Invasion and predation in aquatic ecosystems

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Abstract This article reviews biological invasions in which predation (or its absence) plays a major role in the success of the invader. Examples are described in which the invader out-competes native species for the same food, and cases in which the invader consumes valued native species. In many instances, better predator avoidance by the invasive species or the absence of predators in the new habitat contributes to the success of the invaders; in other cases native or introduced predators appear to be able to keep the invasive species in check. A relatively new management approach in the US is the idea of adding another trophic level – to have humans act as the predators and consume the invasive species. This approach is being utilized in Florida and throughout the Caribbean against the lionfish, but could be extended to other fishes, as well as to various invasive crustaceans and mollusks. This idea is controversial, and current regulations prohibiting the possession of individuals of the invasive species (e.g., mitten crabs or snakefish) would preclude the development of a fishery for them [Current Zoology 57 (5): 613–624, 2011].

Keywords Predator, Prey, Trophic interactions, Feeding, Food web

1 Feeding

1.1 Outcompeting native species

Invasive species may out-compete native species for the same food. There are a number of documented cases of this phenomenon, generally from laboratory studies. Gherardi et al. (2001) compared the predation of the invasive red swamp crayfish *Procambarus clarkii* on different species of tadpoles with that of a native crayfish, *Austropotamobius pallipes*, and found that the invasive crayfish caught them more rapidly and appeared to be faster in switching to different prey than the native species, which they appear to be displacing in Italy (Barbaresi and Gherardi, 2000).

A non-indigenous species without a natural predator in the new environment similarly can become very abundant (Elton, 1958).

This paper focuses on trophic interactions, and the role of feeding and predator avoidance in the success of some selected aquatic invasive species, with emphasis on species in the United States.

1 Feeding

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Competition was also studied between invasive green crabs *Carcinus maenas* and native blue crabs *Callinectes sapidus* in which size-matched pairs were placed in competition experiments for a mussel. Green crabs were far better competitors and ate the food more often than the blue crabs, despite the greater aggression exhibited by the latter. Typically, blue crabs placed in the experi-
mental tank with green crabs extended their claws in an aggressive display, while the green crabs scuttled in and took the food (MacDonald et al., 2007). When fights took place over the food, the native C. sapidus was the “loser” a disproportionate number of times, despite their well-known aggression. These results suggest that juvenile blue crabs are at a disadvantage compared with green crabs; in areas where green crabs are common, juvenile blue crabs may spend more energy in conflict and may be out-competed for desired food items. However, since blue crabs become much larger than green crabs, the larger blue crabs may be able to provide “biotic resistance” to the green crab invasion.

Biotic resistance describes the ability of resident species in a community to reduce the success of invasions (Elton, 1958). Although resistance is well-accepted, the processes that contribute most to it, and whether the processes are strong enough to completely repel invaders are not always understood (Levine et al., 2004). In Chesapeake Bay where blue crabs are more common than further north, green crabs have not successfully expanded their range. Predation rates of large blue crabs on tethered green crabs were much higher in these areas (DeRivera et al., 2005).

A competition was set up between green crabs vs. juvenile lobsters Homarus americanus, in which the green crabs prevailed also. They were the first to the food, fed in more trials than the lobsters, and spent more time with the food than the lobsters (Rosson et al., 2006). They also captured and consumed some of the lobsters.

In competition experiments, introduced populations of the rusty crayfish Orconectes rusticus were better foragers and bolder to forage under predation risk than native populations of the same species. The invasive populations were far better at stealing the food from native crayfish species, something the native populations of O. rusticus did not seem to do (Pintor and Sih, 2009). Thus, there are not only competitive differences between invasive vs. native species, there are also differences between native and introduced populations of the same species. It would appear that individuals who are better foragers are the ones that are most likely to survive when introduced into a new habitat, which may exert selection pressure on the newly arrived animals. It may be that when two populations meet, the better foragers prevail, whichever population it is. It is likely that more often the natives are better adapted to their specific environment.

The Eurasian spiny water flea Bythotrephes longimanus was first detected in 1984 in Lake Huron (Bur et al. 1986) and is now established in all the Great Lakes and many other lakes in the region. B. longimanus consume small zooplankton such as small cladocerans, copepods, and rotifers, competing directly with planktivorous larval fish for food (Berg and Garton, 1988, Evans, 1988). They have been implicated as a factor in the decline of alewife Alosa pseudoharengus throughout the Great Lakes (Evans, 1988).

1.2 Preying on native species

The invader may prey upon the native species of concern. Bythotrephes longimanus, discussed above, not only compete with, but also appear to prey on, Leptodora kindtii and may be a causal factor in the decline of L. kindtii (Branstrator 1995), as the abundances of the two species are often negatively correlated. The invasion has severely altered planktonic food webs. A number of cladoceran species have declined dramatically since the invasion of the Great Lakes, including Eubosmina coregoni, Holopedium gibberum, Daphnia retrocurva, Daphnia pulicaria, and Leptodora kindtii, and overall species richness has decreased as a result (Barbiero and Tuchman, 2004). Their results indicate that invasive invertebrate predators such as Bythotrephes can have pronounced effects on zooplankton community structure. Barbiero and Tuchman (2003) compared the summer crustacean zooplankton communities of 17 invaded and 13 non-invaded (i.e., reference) lakes in Ontario. The communities of the two lake groups differed greatly. Average species richness was 30% higher in the reference compared to the invaded lakes. Total zooplankton biomass was significantly lower in the invaded lakes, mainly because of lower abundances of all common cladoceran species.

Lohrer and Whitlatch (2002) found that the Japanese shore crab H. sanguineus had negative effects on (the prior invader) C. maenas. Asian shore crabs are replacing European green crabs in rocky intertidal habitats in eastern Long Island Sound. H. sanguineus significantly reduced the recruitment of green crabs during field experiments by 50%–75%, but when H. sanguineus were immobilized in mesh bags or had both chelae removed, they did not affect the recruitment of green crabs, suggesting direct predation on the juvenile green crabs. The rising densities of H. sanguineus threaten C. maenas because H. sanguineus preys upon 0-yr green crabs.

As Bailey et al. (2006) demonstrated, the invasive amphipod Gammarus tigrinus in Ireland preys upon both adults and juveniles of the native opossum shrimp Mysis relicta, while adults of the latter preyed only upon juveniles of the former. Furthermore, the presence of G.
tigrinus alters habitat use by *M. relicta*, which then become more vulnerable to fish predation. A more recent invasive freshwater amphipod *Dikerogammarus villosus*, in the Netherlands, preys on both the native *Gammarus duebeni* and on *G. tigrinus*, including both intermolt and recently molted individuals (Dick and Platvoet, 2000). *D. villosus* has been nicknamed “killer shrimp” because of its behavior towards other invertebrates as well as fishes (Casellato et al., 2007). In laboratory studies with various invertebrates, *D. villosus* consumed far more prey and a broader range of prey than other amphipods studied. Adults consumed about one-third of their body weight per day (Krisp and Maier, 2005), suggesting that they may contribute to the decline of these invertebrates in some European streams.

One of the first aquatic invasive species to receive a lot of attention was the zebra mussel *Dreissena polymorpha* that arrived in the Great Lakes in the late 1980s, probably as a result of ballast water discharge from ships from Eastern Europe (They were not native to Europe, either, but moved from their native Caspian Sea and tributaries as a result of shipping canals dug in the 18th century). In its new location, this bivalve had no natural predators and grew very densely, completely covering hard surfaces, clogging up intake pipes for water systems, and causing great economic and ecological harm. However, their extensive filter feeding reduced plankton blooms and improved water clarity. Several years later, the round goby *Neogobius melanostomus* (or *Apollonia melanostomus*) arrived, probably also in ballast water. These fish, unlike any native of the Great Lakes, eat zebra mussels, almost eighty a day (Ray and Corkum, 1997) and can reduce population density of the zebra mussels (Barton et al., 2005). However, round gobies can displace native bottom-dwelling fish. Major reductions in populations of sculpins (*Cottus baikdi* and *C. cognatus*) have occurred in areas where gobies have become established because gobies compete with them for food or drive them from their habitat and spawning areas (Dubs and Corkum, 1996). Gobies also eat darters and other small fishes and feed on eggs and young of lake trout *Salvelinus namaycush*, which already have reduced populations in the Great Lakes (Steinhart et al., 2004).

In addition to eating native fish eggs, round gobies out-compete juvenile sport fish like walleye *Sander vitreus*, yellow perch *Perca flavescens*, and smallmouth bass *Micropterus dolomieu* for habitat, and out-compete adult non-sport fish like darters and sculpin, whose populations have decreased since gobies arrived. However, smallmouth bass that survive long enough to reach about five cm in length can begin to eat gobies, which make up as much as 85 percent of an adult’s diet. Smallmouth bass that eat gobies grow twice as fast as those that do not eat gobies (Winslow, 2010). But if competition with round gobies slows juvenile smallmouth bass growth, then the population may decline. Winslow (2010) found that the presence of gobies causes bottom-dwelling juvenile smallmouth to move up from the bottom into the water column to find food. This not only forces the smallmouth bass to eat tiny zooplankton (rather than the larger bottom-dwelling macroinvertebrates), but it also makes them more vulnerable to predators.

By changing food webs, gobies have increased the potential of contaminants to reach humans. Zebra mussels accumulate pollutants, which can be transferred to the gobies that eat them (Hogan et al., 2007). This is of concern because gobies are eaten by sport fish (smallmouth and rock bass, walleyes, yellow perch, and brown trout), which accumulate the contaminants and transfer them to human consumers. Another example of an invasion potentially affecting water quality is clam *Corbicula fluminea* on the East Coast of North America, which arrived in the late 1970s and is abundant in the Potomac River. When it was discovered, there was concern that it would cause major problems like the zebra mussel in the Great Lakes (attaching to surfaces, blocking intake pipes for water supply systems etc), but it lacks byssus threads and does not attach to hard surfaces. This clam instead settled on sandy bottom sediments; after it arrived there were unexpected increases in submerged aquatic vegetation and fish populations. The clam also serves as food for some fish, birds and muskrats (Darrigren, 2002) and after its arrival the water quality and clarity improved considerably, possibly caused in part by the filter feeding of *Corbicula* (Cohen et al., 1984). Increased clarity of the water would benefit the growth of SAV, which could provide more habitat for fish. The improvement in water quality may also have been due to improved sewage treatment and a ban on phosphorus in laundry detergents, but at the very least, this outcome indicates not all invasions are ecological disasters.

In the late 1980s, the Asian clam *Potamocorbula amurensis* became established in San Francisco Bay, replacing the native clam, *Macoma balthica*, as the dominant benthic macroinvertebrate in the area. It is a filter feeder, and its rapid spread has resulted in reduced phytoplankton in the bay, which means less food for
Veined rapa whelks _Rapa venosa_ are carnivorous gastropods whose main diet consists of a variety of other mollusks such as oysters and other bivalves that they smother by wrapping around the hinged region of the shell; they then feed between the opened valves. Native to the western Pacific, this species favors compact sandy bottoms where it can burrow into the substrate, and tolerates low salinities, water pollution, and low oxygen (Mann and Harding, 2003). _Rapana venosa_ was introduced into the Black Sea in the 1940s and spread along the Caucasian and Crimean coasts and to the Sea of Azov, and the coastlines of Romania, Bulgaria, and Turkey. It has become established in the northern Adriatic and Aegean Seas and is present along the southeast coast of South America. The first specimen in the United States was collected in Chesapeake Bay in 1998. This predatory gastropod grows to a large size (over 150 mm shell length) and has a thick shell. Because of their predatory ability and lack of significant predators, they have caused major changes in the ecology of benthic organisms in the Black Sea. Although scientists are not completely aware of the impacts of the whelk, they are very concerned about its potential impacts on Chesapeake Bay. However, juvenile rapa whelks in Chesapeake Bay may be kept in check by predation by the blue crab. Feeding experiments were performed by Harding (2003) using three size classes of blue crab predators and a size range of rapa whelks. Blue crabs of all sizes consumed Age 1 rapa whelks; Age 2 rapa whelks were consumed by medium and large crabs but not small crabs. The attack methods of medium and large crabs changed with whelk age and size. Rapa whelks less than approximately 35 mm SL were vulnerable to predation by all sizes of blue crabs tested, which may be one reason that the whelk does not appear to be doing great damage in the Chesapeake.

The comb jelly _Mnemiopsis leidyi_ was introduced into the Black Sea in the 1980s, and by 1989, the Black Sea population had reached 400 specimens per m³ of water in optimal conditions. Afterwards, due to depletion of food the population dropped somewhat. In 1999, the species was introduced into the Caspian Sea, where 75% of the zooplankton were depleted, affecting the entire food chain (Finenko et al., 2006). _M. leidyi_ eats eggs and larvae of pelagic fish and caused a dramatic drop in fish populations, including the commercially important anchovy, _Engraulis encrasicolus_, by competing for the same food sources as well as eating the young and eggs. This invasion caused cascading effects. Bottom-up effects included the collapse of planktivorous fish, dolphins in the Black Sea, and seals in the Caspian Sea. Top-down effects included an increase in phytoplankton due to release from grazing pressure, and increasing bacterioplankton populations, triggering increases in zooflagellate populations.

Purcell et al. (2001) reviewed the population distributions and compared population dynamics of _M. leidyi_ in U.S. waters where it is native, and in the Black Sea region, and examined effects of temperature and salinity, zooplankton availability, and predator abundance on _M. leidyi_ population size in both regions. In both regions, _M. leidyi_ populations are restricted by low winter temperatures. In Chesapeake Bay, however, they are limited by zooplanktivorous fish which compete with the ctenophores for food. In contrast, in the Black Sea region, no obvious predators of _M. leidyi_ were present during the decade after its introduction when the ctenophore populations flourished. Zooplanktivorous fish populations had already been severely reduced by over-fishing in the Black Sea prior to the ctenophore outbreak. Thus, reduced populations of potential predators and competitors for food enabled the _M. leidyi_ populations to grow enormously in the new habitat. In Chesapeake Bay, _M. leidyi_ also consumes substantial amounts of zooplankton daily, but may only reduce zooplankton populations significantly when its own predators are rare. _M. leidyi_ is an important predator of fish eggs in both locations. Purcell et al. (2001) concluded that the enormous impact of _Mnemiopsis_ on the Black Sea ecosystem occurred because of the shortage of predators and competitors in the late 1980s and early 1990s. In Figure 1, a conceptual diagram of trophic effects of invasives, _M. leidyi_ is used as an example of a species that is an effective consumer, and lacks predators.

Subsequent accidental introduction of another comb jelly _Beroe ovata_ in the Black Sea resulted in a decline in _M. leidyi_ because _B. ovata_ was a predator on the smaller comb jelly. Shiganova et al. (2001) calculated that the measured population of _B. ovata_ ingested up to 10% of the _M. leidyi_ population daily. A marked decrease in _M. leidyi_ density was recorded along with increased abundance of zooplankton (about 5-fold) and ichthyoplankton (about 20-fold) compared with years
WEIS JS: Invasion and predation in aquatic ecosystems

Fig. 1A  Conceptual diagram of simplified aquatic food web, prior to invader

Fig. 1B  Conceptual diagram of altered food web after arrival of species that is an effective consumer and lacks a predator, using *Mnemiopsis leidyi* as the example

Zooplankton and all fish populations have decreased, while phytoplankton have increased

after the *M. leidyi* invasion but before the *B. ovata* invasion. The *B. ovata* population underwent an initial explosion until the numbers of both ctenophores stabilized. Nevertheless, both *Mnemiopsis leidyi* and *Beroe ovata* remain today in the Black Sea. Currently intentional introduction of *B. ovata* is suggested for biological control of *M. leidyi* in the Caspian.

Invasive fish species in the Pacific Northwest pose a threat to native salmon by predation. Sanderson et al. (2009) identified a number of nonindigenous freshwater fishes – channel catfish *Ictalurus punctatus*, black and white crappie (*Pomoxis nigromaculatus* and *P. annularis*), largemouth bass *Micropterus salmoides*, smallmouth bass *Micropterus dolomieu*, walleye *Sander vitreus*, and yellow perch *Perca flavescens*—that were consuming hundreds of thousands to millions of endangered juvenile salmon at just a few sites. Salmon constituted a large fraction of the diet of some of these in-
Invasive species. This predation by invasive species appears to be a major source of salmon mortality, comparable to better-known threats such as fishing, hatcheries, dams, and habitat alteration.

During the summer of 2002, exotic fish called the northern snakehead \textit{Channa argus} were found in a pond in Maryland, near Washington, D.C. The potential impact was considered so damaging that the event made national headlines. By the time the fish were eradicated from the pond, they appeared in the Potomac River and established a population. The northern snakehead is a voracious predator with no natural enemies. Most of their diet is other fish, though they also eat crustaceans, insects, and plants. They can live at a wide variety of temperatures and in muddy or vegetated ponds, swamps, and slow-moving streams. They can breathe air and survive up to four days out of water, which enables them to travel over land to new bodies of water by wriggling over the ground, allowing them to disperse widely. Reproducing populations have now been discovered in Maryland, California, and Florida. Scientists are concerned that established populations will have disastrous consequences for their new habitat. Landis et al. (2011) found that growth of Potomac River fish was lower than for fish from China, Russia, and Uzbekistan (its native range). This is different than some other invasive species that become larger in their new location than in their native range. Although overall growth was lower than in other populations, these fish demonstrated plasticity in timing of reproduction and rapid larval growth, which likely contribute to the success of the species in its new environment.

The rainbow trout \textit{Oncorhynchus mykiss} has been introduced for food or sport in over forty countries. Salmonid invasions are often driven by repeated authorized introductions of large numbers of fish, escapes from fish culture, and illegal introductions by anglers. Rainbow trout have spread throughout the world and are included among the world's worst invasive species (Fausch, 2007). Invading salmonids can have both direct effects on native salmonids and other fishes through biological interactions (i.e., predation, competition), and indirect effects by fragmenting their habitat and isolating native populations. In addition, these invaders can alter entire aquatic food webs through cascading effects. Research has shown that they can displace native trout and can alter the aquatic invertebrate community, to the detriment of other fish species. They are also a threat to various species of frogs, which are already in decline throughout the world. Introduced trout in California have diminished the distribution and abundance of a native ranid frog, \textit{Rana (=Lithobates) cascadae}. This is primarily the result of predation on frog larvae. However, trout also feed on larval aquatic insects and compete for food with the declining native amphibian (Joseph et al., 2011). Their impact on native fish seems to be greatest in places that never had trout (e.g., Australia and New Zealand). In Southern Europe, Australia, and South America, they have had serious negative impacts on native freshwater fish by eating them, outcompeting, transmitting diseases, or hybridizing with closely related species (Crowl et al., 2011). Hitt et al. (2003) found much hybridization between native westslope cutthroat trout \textit{Oncorhynchus clarki lewisi} and nonnative rainbow trout \textit{O. mykiss} in streams of the Flathead River system in Montana. Seiler and Keeley (2007) found that the introduced rainbow trout and their hybrids with cutthroat trout have higher sustained swimming stamina than native cutthroat trout, and thus are likely to be better predators and better at avoiding predation than the native species.

Red lionfish \textit{Pterois volitans} a venomous species from the western Pacific Ocean, have been found in the past decade along the Atlantic Coast of the Americas from the Carolinas south into the Caribbean. Lionfish are naturally found in the Pacific and Indian Oceans, but they appeared in the Atlantic in the 1990s and have now spread throughout the Caribbean and into the Gulf of Mexico. They were probably introduced in the early 1990s, perhaps escaping from Florida tanks during flooding from Hurricane Andrew in 1992. They are found from shallow mangrove areas to nearly 1000 feet deep. They tolerate temperatures as low as 16 °C, so they can probably survive year-round as far north as North Carolina and have been found even further north along the Atlantic Coast. It is likely with rising temperatures they will become established further north. They compete with local fish for space and food (including smaller fish that they eat). They are solitary ambush-predators that use their fan-like pectoral fans to herd or corner prey against corals or ledges, then consume them whole in a single strike. They devour juveniles of many important commercial species, like snappers, groupers, and shrimp. Albins and Hixon (2008) found lionfish caused significant reductions in the recruitment of native fishes by an average of 79% over the 5 wk duration of the experiment. This strong effect on a key life stage of coral-reef fishes suggests that invasive lionfish are already having substantial negative impacts on Atlantic coral reefs. Morris and Akins (2009) found
that twenty-one families and 41 species of teleosts were represented in the diet of lionfish in the Bahamas.

A lionfish’s stomach can expand to 30 times its normal size. This ability and its voracious appetite make it an effective invasive predator. Côté and Maljkovi (2010) estimated rates of predation by lionfish from field observations on natural reefs in the Bahamas. Lionfish were active during daylight hours and were observed hunting about 20 reef fish species in at least 9 families. They consumed native fish at an average rate of over one kill per hour on clear days and over two kills per hour on overcast days, higher than its predation rate in its native range. Barbour et al. (2010) noted that in the Western Atlantic this top predator occurs at higher densities and forages more successfully than in its native range. Lacking significant predators as an adult, it reduces reef fish recruitment. They compared its population size-structure and stomach contents in mangroves vs coral reefs in the Bahamas and found that in each habitat, >80% of lionfish stomachs contained prey with similar weight and similar prey items. This demonstrates that lionfish colonize and feed in mangrove habitat, an important nursery area for reef fishes.

On the West Coast of North America, the green crab C. maenas is a predator of the native crab Hemigrapsus oregonensis, which showed 5-fold to 10-fold declines within three years of the arrival of green crabs. Field and laboratory experiments indicated that green crab predation caused these declines (Grosholz et al., 2000). The green crab also preferentially preys on native clams in the genus Natricola (Grosholz, 2005) along the Pacific coast. The major decline of these clams following the green crab invasion has allowed an exotic clam Gemma gemma, which had been present in low numbers, to increase their population and become invasive. This phenomenon was referred to as an “invasion meltdown,” in which invasion by one exotic species facilitates subsequent invasions by other species. The “invasion meltdown” model posits that ecosystems become more easily invaded as the cumulative number of species introductions increases, and that facilitative interactions can exacerbate the impact of invaders (Ricciardi, 2001).

In a shelter experiment, in which a refuge to hide was provided in the experimental tank, invasive green crabs were paired with juvenile American lobsters H. americanus. Using crabs of 53–76 mm carapace width and lobsters of 28–57 mm carapace length, Rossong et al. (2006) found that green crabs were able to capture and consume lobsters in 6 of 11 trials. The lobsters that survived spent more time in the shelter. There was no clear relationship between shelter use and size of the lobster. Contrary to expectations, the lobsters that were larger in relation to the green crabs suffered a higher rate of predation, which authors believed to be due to more conspicuous activity and less use of the shelter. The authors concluded that green crabs have the potential to negatively impact native juvenile lobsters by both competition and predation.

Non-lethal negative effects of predatory invaders have also been noted. In response to the invasive cladoceran Bythotrephes longimanus, daphnids move deeper in the water column to avoid predation, but this reduces their growth rate. In the presence of Bythotrephes longimanus kairomones, daphnids migrated vertically, occupying a middle region by night and a low, cold region during the day (Pangle and Peacor, 2006). Over a 4-day experiment, the vertical migration induced by B. longimanus caused a 36% reduction in the somatic growth rate of daphnids, a level that is sufficient to have an effect on their population growth rate. Concentrations of B. longimanus kairomones in water taken directly from the field (Lake Michigan) were high enough to induce behavioral shifts that led to these large reductions in somatic growth rate.

2 Predator Avoidance

One reason for the success of some invasive species is the absence of predators in the new environment. In addition, they may be more effective in avoiding predators than some native species. The exotic crayfish Oronectes rusticus had more effective antipredator behavior against fish than the native crayfish O. virilis. While the latter swims away and is easily captured by the fish, the former approaches fish aggressively with claws extended and generally escapes the predators (Garvey et al., 1994). Gherardi et al. (2011) studied the invasive North American crayfish Procambarus clarkia to investigate the relative effectiveness of odors emitted by fish predators compared with conspecific alarm odor. They studied introduced populations of P. clarkii in two sites with different fish assemblages. Crayfish from both populations responded with a greater reduction in feeding to conspecific alarm odor than to predator odors. P. clarkii seems to perceive a general fish odor that alerts it to possible predation risk. Where they coexist with fish, crayfish become able to distinguish among species, adjusting the intensity of their response to the risk of predation. These results indicate a high capacity for learning and predator recognition in this very successful in-
The invasive amphipod *Gammarus roeseli* was compared with the native *G. pulex* for susceptibility to fish predators. Brown trout *Salmo trutta* preyed more on *G. pulex*, although there was no significant difference observed in antipredator behavior between the two amphipod species. *G. roeseli* spent more time under shelters, but this did not appear to be important for differential predation. Rather, the presence of spines on *G. roeseli* appeared to be responsible for the differential predation (Bollache et al., 2006), a morphological rather than behavioral trait.

The spiny water flea *Bythotrephes* is a food source for many fish species (Bur et al., 1986; Makarewitz and Jones, 1990; Branstrator and Lehman, 1996), but their spines probably reduce predation on them compared with other water flea species. Less effective anti-predator behavior by green crabs was found to facilitate their replacement by another invasive species, the Asian shore crab *H. sanguineus* along the East coast of the U. S. While juvenile shore crabs tend to move away from larger crabs and escape attack, juvenile green crabs tend to remain inactive and rely on protective coloration, which is less effective against crab predators that are tactile hunters (Lohrer and Whitlatch, 2002). MacDonald et al. (2007) compared the shell strength of the carapaces of green crabs and Asian shore crabs vs size-matched native blue crabs *Callinectes sapidus*. Green crabs and Asian shore crabs had thicker, heavier carapaces that did not break as easily as those of blue crabs, implying that this morphological, rather than behavioral defense would make them less likely to be preyed upon by larger predatory animals.

In the Atlantic and Caribbean, lionfish have no natural predators. With a plume of feathery spines that contain a potent toxin, they are resistant to predators and are a menace to divers and anglers who may come in contact and be stung. The sting is extremely painful, but generally not life-threatening. They have become extremely successful and abundant in this new habitat, where they eat large numbers of native fish and have reduced their populations.

### 3 Management Option: Adding Another Trophic Level, Human Beings

It is obvious that the best and most cost-effective management for invasive species is prevention. It is easier and cheaper to prevent an invasion than to cope with invasive species after they are established. If prevention fails, management should focus on early detection and response – this requires monitoring and early detection of incoming organisms. Rapid response can lead to successful eradication. It is more feasible to eliminate a small number of organisms than an established population. Monitoring efforts and public awareness are essential to its success. However, if this is not successful and populations of invasive species become established, management options are limited and costly (Carlton, 2001). Eradication programs or programs to slow the spread of the invasion may be possible. Such programs include quarantining invaded habitats and education to prevent people from moving animals away from the invaded site. If species become established and abundant, the remaining management options involve adaptation, namely adjusting human behavior (Carlton, 2001).

Many invasive species benefit from the absence of predators in their new environment. The idea of humans eating invasive species has been suggested as a way to compensate for this predator release and control the spread of invasive species, although it probably cannot eliminate them entirely. Overfishing has led to the near extinction of many species, but the traits of invasive species tend to be different from those of species susceptible to overfishing, since invaders generally have high growth rates, mature early, and have wide dietary breadth and environmental tolerances while the vulnerable species tend to be the opposite. Direct harvest of abundant invaders is not likely to remove them, but it can reduce their numbers, and therefore their ecological and economic impacts.

Recognizing the near impossibility of eliminating an established invasive species, some biologists and residents of affected regions are encouraging people to catch and eat them. Since successful invaders have few natural predators, humans can fill that role. Philip Rainbow of London’s Natural History museum has called on commercial fishermen to target invasive Chinese mitten crabs in England. “The Chinese love them, especially when they’re full of gonads during the breeding season. The carapace of a large one measures eight centimeters (about three inches) across — that’s a decent-sized meal.” An “Invasive Species Cookbook” (Franke, 2007) is available (“if you can’t beat ‘em, eat ‘em”); the idea of the cook book is to increase interest in the issue of invasive species and to reduce their populations by harvesting them as food sources.

Nutria *Myocaster coypus* are large rodents that were brought from South America into salt marshes in southern states from Maryland to the Gulf of Mexico for their...
Weis JS: Invasion and predation in aquatic ecosystems

Attractive pelts. When the market for fur diminished, these herbivores that consume huge quantities of marsh vegetation, became pests, destroying many acres of marshes. Attempts have been made to establish them as a food for people as a way to control their population explosion. The Invasive Species Cook Book has a recipe for "heart-healthy crock-pot nutria" which is supposed to taste like turkey.

This approach has been widely adopted for lionfish in the Atlantic and Caribbean. Efforts are underway to educate anglers about how to catch, clean, and eat them safely. A tournament was organized in Florida Keys in Sept. 2010 in which 100 divers collected 534 lionfish during the first tournament dedicated to reducing the population of this invasive species. A tournament in Key Largo, organized by REEF (Reef Environmental Education Foundation) and the Florida Keys National Marine Sanctuary, attracted 27 teams that competed to catch the most, largest and smallest lionfish. The Shifting Baselines Ocean Media Campaign put out a public service announcement about lionfish. It presents a humorous vision of the future – a Caribbean restaurant in which the only fish left to serve are lionfish. To view the PSA (Public Service Announcement), see a collection of recipes, and to learn more about the lionfish invasion, one can visit the lionfish PSA website at www.deathtolionfish.org and facebook.com/deathtolionfish.

The federal government and environmental groups have supported and joined in the efforts to eat lionfish. NOAA (National Oceanic and Atmospheric Administration) and environmental groups like REEF have launched EAT LIONFISH campaigns, since in places where people actively remove lionfish, populations are significantly reduced. Developing the food-fishery has the potential to help coral reefs and other marine habitats. In the Bahamas, Maurice White has created Lionfishhunter.com, which contains a large collection of lionfish recipes. He also has video showing how to snip the fins while avoiding getting stung.

Professional tasters have ranked the fish high for taste and texture, and a pilot project which brought the fish to New York and Chicago restaurants proved very successful. The eating of lionfish has become a grass-roots cause in some areas, and several restaurants in the US and the Caribbean are serving it whenever they can. NOAA’s National Centers for Coastal Ocean Science have conducted extensive lionfish research and have conceived an “Eat Lionfish” campaign that builds upon the original New York/Chicago pilot project. A media campaign will include major print outlets and also television producers for The Food Network and The Travel Channel.

In an attempt to recruit additional predators for lionfish, divers in Roatan Marine Park in Honduras are attempting to train sharks to eat them. Local dive masters familiar with the sharks are trying to encourage them to eat invasive lionfish (National Geographic, 2011). If the sharks perceive lionfish as prey, eventually the lionfish may be controlled.

There are no existing regulatory impediments to selling lionfish commercially in the US. Currently there are no federal regulations concerning the landing and sales of lionfish; however, state regulations concerning diving and commercial licensing do apply. Similarly, there are no specific regulations concerning the importation of lionfish for human consumption into the US except those associated with all species, such as safe handling requirements, etc. The FDA has agreed to add the red lionfish to the list of species approved for commercial sale. However, for some other species, the idea of developing a fishery and eating them has been more controversial and difficult.

Asian carps are voracious eaters that can grow up to six feet and 110 pounds. These non-native species were first imported and used in Louisiana catfish farms in the 1970s to control snails and vegetation. In the mid-1990s, flooding allowed the Asian carp to escape from fish farms. They have spread to most of the Mississippi River watershed and the Missouri River, devastating food resources and habitats of native and sport fish populations. The bighead carp Hypophthalmichthys nobilis, along with the other species of Asian carp, now account for the majority of fish in the Missouri River. They are threatening to invade the Great Lakes. They thrive in the Mississippi and Illinois rivers, and because DNA traces and individual fish have been found near Lake Michigan, concerns are high regarding their potentially devastating impact on the Great Lakes.

An Asian Carp Marketing Summit in Illinois was convened in the fall of 2010 to identify opportunities to

market the species as a way to reduce their numbers, and recommended that eating bighead and silver carp may be feasible. Representatives from restaurants, commercial fishing, processing businesses, government agencies, and academic institutions attended the summit and agreed that Asian carp fillets marketed to restaurants and retailers could provide a financial incentive for extensive harvesting of these fish. Because they are filter feeders, bighead *H. nobilis* and silver carp, *H. malcolmii*, are generally low in contaminants, making them healthy to eat. They are low in fat and taste like cod. They also recommended that the large numbers of harvested fish be exported to Asian markets, where these species are popular food fish, and that carp by-products be converted into pet food to eliminate waste and maximize efficiency and profit (ACES News [http://www.aces.uiuc.edu/news]). However, the U.S. Fish and Wildlife Service has published a rule that prohibits the importation and transportation of bighead carp. The efforts recommended by the marketing summit would appear to be an infraction of the Fish and Wildlife rule prohibiting transportation of the species.

There is also a group of grass-roots activists. A group of environmentally conscious “foodies” call themselves “invasivores”. A website called invasivore.org has a goal of promoting awareness of invasive species by encouraging people to eat them. They post recipes and information on finding and preparing a variety of edible invasive species. The Heaven City Restaurant near Mukwonago, WI had an “invasivore” dinner in February 2011, where they served carp cakes, smoked carp steak, and carp Napoleon, featuring invasive Asian carp from the Illinois River. This probably also was an infraction of the Fish and Wildlife rule.

Some biologists and environmental groups warn that trying to get rid of invasive species by eating them is a risky approach. They acknowledge that human predation could slow the Asian carp’s progress toward the Great Lakes and buy valuable time for developing a permanent solution, but they are concerned that creating a taste for Asian carp (or other invasives) in the U.S could promote the development of a sustainable fishery instead of eliminating the fish, which would threaten additional aquatic systems. On the other hand, expanding the commercial Asian carp export market to China is included in the Obama administration’s “2011 Asian Carp Control Strategy Framework,” a plan to prevent the carp from infesting the Great Lakes. Illinois Gov. Pat Quinn announced a program to boost commercial fishing for Asian carp on the Illinois River to sell to China. The state contracted with a Chinese meat processing company and an Illinois commercial fishing company to harvest 30 million pounds.

However, in addition to the U.S. Fish and Wildlife rule regarding Asian carp, there are state regulations, designed to reduce the spread of exotic species, which would appear to prevent the development of fisheries for them. For example, in California, it is illegal to import, transport, or possess live Chinese mitten crabs (Title 14, Section 671 of the California Code of Regulations). However, it is possible to fish for them with a valid sport fishing license. In some areas you can fish only by hook and line and there are no bag or size limits, in other areas you can use traps as well, but the limit is 35 per day. (It is confusing that they would set a limit on a species they would rather exterminate.) These regulations require that fishers immediately kill whatever crabs they catch. Similarly, New York State Fish and Wildlife regulations prohibit releasing Chinese mitten crab into waters of New York State, but also prohibit their possession, importation, transportation, purchase or sale, or offer of purchase or sale, whether dead or live. This regulation requires any Chinese mitten crab to be destroyed unless lawfully held under a license or scientific collector’s permit. Maryland regulations prohibit the possession of live snakehead fish. In North Carolina, the Wildlife Resources Commission banned the transport, possession, purchase or sale, and release of all snakeheads. These regulations would allow someone that caught it to eat it, but they would have to kill it immediately. This sort of regulation makes sense for a species that has not undergone a huge population increase, but would appear to preclude development of a fishery for a species that has become abundant. Opponents of developing a fishery argue that creating demand for these species goes against the goal of eradicating them, so it is better to eradicate them another way.

Other species that potentially could be included in this top-down management approach to invasive species are other species of crabs and fishes, as well as mussels and whelks that are tasty seafood and frequently components of the human diet. There are, of course, limits to what can be accomplished by eating invasive species. Eating invasive species will not solve the problem by eradicating them, but it will lessen their impacts and at the same time provide a new food source for this hungry world, in which many traditional food fishes are in short supply because of overfishing, habitat loss and pollution.
References


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