

PERSPECTIVE

Evolutionary and physiological adaptations of aquatic invasive animals: *r* selection versus resistance¹

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Abstract: Invasive species have been characterized as tolerant of environmental extremes. This hypothesis was evaluated for invasive aquatic species in North America, particularly Asian clams, *Corbicula fluminea*, and zebra mussels, *Dreissena polymorpha*. Both species have rapid growth, early maturity, short life spans, and elevated fecundity, allowing rapid population recovery after reductions by refractive, environmental extremes. Extensive resistance capacities offer little adaptive value to invasive, *r*-selected species, because population reductions occur in their unstable habitats regardless of degree of stress tolerance. Thus, both species have relatively poor physiologic resistance, depending instead on elevated growth and fecundity for rapid population recovery. In contrast, native North American bivalve species are often adapted to stable habitats where perturbation is infrequent (i.e., freshwater unionoidean bivalves). They are characterized by slow growth, extended life spans, and low effective fecundities, slowing population recoveries (*K*-selected), and have evolved extensive resistance adaptations to avoid extirpation during environmental extremes. Review of resistance adaptations in other North American aquatic invaders revealed poorer or equivalent physiological tolerance relative to taxonomically related native species, suggesting that extensive physiological tolerance is not required for invasive success.

Résumé : Les espèces envahissantes sont considérées comme tolérantes aux conditions environnementales extrêmes. Cette hypothèse est évaluée chez des espèces envahissantes d'Amérique du Nord, en particulier, la moule asiatique, *Corbicula fluminea*, et la moule zébrée, *Dreissena polymorpha*. Chez les deux espèces, la croissance est rapide, la maturité précoce, la longévité réduite et la fécondité élevée, ce qui permet une récupération rapide de la population lorsque les conditions extrêmes du milieu causent une réduction de la densité. Une forte capacité de résistance est peu avantageuse chez des espèces envahissantes à sélection *r*, parce que les réductions de population se produisent dans leurs habitats instables, quelle que soit leur résistance au stress. Ainsi, les deux espèces possèdent peu de résistance physiologique, car elles dépendent plutôt de leurs fortes croissance et fécondité pour rétablir rapidement leur densité. En revanche, les espèces indigènes de bivalves d'Amérique du Nord sont souvent adaptées à des environnements stables où les perturbations sont rares (i.e. les bivalves unionoïdés d'eau douce). Elles se caractérisent par une croissance lente, une longévité élevée et une fécondité effective faible, qui ralentissent le rétablissement de leur densité (sélection *K*) et elles ont acquis d'importantes adaptations de résistance pour éviter l'élimination durant les périodes de conditions extrêmes du milieu. L'examen des adaptations de résistance chez d'autres espèces envahissantes d'Amérique du Nord montre que, chez ces espèces, la tolérance physiologique est inférieure ou similaire à celle des taxons indigènes apparentés, ce qui laisse croire qu'une forte tolérance physiologique n'est pas nécessaire pour assurer le succès d'une invasion.

[Traduit par la Rédaction]

Introduction

In an influential paper, Ehrlich (1984) suggested that successful invasive species should have the following attributes: (1) abundance in their original range, (2) polyphagous (i.e.,

wide feeding niche), (3) short generation times, (4) much genetic variability, (5) fertilized female able to colonize alone, (6) larger than most related species, (7) associated with *Homo sapiens*, and (8) able to function in a wide range of physical conditions. Lodge (1993) added the attributes of high dispersal rate, single-parent reproduction, vegetative reproduction, phenotypic plasticity, a large native range, eurytropy, and human commensalism to this list of invasive species traits. Although there are examples of invading aquatic species with many of the above traits, there is little evidence suggesting that physiological capacity to tolerate and function in a wide range of physical conditions (i.e., physiological phenotypic plasticity) is a prerequisite for successful invasion of aquatic habitats. Instead, it has been assumed that tolerance of a wide range of physical conditions allows

Received 21 June 2002. Accepted 28 June 2002. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 13 August 2002.
J16958

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¹From the series "Biological invasions of aquatic habitats in Europe and the Great Lakes".

invasive species to colonize a variety of habitats. This paper reviews evidence for increased physiologic tolerance in invasive nonindigenous species relative to that of taxonomically related native North American species whose habitats they have invaded.

Methods

I examined the physiological adaptations of a number of aquatic invasive, nonindigenous animals in North America and some of those considered likely to invade North American aquatic habitats. A review of major treatises on invasive species (Mooney and Drake 1986; MacDonald et al. 1986; Hengeveld 1989; Drake et al. 1989; di Castri et al. 1990; Williamson 1996; Shigesada and Kawasaki 1997) revealed that none discussed their physiology. I then searched *Zoological Record* for published literature from 1978 to 2001 for information on physiological adaptations in a number of aquatic species recently introduced or likely to be introduced to North America. These included the gastropods *Bithynia tentaculata*, *Melanoides tuberculata* (red-rim melania) and *Potamopyrgus antipodarum* (= *jenkinsi*) (New Zealand mud snail), the bivalves *Corbicula fluminea* (Asian clam), *Dreissena polymorpha* (zebra mussel), and *Limnoperna fortunei* (Asian freshwater mussel), the planktonic cladocerans *Daphnia lumholtzi* and *Bythotrephes cederstroemi* (spiny water flea), and the fishes *Gymnocephalus cernuus* (Ruffe), *Neogobius melanostomus* (round goby), and *Proterorhinus marmoratus* (tubenose goby). This search revealed that although there were some physiological studies for almost all of these species, comprehensive, comparative analysis of physiological traits had only been completed for the bivalves *C. fluminea* (for a review, see McMahon (1999)) and *D. polymorpha* (for a review, see McMahon (1996)). Thus, I have focused my discussions on these species and will present data for other species within the framework provided by *C. fluminea* and *D. polymorpha*.

Basic approach and hypothesis

To evaluate a species' tolerance of environmental conditions, its "resistance" and "capacity" adaptations must be assessed. Resistance adaptations permit function at or near tolerable limits of environmental stress, whereas capacity adaptations allow maintenance of normal physiological function in response to changing environmental conditions (Prosser 1991). My review indicated that the resistance and capacity adaptations of the invasive *C. fluminea* and *D. polymorpha* were generally less extensive than that of endemic native unionoidean mussels, suggesting that extensive resistance and capacity adaptation may not be a requirement for successful aquatic invaders. Review of data for other investigated species revealed that none was characterized by extensive resistance or capacity adaptations. Many invasive aquatic species with significant ecological impacts, including *C. fluminea* and *D. polymorpha*, are characterized by adaptations supporting rapid population growth, including rapid individual growth, early maturity, short life spans, a limited number of reproductive periods, high fecundities, small egg-offspring size, and extensive dispersal capacity. Such traits are generally characteristic of species (i.e., *r*-selected species) adapted to unstable habitats, where intraspecific com-

petition is low or unlikely due to frequent population density reductions or extirpations associated with unpredictable, catastrophic, natural environmental events (Sibly and Calow 1986). Such *r*-selected traits are generally characteristic of invasive species (Lodge 1993; Williamson 1996). This review provides evidence that there is little selective pressure for evolution of extensive resistance and capacity adaptations in *r*-selected invasive species from unstable habitats, because periodic catastrophic environmental events result in massive population mortality regardless of their capacity to tolerate environmental stress. A corollary of this hypothesis is that *r*-selected invasive species such as *C. fluminea* and *D. polymorpha* can rapidly reach densities approaching carrying capacity (i.e., *K*) on introduction to stable habitats outside their endemic range where their densities are not regulated by periodic catastrophic environmental events, disease, or predators.

In contrast, endemic species such as unionoidean freshwater mussels that inhabit only infrequently disturbed aquatic habitats tend to achieve densities approaching the carrying capacity of the environment (i.e., *K*-selected species), resulting in extensive intra- and inter-specific competition for limited resources. Life-history traits associated with species adapted to stable habitats include slow individual growth rates, delayed maturity, long life spans, low fecundity, extensive iteroparity, large egg-offspring size, and limited capacity for dispersal (Sibly and Calow 1986). These life-history traits slow population growth, preventing rapid population recovery after extirpation or reduction by refractive, catastrophic environmental disturbance. Inability of species with *K*-selected life-history traits to recover from disturbance should result in strong selection pressures for development of extensive resistance and capacity adaptations in order to avoid population reduction or extirpation during environmental extremes. In this perspective, I provide examples supporting this hypothesis.

Life-history traits of Asian clams, zebra mussels, and unionoidean mussels

The principle bivalve fauna of North American rivers and lakes are freshwater mussels of the superfamily Unionoidea. They are most common in stable habitats such as large lakes and rivers. In riverine habitats, they inhabit stable substrata of course, sand-gravel mixtures subjected to moderate current flows. They are rarely found in small, unstable stream habitats subjected to periodic flooding and temperature extremes (McMahon and Bogan 2001). Although there is interspecific variation, members of the Unionoidea display most of the *K*-selected characteristics expected of species adapted to the intense competition associated with stable habitats (Table 1). They have long life spans (6–100 years) and delayed maturity (6–12 years), are gonochoristic, grow rapidly to maturity and, thereafter, grow slowly, have extremely low juvenile survivorship but high adult survivorship, are highly iteroparous (i.e., have many reproductive periods within their extended life spans) with one reproductive period per year, and tend to allocate high proportions of nonrespired assimilated energy (85.2–97.5%) to growth and low proportions to reproduction (2.8–14.8%) (Table 1; McMahon and Bogan 2001). Low juvenile survival and low adult growth rates lead

Table 1. Summary of the life-history characteristics of native, North American freshwater bivalves (Unionoidea) and the nonindigenous *Corbicula fluminea* and *Dreissena polymorpha* (based on information in McMahon (1996, 1999), McMahon and Bogan (2001), and Stoeckmann and Garton (2001)).

Life-history trait	Unionoidea	<i>Corbicula fluminea</i>	<i>Dreissena polymorpha</i>
Life span (years)	<6 to >100 depending on species	1–4	4–7
Age at maturity (years)	6–12	0.25–0.75	0.5–2
Reproductive mode	Gonochoristic (few hermaphroditic species)	Hermaphroditic (self-fertilizing)	Gonochoristic
Growth rate	Rapid before maturity, much slower thereafter	Rapid throughout life	Relatively rapid throughout life
Fecundity (no. young per average adult per breeding season)	200 000 – 17 000 000 per female depending on species	35 000 per hermaphroditic individual	30 000 – 1 000 000 per female
Juvenile size at release	Very small, 50–450 µm depending on species	Small, 250 µm	Extremely small, 40 µm
Relative juvenile survivorship	Extremely low	Extremely low	Extremely low
Relative adult survivorship	High	Low, 2–41% per year	Intermediate, 26–88% per year
Degree of iteroparity	Highly iteroparous, generally >10 reproductive periods	Moderately iteroparous, 1–7 reproductive periods	Moderately iteroparous, 1–4 reproductive periods
Reproductive efforts per year	One	Two (spring and fall)	One (2–8 months long)
Assimilated energy respired (%)	—	11–42%	>90% from May to October
Nonrespired energy allocated to growth (%)	85.2–97.5% depending on species	58–71% depending on cohort and season	10–26% depending on temperature and ration
Nonrespired energy allocated to reproduction (%)	2.8–14.8% depending on species	5–15% depending on cohort and season	74–90% depending on temperature and ration
Turnover time in days (= mean standing crop biomass : biomass produced per day)	1790–2849 depending on species	73–91 depending on cohort	53–869 depending on habitat
Habitat stability	Generally stable	Stable to unstable	Stable to moderately unstable (can inhabit high-flow habitats)

to low population productivity, reflected in extended turnover times (i.e., time in days for population production to produce the equivalent of mean population standing crop biomass) of 1790–2849 days (Table 1). High adult survival, long life spans, and low juvenile survival result in domination of unionoidean populations by adults relative to juveniles, a trait characteristic of species adapted to stable habitats (Sibly and Calow 1986).

Unionoideans deviate from the life-history traits expected of species adapted to stable habitats in that females produce very large numbers (200 000 – 17 000 000) of small young (size = 50–450 µm) (Table 1). Females retain eggs in marsupial chambers within the exhalant water channels of their outer gills where they are fertilized by sperm carried to them on inhalant currents. After fertilization, eggs develop into a small, externally released, bivalved larva called a glochidium (McMahon and Bogan 2001). The glochidium is parasitic on specific fish hosts, encysting in their fins or gills for periods of less than 200 days to more than 1000 days depending on species, allowing dispersal and growth to a more competitive size before excystment as a free-living juvenile (Bauer 1994). Thus, elevated fecundity and small offspring size in unionoideans are adaptations that ensure a sufficiently high probability of glochidial contact with appropriate fish hosts to maintain adequate juvenile recruitment (McMahon and Bogan 2001). Low success of glochidial host-fish contact, high levels of host-fish immune rejection of encysted glochidia, and host-fish mortality before excystment of the

transformed juvenile allow only a tiny fraction of released glochidia to transform into relatively large well-developed juveniles. Thus, the effective fecundity of unionoidean species is quite low and leads to production of a few, large, well-developed offspring (i.e., excysted juveniles), a characteristic of *K*-selected species from stable habitats (Sibly and Calow 1986).

Unionoidean species' specific glochidial host-fish species are often closely associated with their preferred adult habitat (McMahon and Bogan 2001), increasing chances for excystment of juveniles into habitats favorable for survival to maturity. However, utilization of fish hosts associated with habitat of the adult reduces chances for long-distance juvenile dispersal. Limited dispersal capacity is hypothesized to have resulted in high levels of diversity and endemism within the North American unionoidean fauna (McMahon and Bogan 2001).

Extended life spans, delayed maturity, low effective fecundities, reduced powers of dispersal, high habitat selectivity, poor juvenile survival, and long turnover times (Table 1) make unionoidean populations highly susceptible to human perturbations (Strayer et al. 1999; McMahon and Bogan 2001). These unionoidean life-history traits (particularly long life spans and low effective fecundities) slow population recovery from human- or naturally mediated habitat disturbances (Strayer et al. 1999; McMahon and Bogan 2001).

The introduced Asian freshwater clam, *Corbicula fluminea*, unlike unionoideans, displays a majority of the life-history

traits (Table 1) that adapt it for life in unstable, unpredictable habitats (McMahon 1999). Arguably, it is the most invasive of all freshwater bivalves, occurring endemically in southern Asia, Australia, and Africa and having been introduced to North America, South America, and Europe within the last 100 years (McMahon 1999). *Corbicula fluminea* grows rapidly, in part because it has higher filtration and assimilation rates than other freshwater bivalve species. Only a relatively small proportion of its assimilation (29%) is devoted to respiration, the majority (71%) being allocated to growth and reproduction. This species allocates a high proportion (85–95%) of nonrespired assimilation to growth, allowing individuals to reach 15–30 mm in shell length in the first year of life and 35–50 mm in the terminal third to fourth year (McMahon 1999). Thus, *C. fluminea* has the highest net production efficiencies recorded for any freshwater bivalve, reflected by short turnover times of 73–91 days (Table 1).

Newly released juveniles of *C. fluminea* are small (shell length \approx 250 μ m) but completely formed, with a well-developed bivalved shell, adductor muscles, foot, statocysts, gills, and digestive system. They anchor to sediments or hard surfaces with a mucilaginous byssal thread but can be resuspended in turbulent flows to be dispersed long distances downstream (McMahon 1999). A relatively low percentage of nonrespired assimilation in *C. fluminea* is allocated to reproduction (5–15%, equivalent to that expended by unionoideans); however, its elevated assimilation rates allow higher absolute energy allocation to reproduction than in other freshwater bivalves. Fecundity is high, estimated at 68 678 juveniles-average adult⁻¹·year⁻¹ (Aldridge and McMahon 1978). Juvenile survivorship, while higher than that of unionoideans, is still low, and unlike unionoideans, mortality rates remain high throughout adult life (74–98% in the first year, 59–69% in the second year, and 93–97% in the third year of life). Low adult survivorship leads to populations dominated by juveniles and immature individuals (McMahon 1999), a characteristic of species adapted to unstable habitats (Sibly and Calow 1986). Most North American *C. fluminea* populations have two annual reproductive periods (i.e., spring through early summer and late summer through early fall; McMahon 1999). *Corbicula fluminea* is hermaphroditic and self-fertilizing (Kraemer et al. 1986), allowing single individuals to found new populations. Maturation occurs within 3 to 6 months at a shell length of 6–10 mm, thus spring-born juveniles can participate in fall reproduction. Maximum life span is highly variable, ranging from 1 to 4 years, within which early maturity and bivoltine reproduction allows individuals to participate in one to seven reproductive efforts (Table 1; McMahon 1999).

The relatively short life span, early maturity, high fecundity, bivoltine juvenile release patterns, high growth rates, small juvenile size, and capacity for downstream dispersal of *C. fluminea* makes it both highly invasive and adapted for life in unstable lotic habitats subject to unpredictable catastrophic environmental disturbance. Its high reproductive potential and growth rate allow it to achieve high densities after invading a new habitat or re-establish dense populations soon after experiencing catastrophic population declines. Its high metabolic rates allow rapid burrowing and it

is tolerant of suspended silt (McMahon 1999). Thus, it is highly successful in North American drainage systems subject to periodic anthropomorphic interference such as channelization, navigational dredging, “pearling” activities in unionoidean beds, sand and gravel dredging, commercial and (or) recreational boating, and organic and (or) chemical pollution, compared with less resilient native unionoidean species (McMahon and Bogan 2001).

Unlike unionoideans in which dispersal generally occurs within a population’s drainage by host-fish glochidial transport, *C. fluminea* is adapted for transport between isolated drainages. The juvenile’s long mucilaginous byssal thread or the filamentous algae on which it settles entangles in the feet or feathers of shore birds and water fowl, which then transport them between drainages (McMahon 1999). Its capacity for natural dispersal is highlighted by its spread into regions of Mexico, where human-mediated transport is highly unlikely (Hillis and Mayden 1985), and into southern England during interglacial periods (Miller et al. 1979).

The zebra mussel, *Dreissena polymorpha*, is the most recently introduced freshwater bivalve in North America (Mackie and Schloesser 1996). Like *C. fluminea*, many of its life-history characteristics (reviewed in McMahon 1996; Mackie and Schloesser 1996; Nichols 1996) make it highly invasive (Table 1). Unlike all other North American bivalve species, it has external fertilization that results in development of a free-swimming, planktonic veliger larva. The veliger remains in the water column for 8–10 days before settlement, allowing long-distance downstream dispersal (Nichols 1996). Veligers released into the Illinois River were estimated to travel >306 km downstream before settlement, with total annual veliger flux being approximately 1.94×10^{14} veligers·year⁻¹ to 2.13×10^{14} veligers·year⁻¹ (Stoeckel et al. 1997). Adults byssally attached to floating objects can be transported long distances downstream, and juveniles attached to macrophytic vegetation can be carried between drainages by waterfowl. Thus, zebra mussels may be dispersed by a number of passive and active mechanisms (Carlton 1993).

Zebra mussels sustain relatively high growth rates throughout their 2- to 3-year life span, becoming sexually mature in the first year of life and reaching a terminal adult shell length of 3.5–5.0 cm in North American populations (Table 1). *Dreissena polymorpha* is gonochoristic, iteroparous, and univoltine, with individuals participating in three to four annual reproductive periods within their 3- to 4-year life span (Mackie and Schloesser 1996). The egg and freshly hatched veliger larvae are small (diameter = 40–70 μ m). *Dreissena polymorpha* allocates a somewhat lower percentage (10–26%) than *C. fluminea* (58–71%) of nonrespired assimilation to somatic growth, leaving 74–90% for reproduction (Table 1; Stoeckmann and Garton 2001). Allocation of a relatively large proportion of nonrespired assimilation to growth allows individuals to rapidly increase in size, making them more intraspecifically competitive and less vulnerable to predation (Sibly and Calow 1986). The elevated levels of energy devoted to reproduction by *D. polymorpha* relative to *C. fluminea* and its very small egg size allow high fecundity, ranging from 30 000 – 40 000 to >10⁶ eggs·female⁻¹·year⁻¹, depending on female size (Table 1; Sprung 1991; Mackie and Schloesser 1996).

Dreissena polymorpha population densities range from 7000 to 114 000 individuals·m⁻², and standing crop biomasses range from 0.05 to 15 kg·m⁻² (Table 1; Claudi and Mackie 1993; Mackie and Schloesser 1996). High standing crop biomass results from juveniles settling on the shells of adults and substrata inhabited by adults, forming dense mats. High individual growth rates and population densities lead to high population productivity, estimated to be 0.05–15 g C·m⁻²·year⁻¹ in European populations and approximately 75 g C·m⁻²·year⁻¹ in North American, Great Lakes populations (converted from dry tissue mass productivity values in Mackie and Schloesser (1996)). These *D. polymorpha* productivity values, although higher than those of unionoideans, are still relatively low compared with those of 1000–4500 g C·m⁻²·year⁻¹ estimated for dense North American *C. fluminea* populations (McMahon and Bogan 2001). Population growth and productivity are habitat-dependent in *D. polymorpha*, yielding variable turnover times, ranging from 53 days (high productivity) to 869 days (low productivity) (Table 1; McMahon and Bogan 2001). Like *C. fluminea*, the life-history traits of *D. polymorpha* cause its populations to be dominated by juvenile and immature individuals (Smit et al. 1993), characteristic of a species adapted to unstable habitats (Sibly and Calow 1986).

The *r*-selected life-history traits of high growth rate throughout life, elevated fecundity, short life spans, and long-distance downstream dispersal of adult and larval stages make *D. polymorpha* a successful invasive species. However, unlike *C. fluminea*, *D. polymorpha* populations tend to be characterized by restriction to more stable habitats in medium- to large-sized lakes and rivers, reflected by its original distribution in the Caspian Sea and Ural River, avoidance of shallow, nearshore, lentic habitats and small, variable-flow, lotic habitats, relatively long age to maturity (generally at least 1 year), iteroparity, gonochorism, and relatively high adult survivorship (26–88% per year) (Mackie and Schloesser 1996). Thus, *D. polymorpha*, while adapted to rapidly recover from catastrophic reductions in population densities, appears less *r*-selected than *C. fluminea* but is more *r*-selected than most members of the Unionoidea.

Restriction of the original range of *D. polymorpha* to the Caspian Sea and Ural River also suggests a limited natural capacity for dispersal between isolated drainage systems compared with *C. fluminea*, which has an endemic range that spans three continents (i.e., Asia, Australia, Africa). Certainly, the gonochoristic habit and external fertilization of *D. polymorpha* would require introduction of a relatively large number of individuals to found a new population, whereas introduction of only one hermaphroditic, self-fertilizing individual of *C. fluminea* is required. Thus, cross-drainage-system dispersal of the *D. polymorpha* through Europe occurred only in the nineteenth and twentieth centuries through human vectors such as transport of adults attached to boat hulls, ballast water dumping, and transport of veligers through canal systems connecting catchments (Mackie and Schloesser 1996). The main natural means of dispersal of *D. polymorpha* between drainage systems is shore bird and duck transport of mussel-infested macrophytic aquatic vegetation for nest building or entrapment of planktonic larval stages in feathers; however, natural dispersal via these modes appears limited (Johnson and Carlton 1996). Without anthropomorphic vectors, dispersal of *D. polymorpha* be-

tween isolated drainages in North American would almost certainly have proceeded at a slower pace than that of *C. fluminea*. Thus, although *D. polymorpha* and *C. fluminea* have similar capacities for rapid population growth after introduction to a new environment, the more limited cross-drainage-system dispersal capacities of *D. polymorpha* make it less invasive than *C. fluminea*.

Physiological adaptations of Asian clams, zebra mussels, and unionoidean mussels

There are differences in the resistance and capacity adaptations of freshwater unionoidean mussels, *C. fluminea* and *D. polymorpha* (Table 2). *Corbicula fluminea* is very tolerant of turbidity (Way et al. 1990) and *D. polymorpha* (Alexander et al. 1994; Lei et al. 1996) is more turbidity tolerant than many unionacean species (Aldridge et al. 1987). Both *C. fluminea* and *D. polymorpha* have higher metabolic rates than unionoideans (Alimov 1975; McMahon 1996, 1999). These adaptations are associated with their capacity to colonize disturbance-prone lotic habitats with higher flow rates and greater suspended solids than tolerated by most unionoidean species (McMahon 1996, 1999; Strayer 1999). The elevated metabolic rates of *C. fluminea* allow for rapid burrowing if individuals become dislodged from the substratum by currents (McMahon 1999), whereas the somewhat lower metabolic rates of *D. polymorpha* (Alimov 1975) may result from byssal attachment to hard surfaces, which eliminates necessity for burrowing or other locomotory activity. Elevated metabolic rates in both species support higher relative filtration rates than achieved by unionids (MacIsaac 1996; McMahon 1999; McMahon and Bogan 2001), likely accounting for their elevated assimilation and growth rates (Table 1). The elevated hemolymph ionic and osmotic concentrations of *C. fluminea* relative to unionoideans or *D. polymorpha* (Table 2; Dietz 1985; Dietz et al. 1996) are believed to support its elevated metabolic rates (McMahon 1999). Capacities for rapid burrowing and tolerance of suspended slit allow *C. fluminea* to colonize smaller, more variable lotic habitats than *D. polymorpha*, which, in turn, appears better adapted to more variable, periodically high-flow habitats than many unionoidean species.

Inspection of Table 2 reveals that in all aspects other than adaptations associated directly with life in disturbance-prone, variable-flow habitats, both *C. fluminea* and *D. polymorpha* are generally less tolerant of environmental stress than most unionoidean species. *Corbicula fluminea* and *D. polymorpha* appear to be less tolerant of elevated temperatures (McMahon 1996, 1999), hypoxia (Johnson and McMahon 1998; McMahon and Bogan 2001), emersion (Byrne and McMahon 1994; McMahon 1996, 1999), low pH, and low calcium concentration than unionoidean mussels (McMahon 1996, 1999; McMahon and Bogan 2001). Unionoideans, *C. fluminea*, and *D. polymorpha* all have poorly developed capacities for respiratory temperature acclimation such that the oxygen uptake rates of individuals are relatively unaffected by their prior long-term temperature experience (Table 2; McMahon and Bogan 2001). In contrast, unionoideans appear better at maintaining O₂ uptake rates with progressive hypoxia (i.e., O₂ regulation of O₂ consumption rate; McMahon and Bogan 2001) than either

Table 2. Summary of the major physiological resistance and capacity adaptations of native, North American freshwater bivalves (Unionoidea) and the nonindigenous *Corbicula fluminea* and *Dreissena polymorpha* (based on information in McMahon (1996, 1999) and McMahon and Bogan (2001)).

Physiological adaptation	Unionoidea	<i>Corbicula fluminea</i>	<i>Dreissena polymorpha</i>
Temperature tolerance	Generally higher than <i>C. fluminea</i> or <i>D. polymorpha</i> in species ranging over similar latitudes	Cannot tolerate >36°C or <2°C	Cannot tolerate >30°C
Metabolic rate	Low	High	Intermediate
Respiratory response to temperature	No temperature regulation of O ₂ uptake rate	No temperature regulation of O ₂ uptake rate	No temperature regulation of O ₂ uptake rate
Capacity for respiratory temperature acclimation	Little capacity for respiratory temperature acclimation	Little capacity for respiratory temperature acclimation	Little capacity for respiratory temperature acclimation
Capacity to regulate oxygen uptake rate with progressive hypoxia	Many species are good regulators of O ₂ consumption with progressive hypoxia	Nonregulators of O ₂ consumption with progressive hypoxia	Poor regulators of O ₂ consumption with progressive hypoxia
Hemolymph osmotic concentration	Intermediate, 40–50 mosmols·L ⁻¹	High, 65 mosmols·L ⁻¹	Low, 30–36 mosmols·L ⁻¹
Emersion tolerance	Most species are emersion tolerant, 32–578 days at 15°C in high relative humidity depending on species	Intermediate emersion tolerance, 36 days at 20°C in high relative humidity	Low emersion tolerance, 13 days at 15°C in high relative humidity
Lower pH limit	Low, ≈4.7 for some species	Intermediate, ≈5.6	High, ≈6.5
Calcium concentration limits	Low, >2.5 mg Ca·L ⁻¹	Unknown, likely to be greater than those of unionids	High, requires >25 mg Ca·L ⁻¹ for good growth
Turbidity tolerance	Variable, ranging from low to very high depending on species	Very high	Intermediate

C. fluminea with no capacity for O₂ regulation (McMahon 1999) or *D. polymorpha* with a very limited capacity for O₂ regulation (McMahon 1996; Table 2), perhaps explaining the generally greater hypoxia tolerance of unionoideans relative to the latter two species.

Thus, although *K*-selected, noninvasive, and generally restricted to stable lotic or lentic habitats, North American unionoidean bivalves appear to have more extensively developed resistance and capacity adaptations than the invasive, *r*-selected, nonindigenous species *C. fluminea* and *D. polymorpha*, adapted for life in less stable habitats. Therefore, neither of these successful nonindigenous freshwater bivalve species appears to support the hypothesis (Ehrlich 1984; Lodge 1993) that a successful invader should be able to function in or tolerate a wider range of physical conditions or stresses than indigenous species.

Physiological adaptations of other nonindigenous invaders of North American freshwaters

To examine whether or not the underdeveloped resistance adaptations of the invasive bivalve species *C. fluminea* and *D. polymorpha* relative to those of indigenous unionoidean freshwater mussels was an unusual occurrence, I examined the literature for descriptions of physiological adaptation in other recent invaders of North American freshwaters with a focus on comparative studies with potentially competing, taxonomically related, native species. Although literature on this subject for other invasive species was not nearly as ex-

tensive as that for *C. fluminea* and *D. polymorpha*, it appeared that the most successful invading species in North American freshwaters do not have greater resistance and capacity adaptations than taxonomically related indigenous species.

The freshwater gastropods *Potamopyrgus antipodarum*, *Melanooides tuberculata*, and *Bithynia tentaculata* have been introduced to North America from Europe, Africa, and Europe, respectively. *Bithynia tentaculata* endemically ranges from Europe into Asia and northern Africa, where it broadly ranges from stable lakes and rivers to small ponds and streams (Ellis 1969). It is not tolerant of elevated temperatures compared with other freshwater gastropods (Fantin et al. 1981; Dregol'skaya and Korotneva 1988), which may explain its high degree of temporal population density variation (Vincent and Létourneau 1985; Subramanian and Thomas 1991). *Melanooides tuberculata* is native to subtropical and tropical regions of northern and eastern Africa, southern Asia, and Northern Australia, where it inhabits shallow seepages, irrigation channels, pools fed by perennial springs, and lakes (Brown 1980). It has an intermediate tolerance of emersion compared with two other freshwater gastropod species in Hong Kong (Dudgeon 1982) but was somewhat more desiccation-tolerant than two native gastropods in the Potomac River, Virginia (Hamilton 1979). It is excluded from small streams that exhibit marked flow variation (Neck 1985; de Freitas and Loureiro dos Santos 1995) and does best in stable habits (Pointier et al. 1991). *Potamopyrgus antipodarum* is endemic to New Zealand, where it inhabits unstable running-water environments from extremely small streams to fast flowing rivers (Winterbourn 1970; Macon

and Cooper 1977). It has an environmental calcium limit of $1.0\text{--}2.4\text{ mg}\cdot\text{L}^{-1}$ (Vareille-Morel 1985), typical of other freshwater gastropods. With a lower limit of $> 4^\circ\text{C}$ (Vareille-Morel 1986), it is less tolerant of low temperatures than most temperate freshwater gastropods, which may account for winter population declines recorded for this species (Siegismund and Hylleberg 1987). No information on physiological adaptation could be found for the Asian freshwater mytilid mussel, *Limnoperna fortunei*, which is widely distributed in freshwater lakes and rivers throughout southeast Asia (Ricciardi 1998). This species recently invaded South American freshwaters (Darrigran and de Drago 2000) and has *r*-selected life-history tactics that adapt it for life in unstable habitats (Morton 1987).

The planktonic cladocerans *Bythotrephes cederstroemi* and *Daphnia lumholtzi* have both been recently introduced into North America. The predatory Palearctic Eurasian cladoceran *B. cederstroemi* was first recorded in the Great Lakes in 1982 (H.J. MacIsaac, Department of Biological Sciences, University of Windsor, Windsor, ON N9B 3P4, Canada, personal communication), where it was likely introduced from eastern Europe (Garton et al. 1993). In Europe, this species is found in small ponds to large lakes (Lehman 1987). Little is known of its physiology. It inhabits cold, oligotrophic lakes throughout Palearctic Eurasia. It does not tolerate high summer water temperatures, resulting in late-summer population crashes (Garton et al. 1990). Unlike a native, predatory, Great Lakes cladoceran, *Leptodora kindtii*, *B. cederstroemi* has little capacity for temperature acclimation of its upper thermal limits (Garton et al. 1990). It has a narrow temperature tolerance range compared with native predatory cladocerans, which should limit its dispersal into southern North American freshwaters (Garton et al. 1993).

The cladoceran *D. lumholtzi* was first reported in Texas reservoirs in 1990–1991 and has spread to many lentic habitats in the southeastern United States (Havel et al. 1995; Dzialowski et al. 2000). In its native tropical-to-subtropical range (i.e., Africa, the Middle East, India, and Australia), *D. lumholtzi* occupies a variety of habits, ranging from deep permanent lakes to temporary ponds (Havel et al. 1995) but has been generally restricted to lakes in the southern United States (Dzialowski et al. 2000). In southern U.S. lakes, its populations grow rapidly and reach peak densities in summer and early fall at water temperatures greater than $25\text{--}27^\circ\text{C}$ when native cladoceran populations are in decline. However, it is absent or at very low densities during periods of lower water temperature in late fall, winter, and spring (East et al. 1999; Work and Gophen 1999a, 1999b). It has low fecundity and survivorship at ambient temperatures below $10\text{--}15^\circ\text{C}$ (Lennon et al. 2001), which may be the basis for its density reductions in southern U.S. lakes during cooler periods of the year relative to more low-temperature-tolerant native cladoceran species (Work and Gophen 1999b; Johnson and Havel 2001). Thus, the tropical–subtropical *D. lumholtzi* appears to be relatively intolerant of low temperatures compared with native southern U.S. cladoceran species, reducing chances of its invasion of lakes at higher latitudes in North America (Lennon et al. 2001).

Three fish species have recently been introduced to the Great Lakes from Eurasia: the tubenose goby, *Proterorhinus marmoratus*, the round goby, *Neogobius melanostomus* (Jude

et al. 1992), and the European ruffe, *Gymnocephalus cernuus* (Pratt et al. 1992). Little information is available on the physiological adaptations of Ponto-Caspian *P. marmoratus* or *N. melanostomus*. *Proterorhinus marmoratus* inhabits slightly brackish to fresh water rivers and estuaries in the Black and Caspian seas and rivers entering the northern Aegean and Aral seas, whereas *N. melanostomus* is endemic to marine, estuarine, and freshwater habitats in the Black, Caspian, and Azov seas and their tributaries (Miller 1986). *Proterorhinus marmoratus* is considered to inhabit moderately unstable thermal habitats, and *N. melanostomus*, stable thermal habitats, reflected in the greater mean heterozygosity of *P. marmoratus*, with *N. melanostomus* having the lowest mean heterozygosity of nine tested gobiid species (Wallis and Beardmore 1984). Its low heterozygosity suggests that *N. melanostomus* may have a relatively limited temperature range. *Gymnocephalus cernuus* is endemic to fresh and brackish water in lowland lakes and slow-flowing rivers in eastern and northern Europe and Asia and in the Caspian and Oral seas, where it can rapidly increase in numbers when introduced to new habitats (Pratt et al. 1992). The rapid growth rate, short life span, and high fecundity of *G. cernuus* are *r*-selected traits that make this species successful in unstable habitats (Lappalainen and Kjellman 1998). It appears to be restricted to clear, well-oxygenated waters, suggesting poor hypoxia tolerance (Ková 1998), and does not appear particularly thermally tolerant compared with other percids or cohabitant fish species (Hokanson 1977). Its $11\text{--}16^\circ\text{C}$ temperature range for hatching (Fairchild and McCormick 1996), $9\text{--}21^\circ\text{C}$ for early embryonic development (Saat and Veersalu 1996), and 21°C for optimal first year growth (Edsall et al. 1993) are not greatly different from that of other percid species.

Synthesis

Corbicula fluminea and *D. polymorpha* have life-history adaptations that clearly adapt them to periodically disturbed habitats in which their short life spans, early maturity, rapid growth, high fecundities, and extensive capacity for downstream dispersal allow rapid population re-establishment after extirpation or density reduction by chance catastrophic environmental perturbations (Table 1). In contrast, most unionoidean mussels, with their long life spans, delayed maturity, slow growth rates, low effective fecundities, and limited capacity for dispersal, are clearly adapted to stable, *K*-selected habitats (Table 1). Even though it has been postulated that invasive species should have broad physiological tolerance, allowing survival under the variable abiotic conditions of environments into which they are newly introduced (Ehrlich 1984), in almost all aspects, *C. fluminea* and *D. polymorpha* are less tolerant and less capable of adjusting to environmental stress than unionoideans (Table 2). Although data on resistance and capacity adaptations for other recent aquatic invaders of North American freshwaters are sparse, the pattern of invasive species being less or equally tolerant of environmental stress than related endemic species appears generally consistent across a number of taxonomically separate groups (i.e., gastropods, bivalves, planktonic cladocerans, and fish). This suggests that broad resistance of and adaptability to environmental stress is not a general characteristic of successful aquatic invasive animals.

Most invasive species with major ecological impacts, including those for which physiological adaptations were reviewed above, have *r*-selected life-history and reproductive traits that allow them to achieve massive population densities soon after invading a new habitat (Lodge 1993; Williamson 1996). In their native unstable habitats, population densities of invasive species are regulated, in part, through periodic density reduction or extirpation by unpredictable catastrophic events (i.e., floods, hypoxia, thermal stress, drying during droughts) regardless of their capacity to tolerate environmental stress. Thus, many invasive species may experience little selection pressure for evolution of extensive resistance and capacity adaptations within their native habitats. Rather, in most of these species, adaptations center on capacity to rapidly re-establish populations after perturbation-induced density reduction or extirpation. In contrast, the life-history and reproductive traits of species adapted to stable habitats (i.e., *K*-selected species), including slow growth rates, late maturity, long life spans, low fecundity, poor dispersal capacity, preclude rapid re-establishment of populations after perturbation-induced density reductions or extirpation (Sibly and Calow 1986).

Even in stable aquatic habitats, stressful environmental perturbations occur periodically. Thus, selection pressures for evolution of elevated resistance and capacity adaptations allowing survival of rarefactive periodic environmental stress should be greater in long-lived, *K*-selected species such as unionoidean freshwater mussels than in *r*-selected, invasive species such as *C. fluminea* and *D. polymorpha*. Indeed, environmental stress can lead to massive population reductions in both *C. fluminea* and *D. polymorpha* with little or no impact on sympatric, native unionoidean mussels (Sickel 1986; McMahon 1996, 1999). Similar environmental stress-induced population crashes have been described for other invaders of North American freshwaters, including *P. antipodarum* (Siegismund and Hylleberg 1987) and *B. cederstroemi* (Garton et al. 1990), in which sympatric, native populations of taxonomically related species were unaffected. Thus, reduced resistance and capacity adaptation to environmental stress in invasive relative to taxonomically related endemic species may be the rule rather than the exception in most ecologically important aquatic animal introductions.

In their unstable native habitats, population size in *r*-selected, invasive species is partially controlled by periodic perturbation (Williamson 1996). Major ecological consequences can occur if such invasive *r*-selected species become established in stable nonnative habitats (i.e., Great Lakes or Mississippi River drainage of North America) where there are no directly competing native species (i.e., attached epibenthic bivalve in the case of *D. polymorpha*; McMahon and Bogan 2001) or in which anthropomorphic perturbation makes the habitat favorable to the *r*-selected invader (i.e., increased river flow and turbidity owing to channelization in the case of *C. fluminea*; McMahon 1999). Once invading, *r*-selected species become established in a relatively stable, nonnative habitat, their population growth is no longer checked by chance environmental disturbance, thus their capacity for rapid reproduction and growth results in development of high population densities that quickly approach *K*.

As such, invasions by nonindigenous aquatic species can result in massive direct and indirect impacts on native flora and fauna and alternation of abiotic habitat conditions. Certainly, among introductions of nonindigenous aquatic species to North America, *C. fluminea* and *D. polymorpha* have had some of the most profound biological and abiotic impacts (MacIsaac 1996; Strayer et al. 1999; McMahon and Bogan 2001) and yet have reduced resistance and capacity adaptations to environmental stress compared with native unionoidean mussels (Table 2).

My examination of the physiological adaptations of successful North American nonindigenous aquatic animals suggests that the hypothesis that successful invaders are characterized by broad physiological tolerance–ecophenotypic plasticity (Ehrlich 1984) may require re-examination, at least for aquatic species. Instead, many successful aquatic invaders are generally *r*-selected and have life-history traits that allow rapid population recovery in their perturbed native environments where physiological tolerance is of little adaptive value. In contrast, among native *K*-selected species, with limited capacity for recovery from catastrophic population reductions, tolerance of physiological stress is of high adaptive value as it prevents population reductions during rarefactive environmental extremes. It is when a nonindigenous, *r*-selected species becomes established in a nonnative, stable habitat where it is no longer subject to environmental stress-induced population reductions, that it can attain massive population densities approaching *K* never achieved in its perturbed native habits. Development of dense invader populations results in major biotic and abiotic perturbations of the invaded habitat that place slowly recovering, *K*-selected, native species' populations requiring habitat stability at risk.

Acknowledgments

David Torsiello of the University of Texas at Arlington assisted with the literature search on which this review was based. Hugh MacIsaac of the University of Windsor, Ontario, and William Stickle of Louisiana State University critically reviewed the manuscript and made many valuable suggestions for its improvement.

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