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CHAPTER 24

Alien Fishes

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Introduction

Over 90 species and subspecies of fish have been introduced into the waters of California; 69 of these have become established (Dill and Cordone, 1997). Although a majority of these fish are freshwater species, alien species have also become established in estuaries, bays and open water marine habitats along the Pacific Coast (Dill and Cordone, 1997; Moyle, 2002). So far, alien marine species that have achieved the greatest success are estuarine and anadromous species, although few attempts have been made to introduce true (stenohaline) marine species into coastal California waters (Dill and Cordone, 1997). The only major attempt in California to move marine fishes into new waters was the translocation of over 30 species of marine fish into the Salton Sea in southern California, resulting in the establishment of 4 species. However, given the widespread and on going introduction of alien marine organisms into coastal environments (Carlton, 1996, 2000), it is likely that additional alien fishes will become established in California. The purpose of this chapter is to describe the species and patterns of alien fish invasions in the marine environments of California in order to provide a better understanding of their past, present, and future impacts.

We begin this chapter by providing an overview of marine fish introductions to date. We then provide accounts of alien fishes currently found within the marine (estuaries and open water marine) environments of California, including their origin, distribution and effects on other marine organisms, especially fishes. We conclude by briefly answering the following questions: 1) Why are there so few successful alien fishes in the marine environments of California?, 2) What has been the impact of alien fishes in the marine environments?, 3) What marine environments in California are most invasible?, and 4) What is the future of alien fishes in California, especially in conjunction with environmental change?

Overview of Marine Introductions

Introductions into marine systems have been increasing as a result of intentional movement of fish and as by-products of other human activities, such as transoceanic shipping, aquaculture, and the artificial connection of major water bodies (Cohen, 1987; Baltz, 1991; Cohen and Carlton, 1998). The most common means of by-product introductions is the movement of organisms in ballast water of ships. However, alien organisms have also been introduced following their attachment to ship hulls and to oysters and other invertebrates brought in for food or bait. In addition, introductions of plants and invertebrates that adversely affect fish populations through alteration of food webs and habitats have been on the rise (Caddy, 1993; Ruiz et al., 1997; Cohen and Carlton, 1998; Berdnikov et al., 1999). The full extent of alien introductions into marine waters worldwide has been difficult to determine given that accurate species accounts are largely unavailable, many introductions are not reported, and many species are considered to be cryptogenic (place of natural origin unknown) (Baltz, 1991; Cohen and Carlton, 1998). Nonetheless, alien fishes are now common in marine waters worldwide (Carlton, 1985; Baltz, 1991).

In general, intentional and by-product fish introductions have been most successful and have had the greatest impact within estuaries and inland seas (Baltz, 1991). Moyle (1999) attributed this success to the fact that estuaries and inland seas are often significantly altered through water diversion, development and pollution; they are also places where the frequency of introductions is high and species intentionally introduced are often well matched to the environment. In addition, large numbers of non-fish invaders have become established in these waters, resulting in significant changes to the function and structure of the ecosystems (Cohen and Carlton, 1998). These changes may make these systems even more vulnerable to invasion through a process termed invasional meltdown by Simberloff and Van Holle (1999). Invasional meltdown occurs when one or more alien species change the physical or biological conditions present in an ecosystem, which in turn facilitates the invasion of additional alien species. In this situation both the biotic resistance (e.g., competition and predation by native organisms) and environmental resistance (physical and chemical conditions adverse to establishment) to invasion are reduced. The often drastic changes in aquatic communities caused by alien species in estuaries and inland seas suggests possible scenarios for other marine environments as alien species become more pervasive. In open water marine systems, the introduction of

TABLE 24-1
Alien Fishes Introduced Into Marine Waters of California

Species	*Date*	*Reason*	*Environment*	*Marine Status*
Striped bass, *Morone saxatilis*	1879	food, sport	F, E, B, M	Common
American shad, *Alosa sapidissima*	1871	food, sport	F, E, B, M	Common
Brown trout, *Salmo trutta*	1893	sport	F, E, M	Rare
Western mosquitofish, *Gambusia affinis*	1922	insect control	F, E	Locally abundant
Threadfin shad, *Dorosoma petenense*	1954	forage	F, E	Locally abundant
Rainwater killifish, *Lucania parva*	1950s	by-product	E, B	Locally abundant
Wakasagi, *Hypomesus nipponensis*	1959	forage	F, E, B?	Invading
Chameleon goby, *Tridentiger trigonocephalus*	1960	by-product	B, M	Locally common
Yellowfin goby, *Acanthogobius flavimanus*	1960s	by-product	E, B, M	common, spreading
Mozambique tilapia, *Oreochromis mossambica*	1960s	aquaculture	E, B	Uncommon
Redbelly tilapia, *Tilapia zilli*	1960s	weed control	F, E	Locally common
Sailfin molly, *Poecilia latipinna*	1960s	pet release	F, E, B	Locally abundant
Inland silverside, *Menidia beryllina*	1967	insect control	F, E, B	Locally abundant, spreading
Shimofuri goby, *Tridentiger bifasciatus*	1980	by-product	F, E	Invading
Shokihaze goby, *Tridentiger barbatus*	1995	by-product	E, B	Invading
American eel, *Anguilla rostrata*.	1874	food	F, E, B, M	Failed
Milkfish, *Chanos chanos*	1877	food	E, B, M	Failed
Ayu, *Plecoglossu altivelis*	1961	food, sport	F, E, B, M	Failed
Atlantic salmon, *Salmo salar*	1874	Food, sport	F, E, B, M	Failed
Tautog, *Tautoga unitis*	1874	Food	B, M	Failed

NOTE: Date corresponds to the date of initial stocking or when species was first discovered. F = freshwater, E = estuarine, B = Bay, and M = marine.

alien species has thus far had little impact, which is likely the result of few species successfully invading these habitats (see Baltz, 1991 for exceptions).

Patterns of fish introductions into California marine waters are similar to those observed worldwide. Twenty fish species, which inhabit estuaries and open marine waters in their native range, are known to have been introduced into California. Fifteen of 20 species were introduced intentionally, to provide sport, food, pets, and control of nuisance organisms (table 24-1). Only 5 of these intentional plants were unsuccessful: American eel, Atlantic salmon, ayu, milkfish and the only true open water marine introduction attempt, the tautog (Dill and Cordone, 1997). In addition, at least 2 other species of catadromous eels have been found in California waters but they seem to be individual escapees from illegal attempts to import them for food (Dill and Cordone, 1997). A majority of the established alien fish species are found in estuaries and bays, although two anadromous species, striped bass and American shad, are commonly found in the open ocean waters off the California coast.

While only 5 of the 15 alien marine fishes found within estuarine and coastal habitats of California are the result of by-product introductions (table 24-1), by-product introductions have been increasing in recent years (Moyle, 1999). In fact, Cohen and Carlton (1998) have dubbed the San Francisco Estuary "the most invaded estuary in the world" as a result of the phenomenal numbers of by-product introductions of plants, invertebrates, and fish. The most common means of by-product introductions of alien fish into California's waters is in the ballast water of ships. Such is the case with the chameleon goby, yellowfin goby, shimofuri goby, and shokihaze goby. The most recent of the ballast water introductions is the shokihaze goby, which was first captured in the San Francisco Estuary in 1997 and has recently become abundant. The rainwater killifish apparently arrived in the railroad cars full of oyster shells and spat brought in for rearing in San Francisco Bay. Other fish species may have already found their way into California waters, but remain undetected.

Species Accounts

In the following section, we provide descriptions of alien marine species currently found in California including their origin, current patterns of distribution, environmental tolerances relating to potential range expansions and their known and potential effects on the aquatic communities. Our discussion is limited to species that are likely to occur on a regular basis in water with salinities greater than 10–15 ppt. Consequently, we exclude many freshwater fishes that occasionally occur in estuarine environments. The species accounts are organized by physiological tolerances: a) euryhaline marine species, b) estuarine species, c) anadromous species, and d) euryhaline freshwater species.

Euryhaline Marine Species

CHAMELEON GOBY

The chameleon goby (Gobiidae) is one of three species from the genus *Tridentiger* introduced into California waters (see fig. 24-1). It was first found in Los Angeles harbor in 1960 and was found in San Francisco Bay in 1962 (Dill and Cordone, 1997). More recently (1995 and 1998), the chameleon goby has been found in San Diego Bay (Pondella and Chinn, 2005) providing evidence that its range continues to expand either through continued shipping transport or active migration. It is native to the Asian Pacific and is typically restricted to marine habitats, being found only occasionally in brackish waters (Matern and Fleming, 1995). The chameleon goby was likely introduced into California waters through ballast water transport (Matern and Fleming, 1995) but attachment to

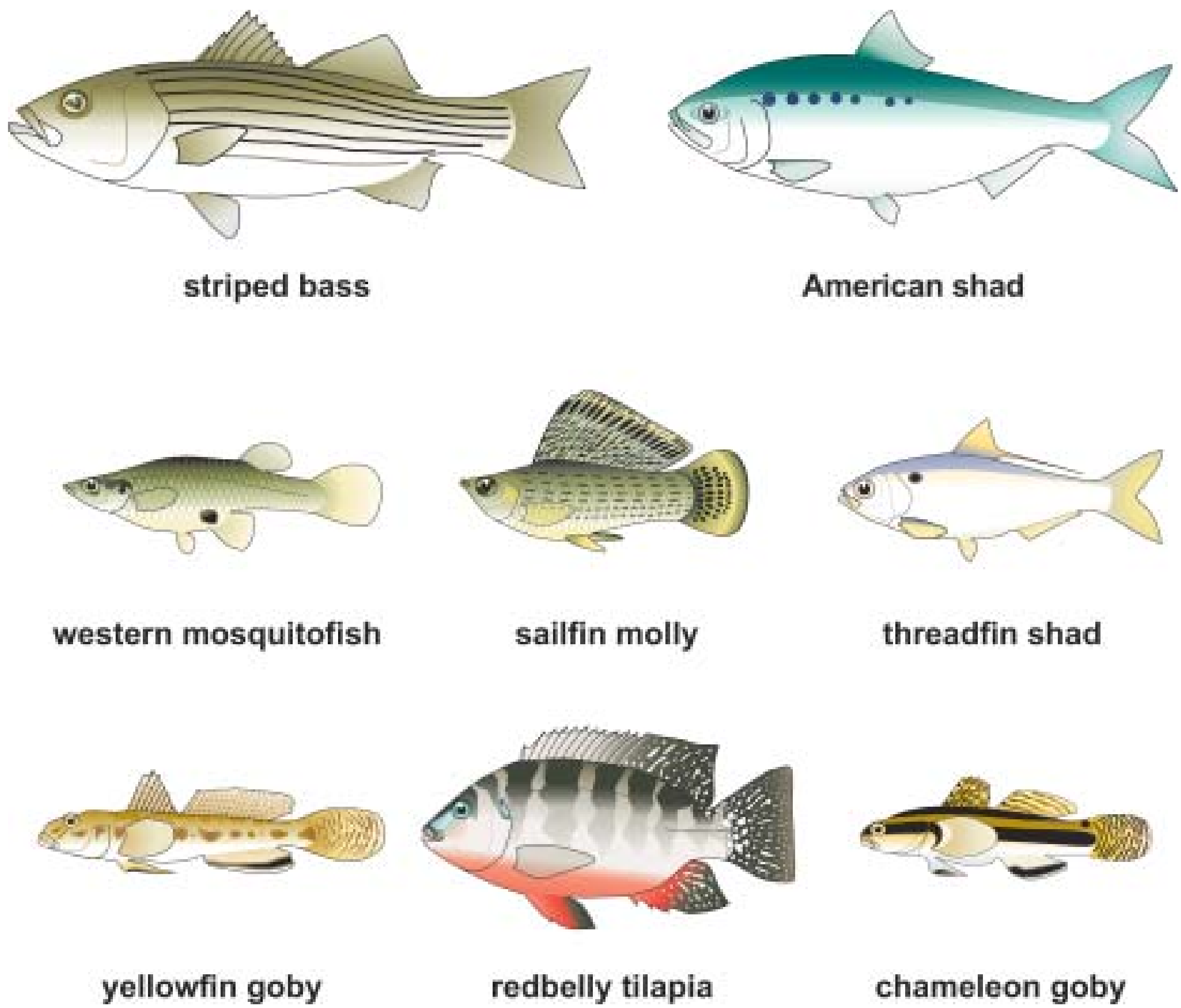

FIGURE 24.1 Examples of alien fishes that have established populations in coastal marine waters in California.

fouling organisms on ships and on imported giant Pacific or Japanese oysters have also been suggested as transport mechanisms (Dill and Cordone, 1997).

Within San Francisco Bay, chameleon goby rarely exceed 90 mm in total length and are typically short lived, with only a few individuals reaching two years of age (Baxter et al., 1999). Chameleon goby are found in a wide range of temperatures, but appear to have a restricted distribution depending on salinity. In San Francisco Bay, they are routinely found in salinities ranging from 10–35 ppt (mean salinity 27 ppt), but are most abundant in waters with salinities between 24–32 ppt (Baxter et al., 1999).

The impact of chameleon goby on native fishes has not been investigated. Given their benthic habits, they may be interacting competitively with other small bottom fishes, which in San Francisco Bay, includes species in the families Gobiidae (longjaw mudsucker, bay goby, cheekspot goby, and arrow goby); Cottidae (staghorn sculpin); and Batrachoididae (plainfin midshipman). However, their low abundance suggests that it is unlikely that they are having significant adverse effects. Between 1980 and 1995, chameleon goby made up only a small percentage ($<1\%$) of the total otter trawl catch of fish in San Francisco Bay (Baxter et al., 1999).

YELLOWFIN GOBY

The yellowfin goby is native to the shallow coastal waters of Japan, Korea, and China (see fig. 24-1). They were first collected in the San Francisco Estuary in 1963 and were found in the Los Angeles Harbor around 1977 (Brittan et al., 1963; Moyle, 2002). These populations were likely established as a result of the transfer of larvae or small juveniles in the ballast water of ships. From these two areas, yellowfin goby have spread along the California coast as far north as Tomales Bay. In northern California, they are most abundant between Elkhorn Slough and Tomales Bay (Miller and Lea, 1972). In southern California, they have spread south as far as San Diego County and have been captured in various coastal lagoons and marshes (Swift et al., 1993) including the Tijuana Estuary (Zedler, Nordby and Kus, 1992) and Sweetwater Marsh National Wildlife Refuge in San Diego Bay (Gregory et al., 1998). Within the San Francisco Estuary, the yellowfin goby is one of the most common bottom fishes and it continues to expand its range into both fresh and brackish water habitats (Baxter, 1999).

The effects of the introduction of the yellowfin goby on California fishes are largely unknown, due to the lack of studies.

One exception is Usui (1981), who found no impact of yellowfin goby on native staghorn sculpin in Newport Bay. Nonetheless, it appears that given their high abundance, broad tolerance of environmental conditions (freshwater to 40 ppt; temperatures to 28°C), relatively large size (17 + cm SL), and predatory feeding habits as adults, yellowfin goby may be adversely affecting other bottom fishes found within the same habitats. One native species, which appears to be especially vulnerable is the tidewater goby, *Eucyclogobius newberryi,* a federally threatened species (U.S. Fish and Wildlife Service, 1994). The tidewater goby is a small (<50 mm SL) benthic fish, which is endemic to the coastal lagoons, marshes and creeks of California (Swift et al, 1989; Moyle, 2002) and would seem to be very vulnerable to yellowfin goby predation. Fortunately, the yellowfin goby has so far had difficulty in establishing itself in small lagoon habitats where tidewater goby are most likely to be found. This may be because these small lagoon habitats typically are disconnected from the ocean most of the year, which results in salinities too low for successful yellowfin goby reproduction (breeding requires at least 5 ppt; Moyle, 2002).

Estuarine Species

SHIMOFURI GOBY

The shimofuri goby is the second of three species within the genus *Tridentiger* to become established into California waters. It is native to Japan and the coast of northern Asia (Moyle, 2002). It was likely introduced into the San Francisco Estuary through ballast water discharge (Matern and Fleming, 1995). Shimofuri goby were first identified in Suisun Marsh, in the upper San Francisco Estuary in 1985, thus were likely introduced into the San Francisco Estuary a few years earlier. Following its introduction, it quickly became one of the most abundant species in the estuary, reflecting its high reproductive potential and pelagic larvae (Matern, 1999). It is now widely distributed in tidal habitats, but prefers shallow water habitat (<2 m) in areas with complex structure including rocks, logs, and tule root masses, which are used for cover and breeding (Moyle, 2002). The shimofuri goby inhabits fresh and estuarine waters with salinities up to 17 ppt and is tolerant of a wide range of temperatures (to 37°C) (Matern, 2001). It is eclectic in its diet, but often eats alien invertebrates (barnacles, hydroids) that have few other predators.

While the salinity tolerances of the shimofuri goby will keep it from colonizing new areas by moving through the ocean, it has demonstrated a surprising capacity to move through fresh water. It has been able move through the California Aqueduct and colonize reservoirs in southern California. By 1990, the shimofuri goby was found in Pyramid Reservoir, approximately 513 km from the San Francisco Estuary and in Piru Creek below the reservoir (Matern and Fleming, 1995). This range expansion indicates that the shimofuri goby can be expected in any of the reservoirs fed by water from the California Aqueduct and will ultimately colonize the estuaries downstream from them (Moyle, 2002).

The shimofuri goby is a highly aggressive species, especially adult males, which defend territories vigorously. In a laboratory experiment it was found that the tidewater goby was considerably disadvantaged during aggressive encounters with the shimofuri goby and was even preyed upon by larger shimofuri gobies (Matern, 1999). These types of aggressive encounters can be expected with other bottom dwelling fishes with competition being most intense for limited resources such as shelters for breeding and predator avoidance. Fish species that are most likely to be adversely affected by shimofuri goby are bottom fishes found within similar habitats such as prickly sculpin, staghorn sculpin, and tidewater goby.

SHOKIHAZE GOBY

The shokihaze goby is the most recent *Tridentiger* species to become established in the San Francisco Estuary. It was first collected in 1997, but has increased in abundance and distribution in recent years (Slater, 2005). As is the case with the other *Tridentiger* species, the shokihaze goby was probably introduced into the San Francisco Estuary as a result of a ballast water transfer from Asia.

Little is known about the shokihaze goby in the San Francisco Estuary, except that it has been found in both fresh and brackish water environments with salinities as high as 28 ppt (Greiner, 2002). According to Dotu (1956), shokihaze goby in Ariake Sound, Japan, can live longer than 3 years and reach a size greater than 120 mm, but may mature as early as the first year at a size of 40–85 mm. The largest shokihaze goby captured in the San Francisco Estuary was greater than 120 mm total length (Steve Slater, CDFG, personal communication). In Japan, shokihaze goby inhabit oyster beds on muddy tide flats (Dotu, 1956). Within the San Francisco Estuary, shokihaze goby are typically found in deep channel habitats. The diet of shokihaze goby in the San Francisco Estuary is unknown, but those captured in Ariake Sound consumed annelids, small crustaceans squid, and young fish including other gobies (Dotu, 1956). The shokihaze goby thus has the potential to have negative effects on small benthic fishes and invertebrates in newly invaded habitats.

RAINWATER KILLIFISH

The rainwater killifish (Fundulidae) is native to the eastern United States from Cape Cod to Texas, with inland populations in New Mexico and Florida (Moyle, 2002). The first California specimens were found in 1958 in both fresh and brackish waters tributary to San Francisco Bay (Dill and Cordone, 1997). The original source of introduction in the San Francisco Bay is unknown, but may have resulted from a ballast water introduction or as a hitchhiker (as eggs) on transported eastern oysters (Hubbs and Miller, 1965). Rainwater killifish are currently found in low abundance in the San Francisco Estuary, but are locally abundant within salt marshes in the lower bay (Moyle, 2002). Outside San Francisco Bay, rainwater killifish have been collected in Orange County (Irvine Lake), Riverside County (Arroyo Seco Creek—tributary of Vail Lake) and Santa Barbara County (Swift et al., 1993). The introduction of the Irvine Lake and Arroyo Seco Creek populations may have resulted when game fish collected from the Pecos River, New Mexico, were introduced into the region (Hubbs and Miller, 1965; Dill and Cordone, 1997).

Because of the small size of rainwater killifish, their current low abundance, and diet consisting mostly of small invertebrates including copepods and mosquitos (Dill and Cordone, 1997), it is unlikely that they are having a significant impact on the native species found within the system. They are, however, capable of tolerating both fresh water and highly saline conditions (twice that of seawater), so it is likely that they will expand their range along the coast of California, if they have not done so already. Rainwater killifish are easily confused with the widely introduced western mosquitofish; thus its current range may be under-estimated.

Anadromous Species

STRIPED BASS

The striped bass (Moronidae) is a large voracious piscivore native to the streams and bays of the Atlantic Coast and the Gulf of Mexico extending from the St. Lawrence River in the north to Louisiana in the south (see fig. 24-1). It was first introduced to the Pacific Coast in 1879 with a plant of 135 fish from the Navasink River, New Jersey released into the San Francisco Estuary. A second plant of 300 fish from New Jersey was made in 1882 (Dill and Cordone, 1997). The introduction of striped bass was so successful that a commercial fishery for striped bass began operation as early as 1888, and by 1899 over 1.2 million pounds of striped bass were harvested (Skinner, 1962).

Striped bass are now widely distributed along the Pacific Coast from 25 miles south of the Mexico border to British Columbia (Moyle, 2002). Warm water conditions associated with El Nino events result in its greatest abundance and distribution in marine waters (Moyle, 2002). Despite its broad distribution, the main breeding population for striped bass on the Pacific Coast remains within the San Francisco Estuary. A smaller breeding population is also present in Coos Bay, Oregon (Moyle, 2002). Striped bass move regularly between salt and fresh water, but spend a majority of their life cycle in estuaries (Moyle, 2002). Striped bass migrate seasonally into rivers in late winter and early spring to spawn with the largest migration occurring up the Sacramento River.

Striped bass are one of the most abundant fish in the San Francisco Estuary, although their numbers have been steadily declining since the 1930s from multiple interactive causes (Moyle, 2002). In recent years there has been a decline in carrying capacity of juveniles as a result of reduced food supplies, which may be partly responsible for the overall decline in this species (Kimmerer et al., 2000), although adult fish have inexplicably increased in abundance in recent years. The marine sport fishery may also have contributed to the decline because many of the fish caught are the largest, oldest, and most fecund females (W. A. Bennett, UC Davis, pers. comm.).

The impacts of striped bass on native fishes in California were likely to have been most severe during the initial years following establishment (Moyle, 2002). During this time, striped bass probably contributed to the decline of native fishes, including salmonids, through predation. Striped bass may also have played a major role in the extinction of native estuarine fishes, but this is difficult to prove with existing information (Moyle, 2002). The continued anthropogenic degradation of estuarine systems in California has made it particularly difficult to determine the effects that striped bass have had on native species. For instance a considerable decline in salmon abundance occurred at the same time as the historic increase in striped bass abundance. Yet, it is difficult to untangle striped bass predation as a cause of salmon decline from other factors that occurred simultaneously, such as excessive fisheries, alteration of the estuary through gold mining activities, watershed development, and pollution.

AMERICAN SHAD

American shad are large clupeids (up to 48 cm FL in California waters) native to the Atlantic Coast from Labrador to the St. Johns River, Florida (Moyle, 2002) (see fig. 24-1). Stemming from their popularity as a food fish on the east Coast, American shad were introduced into California waters in 1871 (Dill and Cordone, 1997). Between 1871 and 1881, over 800,000 fry captured from New York were transported and introduced into California in the Sacramento River (Dill and Cordone, 1997). American shad quickly increased in number and by 1879 a commercial fishery became established (Skinner, 1962). Since their introduction they have rapidly expanded their range to include waters from Todos Santos Bay in Mexico to Cook Inlet, Alaska, with spawning runs occurring in a number of rivers, including the Columbia River (Moyle, 2002). An additional population has also become established in the Kamchatka Peninsula in Russia (Moyle, 2002).

The Pacific Coast populations of American shad spend 3–5 years of their life at sea where their migration routes and activities are largely unknown. What little direct information exists on extent of American shad migrations consists of data collected from a tagging study conducted in the Sacramento River, which found that tagged fish migrated as far south as Monterey Bay and north to Eureka (Moyle, 2002). The rapid and widespread colonization of habitats thousands of kilometers away from the point of original stocking clearly indicates that American shad have the ability and tendency to migrate considerable distances. Return migrations to the rivers in California tend to take place beginning in autumn and extend through early June with largest migrations occurring as water temperatures warm to 17–24°C. As juveniles, American shad rear within rivers and estuaries feeding on a variety of prey including zooplankton, mysid shrimp, copepods and amphipods (Moyle, 2002). Juveniles typically spend 1-2 years in fresh water and brackish water habitats prior to migrating to the sea, with the timing being largely influenced by environmental conditions (Moyle, 2002).

The effect that the American shad have had on other species is unknown, but is unlikely to be significant, given their plankton-feeding habits. While their numbers appears to be lower today than they were historically, they still support a popular sport fishery in California (Moyle, 2002).

WAKASAGI

The wakasagi, a smelt (Osmeridae) native to Japan, was introduced into California reservoirs in the 1950s as a forage species. It was originally introduced under the name pond smelt, *Hypomesus olidus*, because it was assumed to be the same species as the native delta smelt, *Hypomesus transpacificus*, now a state and federally threatened California endemic (Stanley et al., 1995; Moyle, 2002). In Japan, wakasagi are anadromous and are found in bays estuaries and coastal waters (Utoh, 1988). The wakasagi has slowly expanded its range in California, which now includes the San Francisco Estuary (Aasen et al., 1998).

The history of this introduction reflects the casual attitude toward introductions of fish that once prevailed in California. By the 1950s, numerous cold-water reservoirs existed and fisheries managers decided that a planktivorous forage fish was needed to improve growth of the various salmonids planted as sport fish. Because it was difficult to collect delta smelt from the San Francisco Estuary, the Japanese pond smelt, for which a well-developed aquaculture program already existed, was selected for introduction (Wales, 1962). The original plants, in six reservoirs, resulted in the wakasagi becoming established in the Klamath and Sacramento watersheds (Moyle, 2002).

The first reported collection of wakasagi in the San Francisco Estuary occurred in 1974 (Aasen et al., 1998) and they are now being found on a regular basis. Wakasagi were likely transported from the foothill reservoirs to the San Francisco Estuary during periods of high reservoir releases.

Swanson et al. (2000) found that wakasagi are well suited to the waters of the San Francisco Estuary and are more tolerant than delta smelt to stressful environmental conditions including maximum temperatures (wakasagi 29.1 ± 1.3°C vs. delta smelt 25.4 ± 1.7°C), minimum temperatures (wakasagi 2.3 ± 0.9°C vs. delta smelt 7.5 ± 1.2°C) and high salinities (wakasagi 26.8 ± 3.0 ppt vs. delta smelt 19.1 ± 2.1 ppt). Given the current overlap in distributions of delta smelt and wakasagi and the increase in wakasagi abundance in recent years, it is likely that wakasagi will adversely affect delta smelt through competition for food and space, predation on their larvae, and hybridization (Stanley et al., 1995; Trenham et al., 1998). They may also have negative effects on the native longfin smelt, *Spirinchus thaleichthys,* which is also in decline in the estuary. The environmental tolerances of wakasagi clearly indicate that it could expand its range to include the more saline San Francisco Bay and surrounding coastal waters.

BROWN TROUT

Brown trout (Salmonidae) were first introduced into California in 1893 from Europe as a sport species (Dill and Cordone, 1997). They are primarily a freshwater fish in California, but adult sea-run brown trout or smolts have been found in both the Sacramento and Klamath rivers (Moyle, 2002). While anadromous populations are common in their native range, anadromous brown trout have remained rare in California, thus have probably had little impact on native fishes.

Euryhaline Freshwater Species

INLAND SILVERSIDE

The inland silverside (Atherinopsidae) is a planktivore native to estuaries and lower reaches of coastal streams along the Atlantic Coast of the United States and the Gulf Coast from Florida to Veracruz, Mexico (Moyle, 2002). It was originally introduced into Clear Lake, Lake County, in 1967 from Texoma Reservoir, Oklahoma. The purpose of the introduction was to control populations of the Clear Lake gnat (*Chaoborus astictopus*). At the time of its introduction, the inland silverside was listed as the Mississippi silverside, *M. audens*, which was thought to be a freshwater form distinct from the estuarine *M. beryllina* (Moyle, 2002).

The two forms are indistinguishable (Chernoff et al., 1981; Moyle, 2002). This finding is supported by the expansion of the inland silversides range in California following its introduction. By 1975, it had colonized the brackish waters of the San Francisco Estuary where they are now abundant (Moyle, 2002). The inland silverside has also managed to disperse through the waterways of the California Aqueduct and by 1988 had become well established in most of the reservoirs connected to this system (Swift et al., 1993). They thus are likely to eventually colonize estuaries and lagoons in southern California.

The inland silverside is tolerant of a wide range of environmental conditions and is well suited for both freshwater and brackish water environments in California. They have been found to occur in waters with temperatures of 8–34°C with optimal growth and survival in environments at 20–25°C (Moyle, 2002). They have been found in waters with salinities as high as 33 ppt and are common in salinities of 10–15 ppt (Moyle, 2002). Optimal salinity for larval growth and survival is 15 ppt although they are also successful in fresh water (Moyle, 2002).

The inland silverside is extremely prolific and is often one of the most abundant littoral zone species in both fresh and brackish water. They can deplete zooplankton populations and are voracious predators on larval fish (Moyle, 2002). They are thus capable of having negative effects on native fishes. Within the San Francisco Estuary, the effects of inland silverside on other organisms has not been thoroughly investigated, but given their high abundance in shallow water areas, they have the potential to affect populations of splittail, juvenile salmon and other fishes. Indeed, the decline of delta smelt has largely coincided with the silverside invasion of the estuary. Bennett and Moyle (1996) have suggested that the delta smelt is particularly vulnerable to inland silverside predation. The silverside is an unusually effective predator on fish larvae (W.A. Bennett, University of California Davis, pers. comm.) and delta smelt spawn in shallow areas where silversides are abundant.

SAILFIN MOLLY

The sailfin molly (Poeciliidae) is native to the southern United States and northern Mexico, where it is found in a variety of habitats including coastal fresh water, brackish water and salt water (Moyle, 2002) (see fig. 24-1). It became established in the Salton Sea in the 1960s, as the result of fish escaping from tropical fish farms and/or releases by aquarists. It was soon present in the Colorado River and, presumably, its delta and brackish areas along the upper Gulf of California. By the 1980s and 1990s, populations were recorded in a number of salt marshes in southern California, from Ventura County to San Diego County [and in Tijuana Marsh in Mexico] (Swift et al., 1993, Gregory, 1998).

Sailfin mollies tolerate a wide range of salinities (0–87 ppt) but generally require temperatures above 20°C for survival and 24–33°C for reproduction and growth (Moyle, 2002). Their temperature requirements limits their ability to colonize many habitats and to move through marine waters to new areas, although their main method of dispersal seems to be humans releasing unwanted pets. They feed primarily on algae and detritus and attain a maximum total length of 15 cm (although fish over 8 cm TL are unusual) (Moyle, 2002).

Sailfin mollies have been implicated in the decline of endemic pupfishes in California and Nevada deserts, but their effects on fishes and invertebrates in coastal salt marshes is not well understood. Given their small size and limited diet, it is unlikely that they have an appreciable effect on other fishes, but they apparently are important prey of herons and other predatory birds.

WESTERN MOSQUITOFISH

The western mosquitofish (Poeciliidae) is native to the southeastern USA and was first introduced into California in 1922 for mosquito control (Dill and Cordone, 1997) (see fig. 24-1). They are regarded as ideal for this purpose because they can survive a wide range of environmental conditions, including salt marshes and estuaries, live in the shallow quiet waters preferred by mosquito larvae, and are relatively non-selective predators on aquatic invertebrates. Mosquitofish can withstand large temperature fluctuations (0.5–42°), but are found mainly where temperatures range from 10 to 35°C. They are also typically found in habitats where salinities do not exceed 25 ppt, although they can survive salinities of up to 58 ppt (Moyle, 2002). These tolerances have allowed them to colonize most coastal marshes in the southern half of the state, often as the result of planting for mosquito control. In freshwater habitats, mosquitofish have been implicated in the decline and extinction of fish, amphibians, and invertebrates through predation and aggression (Moyle, 2002). There is so far no evidence that they have had negative impacts in salt marshes and similar habitats, but they are capable of preying on small fishes like tidewater gobies and in changing the food webs of estuarine channels. Because of their small size and littoral habits their abundance may be underestimated within the estuaries and bays of California.

THREADFIN SHAD

Threadfin shad (Clupeidae) are native to streams, lakes, and estuaries along the coast of the Gulf of Mexico and occur as far south as Belize in South America (see fig. 24-1). They are a small, fast growing planktivore which often form large schools in surface waters. These attributes led resource managers to believe that it would be an ideal forage fish in California's fresh waters (Dill and Cordone, 1997). Initial plantings in the 1950s in reservoirs in southern California and the Colorado River were followed by their introduction throughout the state and their subsequent invasion of estuaries downstream from the reservoirs (Moyle, 2002). They are most abundant in fresh water where summer temperatures exceed 22–24°C. They become less abundant as salinity increases in estuaries, presumably because of their inability to reproduce at low temperatures or high salinities (Moyle, 2002). Within the San Francisco Estuary, threadfin shad experience heavy die offs when water temperatures cool to 6–8°C (Turner, 1966). Nevertheless, they can survive and grow in sea water and are occasionally captured in salt water from Long Beach to Yaquina Bay, Oregon (Miller and Lea, 1972). Threadfin shad are often the most abundant planktivore in the low-salinity (<5 ppt) waters of the San Francisco Estuary, where they may have negative effects on other estuarine fishes through depletion of zooplankton and predation on larvae. However such impacts are undocumented. They are, however, important prey for striped bass and other piscivores (Moyle, 2002). In more saline environments, they are rarely abundant enough to have much effect on other fishes.

TILAPIA

At least four species of African tilapias (Cichlidae) and their hybrids have become established in California, but only two (Mozambique tilapia and redbelly tilapia) occur in saltwater habitats outside this region (Moyle, 2002) (see fig. 24-1). The Salton Sea and the Colorado River (including its delta) are the centers of tilapia abundance in the western United States, but tilapia also are present in some southern California salt marshes and estuaries. Tilapia in general are tropical fishes, so rarely persist in areas where temperatures drop below 10–15°C for extended periods. Redbelly and Mozambique tilapia can both live in sea water and Mozambique tilapia can tolerate salinities as high as 120 ppt (Moyle, 2002).

The redbelly tilapia was widely introduced into southern California in the 1970s for aquatic weed control and it is permanently established in ditches in the Salton Sea area. It became established briefly in marine waters off Huntington Beach and possibly upper Newport Bay (Knaggs, 1977), but is apparently no longer present (Dill and Cordone, 1997). Mozambique tilapia (and/or its hybrids with other tilapia species) is the most widespread tilapia in California. It appears to be established in the upper reaches of what pass for estuaries in Orange and Los Angeles counties (Knaggs, 1977; Dill and Cordone, 1997) but is only locally abundant. Its ability to persist in estuarine systems over the long term is questionable, given its temperature requirements.

Other Species: Fishes of the Salton Sea

The largest experiment in marine fish introductions in California was the attempt to establish fish from the Gulf of California in the Salton Sea, as the sea changed from a freshwater system to a saltwater system as the result of evaporation (Dill and Cordone, 1997; Moyle, 2002). The Salton Sea is a large (980 km^2), shallow (average depth 5 m) inland body of water located in Riverside and Imperial Counties. It was created in 1905–1907 when the Colorado River decided to make a new irrigation ditch its main channel and flowed into the Salton Basin. It started out as a freshwater lake but by the 1940s it was too salty for most freshwater fishes. The first successful marine introduction was a euryhaline goby, the longjaw mudsucker (Gobiidae) brought in from coastal California as bait in the 1930s. Between 1948 and 1956, systematic efforts by the California Department of Fish and Game resulted in about 20,000 fish representing 31 species being introduced, mostly from the Gulf of California (Dill and Cordone, 1997). Three species survived the transplantion experience and became abundant enough to support a sport fishery: bairdiella (Sciaenidae), orangemouth corvina (Sciaenidae) and sargo (Haemulidae). The salinity of the sea is still increasing, so is unlikely to be able to support their populations for much longer. The most abundant species in the sea is the Mozambique tilapia (Moyle, 2002). This experiment in marine fish introductions does demonstrate that stenohaline marine fishes can be moved and established under the right conditions.

Conclusions

Why are there so few successful alien species in the marine environments of California? The patterns of alien fish invasions in marine environments of California are typical of those worldwide: most established aliens live in estuaries, bays, or enclosed basins (Baltz, 1991). There have only been 15 intentional introductions which have resulted in 10 species becoming established in estuarine and open water marine habitats off the coast of California. Eight of the 15 intentional marine introductions discussed in this chapter are freshwater fishes that have unexpectedly spread into estuarine or open marine waters. Five others are anadromous species that were first introduced into fresh water with the intention of establishing them in marine and freshwater habitats. Overall there has been a high degree of success (67%) with intentional introductions. Thus, the low number of alien species currently found in marine waters of California may be due more to the limited number of intentional introductions of estuarine and marine species than to a lack of invisibility of these habitats.

The establishment of alien fish in the estuaries and bays of California as a result of byproduct introductions, primarily ballast water releases, has also been limited (5 species). In contrast, by 1998 over 160 species of alien invertebrates and plants had become established in salt or brackish waters in California (Cohen and Carlton, 1998). Reasons for the limited number of successfully established alien fish species, relative to the number of alien invertebrate and plant species, are unclear and complicated by the fact that the total number of alien fish species introduced, yet unsuccessfully established, is unknown. It is likely that the small number of successful byproduct introductions of alien fish species observed in California marine waters is a result of limited survival ability in ballast water of the early life history stages.

Another way of addressing this question is to examine why some introduced species failed to become established. Marine introductions that failed in California include milkfish, tautog, American eel, ayu and Atlantic salmon. The introduction of milkfish, tautog, American eel and ayu most likely failed as a result of a poor match between the species and the environment into which they were introduced. This may have been the case especially for the amphidromous ayu, which failed despite heavy and repeated stocking of eggs and fry into the Eel River. In the case of the milkfish, tautog and American eel, the relatively few individuals released (100, <1000 and approximately 2000, respectively; Dill and Cordone, 1997) probably also contributed to their poor success. However, over 300,000 Atlantic salmon were stocked over several years in suitable locations in California, but this species never became established, perhaps because of interactions with native salmonids (Dill and Cordone, 1997).

Arguably the high diversity of native fishes (500+ species) found off California decreases the likelihood of an introduced species surviving, through mechanisms of biotic resistance. For example, a behavioral study in British Columbia, Canada, suggests that reduction of biotic resistance may be playing a large role in the establishment of Atlantic salmon there. Volpe et al. (2001) found that despite behavioral differences between steelhead and Atlantic salmon, the species with prior residency held a competitive advantage over the invading species. It has been further hypothesized that the current increase in successful natural reproduction of escaped Atlantic Salmon in British Columbia waters (Volpe et al., 2000) could be related to marked declines in the abundance of steelhead in these same locations (Volpe et al., 2001).

Given the high abundance of steelhead and Pacific salmon in California, during the time Atlantic salmon were stocked (1874, 1891, and 1929–1932), there may have been considerable biotic resistance preventing the successful establishment of Atlantic salmon. If biotic resistance prevented the earlier invasion of Atlantic salmon in California waters, then the low abundance of steelhead and Pacific salmon today may leave many California waters vulnerable to future invasions. Although no Atlantic salmon have recently found their way into California waters, it remains a possibility because of their continued release from aquaculture facilities along the Pacific Coast. Another possibility is an increase in anadromous brown trout in response to reduced native salmonid populations.

In any case, Moyle and Light (1997) argue that under the right circumstances most invaders can overcome biotic resistance. Indeed the ability of yellowfin goby to colonize new areas along the coast of Central California demonstrates that marine invasions are possible, as does the widespread distribution of striped bass and American shad.

What has been the impact of alien fishes in marine environments? Major changes in aquatic communities as a result of invading alien species have been noted mainly in enclosed seas and estuaries (Baltz, 1991). The San Francisco Estuary is often dominated by alien fishes in its fresh and brackish water portions but by native marine fishes in San Francisco Bay proper, where salinities rarely drop below 25 ppt (Matern et al., 2002). Throughout the estuary, including San Francisco Bay, striped bass are the most abundant piscivore and they probably changed the trophic structure of the estuary to some degree, but the introduction occurred before any studies were done and coincided with a period in which many other changes were taking place as well. One of the more recent invaders of the estuary, the shimofuri goby, was intensively studied by Matern (1999), but he could not detect any obvious effects on the existing fauna, despite its high abundance. Presumably the specializations of this fish, combined with rapid changes in estuarine conditions during the invasion period (Bennett and Moyle, 1996), limited its ability to impact other species. Overall, the impacts of alien fishes in California's marine environments appear to have been minimal. However, future impacts remain uncertain.

What marine environments in California are most invasible? Within California, all alien species that have become established are associated with bays and estuaries for at least a portion of their life cycle. No stenohaline marine species have become established in open water marine environments, which suggests that open water marine habitats are less invasible. This is due, at least in part, to the low number of attempts to establish species in open marine waters of California and the reduced opportunity for byproduct introductions. In support of these findings, Baltz (1991) concluded in his review of worldwide marine fish introductions that fish communities in closed or semi-closed systems are more easily invaded than open water systems with only Hawaiian reefs and the Mediterranean Sea being invaded by more than a few species.

Of the marine fish invasions in California waters, those in the bays and estuaries of California have probably been more successful than those in open water marine habitats because 1) bay and estuarine species are more likely to be tolerant of changing seasonal and daily fluctuations in environmental conditions; 2) there is most likely a similarity in environmental conditions and habitats within temperate bays and estuaries worldwide especially between international ports located at similar latitudes on opposite sides of the Pacific Ocean; 3) there is often a high number of larval and juvenile fish vulnerable to ballast water uptake in bays and estuaries stemming from their heavy use as spawning and rearing areas by highly fecund species; 4) few propagules are currently taken from and released into open water marine habitats; 5) susceptibility to invasion may be dependent upon original species richness, with areas of low species richness being more susceptible to invasion than those with higher species richness (Gido and Brown, 1999). The bays and estuaries in California are typically species poor, thus perhaps more invasible. Whereas open water marine habitats of California are species-rich (this volume), thus may be more resistant to invasion.

What is the future of alien fishes in California, especially in conjunction with environmental change? Alien fishes will likely continue to become more abundant in California's marine waters as the result of: 1) expansion of the ranges of established species, 2) new species arriving via ballast water, and 3) species arriving via aquaculture operations.

It is likely that the four alien goby species in California will continue to expand their ranges with negative effects on native gobies and other benthic fishes and on invertebrates in estuaries, lagoons, and bays. They are all aggressive predators that have the potential to disperse by means of their abundant pelagic larvae, either through aqueducts, through ballast water in ships moving up and down the coast, or through natural dispersion by coastal currents. The inland silverside is also likely to invade more estuaries with negative consequences to native fishes.

It is also likely that additional marine fishes commonly found within bays and estuaries in major Pacific Ocean ports will become established via ballast water of ships, unless zero tolerance limits for life in ballast water become standard practice (backed by laws which are actively enforced). Ballast water introductions occur not only from cross-ocean transport, but also from intra-regional transport of organisms from heavily invaded ports to those in outlying areas. Intra-regional transport of invertebrates already is believed to have introduced species into the waters of Elkhorn Slough, an estuary in central California, and is a mechanism that will likely further redistribute species from previously established populations in major ports to those with no international shipping (Wasson et al., 2001).

It is extremely difficult to eliminate ballast water as a source of alien species because of the vast number of ships involved in global and regional transport, the volume of water taken up in ballast, and costs and time associated with current treatment strategies. Current treatment strategies for ships approaching North American ports focus on flushing of ballast tanks while at sea, because most of the organisms are unlikely to survive in the open ocean or in cold ocean water in the tanks. However, this process is time consuming, cannot always be performed for safety reasons (e.g., during rough seas) and may not be completely effective (Locke et al., 1993). Other potential methods to treat ballast water are being investigated including chemical, thermal, ultraviolet, oxygenation, deoxygenation and various combinations of the above (see National Research Council, 1996 for review; also Niimi, 1997; Rigby et al., 1999; Kuzirian et al., 2001; Suttherland et al., 2001; Browning, 2001; Tamburri et al., 2002). However, no alternative solutions have been selected or are being implemented. Thus, ballast water introductions will likely continue at least into the near future.

Given the current high demand for marine fish and shellfish, aquaculture activities including the importation of shellfish and other organisms will likely continue to be a source of alien species. This includes imports for the saltwater aquarium industry (e.g., at least one species of aquarium fish, the lionfish, *Pterois volitans*, has already become established along the coast of Florida). Among the many organisms currently at risk of becoming established is the Atlantic salmon, as discussed previously. The concern over the potential establishment of Atlantic salmon into Pacific waters is warranted given the rapid increase in culture of Atlantic salmon over the past 29 years. By 1998, it was estimated that Atlantic salmon biomass in aquaculture worldwide had already exceeded that in its native range (Gross, 1998). Net pen culture is the primary method of raising Atlantic salmon in marine environments. This method of culture often results in significant invasions of fish into Pacific Coast waters. A single fish farm in Puget Sound, Washington in 1996 and 1997 "accidentally" released over 460,000 Atlantic salmon (Gross, 1998). Significant releases from other fish farm operations have also occurred, such as the release of several million rainbow trout, coho salmon, and Atlantic salmon during heavy storms in 1994 and 1995 in the Pacific waters in Southern Chile (Soto et al., 2001). Although large-scale releases are a major concern, the continuous release (leakage) of fish (Alverson and Ruggerone, 1997) further increases the possibility of eventual establishment of Atlantic salmon in Pacific waters. This reality may be closer than anticipated since natural reproduction of Atlantic salmon has already been documented in coastal British Columbia rivers (Volpe et al., 2000).

The probability of alien species becoming established and spreading has likely increased in recent years because marine systems have become disrupted by pollution, commercial fishing, and other major insults to ecosystem structure. As a rule, alien species are most likely to successfully invade human-disturbed environments (Elton, 1958; Moyle and Light, 1997). Global climate change, especially increases in ocean temperature, is also likely to increase the probability of new invasions being successful and of existing alien species being able to expand their range (Carlton, 2000).

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