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BIOLOGICAL INVASIONS OF FRESH WATER: EMPIRICAL RULES AND ASSEMBLY THEORY

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Abstract

Because the integrity of aquatic ecosystems is being challenged worldwide by invading species, there is a growing need to understand the invasion process and to predict the success and effects of invading species. Case histories of fish invasions in streams, lakes, and estuaries indicate that invading species and systems being invaded interact in idiosyncratic ways that are often hard to predict, largely because of the role of environmental variability in determining the outcomes of invasions. We nevertheless present a conceptual model of aquatic invasions and a dozen empirically-derived rules that seem to govern most aquatic invasions. While these rules are limited in their usefulness, they do seem to have more predictive value than rules derived from community assembly theory. Copyright © 1996 Elsevier Science Limited

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INTRODUCTION

Freshwater and estuarine biotas are changing rapidly worldwide (Moyle & Leidy, 1992; Allan & Flecker, 1993). Human-mediated invasions of aquatic organisms are associated with these changes, which commonly include extirpation of native organisms. Among the more spectacular cases are the elimination of 200+ species of haplochromine cichlids following the introduction of Nile perch *Lates nilotica* into Lake Victoria, Africa, the alteration of the Laurentian Great Lakes ecosystems by invading sea lamprey *Petromyzon marinus*, zebra mussel *Dreissena polymorpha* and other species, and the complete domination of lowland rivers in the Western United States by non-native fish and invertebrates (Moyle, 1986). On the other hand, there are numerous documented instances where invading species have become established without extinctions of native organisms and seem to have become integrated into the local biota. It is clear that our ability to predict the effects of biotic invasions into aquatic systems is still limited (Li & Moyle, 1981; Lodge, 1993*a*,*b*). The general result of deliberate introductions has been termed the 'Frankenstein Effect' because so many well-intentioned introductions have had unexpected consequences, usually negative (Moyle *et al.*, 1986). The need to increase our ability to predict the consequences of invasions and to understand invasion processes has been emphasized by the enormous economic and social costs of some recent invasions, the growing interest in halting biodiversity loss, and the increased difficulty of managing ecosystems subjected to repeated invasions.

Recently, generalizations about aquatic invasions have been coming from two main approaches, analyses of case histories of individual invasions (e.g. Nichols *et al.*, 1990; Moyle & Light, 1996) and applications of recent developments in ecological theory, especially community assembly theory (Pimm, 1989; Case, 1991; Townsend, 1991; Lodge, 1993*a*,*b*). In this paper, we consider both approaches. After providing a brief introduction to community assembly theory, we present a conceptual model of invasions. We then review a series of case histories of biological invasions for which we have some idea of community-level effects of the invasions. Based in part on these examples, we propose a series of empirical rules for use in predicting the effects of fish invasions into freshwater environments. Finally, we ask how useful the predictions of assembly theory are to the study of aquatic invasions.

COMMUNITY ASSEMBLY THEORY

Community assembly theory stresses process and history and seeks explanation for community patterns in the context of dynamic rather than static (equilibrium) community structure. It holds that all present communities were built up by a process of sequential invasions and extinctions, a process which is continuous. This places the study of present-day invasions, human mediated or otherwise, into the larger context of community development, i.e. it focuses on the interaction between the invader and the target community (Lodge, 1993*b*). The discovery of assembly rules could therefore serve

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to put community ecology on a more predictive basis (Nee, 1990; Keddy, 1992). Community assembly has been explored through examination of natural patterns (Diamond, 1975), laboratory and field experimentation (Alford & Wilbur, 1985; Wilbur & Alford, 1985; Gilpin *et al.*, 1986; Robinson & Dickerson, 1987; Robinson & Edgemon, 1988; Drake, 1991), and computer simulation (Post & Pimm, 1983; Drake, 1990*b*; Strange, 1995). A number of generalizations relevant to invasion biology have emerged from this work (Case, 1991). These include:

(1) invasion success decreases with species richness, supporting Elton's (1958) hypothesis, and the amount of time the community has been accumulating species;
(2) there is a priority effect for residents: invasion, even by a superior competitor, is difficult at low numbers of invaders;
(3) invasion resistance increases with the strength of community interaction coefficients;
(4) the final community state depends on invasion order, thus multiple stable states are possible from a single species pool;
(5) communities can shift among alternative, predictable states as invasions and extinctions proceed.

Assembly theory, like much of the literature on biotic invasions (Li & Moyle, 1981; Lodge, 1993*a*,*b*), is concerned primarily with the biological characteristics of the invading species and of the ecosystems being invaded, on the assumption that competition and predation are the major processes determining the outcome of an invasion. Most simulations assume that all members of the species pool are physiologically capable of persisting in the environment (Post & Pimm, 1983; Drake, 1990*b*), while laboratory studies hold the physical environment constant in order to focus on biotic interactions (Robinson & Dickerson, 1987; Drake, 1991). Keddy (1992) depicts the invasion-assembly process as proceeding by a series of deletion rules, with the first filter determined by the environment and subsequent ones by competition, an approach which ignores the interaction between biotic and abiotic factors. Although Drake (1990*b*) suggests that environmental disturbance can reset assembly trajectories, this effect is not explored in either modeling or experimental studies (but see Strange, 1995). We will argue later in this paper that this is the area where assembly theory needs modifying to reflect the reality of biological invasions. Our experience with invading fishes in California streams and estuaries suggests that if abiotic conditions are appropriate for an invader, it is likely to become established, regardless of the biota already present; conversely, invasion failures are best attributed to failure to adapt to abiotic conditions rather than to biotic resistance on the part of the recipient community (Baltz & Moyle, 1993; Moyle & Light, 1996).

A CONCEPTUAL MODEL OF BIOLOGICAL INVASIONS

Most invasion biology is based on a common conceptual model in which the invasion process is depicted as having three basic phases: arrival, establishment, and integration (Vermeij, this issue; Fig. 1). Most invasion studies focus on one or at most two of these phases and ours is no exception, focusing on the establishment and integration of invading species in aquatic communities. Our conceptual model borrows from assembly theory the idea of a community constructed over time from a pool of potential invaders. This species pool has been greatly expanded for most present communities by human activities, both through deliberate introductions or the establishment of new dispersal routes (e.g. Carlton, 1985). Each newly arriving species meets with what Elton (1958) termed 'ecological resistance' to its establishment, which is here considered to consist of three interactive elements: environmental, biotic, and demographic resistance. Assembly theory has emphasized the role of biotic resistance (mainly predation and competition) in the success and failure of invasions (Case, 1991). Demographic factors (e.g. reproductive traits) influence the invasion success of parasites (A. P. Dobson, pers. comm.), social insects (Moller, this issue),

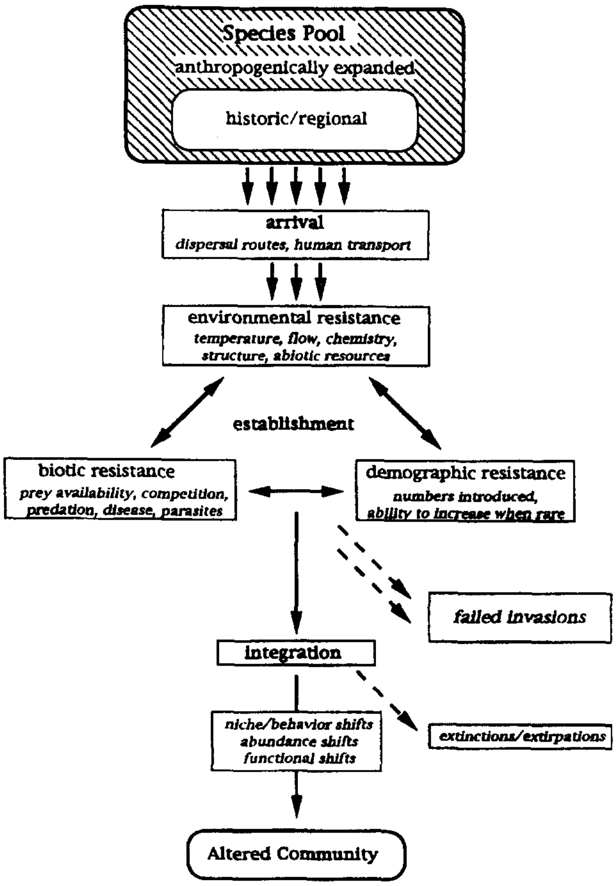

Fig. 1. A conceptual model of invasions, which assumes three basic stages: arrival, establishment, and integration.

and pines (Rejmánek & Richardson, this issue), and are often listed among traits of successful invaders (e.g. *r* vs *K* strategists, Lodge, 1993*a*,*b*). However, we view environmental factors as the most critical in determining the outcome of invasions, at least in the aquatic systems examined here, although clearly the success or failure of most invasions depends on the interaction of all three elements (Lodge, 1993*a*,*b*).

The integration stage of an invasion involves changes in the recipient ecosystem during and following a successful invasion. As indicated by our examples from freshwater systems, few successful invasions seem to create major changes in the receiving systems, although this may be in part an artifact of the scale of most investigations. Certainly only a small percentage of invaders become serious pests to humans (Williamson & Fitter, this issue), or result in global extinctions. However, some changes may consist of more subtle effects, such as local extirpations, behavioral and evolutionary changes of native species, and food web alterations (Power, 1990; Townsend, this issue) which are rarely investigated in detail.

CASE HISTORIES

The following case histories all are aquatic invasions that have been studied by the senior author in the past 10–15 years. They are consequently limited to fish invasions of streams in California and Sri Lanka and of a large California estuary. The invaded ecosystems we discuss represent a wide range of conditions but all have been altered physically or chemically by human activity to some degree. The case histories include (1) Eel River, California, (2) Deer Creek, California, (3) Martis Creek, California, (4) tropical streams, Sri Lanka, and (5) the Sacramento–San Joaquin estuary. Additional case histories dealing with invasions in lakes are presented by Moyle (1986), Craig (1992), Lodge (1993*b*) and Johnson (this issue).

Eel River

The Eel River is a large coastal drainage in northwestern California that has been continuously subjected to invasions by non-native fishes for the past 50 years. The ecology of the fishes of the drainage has been intensively studied in relation to the invasion of Sacramento squawfish *Ptychocheilus grandis*, a piscivorous cyprinid (Brown & Moyle, 1991; Brown *et al.*, 1994). The questions asked during these studies were (1) why have some invading species succeeded, while others have failed? and (2) what effects have squawfish and other successful invaders had on the riverine ecosystem?

The fish fauna of the Eel River has historically consisted principally of saltwater dispersant fishes, including large runs of anadromous salmonids *Oncorhynchus* spp., and Pacific lamprey *Lampetra tridentatus*. The only native freshwater dispersant species is the Sacramento sucker *Catostomus occidentalis*. Although the flow regimes of the river and its tributaries are largely unmodified, the drainage has been altered by human activity. There is a dam and reservoir in the headwaters of the main stem of the river (Pillsbury Reservoir). Much of the drainage has been heavily logged, resulting in large-scale erosion of the steep hillsides in the 1960s which in turn filled much of the stream bed with gravel and sediment. These factors have reduced populations of the native anadromous fishes. The drainage has been successfully invaded by one anadromous species (American shad *Alosa sapidissima*), three species of stream fishes native to neighboring drainages (Sacramento squawfish, California roach *Lavinia symmetricus*, speckled dace *Rhinichthys osculus*, and six species of fish from eastern North America. Of these ten species, only American shad, Sacramento squawfish, and California roach are abundant in the river itself (L. Brown & P. B. Moyle, unpubl. data). Speckled dace only recently (*c.* 1985) became established and their present distribution is limited. The remaining six species are largely confined to Pillsbury Reservoir, although individuals are flushed downstream nearly every spring and small populations become established in downstream pools, especially during periods of extended drought. Some of these populations have persisted for long periods of time, but it is not certain whether or not this results from reproduction or repeated invasion.

The reservoir fishes rarely persist outside the reservoir apparently because they cannot withstand the extremely high, turbid flows that follow winter rains, although lack of suitable habitat (aquatic plant beds) for larvae and juveniles may also play a role. In contrast, Sacramento squawfish and California roach, which are specifically adapted to the fluctuating conditions of California streams (Baltz & Moyle, 1993), have become widespread and abundant in the Eel River within 20 years of their introduction. American shad invaded the system naturally after being introduced into the Sacramento River in the 1870s; they have maintained runs that spawn in the lower river for over 100 years under conditions similar to those of their native streams on the East coast of North America (Moyle, 1976). The invasions of California roach and Sacramento squawfish may have been enhanced by the increase in the amount of shallow, warm water in the main river channels that followed massive erosion of logged hillsides. Interactions with the native fishes seem to have played little role in the success or failure of the various invasions although the native fish populations were depressed at the time of the invasions.

Once established, the two most successful (widespread) invaders, Sacramento squawfish and California roach, caused major changes to the river ecosystem. California roach, which became established around 1960, have acted as 'top-down' predators on the benthos, altering the benthic algae–larval insect community

(Power, 1990). Squawfish (introduced *c.* 1980), which prey on roach and other fishes, may reduce this effect by eliminating roach populations from pools, where the effect of roach on the benthos is especially strong (Power, 1992). Roach show a strong shift in microhabitat preference (to shallower water) in the presence of squawfish, as do other native fishes (Brown & Moyle, 1991). The result is an assemblage of fishes that is more strongly segregated in microhabitat use than the pre-squawfish assemblage (Brown & Moyle, 1991). The segregation seems to be more the result of the disappearance of most small fishes from the pool habitats, where there was great similarity in the use of space by all species, than the result of forced competitive interactions among the displaced fishes. Diets of the species, for example, still showed high overlap (L. Brown & P. Moyle, unpubl. data). In addition, behavioral studies indicate that the microhabitat shifts of some species (California roach, rainbow trout *O. mykiss*) are the result of active avoidance of large squawfish, while that of other species (threespine stickleback *Gasterosteus aculeatus*) is apparently the result of their elimination from pools by direct predation (L. Brown, pers. comm.).

In the Eel River proper, the only successful invaders were fishes adapted to the naturally variable hydrologic regime. The most human-modified habitat (the reservoir) contained the largest number of non-native species and the species least well adapted to the original riverine conditions. This example also indicates that an invaded assemblage can quickly adjust to invading species, including developing a more complex assemblage structure.

Deer Creek

In contrast to the Eel River, Deer Creek, in Tehama County, California, was chosen for study because most of the drainage is free of invading fish species. It is the largest unregulated tributary to the Sacramento River and contains intact native fish assemblages, providing a useful standard of comparison for regulated streams (Moyle & Baltz, 1985). Non-native fishes dominate the fish fauna in two limited areas: a highly disturbed (by grazing, fishing, and roads) meadow system in the upper drainage and the lowermost reach, which is strongly affected by diversion dams and agriculture. Invaders from the altered areas have been found in the natural sections of stream but there is no evidence of self-sustaining populations being established outside the altered sections. Baltz and Moyle (1993) concluded that invasions were primarily prevented by the creek's hydrologic regime (environmental resistance) and only secondarily, if at all, by interactions with the highly organized native fish assemblage (biotic resistance). In the upstream meadow system, exotic brown trout *Salmo trutta* apparently have been favored through a combination of selective fishing for native rainbow trout and the ability of the meadows to modify the effects of the hydrologic regime. The importance of fishing (= predation) in this interaction is indicated by the fact that selective fishing for brown trout has eliminated them from a similar meadow system in nearby Mill Creek, allowing rainbow trout to re-establish themselves (G. Sato, pers. comm.).

This example indicates, that under highly fluctuating natural conditions, well-established natural fish assemblages can maintain their integrity in the face of continuous invasions by non-native fishes. The non-native fishes persist only where the environment has been highly altered by human activity.

Martis Creek

Martis Creek is a small coldwater stream in the Sierra Nevada of California that supports an assemblage of seven fish species, including two non-native trout species, brown trout and rainbow trout. The two trout species have replaced the native cutthroat trout *O. clarki* that was once part of the assemblage (Moyle, 1976). Moyle and Vondracek (1985) found the fish assemblage to be persistent and highly structured, showing segregation by habitat, microhabitat, and diet. Following the completion of this study, the assemblage became almost completely dominated by brown trout and two of the native fishes became extremely rare (Strange *et al.*, 1992). The cause of the shift in assemblage composition has been tied to the timing of reproduction; the brown trout is a fall spawner, while the other species, including rainbow trout, are spring spawners. For several years, environmental conditions favored brown trout spawning but not that of the native species. Once favorable conditions for the native fishes returned, the large population of brown trout apparently continued to suppress the native fishes through predation (Strange *et al.*, 1992). Strange *et al.* (1992) predicted that the assemblage will shift back and forth between a structure dominated by brown trout and one dominated by native fishes, depending on the sequence of environmental conditions over a period of years. Indeed, recent sampling (1992, 1993, 1994) indicates that a shift back to native fishes is taking place (Strange, 1995). However, the brown trout have apparently extirpated Lahontan redside *Richardsonius egregius* from the stream through predation, so complete recovery of the native assemblage will depend on the redside reinvading from outside.

In the long run, brown trout may not be able to persist in Sierran streams like Martis Creek with natural hydrologic regimes; the fact that all the native fishes are spring spawners indicates strong selection pressure favoring this time of reproduction. This factor may also favor spring-spawning rainbow trout over brown trout in the streams. These two species can compete directly for space in streams which may accelerate replacement of one species by the other. However, in streams subject to heavy fishing, anglers remove mainly rainbow trout, thereby acting as selective predators and altering potential long-term outcomes of invasions of the two species (Strange, 1995).

This example indicates that outcomes of invasions of stream fish assemblages are dependent on favorable environmental conditions at the time of the invasion and only secondarily on interactions between invading and resident fishes. However, environmental fluctuations may serve to mediate the effects of the invasion, maintaining a more diverse assemblage than would occur under more constant conditions (e.g. streams regulated by dams).

Sri Lankan streams

The unregulated rainforest streams of southwestern Sri Lanka support a diverse assemblage of small endemic fishes that show a high degree of ecological segregation (Wikramanayake & Moyle, 1989). For zoogeographic reasons, some streams are relatively depauperate (nine vs 20 fish species), although the fishes present also live in the richer streams. Four species of fish from the species-rich streams were introduced (for conservation purposes) into several of the depauperate streams: a water column insect feeder, two benthic omnivores, and one benthic diatom feeder (Wikramanayake & Moyle, 1989; Wikramanayake, 1990). All four introductions were successful and the species became widespread in their new drainages within five years following the introductions. However, the three species with the most specialized habitat requirements were patchily distributed compared to the one less specialized species (Wikramanayake, 1990). For the most part, the new fish assemblages showed the same high degree of ecological segregation observed in the original species-rich assemblages and no major niche shifts of the native fishes were observed. However, in a stream that originally contained just two native species, two of the introduced species showed expanded niches and increased growth rates (Wikramanayake & Moyle, 1989).

The Sri Lanka studies suggest that under certain circumstances, invasions can have relatively small effects on the invaded community or at least on assemblages of similar taxa. The fact that none of the invaders were piscivorous and that piscivorous fishes were largely absent from the introduction areas may have contributed to the success and low impact of the invasions. The invaders were mainly herbivores or omnivores, so food was unlikely to be limiting, and neither the environment nor the species already present were novel to the invaders.

Sacramento–San Joaquin estuary

The Sacramento–San Joaquin (San Francisco Bay) estuary is the largest estuary on the Pacific Coast of North America and has been invaded repeatedly by literally hundreds of species of plants and animals since 1850. The high invasibility of the estuary appears to be the result of a number of interacting factors: (1) the high degree of alteration of estuarine habitats by humans; (2) the enormous extent to which introductions have been made into the estuary; and (3) the naturally high variability in estuarine conditions; and perhaps (4) the young geologic age of the estuary and the consequent comparative lack of species specifically adapted for estuarine conditions. As a consequence of these factors, many of the organisms that dominate ecosystem processes are non-native species, new invaders appear on a regular basis, and assemblages of organisms have developed that are made up of mixtures of native and non-native species (Herbold & Moyle, 1989). Extinctions of native organisms appear to have been surprisingly few, at least until the present era.

The Sacramento–San Joaquin estuary has existed in its present size and configuration for only about 10,000 years, reflecting the great geologic activity characteristic of the California coastline. It contains only one species of native fish (delta smelt *Hypomesus transpacificus*) with a life history completely dependent on the estuary, although there are five to seven other more widely distributed fish species with some degree of estuarine dependence (Herbold & Moyle, 1989). Otherwise, the fishes originally found in the system were euryhaline marine and freshwater fishes. The native invertebrates presumably followed a similar pattern, although they are much more poorly known (Herbold & Moyle, 1989). The rapid settlement of California in the 19th century led to rapid and massive changes in the estuary. Hydraulic mining dumped millions of tons of sediment into the system, the immense marshlands were diked and drained, and pollutants of all kinds flowed in. In the 20th century, urbanization of the estuary's edges and diversion of much of the inflowing fresh water provided further major changes (Nichols *et al.*, 1986).

Invasions of exotic species accompanied the change in conditions. The first invertebrates arrived attached to ship bottoms or swimming in ship ballast water, a source that has steadily increased into the modern era. Carlton (1979) indicates that most invertebrate species in the estuary today are introduced species. The completion of the transcontinental railroad in 1871 became another source of introductions as carloads of marine and estuarine fish and invertebrates were released into the system year after year. Three species of estuarine fish became established in large numbers almost immediately: American shad (1871), white catfish *Ameiurus catus* (1874), and striped bass *Morone saxatilis* (1879). All introductions of stenohaline marine fish from the Atlantic Ocean failed. These failures may have been the result of competition and predation from the diverse assemblage of native marine fishes existing in San Francisco Bay. However, striped bass and two euryhaline gobies are abundant in the Bay, as they are in the more freshwater parts of the estuary. Further introductions have increased the number of exotic fish species in the low-salinity (the Delta and Suisun Bay) portions of the estuary to 27, 60% of the present fish fauna (Herbold & Moyle, 1989). Percentages of exotic species in major invertebrate groups are probably even higher.

There is some evidence that the invasions of the estuary increase when the established assemblages are stressed or depleted. A number of major invasions occurred between 1985 and 1993, a period of severe drought whose effects were accentuated by increasing water diversions (Moyle *et al.*, 1992). In the middle of this period (1989), there was a one-month interval (February) with the highest outflows on record (the result of a series of major storms), an event that turned the entire estuary into a freshwater system for a short period of time. Following the storm, populations of most estuarine organisms were greatly diminished and a number of new species invaded. The most spectacular invasion was that of the Asiatic clam *Potamocorbula amurensis*, which quickly became the dominant filter-feeding organism in the lower half of the estuary, with drastic effects on the established communities of organisms (Nichols *et al.*, 1990). Another prominent invader has been the shimofuri goby *Tridentiger bifasciatus*, which is now one of most abundant fish in the system. Other recent invaders include a number of crustacean species.

One of the interesting questions raised by situations like Sacramento–San Joaquin estuary is the nature of the mixed native–exotic assemblages that have developed. Moyle *et al.* (1986) found that there were co-occurring groups of fishes of mixed origin, each group associated with a distinct set of habitat conditions, that were predictable over a period (1979–1985) of relatively consistent conditions in the estuary. These groups persisted through a much more variable environmental period (1986–1992), but they were less constant in composition from year to year: the shimufuri goby invaded, some native species became extremely rare, and overall fish abundance declined (Meng *et al.*, 1994). The persistence of loose habitat groups of species, as well as studies of the diets of the fishes (Herbold, 1987), indicate that the 'new' fish assemblages have enough structure to resemble assemblages of fishes that have co-existed for thousands of years (Moyle & Vondracek, 1985). However, the overlaps in habitat use and diet are probably higher than in more established assemblages. Segregation may be partly a reflection of the morphological and taxonomic diversity of the mixed assemblages which include representatives from 19 families of fish (Moyle *et al.*, 1985). Whether this diversity is the cause of the segregation observed or the result of it (from competitive or predatory exclusion), is not known. Presumably, segregation is partly the result of morphological limitations of the species, partly the result of interactions among the species, and, perhaps, rapid evolution (Townsend, this issue).

It is also worth noting that the segregation exists despite a changing prey base caused by invertebrate invasions. For the most part, the fishes switch prey readily. Delta smelt and larval striped bass, for example, both switched to preying on non-native copepods when the once-dominant native species declined (Moyle *et al.*, 1992; Meng & Orsi, 1993).

EMPIRICAL RULES FOR AQUATIC INVASIONS

Moyle and Light (1996) present six empirically-derived rules for predicting the fate and impact of biological invasions into California streams and estuaries. In this section we examine the applicability of these rules to other aquatic habitats and regions and add six additional rules that seem to govern invasions into aquatic systems during the establishment and integration phases (Table 1). We regard these rules as the basis for formulating testable hypotheses that in turn can support a theoretical framework.

Most invaders fail to become established

The rate at which species invading aquatic systems become established is not known, largely because most failed invasions are not recorded (Lodge, 1993*b*). The enormous number and variety of organisms in ballast water (Carlton, 1985) suggests that the success rate of estuarine invasions is very low and that the presence of abundant exotic species in most estuaries is the result of the high frequency of introduction. The explosion of new invaders into the Sacramento–San Joaquin estuary during a period of high environmental change also

Table 1. Some proposed rules for biotic invasions into freshwater and estuarine systems during two major phases of the invasions (Vermeij, 1991), initial establishment and long-term integration into the existing fish community

Establishment	Integration
Most invasions fail.	Most successful invasions are accommodated without major community effects.
All aquatic systems are invasible.	Major community effects are most often observed where species richness is low.
Piscivores and detritivore/omnivores are most likely to be successful in systems with low levels of human disturbance.[a]	Piscivores are most likely to alter invaded communities; omnivores/detritivores least likely do so.
Any species with the right physiological and morphological traits can invade, given the opportunity.	Long-term success depends on a close physiological match between the invader and the system being invaded.
Successful invasions are most likely when native assemblages are depleted or disrupted.	Long-term success is most likely in aquatic systems highly altered by human activity.
Invasibility of aquatic systems is related to interactions among environmental variability, predictability, and severity.	Invaders are much more likely to extirpate native species in aquatic systems with either extremely high or extremely low variability or severity.

[a] In lakes, zooplanktivores also show a high rate of invasion success and ability to alter the ecosystems they invade. Likewise insectivores easily invade and alter historically fishless streams or low gradient streams highly altered by human activity.

suggests that having appropriate conditions in the receiving system is very important for successful invasions and that these conditions may only be present for short periods of time. In the Eel River drainage, the six species of fish that have self-sustaining populations in a headwater reservoir are flushed out every year. Downstream populations of these species are either temporary or very small and are presumably periodically eliminated by winter floods. Were another reservoir established in a downstream area, however, it would be quickly colonized by the six species. In Deer Creek, invasions of exotic fishes occur annually from both upstream and downstream sources, but populations do not become established in the undisturbed reaches of stream.

Overall, most successful invasions depend on a coincidence of invaders being present in sufficient numbers to colonize an environment during the narrow windows of time when the environment is available for colonization. It is not surprising therefore that most invasions fail and most successful deliberate introductions into aquatic systems have been made by individuals who understand this relationship.

Most successful invaders are integrated without major negative effects (e.g. extirpations) on the communities being invaded

Moyle and Light (1996) note that in California streams and estuaries, fish assemblages made up of mixtures of native and introduced species resemble co-evolved assemblages in their structural and functional characteristics. This is true even for the fish assemblages in the Sacramento–San Joaquin estuary in which 60% of the 50 species present are non-native (Moyle *et al.*, 1986; Meng *et al.*, 1994). Likewise, the fishes of depauperate Sri Lankan streams quickly become an integrated part of a more complex fish assemblage when additional species are introduced to the streams (Wikramanayake & Moyle, 1989). Similar examples can be found in the complex assemblages fishes in marine systems (Baltz, 1991), in streams of eastern North America (e.g. Bestgen *et al.*, 1989) and in tropical lakes. In Lake Malawi, East Africa, 12 species of bottom-oriented haplochromine ('mbuna') cichlids from one part of the lake were introduced into another part from which they were absent, creating the most diverse mbuna assemblage known from the lake, without any obvious changes in the abundances of the local native species (Trendall, 1988). However, extirpations following invasions do occur, especially if the invader is a piscivore. A relatively small number of species seem to be responsible for most extirpations, reflecting the large number of introductions of predatory fishes, usually for sport fisheries (Moyle, 1986).

All aquatic systems are invasible and invasibility is not related to diversity of the resident organisms

Despite the fact that most invasions fail, the astonishing number and variety of aquatic systems around the world that have been invaded by non-native species is a good indication of (1) the ability of humans to match potential introductions with appropriate habitats; (2) the huge numbers of aquatic organisms that are being moved around the world (e.g. in ballast water of ships); and (3) the naturalness of invasion as a biotic process (Vermeij, 1991; Lodge, 1993*b*). Fish have been introduced at one time or another into most waters that will support them. They have become established in many lakes and streams that initially had no fish, as well as in the complex assemblages characteristic of tropical reefs (Baltz, 1991) and streams of the eastern United States (Moyle, 1986). Moyle and Light (1996) point out that this rule conflicts with one of the most well-established generalizations in the aquatic invasion literature, that communities with low diversity and complexity are the most susceptible to invasion (Lodge, 1993*a*). There are simply too many examples of successful invasions into species-rich communities and of failed invasions into species-poor communities (e.g. Deer Creek, Eagle Lake, Lassen County, CA). The invasibility of most systems is supported by the analysis of Cornell and Lawton (1992), who suggest that ecological communities are rarely saturated with species.

Major community effects of invasions are most often observed where the number of species is low

The reason that simple systems seem more invasible than complex systems is that the results of a successful invasion are likely to be more visible. While no communities (even the Deer Creek fish assemblages) are immune from invasions, invading species do not affect all communities in the same way. Thus predatory fish may cause extinctions of native fish and invertebrates when introduced into isolated spring systems, but their invasions may not significantly change the complex communities of a large reservoir or lake. Streams of eastern North America, with fish assemblages of 20 or more species have suffered repeated invasions of new fishes, usually without equivalent extinctions (e.g. Hocutt *et al.*, 1986; Bestgen *et al.*, 1989). In contrast, in streams of western North America, which typically contain five to 10 native species, extinctions following invasions are common (e.g. Martis Creek).

The reason, in theory, why more complex systems are harder for new invaders to disrupt is that complex assemblages are the result of repeated invasions through evolutionary time (Vermeij, 1991). Repeated invasions result in increased biological resistance to further invasions because species accumulate that have been successful competitors or predators, as demonstrated by the success of their original invasions. One of the apparent exceptions to this hypothesis is Lake Victoria, Africa, which had one of the most speciose fish faunas of any lake in the world until the piscivorous Nile perch *Lates* sp. was introduced into it. Within a decade, the perch apparently eliminated about 200 species of endemic cichlids from the lake (Craig,

1992) and caused radical changes to the lake ecosystem (Goldschmidt *et al.*, 1993). In fact, the Lake Victoria situation may not contradict this hypothesis because most of the extirpated species were part of a 'flock' of closely related haplochromine cichlids that apparently evolved together very rapidly, perhaps within a few hundred years. While this cichlid assemblage had an extraordinarily complex structure, it presumably evolved *in situ* largely in the absence of multiple invasions. From the perspective of an invader like Nile perch, the 200+ haplochromine species behaved like a handful of species and offered no real resistance to invasion.

The high invasibility of the Rift Lake fish communities is also indicated by the fact that four species of tilapiine cichlids were successfully introduced into Lake Victoria at the same time as the Nile perch (Ogutu-Ohwayo, 1990). These omnivorous species were introduced because fisheries had depleted the populations of the native tilapiine species (Craig, 1992). One of the introduced species, *Oreochromis niloticus*, is one of the few fishes to persist in large numbers in face of the Nile perch invasion, which may reflect its past evolutionary experience with similar predators.

In systems that have been minimally altered by human activity, fishes most likely to be successful invaders are top predators and omnivore/detritivores

Moyle and Light (1996) document that, in California, the most successful fish invaders have been piscivores and omnivores. This pattern seems to fit other aquatic systems as well, including Lake Victoria and Sri Lankan streams. Presumably, the success of these two trophic groups is related to the high availability of food during the establishment phase of the invasion. The prey encountered by an invading piscivore is likely to be naive in terms of recognizing the predator and its style of predation. Thus the invading sea lamprey *Petromyzon marinus* virtually eliminated large fish from Lake Michigan, even though some of the same species (e.g. lake trout *Salvelinus namaycush*) coexist with the lamprey in other lakes where the species have been together for thousands of years (Moyle, 1986).

Likewise, invading omnivores/detritivores use a food source that rarely seems to be limiting in aquatic systems, so their success is more likely to be determined by other factors, such as life history strategy. In lakes, zooplanktivores also seem to have a high success rate of invasion. Usually their successful invasion is associated with a decline of the larger zooplankton species, indicating that the fish are a novel predator in the system (O'Brien, 1987).

Piscivorous invaders are most likely to alter the fish assemblages they invade while omnivore and detritivores are least likely to do so

The dramatic effects of piscivores on fish assemblages in lakes and streams have been well documented. The effects of a predator invasion can 'cascade' through the entire ecosystem, altering fundamental ecosystem processes (Carpenter *et al.*, 1985) and the behavior of native organisms (Townsend, this issue). Fisheries managers are increasingly aware of the large-scale consequences of piscivore introductions. In California, for example, large sums of money have been spent attempting to prevent the spread of illegally introduced northern pike *Esox lucius* and white bass *Morone chrysops* into the Sacramento River drainage (Li & Moyle, 1993). In contrast, invading omnivorous and detritivorous fishes seem to have little effect on existing fish assemblages) (Wikramanayake & Moyle, 1992; Moyle & Light, 1996) although they may still have considerable capacity to alter ecosystem functioning (Power, 1990). Because such invaders are presumably harmless in relation to native fishes, three species of detritivores (*Tilapia rendalli*, *Trichogaster pectoralis*, and *Osphronemus gouramy*) have been introduced into the Sepik River, New Guinea, in order to increase fish production for food (Coates, 1993). The conclusion that these introductions presented a low risk to the native assemblages of fishes was reached only after extensive investigations of the native fish fauna (Coates, 1987; Allen & Coates, 1990).

In aquatic systems with intermediate levels of human disturbance, any species with the right physiological and morphological characteristics can become established

The intermediate levels of disturbance refer to fluctuations in environmental conditions that are frequent and unpredictable enough so that it is difficult for any one species or group of species to dominate the system for long. This permits species to coexist at least temporarily that might eliminate one another in more predictable systems or that would be eliminated by environmental conditions in highly altered environments (Connell, 1978). While this rule may be too broad to be very useful for predicting invasion success, it does help to explain the confusing array of fish and invertebrates found in the Sacramento–San Joaquin estuary, in warm-water lakes, or streams of the eastern United States (Moyle & Light, 1996).

In the long term, or in relatively undisturbed aquatic systems, success of an invader will depend on a close match between its physiological and life history requirements and the characteristics of the system being invaded

Thus, fish and other organisms from nearby areas are more likely to be successful invaders into natural systems than those from more distant locations. Moyle and Light (1996) noted that in California streams invading fish species are most likely to be successful if they are adapted to the local, highly seasonal, hydrologic regime. California roach and Sacramento squawfish quickly became widespread and abundant in the Eel River because they evolved in rivers with similar hydrologic regimes. The comparative inability of other species to invade so successfully, despite annual introductions, reflects their lack of adaptations to the riverine conditions. Likewise, Meffe (1991) observed that the failure of bluegill *Lepomis macrochirus* to become established in a stream in the southeastern USA, at the same time as it became abundant in an upstream reservoir, was largely the result of its inability to adapt to the stream conditions. This rule is also supported by Lodge (1993*b*), using examples from midwestern lakes.

Invaders into natural aquatic systems are most likely to become established when native assemblages of organisms have been temporarily disrupted or depleted

This rule of Moyle and Light (1996) reflects the high degree to which California streams and estuaries have been modified and then invaded by non-native species. The successful invasion of the Sacramento–San Joaquin estuary by a number of exotic species in recent years, following the disruption of the existing assemblages by a series of extreme floods and droughts, is an example of the rule. Likewise, the invasion of the Laurentian Great Lakes by salmonids *Oncorhynchus* spp. introduced from the Pacific coast of North America was greatly facilitated by the disruption of the lake ecosystems by two previous invaders, the sea lamprey and the alewife *Alosa pseudoharengeus* (Moyle, 1986). This generality implies that biotic resistance to invasion into freshwater systems does exist to a certain extent, particularly at the early stages of the invasion process.

Long-term success (integration) of an invading species is much more likely in an aquatic system permanently altered by human activity than in a lightly disturbed system

This is due to a number of factors, but most prominently is the fact that human disturbed systems (e.g. reservoirs) tend to resemble one another over broad geographic areas and favor species (such as game fishes) that are also favored by humans. Some of the most altered systems around the world are estuaries because they are the focus of so much urban development and industrial pollution. As a consequence, the hardy species that can survive a trip in a ship's ballast water are likely to be abundant in donor estuaries and find a ready home in recipient estuaries. The result has been the development of a cosmopolitan estuarine fauna that stretches across oceans (Carlton & Geller, 1993).

The invasibility of a natural aquatic system is related to the interactions among environmental variability, predictability, and severity

Variability is defined as the extent to which environmental conditions are likely to fluctuate over a one year period, while predictability refers to the regularity of the annual pattern of environmental fluctuations. Severity is the likelihood that the environment will reach conditions that are stressful or lethal to most freshwater organisms. This scheme is supported by the findings of Poff and Ward (1989) and Poff and Allan (1995), who found that composition of fish communities in streams is determined by the broad hydrological features of watersheds. In general, invaders seem least likely to become established in highly variable but predictable environments and seem most likely to become established in environments that either have low variability in their physical–chemical conditions or have moderate variability but low predictability (Table 2). For example, Deer Creek shows high variability in annual flows but the pattern is predictable; the highest flows occur in the spring, in response to snow-melt, and the lowest flows occur in late summer, at the end of the rainless dry season. The life history patterns of the native fishes show strong adaptations to this cycle, adaptations which are not strongly present in the many fish species introduced into the region (Moyle, 1976; Baltz & Moyle, 1993).

Harshness of the environment in relation to the physiological capabilities of fish also reduces the ability of exotic fishes to invade a system. An example of such a system is Eagle Lake, Lassen County, California, which is a highly alkaline (pH = 8–9) terminal lake containing four native fishes but no exotic fishes or invertebrates (P. B. M., unpubl. data). Numerous attempts have been made to introduce non-native fishes into the lake (unpublished records, California Department of Fish and Game). In the early 20th century, when lake levels were high and alkalinities low, the lake was renowned for its fishery for non-native largemouth bass *Micropterus salmoides*. This fishery disappeared during the 1930s when drought reduced lake levels and increased alkalinities; largemouth bass no longer exist in the lake (P. B. M., unpubl. data). In contrast, nearby Lake Tahoe, with some of the same native fishes but a neutral pH, has been successfully invaded by at least four non-native fishes and two macroinvertebrates (Li & Moyle, 1981). Lake Tahoe is typical of lakes throughout the world; it is rare to find a lake of any size that does not contain one or more non-native species (Li & Moyle, 1993).

Invaders are most likely to extirpate native species in aquatic systems with extremely high or extremely low variability or severity

Aquatic systems that are reasonably benign in their physical and chemical characteristics are likely to support an increased diversity of species, supporting a mixture of native and introduced forms, at least in the short run. Most streams and lakes in temperate North America contain one or more species of introduced fish (Moyle, 1986), usually one of a group of tolerant species (e.g. common carp *Cyprinus carpio*, fathead minnow *Pimephales promelas*, green sunfish *Lepomis cyanellus*). While declines of native fishes usually coincide with the invasions, implying biotic interactions between the invader and the invaded fish assemblage,

Table 2. Susceptibility of relatively undisturbed aquatic environments to invasions by non-native fishes in relation to (1) annual variability in physical characteristics (e.g. stream flow), (2) predictability of the environment, and (3) severity of physical and chemical conditions in relation to ability to support fish life. 1 = low, 2 = moderate, and 3 = high

Variability	Predictability	Severity	Invasibility	Examples
3	3	2–3	1	California streams
2	1	2–3	2	Midwestern streams
1–2	2	3	1	Alkaline lakes
2	2–3	1–2	3	Lakes
1	3	1	3	Springs

the declines are also usually associated with major habitat changes (Burr, 1991; Ross, 1991). Bestgen *et al.* (1989) noted that two species of minnows Cyprinidae introduced into the Pecos River, Texas, from nearby areas have thrived because the artificial flow regime of the river closely resembles that of their native streams (where one of the species is depleted in numbers). In both places, the invaders are still part of complex fish assemblages, a pattern that is common in streams of Eastern North America (e.g. Hocutt *et al.*, 1986). In contrast, introduction of exotic fishes into the constant environments of desert springs or tropical lakes is often a disaster for the native fishes (Courtenay & Moyle, 1992). When streams in the western United States are dammed, creating reservoirs and damping the natural fluctuations in stream flow, they are quickly invaded by non-native fishes, to the detriment of the native species (Moyle, 1976; Minckley & Meffe, 1987).

INVASION BIOLOGY AND ASSEMBLY THEORY

The empirically derived rules listed above suggest that predicting the likelihood of the success of an invading species or predicting the invasiblity of an aquatic system will depend on detailed understanding of the characteristics of the invading species and of the system being invaded. Both are likely to be fairly idiosyncratic, making generalized theory difficult to apply, including community assembly theory. If assembly theory were to work, a list of abundant species within a taxon group (e.g. a fish assemblage) present in a given aquatic system should yield enough information to provide some fairly powerful predictions. Unfortunately, even the five general predictions of assembly theory listed earlier appear to be of limited usefulness for predicting the results of biological invasions. The frequently cited generalization that community diversity reduces invasion success (Lodge, 1993*a*,*b*), for example, is not supported by our examples from aquatic systems. Unlike the predictions of community assembly theory, our empirical 'rules' have little to do with invasion sequence and a great deal to do with the nature of the environment being invaded and the biological characteristics of the invader. Thus existing community structure generally seems to have little to do with the success or failure of invasions. Existence of large populations of predators can presumably prevent invasions but only as long as the environment is constant enough to maintain the large populations (e.g. Strange *et al.*, 1992).

Likewise, numerous field and laboratory studies demonstrate that the outcome of pairwise competition often can depend on the environmental regime (e.g. Baltz *et al.*, 1982) as can the outcome of multispecies competition (e.g. Gilpin *et al.*, 1986). Changes in competitive ability can be related to environmental changes so that in the constantly shifting environment outside the laboratory, no clear winner can emerge. Furthermore, the biotic 'filter' against invasion consists of predation, disease, and prey availability as well as competition. In simulated food webs, the most common reasons for failure of invasions are either inadequacy of the resource base for the invader or heavy predation (Drake, 1990*b*).

Strange (1995), in a modelling study of the dynamics of the Martis Creek fish assemblage, argues that the success of a particular invading species depends on how environmental conditions over a period of several years simultaneously affect both the invader and the community being invaded. Particularly important in understanding this interaction are the life history character- istics of all the species involved because changing flow regimes in the stream alternately favor different life history strategies. Thus there is no one optimal life history strategy for the stream nor is there any one assemblage of fishes that will persist indefinitely, although the present assemblage seems to have just two alternating states. The constantly changing physical environment would seem to make the resident fish assemblage both open to invasion on an irregular basis and resistant to extirpation of any of its members. There are clearly assembly rules that govern the structure of the Martis Creek fish assemblage but they are highly idiosyncratic and probably applicable at best on a regional scale (Strange, 1995).

CONCLUSIONS

In aquatic systems, biotic resistance is usually less important in determining the success or failure of an invasion than environmental resistance, except perhaps in the early stages of invasion when numbers of an invader are small. While there is growing evidence that most invasions of aquatic systems do not cause extirpations of native organisms directly, we are still too far from being able to predict unequivocally the effects of a new species to separate benign introductions from those, like zebra mussel or Nile perch, that cause vast changes to the systems they invade. Our list of empirical rules nevertheless indicates that we think development of a predictive model is possible, at least for aquatic systems on a regional scale. We hope with Pimm (1989) that '... considering introductions in total, ... there are some simple theoretical expectations and there are some equally simple general patterns (p. 366).' Unfortunately, we doubt this is the case, particularly at the level that would be useful to ecosystem managers. At the local level, the patterns are bound to be idiosyncratic and complex. Yet they can still be understood and reasonable predictions made from past experiences, if not from models. However, until our predictive ability improves in a more general arena, it is best to assume that the Frankenstein Effect is the one firm rule: new invasions are likely to have unexpected consequences.

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