Predicting Invasion Success: Freshwater Fishes in California as a Model

PETER B. MOYLE AND MICHAEL P. MARCHETTI

The location, size, and geography of California, combined with extensive knowledge of successful and failed fish invasions, provide an unusual opportunity to test predictors of invasion success. Our analyses show that different characteristics of alien fishes are important at different stages of the invasion process. We found no set of characters that predicted success for all fish invasions, although some characters increase the probability of success. The factors that best predict invasion success are (a) a history of successful establishment outside the species' native range; (b) characters that promote success at multiple stages of the invasion process (e.g., high physiological tolerance); (c) invaded habitat that more or less matches the alien's native habitat; (d) high fish species richness, including other alien fishes; and (e) propagule size exceeding 100 individuals. The difficulty of predicting the invasion success of alien species points to the need to allow only introductions that have proved to be nonharmful and to take quick action to prevent the spread of new invaders.

Keywords: alien species, watersheds, invasion biology, nonindigenous fishes, exotic fishes

Streams, lakes, and estuaries are among the most highly invaded ecosystems in the world; in many of them, alien organisms are now a significant part of the biota (Cohen 2002). The best-documented invaders in these systems are fishes. Because many fish species are widely introduced, there is concern among scientists and managers over the homogenization of freshwater fish faunas worldwide (McKinney and Lockwood 1999, Marchetti et al. 2001, Rahel 2002). Invasions by alien species also have high ecological and economic costs. Efforts to prevent the spread of unwanted fish and other organisms, however, are still small compared with the size of the problem (Meyerson and Reaser 2003), in part because policymakers and the public often fail to appreciate the seriousness of the invasions. Many harmful alien fishes, for example, are also favorite food and game fishes. Thus, to make predictions useful for the management and control of alien species, scientists need to understand the nature of invaders, the invasion process, and the impact of invasions, and to communicate that knowledge effectively.

Because "any species can invade and any environment can be invaded" (Moyle and Light 1996), a search for generalities that would be useful for predicting the success of potential invaders may be futile. Kolar and Lodge (2001) argue, however, that quantitative approaches (including meta-analysis of diverse sources of information) can produce useful predictions. In particular, they argue for the need to analyze data on failed invasions. We think there is also a need to focus analyses at regional scales, because studies at continental or global scales tend to yield results with limited predictive ability (Gido and Brown 1999, Lockwood 1999, Ruesink 2005). In this article we address these issues of approach and scale in relation to fish invasions by synthesizing recent studies in California, mainly our own. We focus on these studies because the scope and completeness of our data sets make our studies widely applicable. After introducing California as a laboratory for the study of fish invasions, we focus on the potential for predicting success and impacts of freshwater fish invasions based on (a) symbiotic characteristics (the relationship of the fish to humans), (b) biological characteristics of the invaders, (c) characteristics of the invasion site, and (d) the invasion process. We then briefly address the question, Do alien fishes alter the ecosystems they invade?

Peter B. Moyle (e-mail: pbmoyle@ucdavis.edu) is with the Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616. Michael P. Marchetti (e-mail: mmarchetti@csuchico.edu) is with the Department of Biology, California State University, Chico, CA 95926.

California: A laboratory for the study of fish invasions

Although the fresh waters of California have been highly invaded and modified by alien fishes, invertebrates, plants, and other organisms, fish invasions are by far the best documented. Thus we have been able to collate a large data set on successful and failed fish introductions from information in Dill and Cordone (1997) and Moyle (2002). We expanded this data set by counting as alien species those fishes native to one watershed that were introduced into other watersheds of the state. California represents a reasonable scale for this type of analysis. It is large enough (over 411,000 square kilometers) and long enough (spanning 10 degrees of latitude) to encompass diverse environments, from desert to temperate rainforest, that contain a wide variety of aquatic habitats (Moyle 2002). The state is also geographically complex, containing distinct zoogeographic regions and numerous watersheds that are largely isolated from one another so that each watershed can be treated as an independent invasion site (figure 1). This means that our analyses were based on invasions into regions with natural rather than political boundaries, unlike most other studies of invasion patterns (Gido and Brown 1999, Ruesink 2005). We have documented invasions, starting in the 1870s, of the state's 44 largest watersheds (Marchetti et al. 2001, 2004a, 2004b, 2004c) by 110 fish species.

Many (43%) of the invasions were unsuccessful. Unsuccessful introductions are primarily those of species for which records exist of temporary establishment in the wild or for agency-documented attempts to establish populations (Dill and Cordone 1997). Presumably other, unrecorded failed introductions also occurred, especially those of aquarium and bait fishes. California's aquatic environments are highly disturbed statewide, with few that qualify as pristine. The extent and nature of the disturbances, from dam building to land-use changes, are also well documented at various scales, so it is possible to examine how invasions relate to environmental change (Meador et al. 2003, Marchetti et al. 2004a).

The native fishes have a relatively low species richness ($N = 66$), but most are endemic to the state, a situation typical of fish faunas in regions with Mediterranean or arid climates (Moyle 2002). By and large, the fauna has a suite of morphological and life history characteristics that reflect adaptations for persisting through long periods of extreme drought (Moyle 2002), which suggests that under wetter (or human-altered) conditions, it is not saturated with species.

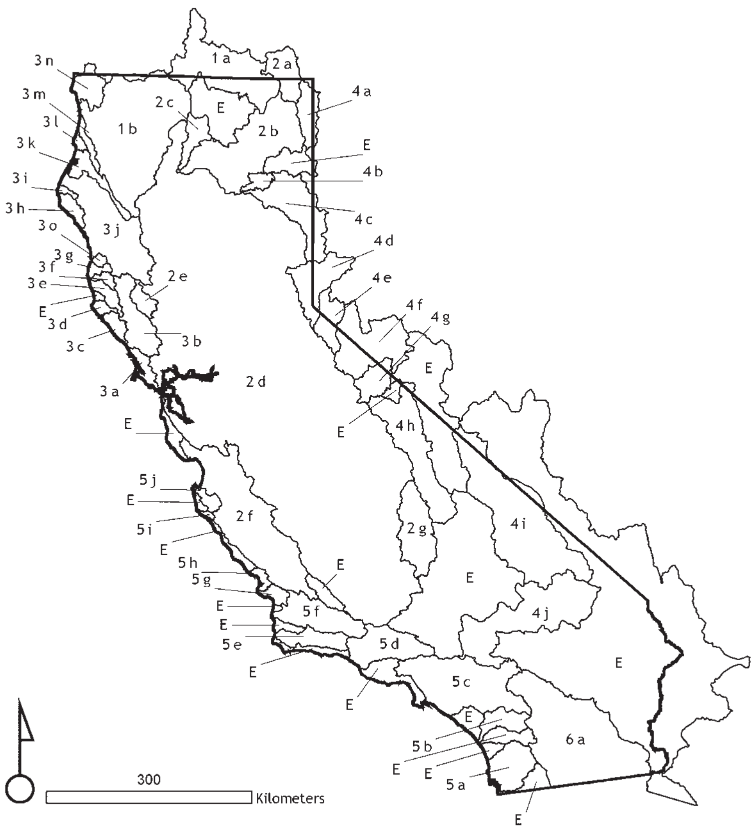

Figure 1. Map of California showing major watersheds used in analysis of fish invasions. Each number represents a major zoogeographic region; each lowercase letter represents a distinct watershed within the basin that is physically separated from the other watersheds or is characterized by a distinct fish fauna, or both (see Moyle 2002 for details). A capital letter E indicates a fishless basin, not used in our analysis. Modified from Moyle (2002).

Symbiotic characteristics

Symbiotic characteristics are aspects of alien species that either make them desirable to humans (mutualism) or allow them to invade as a by-product of human activities (commensalism). Thus fishes can be introduced deliberately for food, sport, or biological control or as by-products of human activity, such as aquaculture operations, shipping, and aqueducts that connect watersheds (Moyle 1998). In California, as in most of the world, the biggest reason for mutualistic fish introductions has consistently been for sport or food (Dill and Cordone 1997). Forty-five percent of fish introductions into the state were made for this purpose, with an approximate 2:1 ratio of success to failure. Another 15% of all introductions were forage and bait fishes, introduced as food for alien game fishes, with a similar rate of success (Moyle 2002). Slightly lower rates of success have been achieved with introductions undertaken as biological control or conservation measures (e.g., endangered native fishes moved to nonnative watersheds).

The high success rates of deliberate fish introductions reflect the ability of anglers and biologists to match characteristics of alien fish to receiving waters and to make repeated introductions of large numbers of individuals (Marchetti et al. 2004c). Less successful (28% success for recorded introductions) have been species introduced as by-products of human activities: unwanted aquarium pets, escapees from tropical fish farms, fish carried in ballast water, and native fishes moved to new watersheds via aqueducts. The importance of aqueducts in the invasion process is just beginning to be fully appreciated. For example, in recent years, at least five species of native fishes and two species of alien fishes from northern California have become established in southern California reservoirs through transfer via aqueducts (Moyle 2002). One of these species, the shimofuri goby (*Tridentiger bifasciatus*), originally became established in northern California through ballast water transported from Japan (Moyle 2002).

Lockwood (1999) and Brooks (2001) suggested that among birds, only certain groups have characteristics prized by humans, and therefore taxonomy can be a good predictor of invasion success. To a certain extent this is true for fish as well: 63% of the established alien species in California come from just five families (Cyprinidae, Ictaluridae, Salmonidae, Centrarchidae, and Cichlidae), which contain many food and game fishes (table 1). The Cyprinidae, Salmonidae, and Centrarchidae contain both native and alien species, as do 5 other families (i.e., 8 of 16 native families), suggesting that local familiarity with a taxon plays a role in its spread. On a global scale, Ruesink (2005) suggested that the bias in alien fishes toward certain families was related to small body size, although this was not true for California aliens.

Another way to look at human preference is to count the countries that an alien species has successfully invaded (Lockwood 1999). Success predicts success. In California, about half of all alien species are not established in any other country, but the ratio of success to failure rises from slightly more than 1:1 for fishes with no previous successes to 4:1 for alien fishes that are established in 10 or more countries. Marchetti and colleagues (2004c) found that frequency of prior invasion success was the best predictor of the species that were most likely to become integrated into the California fish fauna.

Biological characteristics

The biological traits of successful invaders have been hypothesized in a number of papers, supported mainly by anecdotal evidence (Ehrlich 1989, Williamson and Fitter 1996). In this section we examine characters most often cited as associated with successful fish invasions.

Abundance and wide distribution in the native region. This character provided mixed results as a predictor of invasion success in our studies. Introduction failures were as common as successes in widely distributed species, a finding consistent with that of Brooks (2001) for birds. Twenty successful invasions were by species with very small native ranges. These include spring-dwelling pupfish (*Cyprinodon*) species that were transferred to springs outside their native range for conservation purposes. They also include two species endemic to relatively small regions of the eastern United States, bigscale logperch (*Percina macrolepida*) and redeye bass (*Micropterus coosae*), which are now apparently more widely distributed in California than they are in their native ranges (Moyle 2002). However, we did find that large native range was a contributor to some multivariate models predicting invasion success, suggesting that widely distributed species are somewhat more likely to have other features favoring invasion success than those with narrow distributions (Marchetti et al. 2004c), a conclusion supported weakly by Ruesink (2005).

High physiological tolerance. The ability to tolerate wide ranges of temperature, salinity, and other physiologically limiting factors proved to be important for California fishes; 66% of all successful introductions had high to extremely high tolerances (Marchetti et al. 2004b, 2004c). However, 47% of introduction failures had similar tolerances. Lack of physiological tolerance was most obvious as a factor in the failure of tropical aquarium fishes in southern California, where species become temporarily established but die out during

Table 1. Families of fishes found in the fresh waters of California, with number and percentage of extant native species and alien species in each family.

Family	Species	Native species (percentage)		Alien species (percentage)	
Petromyzontidae (lampreys)	6	6	(100)	0	(0)
Acipenseridae (sturgeons)	2	2	(100)	0	(0)
Clupeidae (herrings)	3	1	(33)	2	(67)
Cyprinidae (minnows)	22	14	(64)	8	(36)
Catostomidae (suckers)	10	10	(100)	0	(0)
Ictaluridae (bullhead catfishes)	7	0	(0)	7	(100)
Esocidae (pikes)	1	0	(0)	1	(100)
Osmeridae (smelts)	4	3	(75)	1	(25)
Salmonidae (salmonids)	12	8	(67)	4	(33)
Atherinopsidae (silversides)	2	1	(50)	1	(50)
Fundulidae (topminnows)	2	0	(0)	2	(100)
Poeciliidae (livebearers)	5	0	(0)	5	(100)
Cyprinodontidae (pupfishes)	4	4	(100)	0	(0)
Gasterosteidae (sticklebacks)	2	1	(50)	1	(50)
Cottidae (sculpins)	9	9	(100)	0	(0)
Moronidae (striped basses)	2	0	(0)	2	(100)
Centrarchidae (sunfishes)	12	1	(8)	11	(92)
Percidae (perches)	2	0	(0)	2	(100)
Cichlidae (cichlids)	4	0	(0)	4	(100)
Embiotocidae (surfperches)	2	2	(100)	0	(0)
Gobiidae (gobies)	5	2	(40)	3	(60)
Mugilidae (mullets)	1	1	(100)	0	(0)
Flounders (Pleuronectidae)	1	1	(100)	0	(0)
Total	120	66	(55)	54	(45)

Source: Moyle 2002.

winter when temperatures fall below 18–20 degrees Celsius (°C). Guppies (*Poecilia reticulata*), for example, are widely established in sewage treatment ponds in the state and are no doubt frequently dumped into local waterways by aquarists. Nevertheless, there are no known wild populations in California, presumably because of their inability to tolerate low temperatures.

The importance of physiological tolerances is demonstrated by fishes inhabiting Suisun Marsh, a fresh to brackish estuarine marsh with shallow (< 3-meter) channels, which is part of the San Francisco Estuary. The marsh channels show considerable fluctuation in temperature and salinity but have been highly invaded by alien fish and invertebrates (Matern et al. 2002). Suisun Marsh is directly connected to the Sacramento River, so a pool of 68 freshwater and anadromous species (40 of them aliens) is available to colonize the marsh from fresh water. In nearby Suisun and San Pablo Bays, there are at least 72 species (14 aliens), mostly marine fishes, also available for movement into the marsh. When overlap in the two lists is accounted for, at least 105 species (41 aliens) are available to colonize the marsh, yet only 29 species (14 aliens) are consistently present. The failures are primarily stenohaline or stenothermal marine and freshwater fishes that cannot tolerate the ranges of salinity (0–16 parts per thousand) and temperature (4°C–30°C) regularly encountered in shallow marsh sloughs. Thus the alien chameleon goby (*Tridentiger trigonocephalus*) has never been found in the marsh, even though it is abundant in the San Francisco Bay, a largely marine system. In contrast, the closely related shimofuri goby became abundant in the marsh following its invasion in 1987 (Moyle 2002).

Genetic traits. There is insufficient information to say much about the genetic traits of native versus alien fishes in California. Yet there are hints of perhaps contradictory trends. The first is that at least 22 alien species became established with initial introductions of fewer than 100 individuals, which suggests that a large gene pool and high genetic variability in the short run do not play a major role in invasion success. The second hint is that some of the most widespread alien species (common carp [*Cyprinus carpio*], goldfish [*Carassius auratus*], and various salmonids) are tetraploids, suggesting there may be advantages to high genetic diversity. It also appears that the dominance of alien species may be enhanced if there is strong selection during the invasion process for favorable genetic traits that enhance survival in new environments. Thus the introduction of several species of tilapia (*Oreochromis*) in California has resulted in large populations of hybrid origin that Costa-Pierce (2003) suggests are uniquely adapted to the polluted waters of southern California and may deserve recognition as at least two new taxa.

r-Selected life history strategy. Invading species with small adult size, high fecundity, rapid growth, and early maturity (r-selected traits) are often considered to have an increased likelihood of success because of their ability to colonize new areas rapidly once established (Ruesink 2005). Our analyses do not provide much support for this assertion. We found that introductions of small (< 10 centimeters [cm] adult length) and large (> 80 cm adult length) species tended to fail slightly more often (60% failure for small fishes, $n = 22$; 43% for large fishes, $n = 14$) than introductions of fishes of intermediate size (35% failure, $n = 49$), although large size contributed to multivariate models of invasion success in later stages of the invasion process (Marchetti et al. 2004b). Species with very low fecundity (< 100 eggs per female) tended to succeed only slightly more often than they failed (53% success, $n = 19$), even though low-fecundity fishes also tended to be livebearers or guarders of embryos, a strategy that definitely improves invasion success (3:1 success-to-failure ratio, or 75% success rate; $n = 49$). Fish with modest fecundities (1000 to 10,000 eggs per female) had a success rate (79%, $n = 33$) similar to that of high-fecundity fishes (>10,000 eggs per female; 71%, $n = 42$). As a measure of rapid growth and early maturity, we used an estimate of the typical maximum age of fish in the wild. Fish with low (< 4-year) or high (> 10-year) potential life spans showed no particular pattern of success, but fish with maximum ages of 4 to 10 years had a 79% success rate ($n = 43$). This suggests that r-selected tendencies are an advantage to a fish invader mainly if individuals also live long enough to survive periods of unfavorable conditions. Thus, parental care is a good predictor of the ability of a fish to become established, long life span is a good predictor of its ability to spread following establishment, and moderate size is a good predictor of its ability to become abundant (Marchetti et al. 2004b). Overall, it is evident that fish with almost any life history strategy can successfully invade, but success rates are likely to be highest in fish with intermediate or mixed characteristics (Marchetti et al. 2004b, 2004c).

Generalist diet or habitat. Moyle and Light (1996) predicted that the introduced fishes most likely to become established would be either omnivores or piscivores as adults: omnivores because they would not be limited by food supplies, piscivores because they were likely to be novel predators (see below). Our analyses revealed no such patterns, perhaps because most fishes are omnivorous or at least feed broadly on small invertebrates when young. Specialization is most likely at older ages. In contrast, the broad physiological tolerances of a majority of successful invaders suggest that many of them are habitat generalists, although there are successful specialists as well (e.g., brook trout [*Salvelinus fontinalis*], adapted for cold alpine lakes and streams). Some of the most widespread and abundant California invaders, however, are both habitat and dietary generalists (e.g., common carp, goldfish).

Rapid dispersal. Rapid dispersal is a two-edged sword for invading species. At the early stages of invasion, dispersal by juveniles into surrounding areas presumably decreases the probability of individuals finding each other for reproduction later on. On the other hand, rapid dispersal may reduce the probability of a colony being eliminated by stochastic environmental events. That 64% of successful fish invaders in California have some form of parental care suggests that limiting dispersal of early life history stages is advantageous to invading species. On the other hand, over 40% of successful invaders also have untended pelagic larvae. The California species known to have spread rapidly through aqueducts, with one exception, have pelagic larvae or juveniles.

Migratory behavior is generally regarded as antithetical to invasion success (Lockwood 1999) because of the difficulties invaders face if they require widely spaced habitats at different life history stages, with high mortality during migration. The failure of two species of catadromous eels (*Anguilla* spp.) to become established despite repeated (if small) introductions is presumably related to the lack of suitable spawning habitat in the ocean off the California coast. Likewise, introductions of both anadromous ayu (*Plecoglossus altivelis*) and Atlantic salmon (*Salmo salar*) failed despite massive, repeated introductions of juveniles into apparently suitable streams. Similar efforts to establish anadromous American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*), however, were successful (Dill and Cordone 1997). Thus migratory behavior per se does not appear to be a barrier to invasion.

Traits novel to the invaded community. Novel traits of an alien species are those traits, not found in existing members of the invaded fish community, that allow an invader to overcome biotic or environmental resistance (*sensu* Case 1991) through more efficient use of resources; different styles of predation (on naive prey); or low susceptibility to native predators, parasites, and diseases. Novel traits may be especially useful in altered environments. Thus the shimofuri goby apparently owes its success in California to novel traits such as its ability to feed on invertebrates (mostly alien species) not used by other fishes (Matern and Brown 2005); its aggressiveness toward other benthic species (fish and invertebrates) that use potential nesting sites; and its abundant, tiny larvae. Its pelagic larvae are about half the size of other fish larvae, suggesting an unusual niche for them (Moyle 2002). Brown trout (*Salmo trutta*) have been successful in multiple introductions in part because they spawn in autumn, and thus young-of-year brown trout are larger than those of spring-spawning native trout and so can dominate the best rearing habitats (Moyle 2002).

Invasion site characteristics

Invasion site characteristics hypothesized to favor frequent or rapid invasion include (a) similarity to source areas, (b) a high level of disturbance by human activity, and (c) low native species richness (Elton 1958, Orians 1986, Moyle and Light 1996). A serious problem in using such characteristics for prediction is that each invader uses the environment in a different way. For example, whether a stream can be successfully invaded by rainbow trout (*Oncorhynchus mykiss*) or brown trout (or both) depends on the timing and extent of high-flow events (Strange and Foin 1999, Fausch et al. 2001).

Similarity. Invasion areas likely to have the lowest environmental resistance are those most similar in their characteristics to the home areas of the invaders. Thus, in California, 31 of 66 extant native freshwater species have become established in other major watersheds of the state, including native species that exist only in small or declining populations in their native habitats (Moyle 2002). This success rate reflects the similarities of climate and flow regimes in adjacent watersheds. Fausch and colleagues (2001) found that rainbow trout became established in other regions of the world mainly in streams where flow regimes were similar to the flow regimes of their source streams in California. Likewise, invasive fishes from other climatic regions of North America largely failed to become established in California streams in watersheds that were protected from high levels of human disturbance (Baltz and Moyle 1993, Strange and Foin 1999). A major exception has been the redeye bass, which now dominates the fauna of some natural streams (Moyle 2002, Moyle et al. 2003).

Human disturbance. Human disturbance is clearly associated with high rates of successful invasion in freshwater systems (Moyle and Light 1996, Moyle 1998, Gido et al. 2004). Gido and Brown (1999) found that the number of large reservoirs in major watersheds of North America was a good predictor of the number of alien species, in large part because it reflected both the creation of new lacustrine habitats and a high degree of disruption of natural characteristics of rivers and streams. We have found a similar relationship between alien species and reservoirs in California watersheds, as well as relationships between alien species and various measures of land disturbance, such as miles of canals and extent of urban development (Marchetti et al. 2004b, 2004c). A key reason for these relationships is the presence of habitats that favor alien fishes, such as reservoirs, ponds, and streams with altered flow regimes. Our studies of Putah Creek demonstrate that the success of alien species can be at least partly reversed if a more natural flow regime is restored (Marchetti and Moyle 2001).

Species richness. On theoretical and experimental grounds, ecosystems with high species richness are hypothesized to be much less easy to invade than those with low species richness (Elton 1958, Chapin et al. 1998). For example, both Gido and Brown (1999) and Sax (2001) found that major watersheds with high species richness were less invaded than those with low richness. In contrast, Moyle and Light (1996) suggest that at the local scale, all freshwater systems are highly invasible, regardless of local species richness, depending on conditions at the time of invasion. This contention is supported at the global scale by Ruesink (2005) and at the local scale by Gido and colleagues (2004). In California, the two freshwater regions most invaded by alien fishes and aquatic invertebrates are the lower Colorado River (approximately 6 to 8 species of native fish fauna, mostly extirpated) and the Central Valley (approximately 28 species of native fish fauna, most still present). Both systems support 22 to 24 alien fish species, with new invasions taking place regularly (Moyle

2002). Even with such variability, we have demonstrated a positive relationship between native species richness and the number of successful invasions at the watershed scale (Marchetti et al. 2004a). Watersheds with the most native fishes also have the most diverse aquatic habitats and the most water, suggesting that the watershed is the appropriate scale for analysis. Stohlgren and colleagues (2002) found a similar pattern for plants.

Invasion process

The preceding sections indicate that factors contributing to successful invasions are complex and often confusing. One major source of confusion has been that different characteristics of both the invader and the invaded environment are likely to be important at different stages of the invasion process. The complex interactions among the traits of the invader and the characteristics of the invasion site are best described through multivariate models (Marchetti et al. 2004a, 2004b, 2004c). Developing these models requires understanding the invasion process.

A successful invader must survive a series of events: capture into a transport mechanism, transport to the invasion site, inoculation into an invasion site, initial establishment, population growth in the establishment area, spread to a broad area, and integration into the existing biotic community (Moyle and Light 1996, Kolar and Lodge 2001, Cohen 2002). Not surprisingly, most invasions fail (Moyle and Light 1996, Williamson and Fitter 1996). There are many reasons for failure, including demographic stochasticity (natural fluctuations of small populations), environmental stochasticity (impacts of extreme environmental events), marginal or unsuitable colonization sites (even if in a matrix of suitable sites), and initial dispersal failure (Sax and Brown 2000). The success of invaders with favorable biological characteristics in the face of such formidable obstacles is usually related to frequent invasion attempts (introductions by humans); the presence of novel, unusually favorable environments (created by human disturbance); release from natural enemies (predators, competitors, disease, parasites); and the superior nature, in terms of physiology and behavior, of species evolved as members of diverse continental assemblages (Elton 1958, Sax and Brown 2000, Marchetti et al. 2004c). In this section, we break the process into five stages for the purpose of discussion: transport, inoculation, establishment, spread, and integration (figure 2).

Transport. In these days of fast, global transportation systems, moving aquatic organisms over natural barriers is relatively easy. The movement of millions of fish each year by the aquarium trade and the diversity of organisms carried in ballast water of ships illustrate well how the need for transport is now one of the least important barriers to establishment. Nevertheless, closeness to the nearest source of individuals is an important variable in our models predicting invasion success (Marchetti et al. 2004a, 2004b, 2004c), presumably because it is also related to the likelihood of multiple introductions and of species that are "preadapted" for local conditions.

Inoculation. Many invasions fail because invading organisms are introduced into habitat that is unsuitable or marginal in quality, even if the surrounding environment seems to be suitable (Sax and Brown 2000). Indeed, most species exist in only a small subset of the total habitat available, so it would seem likely that many invasions should fail at this stage, with no reproduction taking place. For example, golden shiners (*Notemigonus crysoleucas*) are the most commonly used bait minnow in California and are probably subject to hundreds of releases annually by anglers in California lakes and streams. Yet the number of isolated populations established from bait bucket introductions is relatively small, suggesting that most fish are released in places where they are quickly consumed by predators or fail to reproduce. Nevertheless, if bait fishing with golden shiners continues to be permitted, the species should eventually become established in all suitable habitats. This inevitability is reflected in our multivariate models,

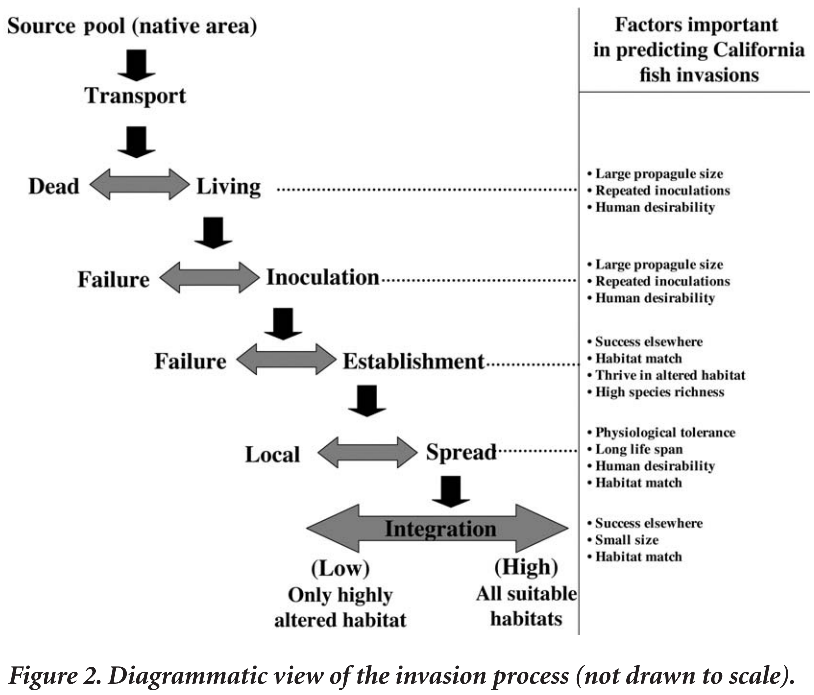

Figure 2. Diagrammatic view of the invasion process (not drawn to scale). At each step, individuals of species encounter factors that cause most of them to die. Successful invasion requires surviving each stage of the process. Once a species is established, a combination of biotic and environmental factors determines whether it will spread and eventually be integrated into the existing assemblages of species. In this diagram, factors affecting success in the transport stage are presumed to be the same as those in the inoculation stage.

in which propagule pressure (number of individuals introduced, usually through multiple introductions) is one of the most important factors related to successful invasions (Marchetti et al. 2004c), a finding consistent with the review of Lockwood and colleagues (2005). We found that 70% of all introductions with fewer than 100 individuals ($n = 40$) failed, and that 68% of all failed introductions ($n = 41$) consisted of fewer than 100 individuals. Yet large propagule size is no guarantee of success: Ayu, Atlantic salmon, and Bonneville cisco (*Prosopium gemmiferum*) failed to become established despite repeated introductions of thousands of individuals into seemingly appropriate habitats.

Establishment. Once the inoculated individuals establish a beachhead population, reproduction becomes essential for establishment. For temporary establishment, the characteristics of the invaders simply have to be compatible with those of the invasion site, so they can survive long enough to reproduce. A new population, however, is subject to extermination by local environmental events (e.g., a sudden flood) or random demographic fluctuations. Thus, for permanent establishment, the initial success of a colony must be followed by dispersal from the invasion site. For example, Arctic grayling (*Thymallus arcticus*) have at least twice established reproducing populations in single California lakes that lasted approximately 25 years before dying out as the result of local environmental conditions (Moyle 2002). On the other hand, Jeschke and Strayer (2005) indicate that over half of the fish species that were moved between North America and Europe, in either direction, and introduced in the wild became permanently established.

Spread. Once a species has become firmly established in an area, rapid spread of the population becomes an asset for long-term persistence. Biologically, a high percentage of successful fish invaders in California have parental care, which suggests that a compromise of limited dispersal in early life stages with rapid dispersal in later stages may be advantageous. Our models also indicate that a long life span, closeness of place of origin, and being a predator on invertebrates or fish are associated with aliens now widespread in the state (Marchetti et al. 2004c), although these characters are not associated with successful fish invaders in the Laurentian Great Lakes (Kolar and Lodge 2002). Virtually all studies agree that the most common characteristic of widespread alien vertebrates is desirability to humans. Common carp, for example, became widespread in the 19th century because of their often exaggerated desirability as a food and game fish.

Integration. A successful invader eventually becomes integrated into local ecosystems to the point where it responds to local environmental conditions and to other members of the biotic community in ways apparently indistinguishable from those of native species. In Suisun Marsh, for example, native and alien fishes largely showed similar population fluctuations in response to changes in conditions over a 24-year period (figure 3), although native fishes showed slower recovery from adverse (drought) conditions (Matern et al. 2002). Many successful invaders become integrated and appear to have only minor negative effects on other species. This fits with the idea that some communities are undersaturated with species (Caley and Schluter 1997), although scientists' understanding of how alien species fit into their host communities is very incomplete (Shea and Chesson 2002). Typically, integration occurs in fish assemblages inhabiting disturbed areas, where other alien species are already present.

How rapidly a species disperses at the beginning of the invasion process and how abundant it eventually becomes are factors strongly related to whether or not it is likely to be regarded as a nuisance species. Thus the inland silverside (*Menidia beryllina*) spread through much of central and southern California in about 25 years and was widespread

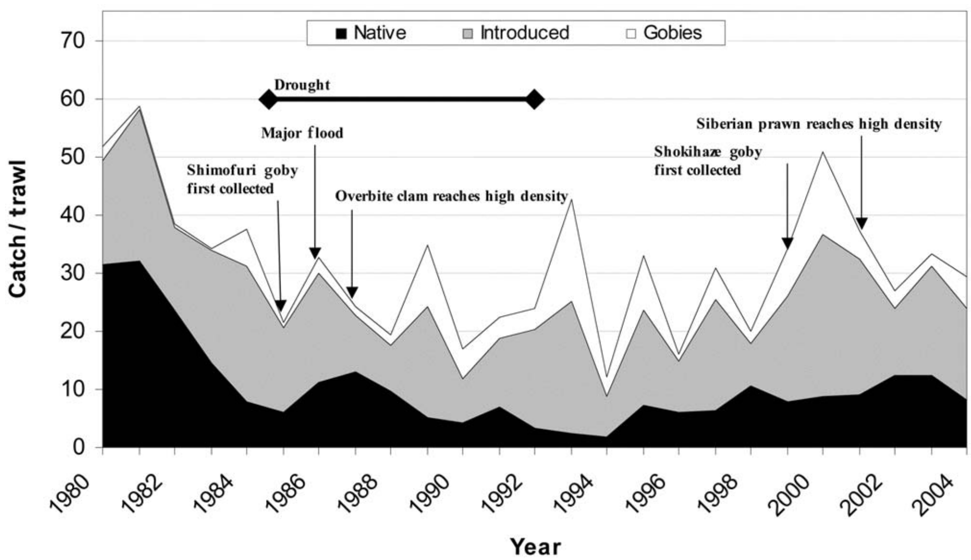

Figure 3. Trends in the populations of native and alien fishes in Suisun Marsh, 1980–2004. The trends are based on the average number of fish caught per trawl haul, assuming 22 trawls per month for all months of every year (approximately 240 trawls per year, updated from Matern et al. 2002). Gobies are graphed separately, because the three goby species are alien and the numbers are dominated by the shimofuri goby, which invaded in the 1980s. Noted on the figure are a major drought, which increased salinities in the marsh, and the first record of the shimofuri goby (arrow on left).

before anyone realized it was probably having detrimental impacts on other fishes through predation on larvae (Moyle 2002). Unfortunately, predicting the impact of an alien species is best done by examining its impact elsewhere (Ricciardi 2003), which may be largely academic if the species is already spreading.

Predicting successful invasions

A successful invasion happens when an invader's symbiotic traits, biological characteristics, and invasion site (at multiple scales) are all favorable (Williamson 1996). The complexity of this three-way interaction means that there are many different combinations of characters that can lead to successful invasions in a given geographic area. Marchetti and colleagues (2004a, 2004b, 2004c) have created numerous multivariate models to look for commonalities in failed and successful invasions. The main points of this body of work suggest that (a) there is a suite of alternative models to predict successful invasions, (b) different models fit different stages of the invasion process, and (c) all models have exceptions (i.e., are statistical and not absolute in their predictive power). Analyses by Gido and colleagues (2004) and Ruesink (2005) show similar results.

The best statistical predictors of a successful invader are the most obvious ones: past history of successful invasion, high desirability by humans, ability to thrive in human-altered habitats, good match between the characteristics of the source environment and the recipient environment, and large propagule size (multiple introductions or more than 100 individuals, or both). The more of these traits a fish possesses, the more likely it is to be introduced and established. Unfortunately, many successful fish invaders may have only one or two of these characteristics, and even these may not be revealed until after the invasion has succeeded. For example, bigscale logperch came into California as a small number of individuals in a shipment of largemouth bass (*Micropterus salmoides;* Moyle 2002). The presence of logperch was not detected until they had escaped from the bass ponds and become locally abundant. At the time of discovery, the bigscale logperch had not even been described as a distinct species, nor were the characteristics known that enabled it to thrive in California (e.g., ability to live and breed in warm, muddy sloughs), because they differ from those of most other members of the same genus (*Percina*). The bigscale logperch is now abundant and widespread in the state, a situation that was largely unpredictable on the basis of knowledge at the time of introduction. In contrast, the huge success of common carp in California was, in retrospect, completely predictable because carp possesses all of the favorable characteristics listed above, as well as a life history pattern very similar to that of many native cyprinids (Moyle 2002).

Perhaps a more useful approach is predicting which potential invaders are likely to have detrimental effects. The bigscale logperch, for example, although widely distributed, is a small species with no known (or likely) negative effects on other fishes or aquatic environments. The common carp, however, is widely regarded as a pest, although its negative effects in California are largely speculative (derived from studies of other areas). Of course, the perception of detrimental effects changes through time. For example, the changing ethnic composition of California may cause a shift in carp status from pest back to favored species (its status when first introduced in the 19th century). The black basses (*Micropterus* spp.) and other centrarchids have always been regarded with great favor in the state as sport fish, even though their negative impacts on native fishes have been documented (Moyle 2002). Thus nuisance status in fish is clearly a cultural designation, but increasingly it is being defined in terms of having a negative impact on native fishes, amphibians, and invertebrates or on existing fisheries. Ruesink and colleagues (1995) suggest that, given the uncertainties in predicting invasion success or in predicting a subsequent change in status from naturalized species to pest, the best strategy is to adopt the precautionary principle: Allow an introduction or invasion to proceed only if it can be demonstrated *not* to be harmful. Thus, eradication of the predatory northern pike (*Esox lucius*) from the single reservoir into which it has become established in California is the best option for management, because its past invasion history suggests it will have a detrimental effect on native fish populations (Moyle 2002).

Do fish invaders alter the systems they invade?

How much alien fishes have altered California ecosystems is often hard to determine, because the ecosystems typically are already altered by human activities, have experienced multiple invasions, and have been studied mainly after invasions have taken place. For example, the shimofuri goby became a major invader of the complex fish community of Suisun Marsh, made up of both native and alien species, yet it appears to have had no impact on other fishes (figure 3). Additions of other fish invaders to the marsh fauna have not been accompanied by disappearances of native species in the past 50 years (Moyle 2002), so total fish species richness has increased. In contrast, the invasion of predatory redeye bass into the Cosumnes River has decimated the native fish fauna—many sections of stream now contain mainly redeye bass (figure 4; Moyle et al. 2002).

One of the species that declines in the face of centrarchid bass predation is the principal native piscivore in central California streams, the Sacramento pikeminnow (*Ptychocheilus grandis;* Gard 2004). The pikeminnow, however, has been introduced into the Eel River drainage in coastal California, where it has become widespread and abundant, causing changes in the structure of the native fish assemblages (Brown and Moyle 1997). White and Harvey (2001) suggest that pikeminnow predation may eventually eliminate some native species from the river. Curiously, the combination of pelagic predation by pikeminnows and benthic predation by two native sculpin (*Cottus*) species is apparently preventing the spread of another fish invader to the system, speckled dace (*Rhinichthys osculus;* Harvey et al. 2004).

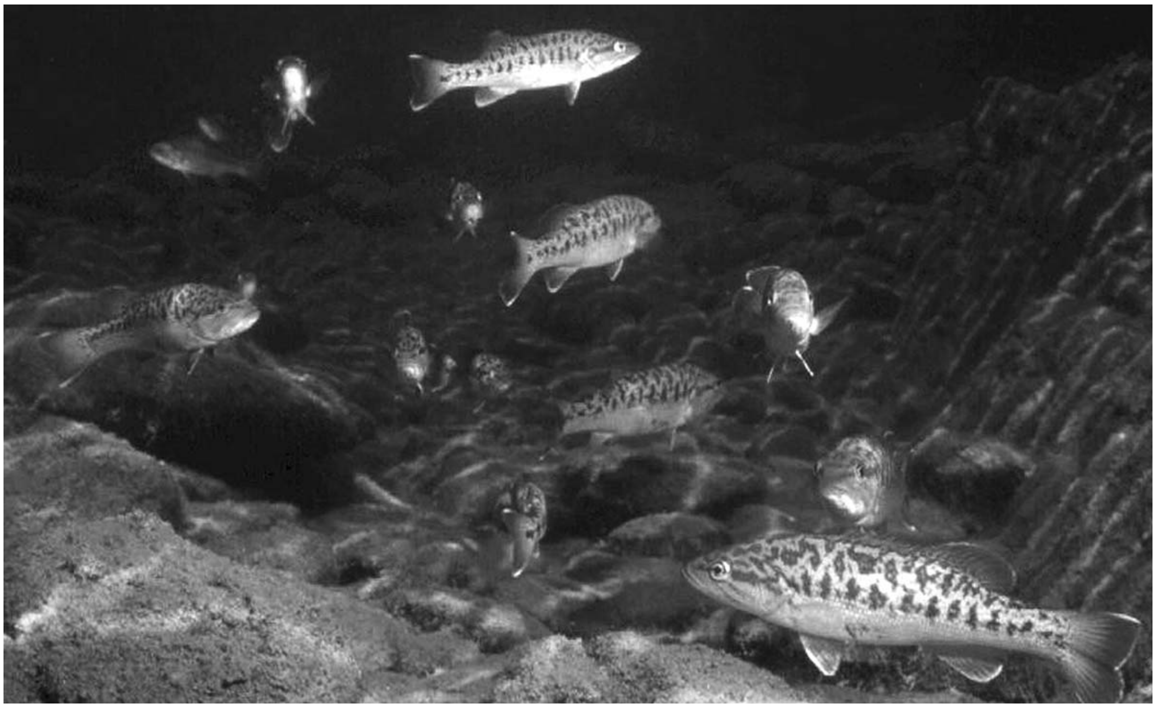

Figure 4. Redeye bass in a pool in the Cosumnes River, California. This alien species can constitute over 90% of the fish present in long stretches of a river once dominated by native species. It is probably more widely distributed now in California than it is in its native range in the southeastern United States. Photograph: Juan Cervantes.

Conclusions

There is no universal set of characters that can predict which aquatic invasions will succeed or which fishes are likely to become nuisance species. Our analyses of California fish invasions do demonstrate, however, that there are a number of characters, both of the invader and of the place being invaded, that increase the probability of an invader being successful. In general, a fish species is likely to be a successful invader if (a) it has a history of successful establishment outside its native range; (b) it has characters likely to promote success at multiple stages of the invasion process; (c) it is introduced into a habitat that more or less matches its native habitat; (d) it is introduced into a region with comparatively high fish species richness, including other alien fishes; and (e) it is introduced repeatedly, with propagule sizes exceeding 100 individuals. Beyond this, there are a wide variety of characteristics, often confined to a particular set of species or environments, that increase (or decrease) the likelihood of successful invasion. Clearly, if a potential invader is well studied before being allowed into a new area, the potential for predicting invasion success and impact will be greatly increased. As much as possible, however, introductions of more alien species should be prevented (Mooney et al. 2005). Given the potential for a new invader to cause harm, even being able to predict success or failure with 85% to 95% confidence may be too high a risk to take (Smith et al. 1999).

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