and Childs, 1992). A diverse assemblage of native endemic cutthroat trout (*O. clarki*) exists in the Western Basin, but many of the subspecies are on the brink of extinction. The resident cutthroat trout are currently recognized as a group of morphologically similar but genetically (Fig. 1) and behaviorally distinct subspecies (Allendorf and Leary, 1988) (Fig. 1b). Based on biogeography and mitochondrial DNA differences, these species have been isolated from one another for 1 to 2 million years (Allendorf and Leary, 1988). Introduction of nonindigenous species—including stocked cutthroat trout subspecies (*O. clarki* spp.), brown trout (*Salmo trutta*), rainbow trout (*O. mykiss*), and brook trout (*Salvinus fontinalis*)—is the greatest threat to this group of subspecies (Allendorf and Leary, 1988; Varley and Gresswell, 1988; Utter and Allendorf, 1994).

Introduced brook and brown trout populations have led to declines in resident populations of cutthroat trout through a variety of ecological interactions. Brook and brown trout outcompete resident cutthroats for food and space, and older individuals prey on juvenile cutthroats (Varley and Gresswell, 1988; Destaso and Rahel, 1994; Wang and Ray, 1994; Dunham et al., 2000). Brook and brown trout, however, are only distantly related to cutthroat trout, and no studies have documented hybridization between either brook or brown trout and either resident cutthroats or introduced rainbow trout.

Introduced rainbow trout have negative impacts on resident cutthroats through competitive interactions, but extensive hybridization represents the most serious threat to the persistence of these endemic species (Dowling and Childs, 1992, and references therein; Dunham et al., 2000). Hybridization between rainbow trout and cutthroat trout has led to the extensive loss of genetic

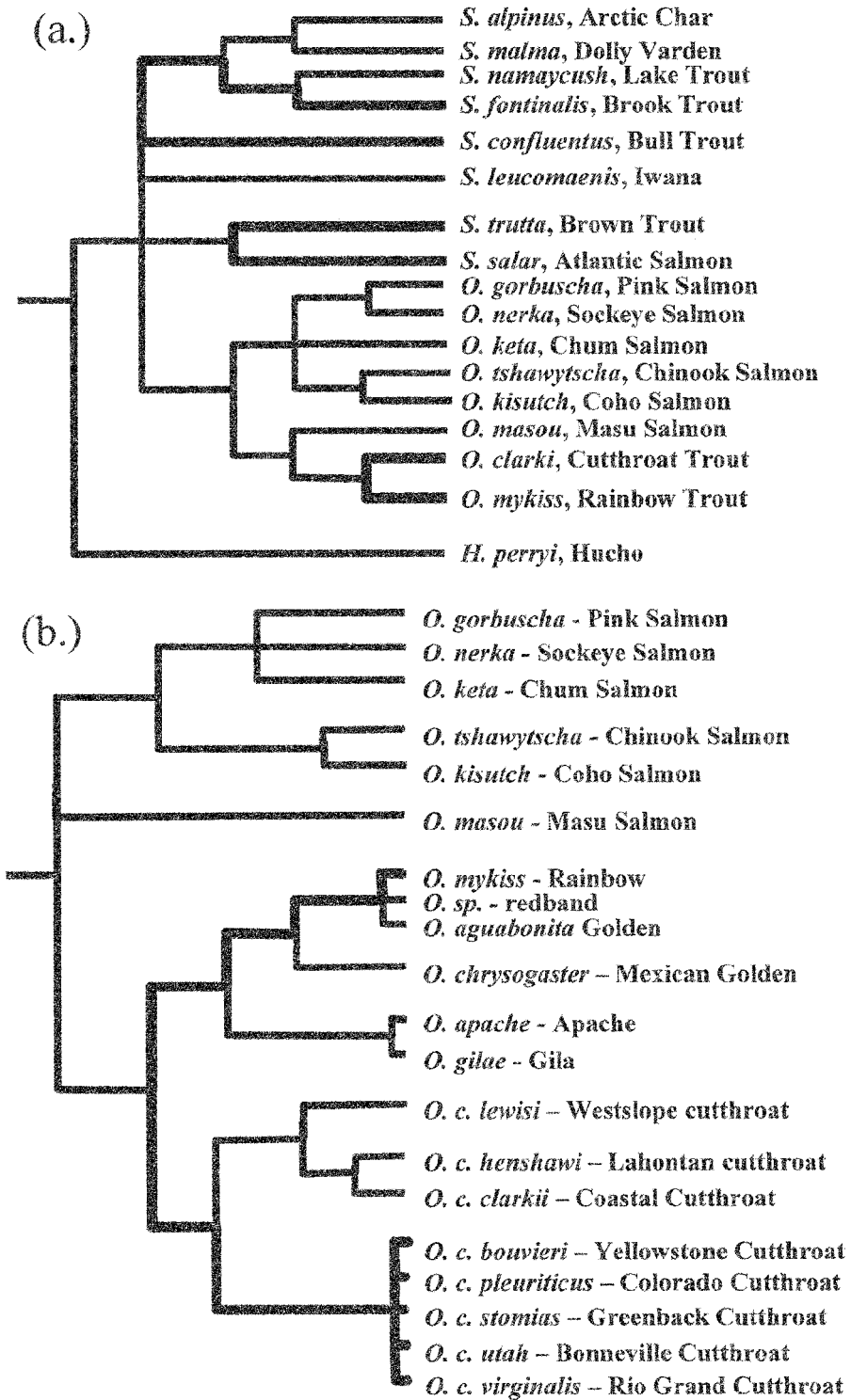


FIGURE 1. (a) Phylogeny of Salmonids, indicating species shown to hybridize as determined using a strict consensus tree from restriction maps of 18S and 28S ribosomal DNA (modified from Phillips et al., 1992). (b) Consensus tree reflecting divergence among the taxa determined by a combination of nuclear, mitochondrial, and ribosomal DNA sequence data and morphological data. Dark lines indicate taxa shown to hybridize (modified from Utter and Allendorf, 1994).

diversity. Stocking of cutthroat trout from one region to another has also resulted in hybrid swarms (Gyllensten et al., 1985; Allendorf and Leary, 1988) and has probably led to the loss of at least one genetically pure subspecies of cutthroat trout, the westslope cutthroat trout, *O. clarki lewisi* (Allendorf and Leary, 1988). Because of the close genetic relatedness of the cutthroat trout subspecies (Fig. 1), the loss of biodiversity through hybridization might have been predicted. Attention to phylogenetic relationships should help evaluate risks in any future planned introductions.

CRAYFISHES

The biodiversity of North American crayfishes is the greatest in the world, but many species are at risk of extinction (Lodge et al., 2000a) (Table 1). The geographic ranges of many of the >333 North American species (75% of the world's total crayfish species) have, until recently, been confined to one or a few catchments, especially in the Cumberland Plateau and Ozark Mountain regions (Fitzpatrick, 1986; Crandall and Templeton, 1999). These small populations and restricted distributions predispose crayfish to the threats of habitat alteration and the introduction of nonindigenous crayfishes (Taylor et al., 1996; Lodge et al., 2000a,b). The primary pathways of crayfish introductions to nonnative ranges are aquaculture, aquarium and pond trades, biological supply trade, and the live bait trade (Lodge et al., 2000a,b). Introduced species and habitat alterations contribute to conservation concern for >50.5% of North American crayfishes (Master et al., 1998; Taylor et al., 1996; Association for Biodiversity Information, 2001). Ecological interactions with introduced species (e.g., competition, predation, and vectors of disease) have contributed to the decline of many native North American crayfishes (Lodge et al., 2000a), but hybridization with invading species is also an important factor to consider (Perry et al., 2001a,b).

Crayfishes are the largest freshwater aquatic invertebrates and often serve as keystone species (Power et al., 1996) capable of controlling the structure and flow of energy in lake (Hobbs, 1993; Lodge et al., 1994; Nystrom et al., 1996) and stream ecosystems (Huryn and Wallace, 1987; Rabeni, 1992; Creed, 1994; Charlebois and Lamberti, 1996;

Perry et al., 1996, 2000). Changes in the crayfish community composition can result in dramatic changes in invertebrate assemblages, affect benthic algal and macrophyte biomass and productivity, and potentially lead to decreased fish populations (Butler and Stein, 1985; Lodge et al., 1985, 1994; Creed, 1994). Because of this central role, any changes in the native crayfish biodiversity also threaten the entire freshwater community structure and ecosystem function. Thus, preservation of resident crayfish biodiversity is important not only for crayfish, but also for all other components of freshwater ecosystems.

The invasion of the rusty crayfish, *Orconectes rusticus*, and resulting extirpation of the resident crayfishes, *O. propinquus* and *O. virilis*, provide a perspective on the role of hybridization and ecological mechanisms of displacement. *Orconectes rusticus* is native to the tributaries of the Ohio River in southwestern Ohio, northern Kentucky, and southeastern Indiana (Page, 1985; Hobbs and Jass, 1988). In recent decades, however, *O. rusticus* has been spread by human activity as far north as Maine and Ontario, south to Tennessee, and west to New Mexico (Page, 1985; Hobbs and Jass, 1988; Momot, 1992; Taylor and Redmer, 1996). Wherever the rusty crayfish has become established, it has altered aquatic ecosystems and extirpated resident crayfishes (Butler and Stein, 1985; Lodge et al., 1985, 1994, 1998, 2000a,b; Butler, 1988; Olsen et al., 1991; Taylor and Redmer, 1996). *Orconectes rusticus* has become a serious pest throughout eastern North America in the past 30 years (Hobbs and Jass, 1988; Lodge et al., 1994, 1998; Taylor and Redmer, 1996).

The dynamics of invasions by *O. rusticus* and the mechanisms through which it displaces resident species have been most intensively studied in northern Wisconsin and Michigan lakes and streams (Fig. 2) (Hill et al., 1993; Hill and Lodge, 1994, 1999). In these ecosystems, *O. rusticus* is displacing two resident taxa, *O. propinquus* and *O. virilis* (Lorman and Magnuson, 1978; Olsen et al., 1991; Hill and Lodge, 1994; Lodge et al., 1994). *Orconectes rusticus* grows significantly faster than does *O. propinquus* and reaches a larger body size (DiDonato and Lodge, 1993; Hill et al., 1993; Garvey et al., 1994). Although *O. rusticus* and *O. virilis* are similar in adult body size, *O. rusticus* has larger

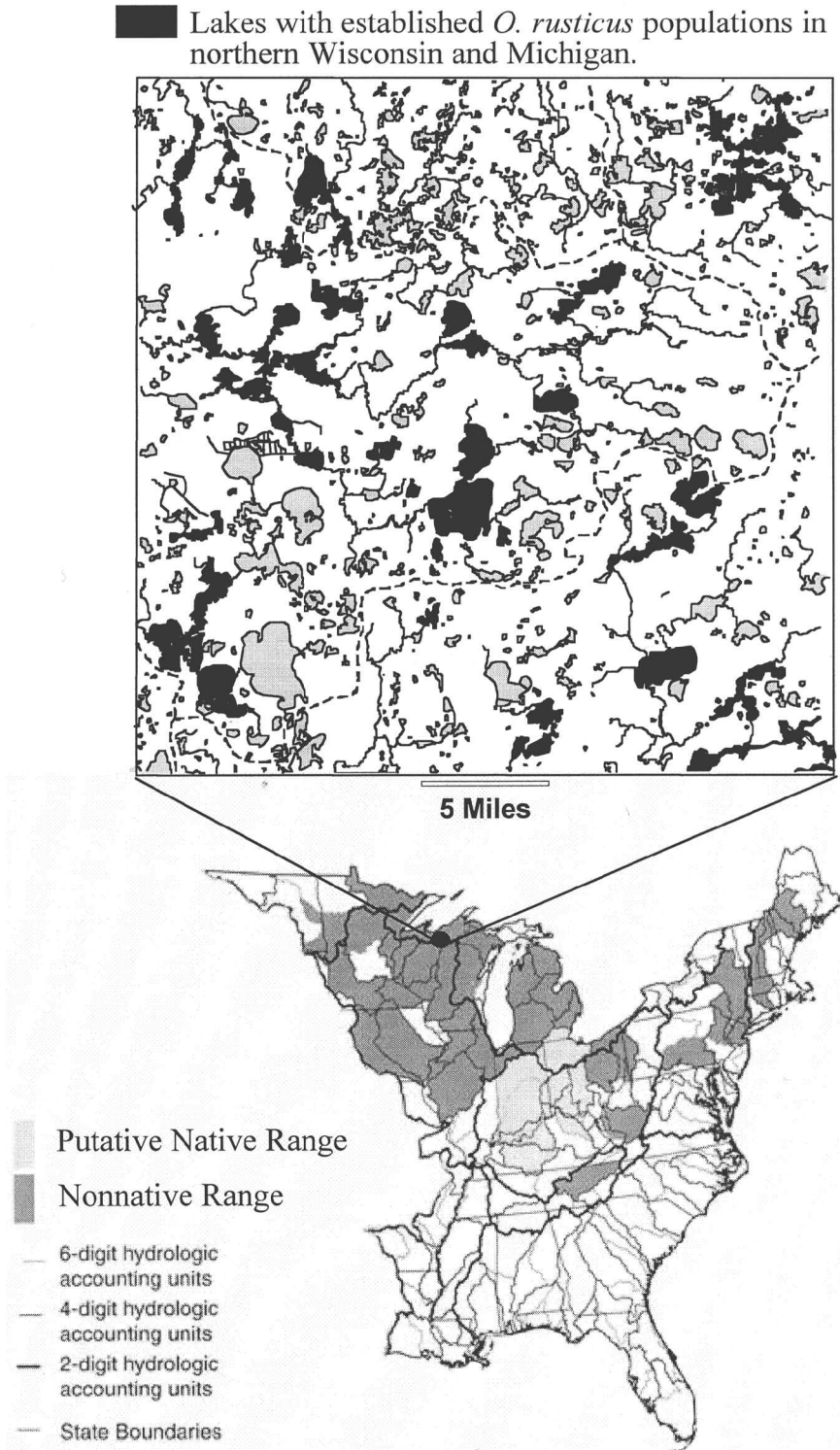


FIGURE 2. Native and current distributions of *O. rusticus* in the eastern USA (modified from Hobbs and Jass, 1988, private communication, Chris Taylor, Illinois Natural History Survey). Areas of northern Wisconsin/Michigan with lakes colonized by *O. rusticus* are indicated in black (Perry et al., 2001b, and references therein). Trout Lake is the large lake in the center of the figure.

chela, greater rate of juvenile survivorship, and greater growth rates than does *O. virilis* (Lodge et al., 1986; Garvey and Stein, 1993; Hill and Lodge, 1999). These features make *O. rusticus* less susceptible than *O. virilis* and *O. propinquus* to predation (DiDonato and Lodge, 1993; Garvey et al., 1994; Kershner and Lodge, 1995) and better able to secure food and shelter (Capelli and Munjal, 1982; Rabeni, 1985; Garvey and Stein, 1993; Hill and Lodge, 1994, 1999). Ecological mechanisms (e.g., competition, predation resistance) and demographic differences (e.g., growth rate, survivorship, individual size) seem to be the only factors driving the extirpation of *O. virilis* by *O. rusticus*. However, hybridization and introgression have recently been shown to be an important driving force in the extirpation of *O. propinquus* by *O. rusticus*.

Morphological studies suggested that *O. rusticus* was hybridizing with resident crayfish species (Crocker and Barr, 1968; Capelli and Capelli, 1980; Smith, 1981; Berrill, 1985; Butler and Stein, 1985). Significant morphological variation between populations of *O. rusticus*, however, made it difficult to definitively establish that these intermediate individuals were hybrids, and not just intraspecific variants resulting from environmental heterogeneity among lakes (Capelli and Capelli, 1980; Tierney, 1982). Until our recent work, this situation was never analyzed genetically. Using diagnostic nuclear markers (genes for isocitrate dehydrogenase [*Idh*] and hydroxyacid dehydrogenase [*Had*]), and diagnostic mitochondrial (mt) DNA markers (16S large ribosomal subunit and cytochrome *c* oxidase II), we found that hybridization occurred between *O. rusticus* and *O. propinquus*, whereas *O. virilis* hybridized with neither of these. Determination of the extent to which hybridization was occurring and what role it might have in the invasion and displacement of *O. propinquus* relative to the already well-documented ecological mechanisms was needed (Perry et al., 2001a,b).

Hybridization was predicted to increase the rate of displacement of *O. propinquus*. On the basis of our detailed understanding of competitive interactions of these species, we hypothesized that male *O. rusticus* would outcompete male *O. propinquus* for females of both species, which would result in biased mating patterns. If hybrid progeny were unfit, then the result would be decreased

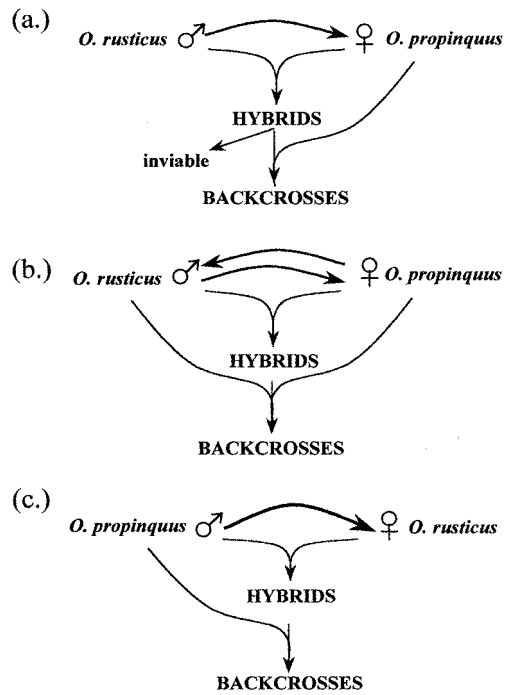


FIGURE 3. Hypothetical models of hybridization between *O. rusticus* and *O. propinquus*: (A) how hybridization would lead to the most rapid displacement of *O. propinquus*; (B) how hybridization and random mating lead to F_1 hybrids and backcrosses, which in the absence of ecological displacement mechanisms would lead to a hybrid swarm; and (C) how directional mating—with resident males mating disproportionately with invading females—might have the least impact on *O. propinquus*.

reproductive output of *O. propinquus* females (Fig. 3A). Moreover, if adults of mixed ancestry were competitively intermediate, they would also be able to outcompete resident *O. propinquus* males for mates, further increasing the rate of extirpation of *O. propinquus* relative to *O. rusticus* through decreased production of pure *O. propinquus* offspring (Fig. 3A). Other potential outcomes of hybridization associated with invasions included random mating and the formation of a hybrid swarm (Fig. 3B), and directional mating of resident males with invading females (Fig. 3C). Through the use of molecular markers, we were able to test the extent of hybridization, the mating patterns leading to the formation of F_1 hybrids, and the existence of later-generation hybrids—which could not have been accomplished with morphological techniques.

We quickly realized that an in-depth understanding of the ecological mechanisms

of the invasion did not translate into an understanding of the potential role of hybridization. The detailed study of the dynamics of hybridization were conducted in the well-studied invasion around the littoral zone of Trout Lake (Fig. 2), where the time of the introduction was known and the progress of invasion had been documented yearly thereafter (Lodge et al., 1986). Because only two diagnostic nuclear markers distinguished *O. rusticus* and *O. propinquus*, maximum likelihood techniques were used to estimate the frequency of hybridization (Nason and Ellstrand, 1993). The F₁ hybrids in Trout Lake accounted for 6% ± 3% (95% confidence interval) of the crayfish community. The F₂ and backcross crayfish were estimated to contain 4% ± 1% and 13% ± 7% of the population, respectively (Perry et al., 2001a). To determine the mating patterns leading to the formation of these crayfish, we used diagnostic mtDNA markers combined with the diagnostic nuclear markers. The majority (95%) of F₁ hybrids were the result of *O. rusticus* females mating with *O. propinquus* males (Fig. 3C); only 1% ± 3% (95% confidence interval) of the total crayfish population was the product of F₁ hybrids backcrossing to *O. propinquus*, whereas 13% ± 5% represent backcrosses to *O. rusticus* (Fig. 3C). The F₁ hybrids, therefore, appear to mate disproportionately with pure *O. rusticus*. The consequences are that genetic introgression of nuclear DNA from *O. propinquus* into *O. rusticus* is much greater than in the reverse direction. These results led to a complex mix of ecological mechanisms to explain the success of *O. rusticus*, hybridization dynamics that were inconsistent with predictions, and an unclear understanding of the relative importance of these invasion mechanisms.

The relative effects of hybridization and ecological mechanisms of displacement were quantified by using a population genetics model modified from Fisher's model of the spread of an advantageous allele (Kot et al., 1996; Perry et al., 2001a). In this model, the relative fitness of the *O. propinquus* alleles was estimated using data from several lakes where morphologically identified *O. rusticus* were the only crayfish present and introgressed *O. propinquus* nuclear markers were assumed to exist in an equilibrium state. If no hybridization was occurring, *O. rusticus* would eventually go to fixation as

O. propinquus individuals were driven locally extinct (the haploid or ecological model). The relative fitness of hybrid individuals relative to *O. rusticus* and *O. propinquus* was estimated from allele frequencies at the invasion front. The model, parameterized with these relative fitness values, suggests that hybridization hastens the spread of the *Idh* 110 allele for *O. rusticus* from 5% to 36% relative to ecological interactions alone. A similar analysis for *Had* suggests that hybridization speeds the advance of the *O. rusticus* 80/90 allele by 1% to 36%. Obviously, several simplifying assumptions were made in the preceding modeling, perhaps the foremost being that the genetics were collapsed into a single-locus problem. In so doing, the effects of epistasis (non-additive genetic interactions among genes) and linkage on selection were discounted. The assumption that linkage is negligible is realistic, given that crayfish generally have a large number of chromosomes. For example, *Astacus trowbridgii*, *Procambarus clarkii*, and *O. virilis* have haploid chromosome numbers of 188, 188, and 100, respectively (Fasten, 1914; Niiyama, 1934; Murofushi et al., 1990), which greatly reduces the likelihood of linkage among loci. This modeling approach is a first attempt at estimating the potential importance of hybridization in crayfish invasions.

The long-term evolutionary consequences of introgression in inland lakes remain unclear because *O. propinquus* alleles may still be selected against in an *O. rusticus* genetic background. If such selection is occurring, then eventually *O. propinquus* genes may gradually be eliminated from the population. Preliminary data show a decline in *O. propinquus* alleles in lakes where *O. propinquus* has been extirpated for longer and longer times (Perry et al., unpubl. data). Thus, *O. propinquus* genes can persist for at least some time after an invasion by *O. rusticus*. Resolution of the introgression issue will clarify whether the *O. rusticus* interaction with *O. propinquus* is best described as genetic assimilation, in which case *O. propinquus* genes remain in the *O. rusticus* population, or as genetic extirpation, where *O. propinquus* genes are eliminated. Details of the hybridization process and its evolutionary implications may differ for other pairs of crayfish species or other

habitats, for example, the Laurentian Great Lakes.

Orconectes rusticus in the Great Lakes

The detailed understanding of the *O. rusticus*-*O. propinquus* invasion in small inland lakes has been extended into the Great Lakes. The historical distributions of the crayfishes in the Great Lakes were reconstructed on the basis of published records of tributaries and limited lake locations since the 1800s. These historical records indicate that *O. propinquus* and *O. virilis* were the dominant crayfishes in the past (Creaser, 1930, 1932). Other species of *Orconectes* and *Cambarus* were found in the tributaries and bays but only rarely in open water areas of the Great Lakes. *Orconectes rusticus* was first documented in one of the Great Lakes near the mouth of the Maumee River (Ohio) in Lake Erie. Creaser (1930) suggests that *O. rusticus* either migrated across a low and often swampy barrier between the Maumee drainage and the Scioto or Wabash River drainages or through a canal constructed in the early 1800s. *Orconectes rusticus* is now commonly found in Lake Erie and is present in parts of Lakes Michigan, Superior, Ontario, and Huron and in many of the tributaries of these lakes.

Collections to document the dynamics of the *O. rusticus* invasion of the Great Lakes were focused on Lake Michigan. Here, *O. propinquus* and *O. virilis* were the dominant species in the tributaries, with *O. propinquus* the dominant species in the lake itself; *O. rusticus* was never documented in the Lake Michigan region (Creaser, 1930, 1932) (Fig. 4). Because the primary route of introduction of *O. rusticus* is through its use as bait, collection efforts were focused on areas near boat launches and bait shops. The presence of *O. rusticus* was documented in the tributaries of Lake Michigan through hand collections and scuba-based sampling in Lake Michigan (Fig. 5). *Orconectes rusticus* was expected to be found in the bays and tributaries, where it would have displaced *O. propinquus* and *O. virilis* as it has in northern Wisconsin and Michigan. From these locations, it was expected *O. rusticus* would colonize offshore sites, where *O. propinquus* would also be displaced.

Orconectes rusticus was found in all major tributaries and bays sampled (Fig. 5).

The extent of movement of *O. rusticus* upstream was not examined because the spread into Lake Michigan was the focus of this study. Sampling efforts of offshore locations were concentrated on rocky reefs, which provide suitable habitat for crayfish. The majority of the habitats surrounding the major tributaries of Lake Michigan consisted of sand plains that provide crayfish no refuge from predation. In the Benton Harbor, Michigan, location (Fig. 5), offshore populations of *O. propinquus* crayfishes but no *O. rusticus* were found among the rocks about a mile from shore in 12–18-m-deep water (Fig. 5). In contrast, *O. rusticus* was the only species found in the harbors (Fig. 5). In shallower regions in Grand Traverse Bay, however, *O. rusticus* was present in rocky habitats near shore. No suitable habitats were found in other eastern shore locations and no crayfish were collected there. Apparently the sand plains between the harbors and offshore rocky habitats along most areas of the eastern shore of Lake Michigan have slowed the invasion of *O. rusticus* into the lake proper.

Even though *O. rusticus* and *O. propinquus* did not occur together at any of the sampling locations on the eastern shore, making the likelihood of finding hybrid individuals low, we conducted genetic analysis of the *O. rusticus* populations to detect backcross individuals. In the harbor population of *O. rusticus* ($N = 120$ crayfish), backcrosses were common (9%; $N = 11$) but, as expected, no F_1 hybrids were discovered. The presence of backcrosses (and lack of F_1 hybrids) indicates hybridization has occurred in the recent past. Nuclear DNA material had introgressed into the *O. rusticus* population from the original *O. propinquus* population that existed in the harbor. Offshore *O. propinquus* populations were also examined for the same genetic markers, but only *O. propinquus* genetic markers were expected to be found because no *O. rusticus* were present. However, of the 120 crayfish sampled, 4% ($N = 4$) were characterized as *O. propinquus* based on morphology and mtDNA, although they possessed *O. rusticus* alleles. These results suggest that even though *O. rusticus* has not invaded these habitats, gene flow is occurring from the harbor to the offshore region.

In this example the direction of backcrossing is contrary to that documented in smaller inland lakes. In the inland lakes,

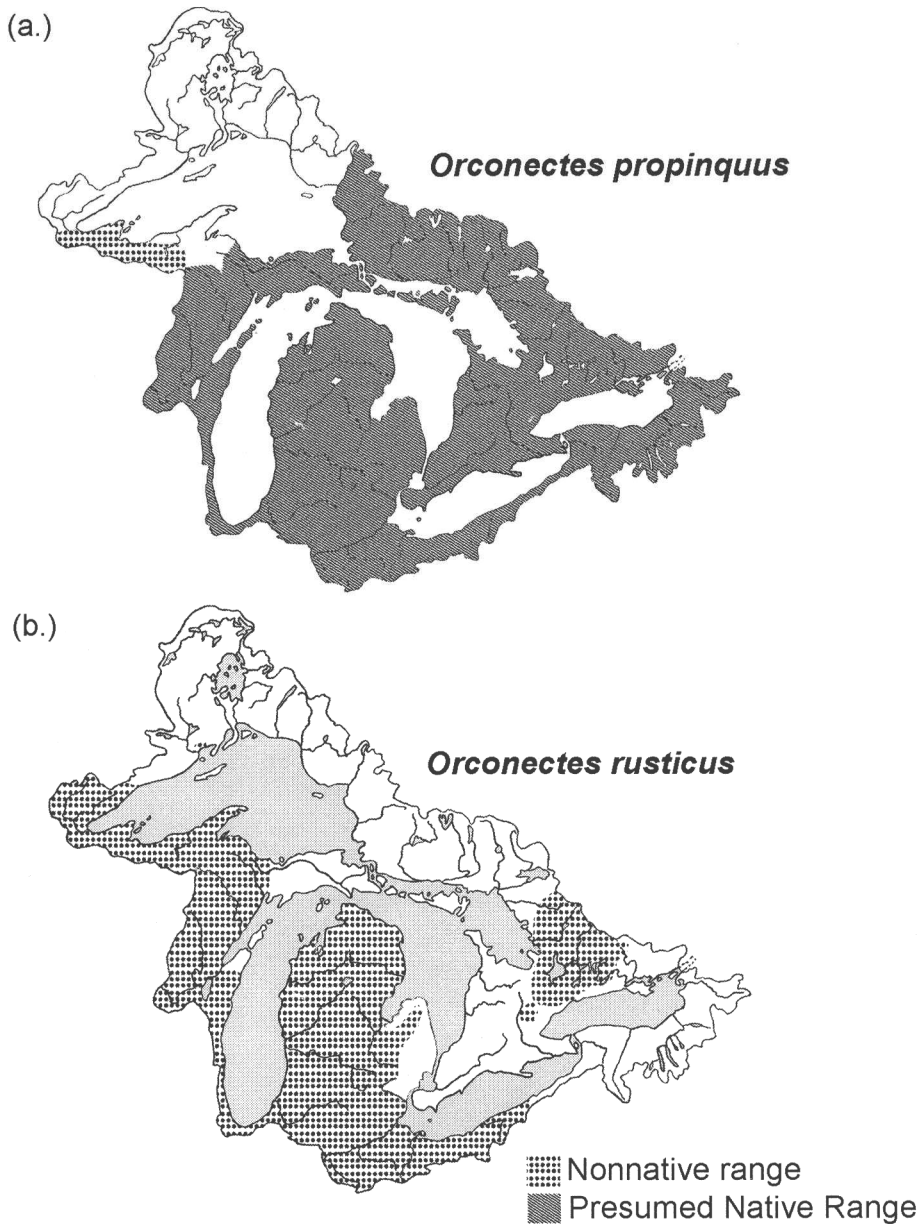


FIGURE 4. Native and introduced ranges of (a) *O. propinquus* and (b) *O. rusticus* in the Great Lakes Watershed (Turner, 1926; Creaser, 1930, 1932; Crocker and Barr, 1968; Hobbs and Jass, 1988; Momot et al., 1988; Page, 1985; Momot, 1992)

O. rusticus invaded in a relatively uniform wave front, and introgression led to *O. propinquus* genes in *O. rusticus* individuals. Along the eastern shore of Lake Michigan, however, invasions of *O. rusticus* appear to be stalled at the river mouths, and *O. rusticus* genes occur in *O. propinquus* individuals. This contrast between inland lakes and Lake

Michigan suggests that the dynamics of invasion, hybridization, and introgression are context-dependent. The introgression pattern in Lake Michigan suggests specifically that in Lake Michigan, hybrids may be backcrossing primarily with *O. propinquus* (not *O. rusticus* as in inland lakes). Clearly, further studies in the Great Lakes, and additional

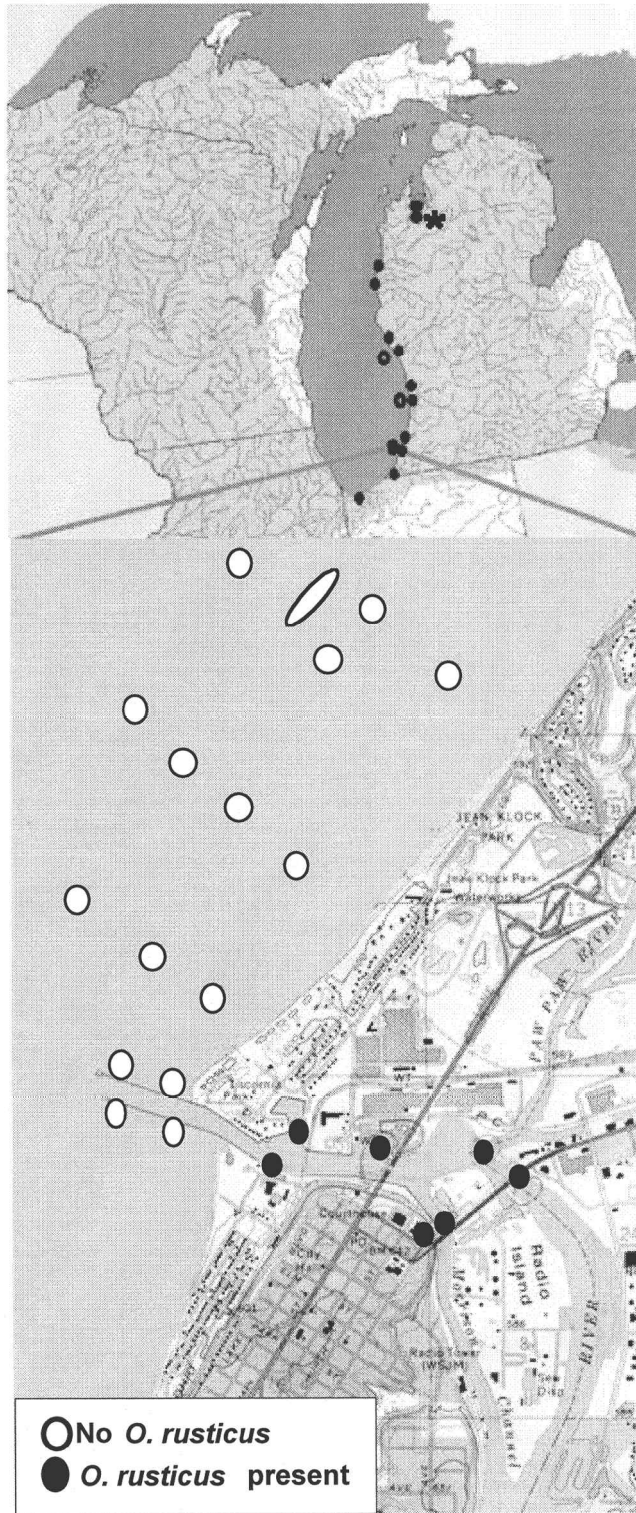


FIGURE 5. (a) Current distribution of *O. rusticus* in Lake Michigan and in the mouths of major tributaries (dots on shoreline). The asterisk indicates Grand Traverse Bay, discussed in the text. (b) Detailed results for the area around the mouth of the St. Joseph River in St. Joseph, Michigan.

studies of other crayfishes in other habitats are required before any generalized patterns can be recognized.

*Predicting the Potential Extent
of Hybridization Among Crayfishes*

Hybridization between *O. rusticus* and *O. propinquus* is the only occurrence of hybridization between crayfishes that has been documented genetically. However, morphological evidence suggests hybridization is much more common than previously recognized. For example, individuals of intermediate morphology suggest that hybridization is occurring between *O. virilis* (Gremicambarus) and *O. immunis* (Gremicambarus) (D. Jensen, pers. comm.); *O. obscurus* (Crockerinus) and *O. propinquus* (Crockerinus) (Capelli and Capelli, 1980); *O. obscurus* (Crockerinus) and *O. rusticus* (Procericambarus) (Capelli and Capelli, 1980); *O. rusticus* (Procericambarus) and *O. jeffersoni* (Crockerinus) (C. Taylor, pers. comm.); and *O. rusticus* (Procericambarus) and *O. sanbornii* (Crockerinus) (Butler and Stein, 1985). These instances of putative hybridization occur in or among closely related lineages, in our current understanding of the phylogenetic relationships of these species (Crandall and Fitzpatrick, 1996) (Fig. 6). Although the phylogenetic relationships among crayfishes are not fully resolved, current theories provide a firm basis for predicting species at risk of hybridization associated with invasions. Further studies of the systematic relationships as well as laboratory mating trials are needed to test the potential for hybridization among these closely related taxa. Nevertheless, the implication is clear that hybridization and introgression pose a substantial threat to the conservation of crayfish and freshwater ecosystems.

FRESHWATER MUSSELS

The diversity of freshwater mussels in the USA is unmatched in the world, with 296 species in two families (Unionidae and Margaritiferidae) (Table 1). More than 56% of the species are considered in need of conservation attention, but only 24% are listed as threatened and endangered species by the federal government. The primary threats to their populations result from habitat modification, pollution, overharvesting, and

interactions with nonindigenous species; 38 species are presumed extinct (Williams et al., 1993; Master et al., 1998; Association for Biodiversity Information, 2001). Like crayfishes, many freshwater mussels occupy limited ranges and have limited dispersal abilities; they are therefore particularly susceptible to anthropogenic effects. Population subdivision and geographic variation of unionids is potentially greater than that of fishes and crayfishes because of the dependence of unionids on specific fish hosts for reproduction.

Mussels may represent the best aquatic example of how an increased understanding of the phylogenetic relationships will be integral in preventing the loss of biodiversity. The limited molecular systematics to date suggests morphologically based identification of mussels may not identify distinct evolutionary entities because morphological similarity between species often conceals cryptic species (Mulvey et al., 1997; Lydeard and Roe, 1998; Roe and Lydeard, 1998). Current estimates of the distribution and status of mussel populations based on morphological identification may improperly designate populations as stable or declining (Berg et al., 1996, 1997; Mulvey et al., 1997; Lydeard and Roe, 1998; Strayer and Fetterman, 1999; Berg and Berg, 2000). Hybridization and introgression in freshwater mussels have been examined in only two studies using either morphology or genetic markers but appear to be common among individuals where these events have been documented (Kat, 1986; Strayer and Fetterman, 1999). Developing genetically and morphologically based phylogenies for unionids is needed to delineate evolutionary distinct entities that require urgent conservation attention (Mulvey et al., 1997; Lydeard and Roe, 1998; Berg and Berg, 2000). Current conservation efforts increasingly rely on relocating mussels to other sites or into artificial breeding facilities (Cope and Waller, 1995; Waller et al., 1995). However, such conservation approaches that involve the mixing of mussel populations may result in mixing species that are not yet reproductively isolated from one another, leading to the loss of future biodiversity.

Molecular tools are needed to determine at what scale—stream, watershed, or ecoregion—mussel populations can be managed in such a way as to preserve the remaining biodiversity (Berg et al., 1996).

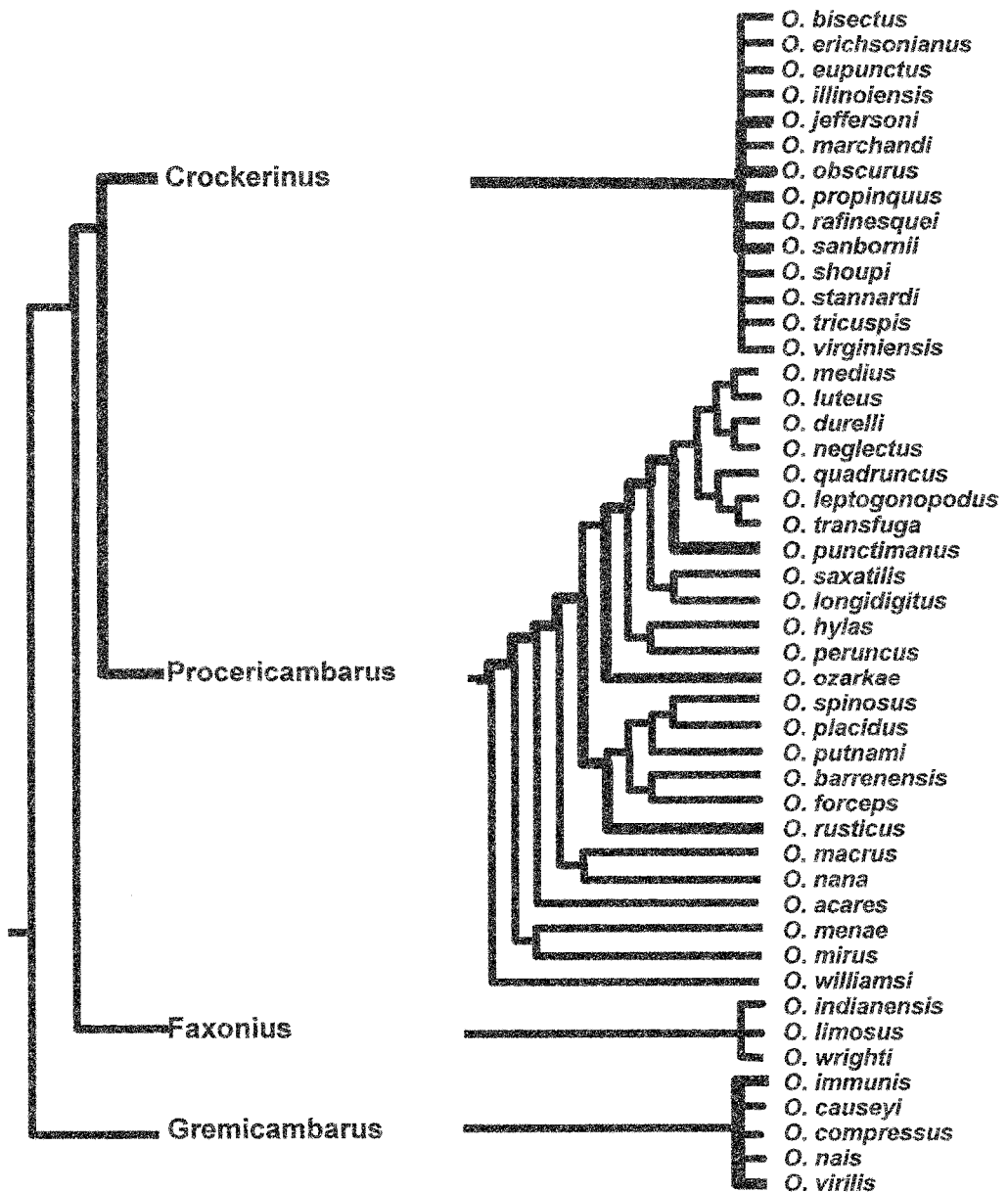


FIGURE 6. Phylogenetic relationships of selected subgenera of *Orconectes* crayfish, based on morphological relationships for all subgenera except those in Procericambarus, which are based on 16S mtDNA sequences (but see Crandall and Fitzpatrick, 1996, for a detailed discussion). Species thought to hybridize with one another because of the presence of morphological intermediates are connected by black lines. Source: Redrawn from Tree of Life <http://phylogeny.arizona.edu/tree/eukaryotes/animals/arthropoda/crustacea/decapoda/astacidea/cambaridae/orconectes/orconectes.html#TOC3>.

This approach to understanding population subdivision has been conducted for only a few aquatic species; in the example of *Quadrula quadrula* (Berg et al., 1996), between-population variation was found based on mtDNA and nuclear markers suggesting that these subdivided populations

should be managed as different management units. Genetic studies of 27 of the 289 unionid species suggest that morphology alone does not indicate true phylogenetic relationships of species; moreover, they report considerable genetic variation within and among populations, which possibly conceals cryptic

species (Kat, 1986; Berg et al., 1997; Johnson et al., 1997; Mulvey et al., 1997; Lydeard and Roe, 1998; Roe and Lydeard, 1998).

Population declines resulting from hybridization between two species have been documented for *Alasmidonta varicose* and *A. marginata*, based on morphological analyses (Strayer and Fetterman, 1999). Only one study using molecular techniques to address hybridization and introgression in freshwater mussels has been examined (Kat, 1986). Hybridization as a result of secondary contact has been documented between *Anodonta cataracta* and *A. grandis*, and to a lesser extent between *Lampsilis radiata* and *L. siliquoidea* (Kat, 1986). Thus, hybridization is probably more common than previously recognized.

The potential for hybridization exists in particular as the result of transport of individuals from one region to another. The planned relocation of a population of *Potamilus inflatus* into another population was prevented when genetic analyses revealed that differences between the populations were greater than those between other congeners, *P. purpuratus* and *P. alatus* (Fig. 7) (Roe and Lydeard, 1998). If the individuals had been introduced, the possibility of their hybridization was high, potentially leading to the loss of an already threatened species, but that possibility was never directly tested (Roe and Lydeard, 1998).

One of the main threats to native unionids is the invasion of the zebra mussel, which has already caused the local extinction of many populations in the Great Lakes and large rivers (Strayer and Smith, 1996; Strayer et al., 1996; Schlosser et al., 1997). One suggestion of how to preserve the threatened populations is relocation to new habitats or to breeding facilities where zebra mussels will be less likely to invade (Cope and Waller, 1995; Waller et al., 1995). However, relocation of unionids from native habitats may lead to the mixing of morphologically similar species that previously had been reproductively isolated by geographic barriers. Until genetic-based phylogenies can be constructed to determine the systematic relationships of unionids, geographically isolated populations should be maintained separately to prevent the potential for hybridization and introgression among closely related lineages (Lydeard and Roe, 1998; Roe and Lydeard, 1998).

HYBRIDIZATION IN OTHER AQUATIC TAXA

In this review, we focused on fishes, crayfishes, and unionids because these are the aquatic taxa for which the best information on invasions and hybridization exists. We do not mean to suggest that hybridization and introgression are not important factors in the invasion and replacement of other aquatic taxa, especially insects. Aquatic taxa are often limited in their dispersal abilities, thereby resulting in low gene flow among populations and genetic subdivision or isolation among populations. Unfortunately, relatively little is known about the conservation status of insects and many other groups of aquatic taxa, and much less is known about the occurrence of hybridization. However, extensive genetic subdivision of populations has been studied for many aquatic taxa, including mayflies (Sweeney et al., 1986, 1987, 1991; Funk et al., 1988; Sweeney and Funk, 1991), stoneflies (Funk and Sweeney, 1990), black flies (Snyder and Linton, 1984), waterstriders (Zera, 1981; Sperling and Spence, 1990; Klingenberg et al., 2000), gammarid amphipods (Gooch and Hetrick, 1979; Gooch and Glazier, 1986; Wit and Hebert, 2000), and pleurocerid snails (Chambers, 1980; Dillion, 1984). These studies suggest that many aquatic invertebrate species that have been identified as a single population based on morphological analyses are actually composed of genetically distinct populations subdivided regionally by watershed boundaries. The potential for hybridization associated with invasions of these morphologically similar but genetically distinct groups is real. However, few instances of hybridization have been documented, and the extent of homogenization of these taxa is not well known. The need for combined morphological and genetic-based phylogenies for these and other taxa is even greater than for fishes, crayfishes, and mollusks. If hybridization is more likely between closely related species, systematics may provide the key to predicting the potential for hybridization. Further studies can be undertaken to assess the potential for extirpation of species through hybridization (Rhymer and Simberloff, 1996).

HYBRIDIZATION IN CONSERVATION

In previous sections, we emphasized the extensive freshwater biodiversity in North

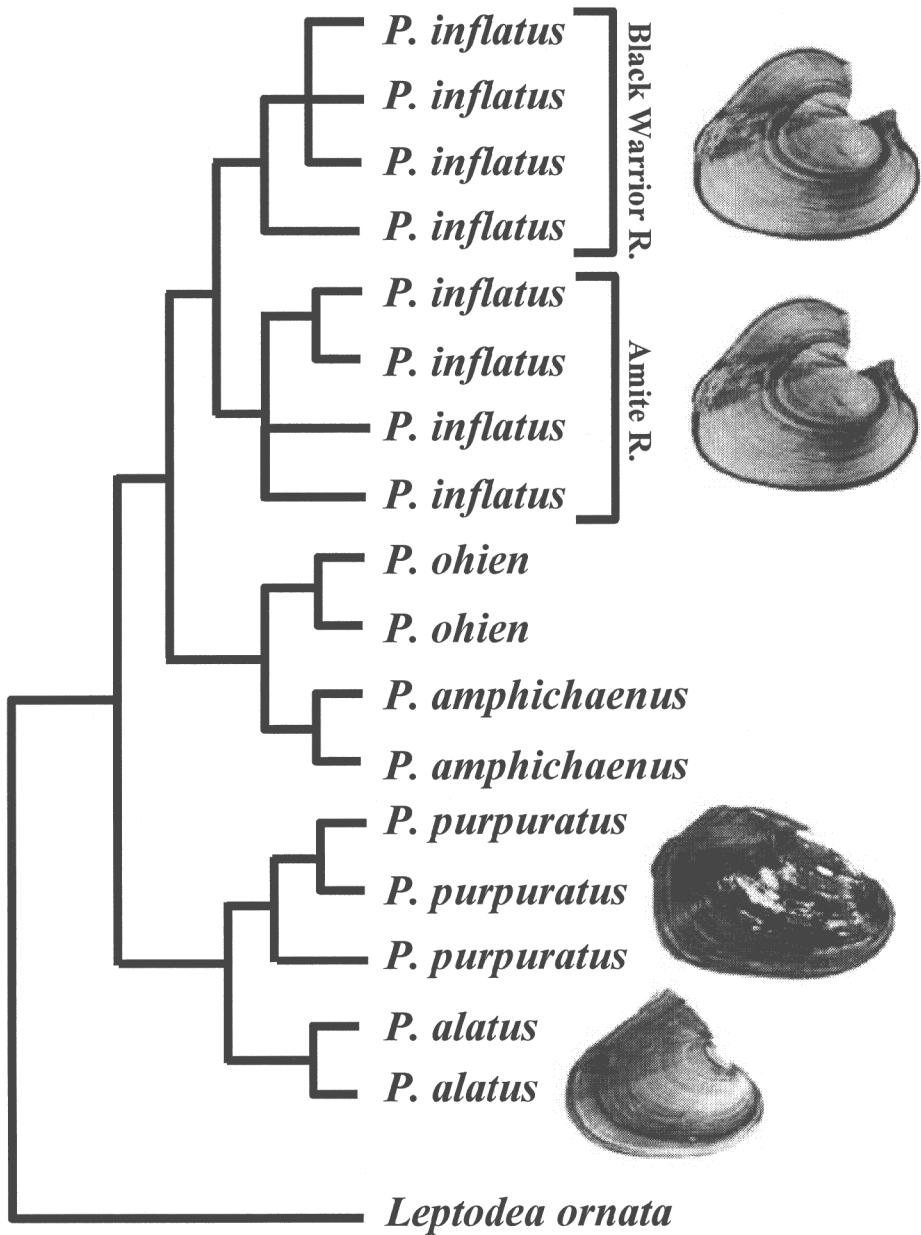


FIGURE 7. Phylogenetic relationships of *Potamilus* modified from Roe and Lydeard (1998) and showing the relationships of selected *Potamilus* species and populations. *Potamilus inflatus* populations from two river drainages (Amite River, Louisiana, and Black Warrior River, Alabama) are as genetically differentiated as *P. purpuratus* and *P. alatus*, which are recognized as two morphologically distinct species.

America and the threats resulting from ecological displacement and hybridization with nonindigenous species. The current state of aquatic biodiversity in North America is emphasized because it is among the most diverse in the world (Table 1), and the many threats to it have gone relatively unnoticed relative to terrestrial flora and fauna

(Allendorf, 1988; Miller et al., 1989; Naiman et al., 1995; Lydeard and Roe, 1998; Rahel, 2000). These unique assemblages of unionids, crayfishes, and fishes are threatened by the continued homogenization of their populations (Rahel, 2000). Because the systematic relationships of many of these species is confounded by recent divergence and their

morphological similarity, a clearer understanding of the systematic relationships is critical for preventing hybridization and introgression among these taxa and directing conservation measures.

For terrestrial vertebrates, the loss of a species, subspecies, or even a race often receives front-page press. Those species are portrayed as important to humans from an aesthetic, economic, and environmental perspective. Conservation efforts for mammals (Taberlet et al., 1997; Taylor et al., 1997), birds (Tegelstrom and Von Essen, 1996; Young and Allard, 1997), and commercially important fish species (Waples, 1990a,b; Waples and Teel, 1990; Vassart et al., 1995) often include genetic analyses (to prevent inbreeding and outbreeding depression and to preserve genetic diversity). Of all of the aquatic taxa, fishes receive the greatest scientific and public attention because of their perceived ecological importance in aquatic food webs and their economic importance to humans. Other diverse taxa in North America are, however, often not included in the list of threatened and endangered species even though they are, in fact, more threatened than some fishes. This bias is portrayed effectively by a comparison of the most recent lists of federally listed threatened and endangered species and of those species considered in need of conservation attention. The federal and nongovernmental lists are similar for mammals, reptiles, and birds, but very different for amphibians, fish, crayfish, and unionids, where the nongovernmental sources judge more species to be at risk than those protected by the Endangered Species Protection Act.

Studies of the loss of biodiversity as a result of introduced species are typically performed on a case-by-case approach after the invasion has occurred and the resident species are being or have been displaced. Developing a predictive approach based on ecological interactions and phylogenetic relationships—to provide a reliable guide to the potential for hybridization and introgression between invaders and resident species—is needed to prevent the further loss of biodiversity. This literature review and others (Rhymer and Simberloff, 1996) suggest that hybridization between closely related taxa or between genetically differentiated populations may pose a serious threat to biodiversity, especially in North American fresh waters. Understanding the

systematic relationships of aquatic taxa will help delineate species boundaries and identify morphologically cryptic taxa and may be the only way to predict the likelihood that a nonindigenous species may hybridize.

Although the threat of species introductions has previously been viewed primarily in terms of ecological mechanisms, aquatic taxa may be particularly prone to extinction as the result of hybridization. However, the delineation of species boundaries is often unclear because of morphological similarity, and relatively few studies have used molecular tools to examine the systematic relationships of aquatic taxa. Invasions resulting in the loss of resident species through both ecological mechanisms and hybridization are often thought of as inconsequential. In contrast, as the examples highlighted in this review suggest strongly, given that many, if not most, species invading North America freshwater habitats are from other habitats in North America, in fact hybridization and introgression are common contributing factors in the demise of many native species in a wide variety of vertebrate and invertebrate taxa. This situation highlights the urgent need for greater application of molecular tools in constructing phylogenies for these taxa. Such phylogenies then would provide the most reliable basis for assessing risks to native species of ecological and genetic interactions with species that have been or may be introduced. Such risk assessments are essential to the development of conservation strategies to slow the losses of North America aquatic biodiversity.

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