What have we learned from aquatic invasions? Ten generalizations

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We can learn much from invasions. A growing number of case studies worldwide have revealed remarkable patterns and generalizations that have both theoretical and applied importance. Some of these are summarized below.

1. Rates of discovery of invaders are increasing worldwide.

The best estimate we have for the rate of invasion in an area is the rate at which invaders are discovered. We are finding more new invaders in our lakes, rivers and estuaries than ever before. In many systems, the cumulative number of species discovered has risen exponentially over the past century. Multiple factors could account for this pattern: (i) we could be getting better at detecting new species; (ii) time lags between introduction and subsequent detection may generate statistical artifacts that create the appearance of increasing rates of invasion; or (iii) the systems are becoming increasingly susceptible to invasion, largely because of the proliferation of human vectors. Since the early 19th century the Great Lakes have been invaded by at least 180 species, most of which were discovered after the opening of the St. Lawrence Seaway in 1959. One new invader is recorded every 7 months, on average. As far as we know, none of the 180+ exotic species that have successfully invaded has subsequently disappeared. So, rather than replace each other, exotic species are rapidly accumulating in the Great Lakes.

2.   Many introductions fail to establish sustainable populations.

In spite of the growing rates of invasion, many species that have been introduced to the Great Lakes and elsewhere have failed to invade – that is, they did not establish persistent populations. In most cases, this is because environmental conditions are inhospitable to them. For example, European flounder and mitten crabs have been released multiple times in ballast water from transoceanic vessels, but apparently cannot reproduce in the low-salinity waters of the Great Lakes. Tropical aquarium fishes (e.g. piranha) have been dumped repeatedly by pet owners into waters throughout the basin, but cannot survive winter temperatures; by contrast, goldfish have managed to do it. Another common cause of failed invasions is that there are too few individuals introduced to build a sustainable population.

3.   Propagule pressure is the most consistent predictor of establishment success.

Propagule pressure is a term that refers to the intensity of introduction – the number of individuals released and the number of release events. Species that are introduced more frequently and in greater numbers tend to be successful invaders. Small numbers of individuals are more likely to be wiped out because they are vulnerable to small-scale disturbances or sudden environmental changes (i.e. bad luck), or because they failed to

locate mates. Frequent releases increase the probability that sufficient numbers of a species will be introduced at a time when conditions are optimal. Therefore, unless the species can reproduce asexually, a single release of a few individuals is not likely to result in an invasion.

4.   All aquatic systems are invasible, but some are more invasible than others.

Regardless of how pristine or productive a system is, or how many native species are present, all aquatic systems are invasible if a sufficiently large number of species are given opportunities to invade. However, areas subject to intense human activity or disturbance tend to be invaded more often. For example, studies have shown that impounded lakes are invaded more often than natural lakes, and are also more likely to support multiple invaders.

5.   The impacts of exotic species are context dependent.

The impacts of an exotic species may vary greatly across its invaded range (for example, an invader may cause the extirpation of a native species at one site, but coexist with it at other sites). This is because the ecological (and economic) effects of a species are a function of its abundance, which varies in space and time in response to local environmental conditions. The context-dependent nature of invasion is the greatest impediment to risk assessment.

6.   The potential impact of an exotic species is not correlated with its invasiveness.

The term "invasive" has taken on a variety of different meanings and has been used to describe, for example, (i) any introduced exotic species; (ii) exotic species that spread rapidly in a new region; or (iii) exotic species that exert harmful environmental impacts, particularly on native species. The second definition in various forms is more commonly used by ecologists (*invasiveness* often refers to a species' ability to rapidly colonize an area), while the third definition is often used in policy papers and legislation. But these definitions are not generally compatible. Exotic species can cause strong local impacts even if they are poor colonizers; there is no correlation between the magnitude of their impact at a given site and their previous establishment success or rate of spread.

7.   The introduction of an uncontrolled generalist consumer often has cascading effects in aquatic food webs.

Many case studies have shown that the greatest disruptions to food webs result from the introduction of a prolific species that has a broad diet and avoids significant predation from resident species. Examples include the introduction of (i) top predators into lakes; (ii) mysid shrimp into lakes lacking planktivorous fishes adapted to feeding on them; and (iii) filter-feeding bivalves into lakes, rivers and estuaries. Such species can affect multiple trophic levels and the productivity of the system.

8.   The largest impacts are caused by species introduced to systems where no similar species exist.

An invader's impact is determined by the invaded system's evolutionary experience with similar species. High-impact invaders (i.e. those that displace native species) are more likely to be ecologically distinct from species already present in a system, because in such cases it is likely that they (i) will use resources differently from resident species; (ii) encounter naïve prey; and (iii) not encounter enemies that can efficiently compete with or prey upon them. For example, the introduction of piscivores into historically fishless lakes in alpine regions has had strong negative effects on native amphibians. Similarly, North American freshwater communities have no evolutionary experience with dominant fouling organisms, which explains the severe impact that zebra mussels have had on our native freshwater mussels.

9.   The invasion history of a species is the best predictor of its invasiveness and impact.

The invasion history of a species, if sufficiently documented, may provide a valuable guide for predicting the ecological consequences of its introduction into a new environment. The magnitude of an impact is often quite variable, but the types and direction of impacts might be consistent (and thus predictable) across sites; for example, the zebra mussel's impacts on benthic invertebrates exhibit predictable patterns across a range of invaded habitats and geographic regions. Therefore, managers might be able to use invasion history to prioritize invasion threats. However, there are some major caveats: (i) most species do not have a well documented history of impacts; (ii) impacts often vary greatly across sites (see generalization #5); and (iii) invaders can modify each other's invasion success and impact (see generalization #10).

To summarize previous generalizations, the most severe ecological impacts are caused by aquatic invaders that possess one or more of the following characteristics: 1) they have high rates of reproduction; 2) they are introduced to a new region where similar species do not exist; 3) they are often top predators or suspension feeders; 4) they can alter the availability of critical resources such as light, nutrients, or habitat space; and 5) they have a history of similar impacts in other invaded regions.

10. Synergistic effects may result from the interactions of multiple invaders.

Invasions are generally treated as independent events, but a growing number of case studies reveal that introduced species can interact in synergistic ways. Rather than compete with each other, these species can sometimes facilitate each other. For example, when the sea lamprey invaded the upper Great Lakes it caused severe declines in the abundance of lake trout, creating a predator-free environment that promoted the subsequent establishment and population explosion of the alewife. Another example involves the zebra mussel, which stimulates the growth of plants (including exotic weeds like Eurasian milfoil) by filtering out suspended material and thus increasing the light transparency of a lake. In return, the plants provide substrate for young settling mussels.

Not only can one exotic species promote the establishment of another, it can also enhance the other's impact, leading to unpredictable ecological disruptions. Every year since 1999, thousands of fish-eating waterfowl such as loons, mergansers and gulls have died in Lake Erie and Lake Ontario, due to a rare type of avian botulism. It is believed that botulism bacteria (*Clostridium botulinum*) proliferate in the bottom sediments because of the activity of zebra and quagga mussels, whose filtration activities stimulate excessive plant growth. The subsequent decomposition of dead plant material at warm temperatures strips the bottom waters of oxygen, creating conditions in which the bacteria thrive. The mussels filter and accumulate the bacteria, and transmit it to their principal predator – the round goby. In turn, the gobies transfer the bacterial toxin to fish-eating birds. Without either the exotic mussels or the gobies, such a massive outbreak probably would not have occurred. Synergistic disruptions should become more frequent with increasing numbers of invaders; if so, even a partial reduction in the rate of invasion is likely to yield disproportionate benefits for ecosystem management.