Native predators and exotic prey – an acquired taste?

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Only a small proportion of exotic species invasions give rise to hyper-successful nuisance species, but those that do have dramatic negative impacts on ecosystems, such as the displacement of native species and disruption of native food webs. For a native predator, such changes may mean a major transformation in its resource base and a decline in its fitness. However, native predators may adapt to become more effective at feeding on exotic prey, either rapidly, via existing phenotypic plasticity, or more slowly, via natural selection. Despite a rapidly growing number of publications on the importance of species invasions as a driver of contemporary evolution in both invading and native species, we know little about how the arrival of exotic prey affects native predators. We propose that native predators could be important in regulating the long-term dynamics of invading species and, consequently, that the overexploitation of predators could facilitate biological invasions.

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Predator–prey interactions are a major driver of the dynamics of populations, communities, and ecosystems (Sergio *et al*. 2006), as well as the evolution of adaptive traits (Johnson and Agrawal 2003). Interactions between predator and prey are also important in invasion biology; indeed, release from natural enemies, including coevolved predators, is often cited as a mechanism enabling exotics to become hyper-successful nuisance species (Colautti *et al*. 2004). A large body of literature is rapidly accumulating on the role of adaptation in predator–prey interactions, but the overwhelming majority of studies focus on how prey respond to predation risk (Lima 2002; Johnson and Agrawal 2003). Likewise, studies of predator–prey interactions in invasion ecology have concentrated largely on how native prey adapt to exotic predators by evolving anti-predator strategies (McIntosh and Townsend 1994) or inducible defenses (Freeman and Byers 2006), not on how exotic prey affect native predators (King *et al*. 2006).

In a nutshell:

- Exotic species can represent an abundant prey resource for predators and displace native prey
- A predator that is able to feed on an exotic species has a fitness advantage over a predator that cannot
- There may be a considerable "adaptive" lag period before native predators become effective at controlling an exotic species
- Overharvest of native predators may compromise their ability to regulate invaders

This emphasis on the responses of prey neglects the reciprocal responses of predators, which may be equally important. In particular, we argue that invasion and evolutionary ecologists should pay more attention to the responses of native predators to exotic prey. Native predators may be an important factor regulating not only native species, but also the long-term dynamics of invading species. Furthermore, the exotic prey/native predator system offers unique opportunities to study selection and contemporary evolution of adaptive traits in predator populations. The tendency of ecologists to focus on exotic prey rather than native predators has left us without the necessary information to assess how important native predators are in controlling populations of exotic species. If native predators are an important control on species invasions, human decimation of predator populations may not only destabilize native ecosystems, but leave them vulnerable to invasion by non-native species as well.

Here, we describe the conditions under which native predators should respond adaptively to the arrival of exotic prey and review evidence indicating that exotic species change the prey base and fitness of native predators. We further examine evidence that native predators change their diets in response to invasion, and may adapt to use exotic prey more efficiently. We argue that native predators could supply considerable biotic resistance to exotic invaders, in some cases after an "adaptive" lag period, and suggest directions for future research on this understudied topic.

■ Why should native predators adapt to exotic prey?

Exotic species may represent an abundant prey resource for predators and also displace the native prey that formerly made up the bulk of a predator's diet. Consequently, a predator that is able to feed on an exotic

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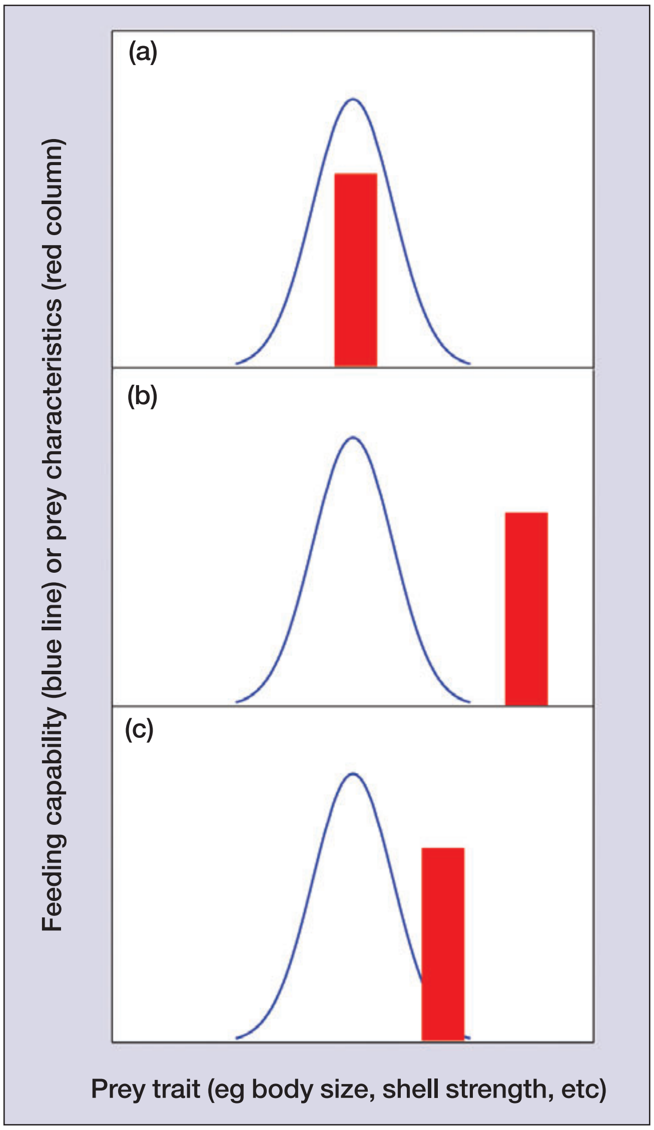

Figure 1. *Exotic prey may be (a) well inside the feeding capabilities of a population of native predators, (b) outside its feeding capabilities, or (c) within the feeding capabilities of only some individuals in the population.*

species will be at an advantage over a predator that cannot. This advantage need not be large to affect predator behavior and evolution, as long as it is persistent. Broadly speaking, there are three possible responses of a predator population to the arrival of an exotic species. (1) The exotic species is well within the existing feeding capabilities of the predator population (Figure 1a). If the predator is abundant, it could supply biotic resistance against the invasion, preventing the exotic from becoming either established or, if already present, hypersuccessful. (2) The exotic species is so far from the feeding capabilities of the predator that evolutionary constraints prevent adaptive predator responses (Figure 1b). In this case, exotics that cause a dramatic change in the prey base should indirectly lead to the decline of native predators and a reduction in the trophic transfer of energy up the food web. (3) The exotic species is near the feeding capabilities of at least some individuals in the predator population, creating scope for adaptive change (Figure 1c). This adaptation can result from several mechanisms operating across a range of time scales, and will be the main subject of our review.

Can predators compete in the arms race?

Theoretical arguments underpin the current strong emphasis on the study of adaptation by prey, rather than that by predators. Loose application of the "arms race" analogy in the evolution of predator–prey interactions has been criticized for failing to recognize that the selective forces on prey and predators may be asymmetrical (Nuismer and Thompson 2006). Prey adapt to avoid death, whereas predators adapt merely to acquire more meals (the "life–dinner" principle; Dawkins and Krebs 1979), making the fitness gradient stronger in prey populations. This asymmetry should drive stronger responses by prey species than by predators. Following this thinking, it seems reasonable to postulate that the evolution of prey defense should be more likely (and thus more rewarding to study) than the evolution of predator offense.

However, the life–dinner asymmetry may not apply universally. The strength and perhaps direction of this asymmetry ought to depend on (1) the degree to which predation from a particular predator is a major cause of mortality in the prey species, and (2) the importance of a particular prey item in the predator diet. If a single predator species is the primary source of mortality for a prey species, whereas that prey item is not the major component of the predator's diet, then there should be strong pressure for the prey to evolve anti-predator defenses and little pressure for the predator to counter these defenses; the life–dinner argument thus applies in such a scenario. Alternatively, the prey may be the major item (or an essential item) in the predator diet, but mortality from the predator may represent a minor risk for the prey. In this case, it is the predator that should be pushed to evolve to more effectively detect, capture, or handle the prey, and the prey will be under little pressure to evolve anti-predator defenses. The latter situation should be especially relevant in many biological invasions, because exotic species often become extremely abundant and may eventually come to constitute a large part of the potential prey base available to native predators (Figure 2). Native predators, on the other hand, represent a small fraction of the mortality sources for prey in the early stages of the invasion.

What evidence suggests adaptation in native predators?

Much evidence now shows that native predators affect the abundance, morphology, and behavior of native prey (Lindström *et al.* 1994; Miner *et al.* 2005; Ripple

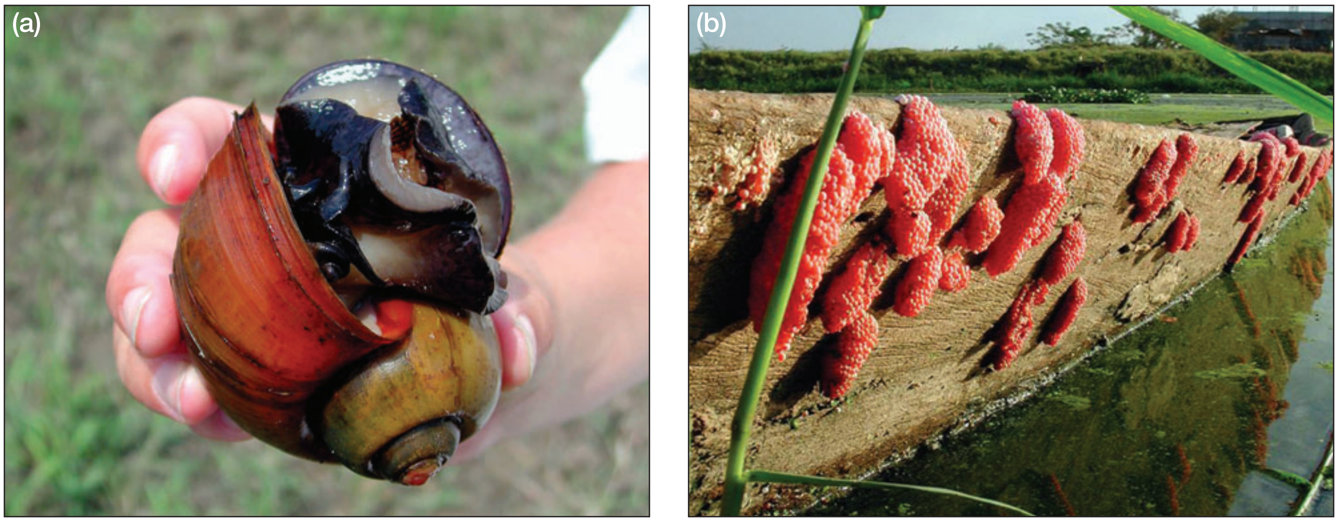

Figure 2. *(a) The South American golden apple snail (*Pomacea canaliculata*) has become a hyper-successful invader throughout Southeast Asia. (b) Canoe in Laos with approximately 100 000 golden apple snail eggs, ready to hatch in two weeks.*

and Beschta 2005), with effects that reverberate throughout the ecosystem (Shurin *et al.* 2002). It therefore seems likely that native predators will have analogous effects on exotic prey species.

In the following sections, we review empirical evidence for (1) dramatic changes in the food base of native predators after exotic invasions, (2) post-invasion declines in native predator fitness, (3) predators switching to exotic prey, (4) rapid changes in predator behavior or morphology in response to a transformed food base, (5) evolutionary responses of native predators, and (6) suppression of exotic prey populations by native predators.

Dramatic changes in the food base of native predators after invasion

It is well established that hyper-successful invaders alter species composition and abundance at lower trophic levels. For example, the New Zealand mud snail (*Potamopyrgus antipodarum*) attained densities of up to several hundred thousand individuals per square meter in streams of Yellowstone National Park (Wyoming) just 7 years after their introduction (Hall *et al.* 2003); native invertebrates in sampled areas within Yellowstone now constitute only 3% of total biomass. Dramatic changes at the food base are also found when species like the freshwater zebra mussel (*Dreissena polymorpha*; Strayer and Smith 2001; Figure 3) and marine blue mussel (*Mytilus galloprovincialis*; Geller 1999) invade and compete with native species for substrate and other resources. Invasive ants also drastically reduce the populations of both native ants and other arthropods in invaded areas around the globe (Holway *et al.* 2002).

Post-invasion declines in native predator fitness

The changes in the benthic animal community that followed the zebra mussel invasion of Lake Michigan led to steep declines in growth rates and health of several fish species, including the most important commercial fish in the Laurentian Great Lakes, lake whitefish (*Coregonus clupeaformis*; Pothoven *et al.* 2001; Pothoven and Madenjian 2008; Figure 4b). Size and body condition greatly influence survival and the number and quality of offspring in fish (Birkeland and Dayton 2005), making it likely that the change in prey base negatively affected whitefish fitness. Likewise, native ants are rapidly being displaced by the invasive Argentine ant (*Linopithema humile*) in California (Suarez *et al.* 2000). The threatened coastal horned lizard (*Phrynosoma coronatum*) is a specialized predator of ants, but horned lizards avoid eating Argentine ants. Juvenile coastal horned lizards reared on only Argentine ants do not gain weight (Suarez and Case 2002), thus leaving few resources for reproduction in areas where the prey base is dominated by exotic ants.

Predators switching to exotic prey

There are numerous examples of native predators consuming exotic prey; for example, > 90% of the diet of the threatened Lake Erie water snake (*Nerodia sipedon insularum*) now consists of Eurasian round goby (*Neogobius melanostomus*), which invaded the Great Lakes in the early 1990s (King *et al.* 2006). Zebra mussels have become an important food item for many North American turtles (Bulté and Blouin-Demers 2008), birds (Petrie and Knapton 1999), fish (Magoulick and Lewis 2002), and decapods (Molloy *et al.* 1994), and now constitute a large proportion of the whitefish diet as well (Figure 4c). However, we do not know if per capita consumption rates of exotic prey by these native predators increased over time after invasion – that is, whether the native species responded adaptively to a dramatically altered food base. An adap-

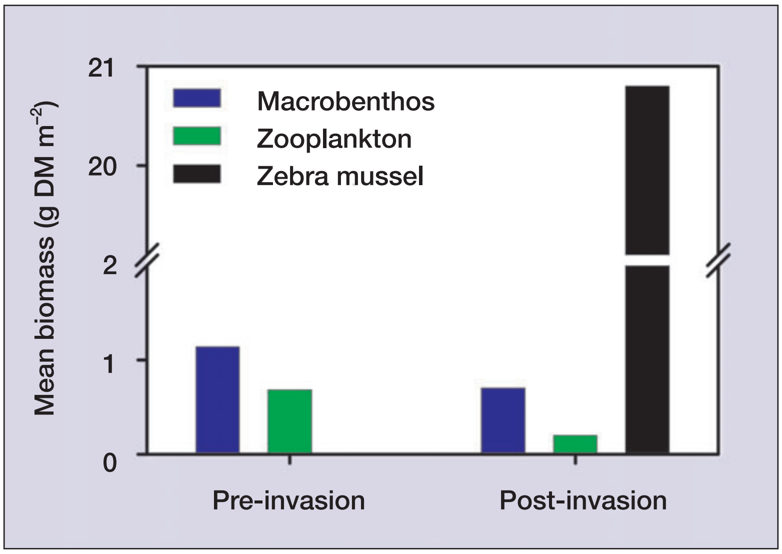

Figure 3. *Macrobenthos and zooplankton (mean biomass [g DM m^{-2}]; DM = dry mass) in the Hudson River, before and after zebra mussel invasion. Modified from Strayer and Smith (2001).*

tive response might help explain the enormous increase in waterfowl use of Long Point Bay in southern Ontario following the zebra mussel invasion (from 43 200 waterfowl-days [ie one waterfowl for one day] in 1986 to 3.6 million in 1997; Petrie and Knapton 1999), or higher rates of zebra mussel disappearance in the Mississippi River in cages open to fish predation in 1998 (7 years after invasion; Bartsch *et al.* 2005) versus that in 1994 (3 years after the invasion; Thorp *et al.* 1998).

There are several mechanisms by which native predators may become better able to use exotic species as prey, including learning, social transmission, ontological changes in morphology, and evolutionary adaptations. These mechanisms operate over a wide range of time scales, from the lifetime of an individual to many generations.

Rapid changes in predator behavior or morphology

Predators can modify their behavior from experience. For example, predatory wasps learn to overcome the defenses of their sheltered prey (Weiss *et al.* 2004), and European green crabs (*Carcinus maenas*) can transfer handling skills learned from previous prey encounters to new and similar food items (Hughes and O'Brien 2001). Numerous examples show that predators aggregate in patches with high prey densities (eg Petrie and Knapton 1999). It is well known that higher-order (including mammalian) predators teach their young what to eat and what to avoid, but social learning is important in lower-order predators as well (eg fish; Brown and Laland 2003).

Phenotypic plasticity – where organisms fine-tune their behavior, life history, or morphology during the individual's lifetime to match a changing environment – is common in nature (Nussey *et al.* 2005). Predators may change morphologically to become more efficient at consuming abundant prey. Red rock crabs (*Cancer productus*) that are grown on fully shelled prey, for example, grow larger and stronger claws than conspecifics that are raised on nutritionally equivalent but unshelled prey (Smith and Palmer 1994). During ontogeny, the mouth morphology or gape size of many fish (Mittelbach *et al.* 1999) and snakes (Aubret *et al.* 2004) develops to match the size of the most important prey. Such modest changes in behavior or morphology could make some predators more effective at consuming exotic prey almost immediately, an example of our third scenario (Figure 1c).

Evolutionary responses of native predators

Over time, however, drastic and directional change caused by a hyper-successful invader should favor the most adaptive traits in a predator – be they tooth or gape size, search image, or otherwise – through natural selection. Existing variability within predator populations, such as individual foraging specializations (eg Schindler *et al.* 1997), may serve as raw material for rapid evolution in habitats invaded by hyper-successful invaders. Natural selection should favor traits that increase detection, capture, and use of abundant and energetically profitable prey or avoidance of unprofitable or poisonous prey. To our knowledge, such rapid evolution by predators has rarely been studied in the specific context of native predators and exotic prey, but empirical studies on related subjects suggest that evolutionary adaptation of predators should be common (Agrawal 2001; Strauss *et al.* 2006). For instance, it is well known that native herbivores evolve to feed more effectively on exotic plants – the Australian soapberry bug (*Leptocoris tagalicus*) has evolved larger mouthparts to increase foraging on fruit of the invasive balloon vine (*Cardiospermum grandiflorum*) in just a few decades, for example (Carroll *et al.* 2005).

Likewise, predators that suffer reductions in fitness from exotic species invasions, such as lake whitefish, should evolve through natural selection or undergo decline. For example, it is especially difficult for small whitefish to consume larger, more energetically profitable zebra mussels (Pothoven and Nalepa 2006). In this case, then, whitefish individuals that are better at consuming larger mussels at an earlier age (Figure 1c) would have a fitness advantage.

A few studies indicate that predator populations can evolve adaptations to overcome prey defenses. The best known are of cases in which the prey species negatively affects predator fitness, such as when the prey is toxic

(Brodie and Brodie 1999), or when the predator–prey relationship is tightly linked (eg Kishida *et al.* 2006). These adaptations do not always require a long coevolutionary history. In Australia, two snakes, the red-bellied blacksnake (*Pseudechis porphyriacus*) and the green tree snake (*Dendrelaphis punctulatus*), evolved an altered morphology (a smaller head to avoid swallowing large doses of toxin and a larger body size to dilute ingested toxin) in response to the invasion of the poisonous cane toad (*Bufo marinus*) over approximately 20 predator generations, or roughly 60 years (Phillips and Shine 2004). We suggest that evolutionary responses by other native predators that experience reduced fitness in habitats invaded by hyper-successful exotic species may be both common and important.

In contrast, some populations will have evolutionary constraints that slow or prevent adaptation to exotic prey. For instance, mainland and island populations of tiger snakes (*Notechis scutatus*) vary with respect to phenotypic plasticity in head size. Full-sibling experiments have shown that head size in the island population is a phenotypically plastic response to feeding on bigger prey as juveniles. Mainland tiger snakes show no such plasticity (Aubret *et al.* 2004), suggesting that the mainland population would respond more slowly, if at all, to a large-bodied invader (Figure 1b).

Do native predators suppress exotic populations?

There are several examples of native predators controlling both the abundance and distribution of exotic species. Gruner (2005) reported up to an 80-fold increase in the abundance of an established but uncommon exotic spider when native birds were excluded from an area, indicating that native birds kept this spider from becoming hyper-successful. The exotic European green crab (*Carcinus maenas*) is limited by predation from the blue crab (*Callinectes sapidus*) in eastern North America (deRivera *et al.* 2005) and by predation by red rock crabs (*Cancer productus*) in southwestern North America (Jensen *et al.* 2007). Interestingly, blue crabs may also suppress invasive rapa whelks (*Rapana venosa*; Harding 2003) and zebra mussels in the Hudson River (Molloy *et al.* 1994; Figure 5), which suggests the importance of this heavily harvested native predator as an agent of biotic resistance.

■ What can we conclude about predator adaptation to exotic prey?

Although empirical studies on predator adaptation to exotic prey are few, we propose several general conclusions: (1) hyper-successful invasive species strongly alter the food base of native predators; (2) this change is often directional and persistent; (3) exotic prey are often included in the diet of native predators, sometimes even as the main food item; and (4) switching to exotic prey may affect predator growth and body condition, which strongly relate to fitness. There is large genetic variation in natural populations, not only in terms of fixed traits, but also in phenotypic plasticity, which allows adaptive traits to evolve in response to a world that has been dramatically restructured by exotic invasions. Successful invasions by exotic prey may therefore trigger adaptation in native predator populations. We do not know how common evolutionary adaptation in predator populations may be, but it is likely

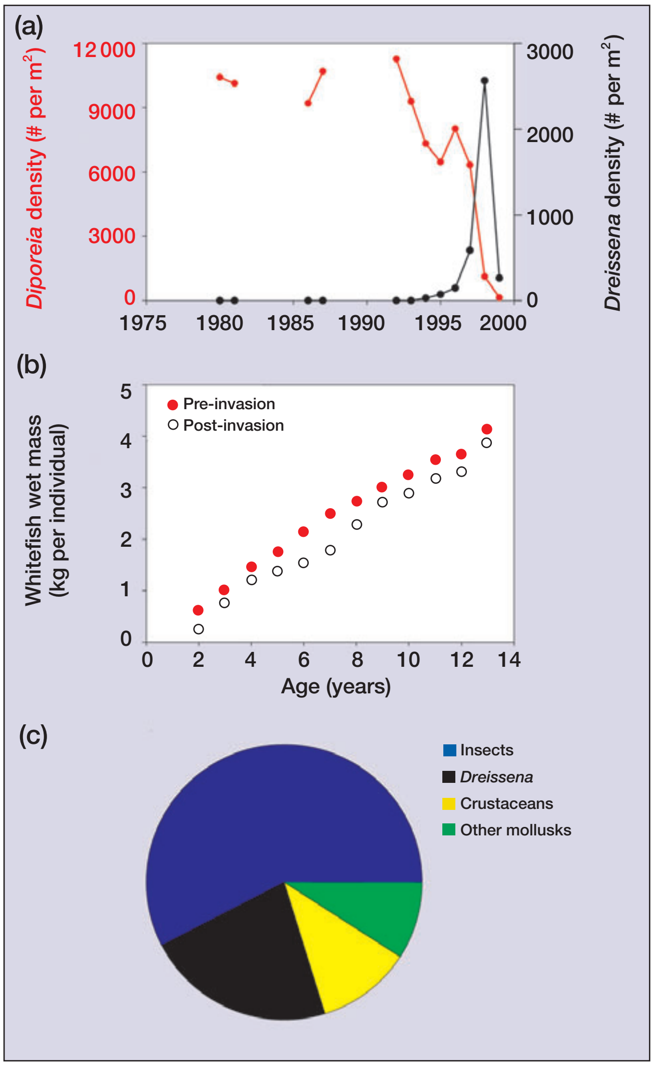

Figure 4. *Effects of the zebra mussel (*Dreissena polymorpha*) invasion of Lake Michigan on a native benthic amphipod crustacean (*Diporeia sp*) and the lake whitefish (*Coregonus clupeaformis*). The lake whitefish is the chief commercial fish of the Great Lakes, and* Diporeia *was its predominant food before the zebra mussel invasion. (a) The density of* Diporeia *declined sharply after the arrival of zebra mussels. (b) Growth rates of lake whitefish fell after the zebra mussel invasion. (c) Lake whitefish began to eat zebra mussels after the invasion. Diet composition is expressed as dry mass of gut contents. Note that the proportion of* Diporeia *in the post-invasion diet was too small (< 1%, by dry mass) to show in this diagram. Modified from Pothoven* et al. *(2001).*

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Figure 5. *Native blue crab (*Callinectes sapidus*) eating invasive zebra mussels.*

that, over time, evolution allows some predator populations to recover from decreased fitness. The relative paucity of examples of predator evolution in response to exotic prey may not reflect its rarity in nature, but rather a lack of scientific attention, especially given the obstacles associated with long-term studies.

Given that there may be a considerable lag period before native predators become effective at controlling an exotic species, short-term snapshots of biotic resistance may provide a false impression of the long-term regulatory potential of native predators. For example, the imported red fire ant (*Solenopsis invicta*) initially had drastic negative impacts on abundance and species richness of native ants and other arthropods in Texas. Studies conducted a decade later, however, showed that red fire ants had declined, while native ant and arthropod diversity had recovered to pre-invasion levels (Morrison 2002). The mechanisms behind this decline are not known, but acquisition of natural enemies, such as predators, is one plausible explanation. The timing and strength of predator adaptation to novel prey may strongly influence the dynamics of nuisance exotic species. Lack of long-term data on the population dynamics of hyper-successful exotic species (Strayer *et al.* 2006), however, makes it difficult to assess this influence.

■ Future research

One approach to the study of predator adaptation in the context of invasion is to compare native populations of a given species that have and have not coexisted with an exotic prey species, in terms of their relative abilities to recognize, handle, and consume the exotic. Full-sibling experiments with second-generation predators could then establish whether the feeding adaptations are primarily phenotypically plastic or genetically based. Such studies could also be coupled to observations of how the defenses of the exotic vary across habitats with and without specific native predators. Another approach is to quantify the responses of exotic prey to predator removal, either via controlled field experiments (eg Gruner 2005) or "natural" experiments, such as when disease outbreaks decimate native predator populations. Finally, unexplained crashes of previously hyper-successful exotics (Simberloff and Gibbons 2004) provide opportunities to test hypotheses about the mechanisms leading to collapse, and may lead to the discovery of examples of latent biotic resistance.

■ Conclusions

Drastic changes in the food base may be a strong selective force on native predator populations, and this phenomenon deserves more study in both basic and applied ecology. Invasions by exotic species are a growing threat to biodiversity, ecosystem function, and local economies (Mack *et al.* 2000; Holway *et al.* 2002; Carlsson *et al.* 2004), but there are still many gaps in our understanding about why many species do not establish, why well-established exotic species suddenly crash or even go extinct (Simberloff and Gibbons 2004), and why some exotic species become hyper-abundant. It is likely that native predators are one important but overlooked factor in controlling the long-term population dynamics of invasive species and mitigating their impacts on ecosystems.

Native predators structure ecosystems and may also contribute to biotic resistance against exotic invaders. The latter is often thought of as an "all-or-nothing" factor, so that tests for biotic resistance typically assess only the failure or success of an invasion (Mack *et al.* 2000; Jeschke and Strayer 2006; Lockwood *et al.* 2007). However, partial biotic resistance may be important in reducing the population size and detrimental impacts of an exotic species. Consequently, there is a pressing need for quantitative measurements of biotic resistance and the extent to which individual predator species (or competitors, or diseases) contribute to such resistance.

Finally, the prospect that predators may provide substantial biotic resistance to invasion raises the possibility that widespread human-driven declines in predator populations could lead to trophic cascades – with unknown effects to the ecosystem – and contribute to hyper-successful biological invasions. Populations of many predators have been reduced to a fraction of their original abundance because of control programs targeting "undesirable" species (eg wolves, coyotes) or overexploitation of species that are valuable (eg many large, predatory fish species; Pauly *et al.* 1998). For instance, intense fishing for blue crabs, red rock crabs, and Great Lakes whitefish may undermine the biotic resistance provided by these native populations, but we know little about how these reductions affect the success of invading exotics. Steep declines in predator populations could reduce not only the size of the predator population but also the phenotypic and genotypic variation that it contains, which, in turn, could then reduce the ability of the native predator to respond over time to exotic species (Layman *et al.* 2007). If the harvesting of predators substantially reduces biotic resistance to harmful invaders, then we need to count the costs of these invasions against the economic benefits provided by the harvesting of wild predators.

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