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Further Investigations into the Natural History of San Francisco Bay and Delta
With Reference to the Influence of Man

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BENNETT & MOYLE: FISH DECLINES IN THE ESTUARY

WHERE HAVE ALL THE FISHES GONE? INTERACTIVE FACTORS PRODUCING FISH DECLINES IN THE SACRAMENTO-SAN JOAQUIN ESTUARY

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Fish populations have declined markedly in the Sacramento- San Joaquin estuary. We review evidence for factors contributing to the declining abundance of fishes in the context of a conceptual model that emphasizes the interactive nature of six main pathways by which alteration of freshwater outflow to the estuary affects the survival of larval and juvenile fishes (recruitment success). Specific pathways include the influence of freshwater outflow on (1) transport and entrainment, (2) retention in and/or advection from preferred habitats, (3) the success and effects of invading species, (4) primary production and food web dynamics, (5) dilution and/or flushing of toxic compounds, and (6) the quantity and quality of shallow-water spawning/rearing habitat. The collective evidence suggests that within and among years recruitment success may be regulated by several pathways acting in concert or synergistically, indicating the futility of promoting single-factor, or single-pathway, explanations for fish declines. Clearly, ameliorating the effects of various factors (*e.g.*, reducing entrainment, toxic runoff, and improving shallow-water habitat) will improve conditions for fish. However, recovery of many depressed populations may be precluded by the continuously changing composition of the estuarine food web by exotic species. The current lack of life history information on several of the more severely affected species and the need to prevent extinctions suggests that the most pragmatic and promising solution is to ensure adequate outflow to the estuary.

The fish populations of the Sacramento-San Joaquin estuary have declined dramatically in recent years (Herbold *et al.* 1992; Jassby *et al.* 1995; Meng *et al.* 1994). The majority of species about which we have adequate information reflect this overall decline. Most dramatically, the winter-run chinook salmon is now listed as an endangered species, the delta smelt is listed as a threatened species, and Sacramento splittail has been proposed for listing. In addition, major fisheries for striped bass, chinook salmon, and others have been reduced to low levels. The simultaneous declines of so many species with different habitat requirements and life history strategies is an indication of broad problems with the estuarine environment, especially in the Delta, the uppermost part of the estuary (Fig. 1). Drought and diversion of inflowing freshwater have been implicated as the overriding factors in the fish declines (Stevens *et al.* 1985; Herbold *et al.* 1992; Moyle *et al.* 1992). However, it is difficult to elucidate how lack of freshwater outflow directly affects fish populations, as well as how other factors (*e.g.*, toxic runoff, species invasions, see Nichols *et al.* 1986; Herbold & Moyle 1989; Jassby *et al.* 1995;

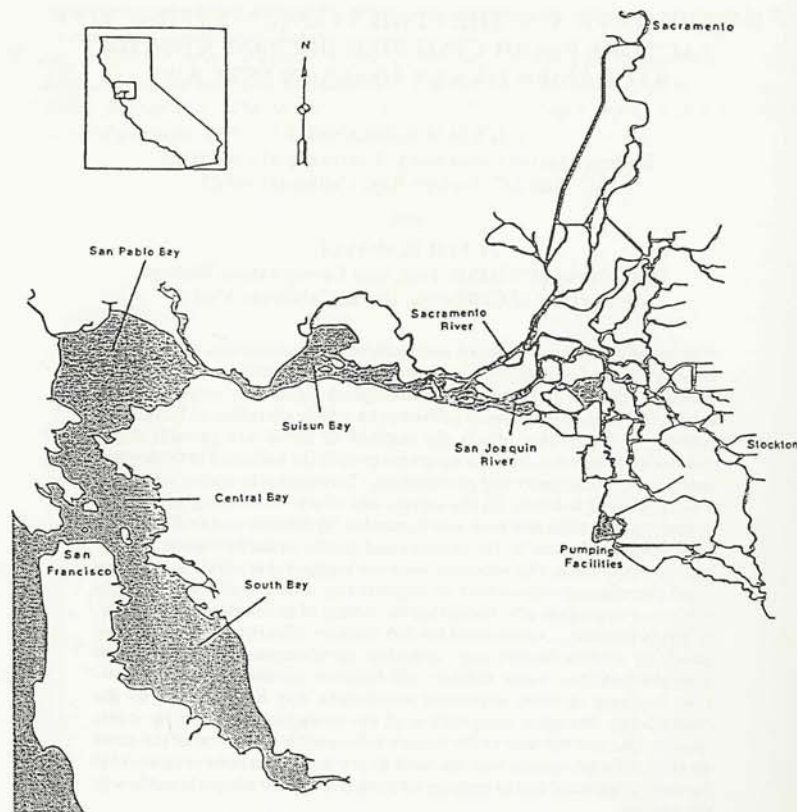


FIGURE 1. The Sacramento-San Joaquin estuary showing four sub-embayments, rivers and Delta region extending from Sacramento to Stockton and the State and Federal water projects.

Bennett *et al.* 1995) are affected by outflow to act synergistically with drought and diversions to maintain populations at low abundance.

In recent years, the majority of species appear to be recruitment limited (Herbold *et al.* 1992; Moyle *et al.* 1992), which we define operationally as poor survival through the first year of life. Because many species are short-lived (1-3 years) such recruitment limitation may regulate population dynamics. Recruitment is naturally a highly variable process, and generally considered to be influenced by the interaction of environmental factors with food web and demographic factors (Sissenwine 1984; Rothschild 1986). However, the relative importance of factors producing variability are rarely well understood (Shepherd & Cushing 1990). This is especially true for the Sacramento-San Joaquin estuary, because we know very little about the early life stages of many of the most severely affected species.

In this paper we review the factors contributing to fish declines in the Sacra-

mento-San Joaquin estuary in the context of a conceptual model (Fig. 2) that outlines various pathways by which freshwater outflow affects recruitment. We then show how several pathways may act together to produce the poor recruitment of selected species (striped bass, Fig. 3; delta smelt, Fig. 4). Finally, by examining life history characteristics, we attempt to extrapolate to other native (Fig. 5) and introduced (Fig. 6) species about which there is considerably less biological information. Model pathways are intended to organize discussion, illuminating interactions among factors and should not be interpreted as statistically derived pathways (*e.g.*, path analysis, Wootton 1994), or as pathways of energy flow which typify many estuarine models (Kremer & Nixon 1978; Baird & Ulanowicz 1989). Clearly, various pathways could be expanded into formal models, however, suitable information is currently incomplete. Therefore, we seek to provide a framework for evaluating the relative importance of contributing factors and their interrelated pathways as well as to identify important gaps in our understanding of the causes of the fish declines.

FRESHWATER OUTFLOW AND RECRUITMENT SUCCESS THE PROBLEM

Reduction of freshwater inflow to estuaries has often been associated with declines in productivity and fish recruitment (Stevens *et al.* 1985; Nixon *et al.* 1986; Skreslet 1986; Houde & Rutherford 1993). However, the relative importance of mechanisms underlying apparent outflow-recruitment relationships remain unclear in most cases (Sutcliffe 1973; Stevens *et al.* 1985; Sinclair *et al.* 1986; Jassby *et al.* 1995). In the Sacramento-San Joaquin estuary (Fig. 1), freshwater diversions and reduced outflow are highly associated with declining recruitment and abundance of the majority of fish species (Stevens *et al.* 1985; Herbold *et al.* 1992; Jassby *et al.* 1995). While entrainment in the major state and federal water projects is the most identifiable explanation for fish declines (Turner & Chadwick 1972; Stevens & Miller 1983; Stevens *et al.* 1985; CDFG 1987), current focus has shifted to distinguishing the effects of entrainment from those of food web alteration, loss of low salinity nursery habitat, pollution, and other factors that are considerably more difficult to quantify (Herbold *et al.* 1992; Moyle *et al.* 1992; Jassby *et al.* 1995; Bennett *et al.* 1995). Progress in understanding recruitment failure, however, remains burdened by the promotion of competing single-factor hypotheses (*e.g.*, entrainment vs. toxic exposure).

In this light, we provide a flow diagram (Fig. 2) to organize discussion of several direct and indirect pathways by which freshwater outflow interacts with various factors to regulate recruitment. Our thesis is supported by the growing awareness that recruitment in marine and estuarine systems may often be regulated by the effects of 2 or more factors acting simultaneously (Lasker 1981; Rothschild 1991; Lawrence 1990; Cowan *et al.* 1993). This review is not meant to be a comprehensive history of effects, but summarizes and updates the reviews in Smith & Kato (1979), Nichols *et al.* (1986), Herbold *et al.* (1992), and Moyle *et al.* (1992) to specifically address how freshwater outflow affects the survival of young fishes.

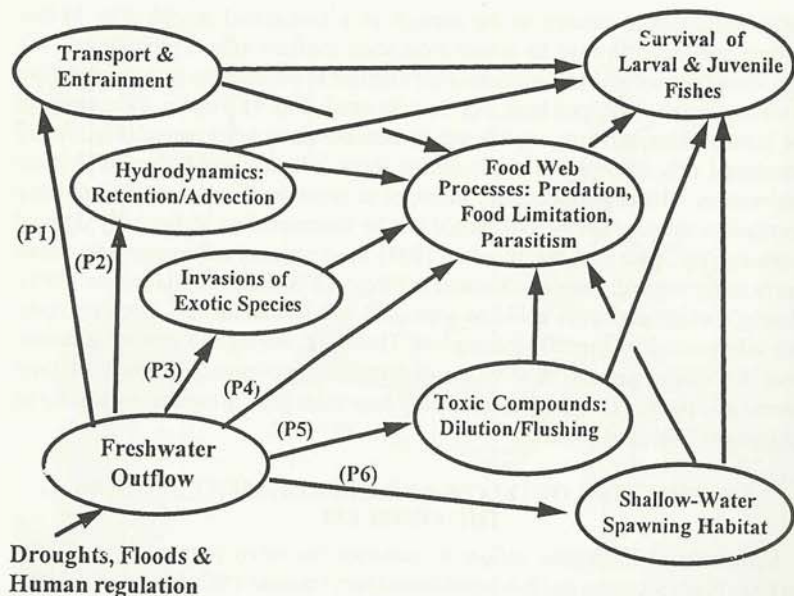


FIGURE 2. Conceptual model illustrating pathways (P1-P6) by which the amount of freshwater outflow to the estuary affects recruitment of young fishes. Various factors may affect recruitment simultaneously by direct and/or indirect pathways with various food web processes.

A CONCEPTUAL MODEL

Climatic and Human Regulation of Freshwater Outflow.—The amount and timing of freshwater entering the estuary is controlled by human response to and possible influence on the effects of natural climatic variability. The Sacramento-San Joaquin estuary receives runoff from 40% of the state's surface area and is located in a region where annually winters are cool and wet, while summers are hot and dry. High interannual variability in wintertime precipitation affects the amount of freshwater available to the estuary (Peterson *et al.* 1995). Moreover, because 70% of California's rainfall occurs north of the estuary, while 80% of its water consumption occurs south of the estuary, considerable freshwater outflow is diverted south by an elaborate system of water development (Nichols *et al.* 1986; Moyle *et al.* 1992). Complicating this picture further is a twenty-year period (1974-1994) with much more variable precipitation than the previous 50-100 years (Peterson *et al.* 1995). 1976 and 1977 were severe drought years, while 1983 was an extreme wet year. The drought years (1985-1994) were broken by the wettest month on record (February 1986) and the wet year 1993 (Peterson *et al.* 1995). The 1986 rain event had a particularly strong effect, flushing many organisms out of the estuary that already had depleted populations (*e.g.*, delta smelt, Moyle *et al.* 1992). Subsequently, a number of new invading species became established (Path

3 below, Nichols *et al.* 1990; Kimmerer *et al.* 1995; Meng *et al.* 1994; Matern & Fleming, in press).

Diversion of freshwater is the single biggest factor altering flows through the estuary today (Moyle *et al.* 1992; Arthur *et al.*, this volume). Water is diverted in three main areas: upstream of the Delta, within the Delta, and at the south Delta pumps of the State Water Project (SWP) and the Central Valley Project (CVP). Upstream diversions range from the myriad of small riparian diversions to large diversion dams such as Red Bluff Diversion Dam, to major water storage facilities such as Shasta, Friant, and Oroville dams. The effects of these diversions include reduced stream flows, reduced variability in flows, altered channel morphology, and changes in water quality, especially water temperatures. About 30% of the mean annual unimpaired flow to the estuary is diverted upstream, although some of it eventually reaches the Delta as polluted irrigation return water. Within Delta diversions for agriculture amount to about 1 million acre feet per year in about 2,000 small diversions. How these diversions affect within-Delta hydraulics is not well understood, although the requirement that such diversions must be allowed in order to satisfy riparian water rights maintains the Delta as a largely freshwater system. The south Delta pumps have been taking increasing amounts of water from the estuary in recent decades (Moyle *et al.* 1992; Arthur *et al.*, this symposium) although actions to protect endangered fishes have reduced this take in the past several years. These pumps have taken as much as 60% of the inflowing water in some years and in most years drastically alter the way water flows through the estuary, often producing reverse flows in the San Joaquin river (Moyle *et al.* 1992; Arthur *et al.*, this volume).

A major problem for understanding the effects of water development on fish recruitment is the cumulative effects of all the diversions, big and small, such that it is often hard to separate the effects of one diversion or set of diversions from others. The effect of water development on inflow to the estuary, in many respects, reduces variability often creating prolonged drought conditions.

Oceanic conditions can also affect estuarine fish, especially anadromous forms, in ways other than by influencing freshwater outflow. El Niño events, such as those that happened in 1976-77 and 1983, can significantly reduce ocean productivity, which in turn can reduce growth and survival of fish such as chinook salmon and Pacific herring (Herbold *et al.* 1992). The 1976-77 El Niño initiated a dramatic step-change, persisting to the late 1980s, in at least 40 climatic, oceanic, and biotic variables in the Pacific (Ebbesmeyer *et al.* 1991; Kerr 1922) that may have also affected resident estuarine fishes. For example, both adult and young-of-the-year (38mm) striped bass experienced a similar drop in abundance in 1976 and 1977 which has persisted and worsened (Fig. 3). Because poor recruitment would not produce a change in the adult population for at least 3 years, the concurrent drop in adult abundance may reflect this climatic shift, perhaps by inducing migration from the estuary. However, while this well-documented decline of striped bass in the mid-1970s (Fig. 3; Stevens *et al.* 1985) does not appear to be due to recruitment failure, poor year-class success as well as large-scale stocking of juveniles during

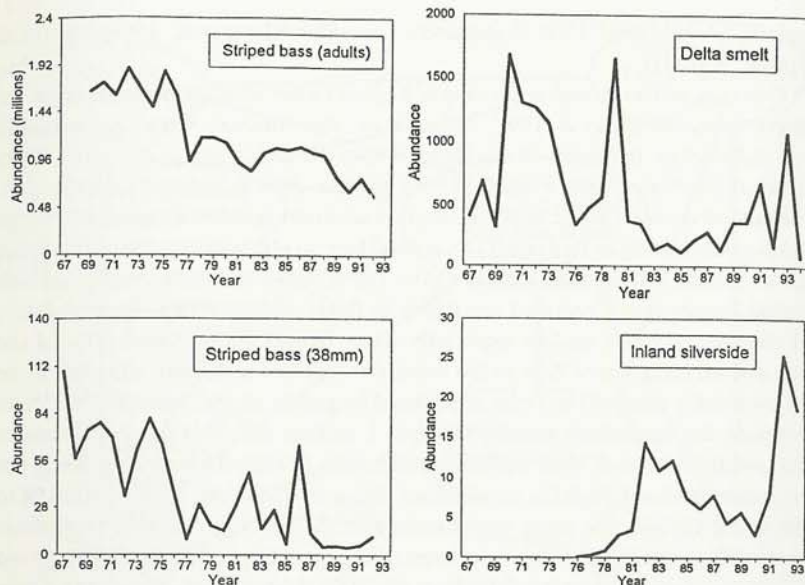


FIGURE 3. Changes in abundance of adult (406mm, age 2 yrs.) and young-of-the-year (38mm, age 3-4 months) striped bass. Data for adult abundances are Peterson population estimates, and young-of-the-year abundances are indices derived from summer tow-net surveys weighted by the volume of water at each sampling site (see Stevens *et al.* 1985).

FIGURE 4. Change in abundance of delta smelt (native) and inland silversides (introduced in 1975, Moyle 1976). Data for delta smelt are abundance indices derived from CDFG's fall mid-water trawl survey (see Moyle *et al.* 1992). Data for inland silversides are catch-per-haul estimates from USFWS's salmon smolt beach seine survey.

most of the past 15 years have not replenished the population, indicating conditions in the estuary remain poor for young fish.

PATHWAYS AFFECTING RECRUITMENT

Below we outline how alteration of the amount, variability, and timing of freshwater outflow can affect recruitment success via six main pathways (Fig. 2). All pathways can produce direct and interactive effects (with food web processes) on larval and juvenile fish survival.

Path 1. Transport and Entrainment.—The effects of altered transport and entrainment in water diversions are covered in detail by Arthur *et al.* and Brown *et al.* (this volume), therefore our discussion will be brief. Water diversions alter the typical pattern of outflow seaward, producing cross-Delta flow towards the state and federal pumping facilities located in the south Delta (Fig. 1). Consequently, millions of juvenile and larval fishes are entrained in the diversions. In addition, the migration routes of young fishes (in particular, salmon smolts) are altered such that they accumulate in the proximity of the pumping facilities (*e.g.*, Clifton Court Forebay, Fig. 1) where they experience substantial predation by aggregations of

larger fishes (typically adult striped bass) in addition to entrainment (Arthur *et al.*, this volume).

Path 2. Physical processes of retention and advection.—Diversion of freshwater outflow alters estuarine hydrodynamics, which can influence the retention or advection of young fishes and their food in the upper estuary. Under conditions of reduced outflow, estuarine circulation becomes dominated by tidal mixing rather than gravitational mixing that results from stratification of freshwater outflowing over denser, inflowing saltwater (Kimmerer 1992). In the St. Lawrence estuaries, the interaction of vertical movements of fishes and zooplankton with tidal currents and gravitational circulation acts to retain populations in the upper estuary (Fortier & Leggett 1983; Laprise & Dodson 1989, 1990). This also allows organisms to co-occur with food patches (Dauvin & Dodson 1990), and it may provide an isolation mechanism during their evolution (Sinclair 1988). Domination of tidal mixing during times of low outflow may reduce the effectiveness of this process such that organisms are lost from optimal habitat by diffusive or advective processes. Recent investigations during a dry year (1994) indicate larval striped bass and juvenile longfin smelt migrate vertically, occurring near the surface on flood tides and near the bottom on ebb tides apparently facilitating maintenance of longitudinal position (Bennett, Kimmerer, Burau, Arthur, unpublished data). In addition, flood events flush estuarine organisms out of the system (*e.g.*, delta smelt, Moyle *et al.* 1992).

Path 3. Riverine Input / The Agricultural Model.—Estuaries are among the most productive of aquatic systems, in part because riverine transport of nutrients and carbon provides fertilizer, enhancing the estuarine food web. This phenomenon, called the agricultural model (Nixon *et al.* 1986; Houde & Rutherford 1993), provides an intuitively appealing mechanism for the association between river outflow and recruitment success of invertebrates and fishes, because it invokes the traditional notion of a linear food chain (Carpenter & Kitchell 1993). The basic assumption of this pathway is that larval and/or juvenile fishes are food limited during times of low freshwater outflow, such that recruitment is regulated by starvation and/or predation on malnourished individuals. However, evidence for starvation in estuarine and marine systems is rare, especially considering the number of cases in which it has been investigated (see reviews by May 1974; Leggett 1986; Houde 1987).

During the recent drought, 1987-1992, the importance of food limitation was investigated for larval striped bass (Bennett *et al.* 1995), because growing evidence suggested food limitation may be an important source of larval mortality. Drought, diversions, and grazing by introduced benthic mollusks reduced primary productivity in the larval habitat (Jassby & Powell 1994), and the preferred food for first-feeding larvae, notably the copepod *Eurytemora affinis*, also declined in abundance by about two orders of magnitude (Kimmerer *et al.* 1995; Kimmerer & Orsi, this symposium). In addition, an increasingly abundant copepod, *Sinocalanus doerrii*, an exotic from Asia, appeared difficult for first-feeding larval fish to capture (Meng & Orsi 1991). However, morphological and histological evaluations of field-caught larvae from 1988-1991, indicated that all larvae examined (N = 980)

had been feeding, and lacked alterations attributable to starvation (Bennett *et al.* 1995). To examine the interaction of predation with food limitation, field experiments were conducted presenting an inland silverside (*Menidia beryllina*) predator with a choice between starved and fed striped bass larvae in large enclosures (Bennett & Rogers-Bennett, submitted manuscript). Our results indicated that starved and fed larvae were consumed at similar rates, but that predation rate declined exponentially over a 5-7 mm larval size range. This suggests that slower growth will dramatically enhance the effect of predation during the larval period.

Additional evidence suggests that while larval food supplies may be recovering, larval growth appears slow. After 1988, another exotic copepod, *Pseudodiaptomus forbesi*, became abundant (see Kimmerer & Orsi, this volume) and appears to be suitable food, replacing native species in larval stomachs (Meng & Orsi 1991; L. Miller, CDFG, pers. commun.). Switching to a new and abundant food item would sufficiently augment the larval food base, decreasing the probability of slow growth. However, otolith analyses of field-caught larvae by CDFG (L. Miller pers. commun.) indicate mean larval growth ranged from 0.15 to 0.22 mm d⁻¹ during the drought years with record low survival (1988-1991), whereas during a wet year (1986) larvae grew 0.25 mm d⁻¹ and exhibited high survival (L. Miller, pers. commun.; Jassby *et al.* 1995; Fig. 3). In contrast, growth rates of Chesapeake Bay striped bass larvae are typically much higher (about 0.30 mm d⁻¹, Chesney 1989), suggesting larvae in the Sacramento-San Joaquin estuary may grow slowly, increasing the period when they are most vulnerable to predators (Bennett & Rogers-Bennett, submitted manuscript; Rose *et al.*, unpublished manuscript). Comparisons of results from individual-based-modeling (IBM) of Chesapeake (Cowan *et al.* 1993) and California (Rose *et al.*, unpublished manuscript) young striped bass populations also support the slow-growth hypothesis. Therefore, factors which influence growth (*e.g.*, food, temperature, pollutants) may be important, if subtle, sources of mortality.

Path 4. Success of Species Introductions. — Invasions of exotic species accompanied the massive alterations of habitats and flows during the late 1800s. With the completion of the transcontinental railroad in 1871, many carloads of marine and estuarine fishes and invertebrates from the Atlantic coast were released into the highly altered estuarine system. Three species of estuarine fish became established in large numbers almost immediately: American shad (1871), white catfish (1874), and striped bass (1879). These introductions, and many others that have taken place since the 19th century suggest that invasions of the estuary have a higher potential for success when the established assemblages are stressed or depleted from habitat alteration and/or reduced outflow (Moyle 1986; Baltz & Moyle 1993).

Further evidence for this 'rule' is the number of major invasions that occurred between 1985 and 1993, a period of severe drought whose effects were exacerbated by increasing water diversions (Nichols *et al.* 1990; Moyle *et al.* 1992; Kimmerer *et al.* 1995; Matern & Fleming, in press). Following the extreme flood event of February, 1986, populations of many estuarine organisms (particularly benthic organisms) were greatly diminished and a number of new species invaded. The most spectacular invasion was that of the Asiatic clam, *Potamocorbula amurensis*,

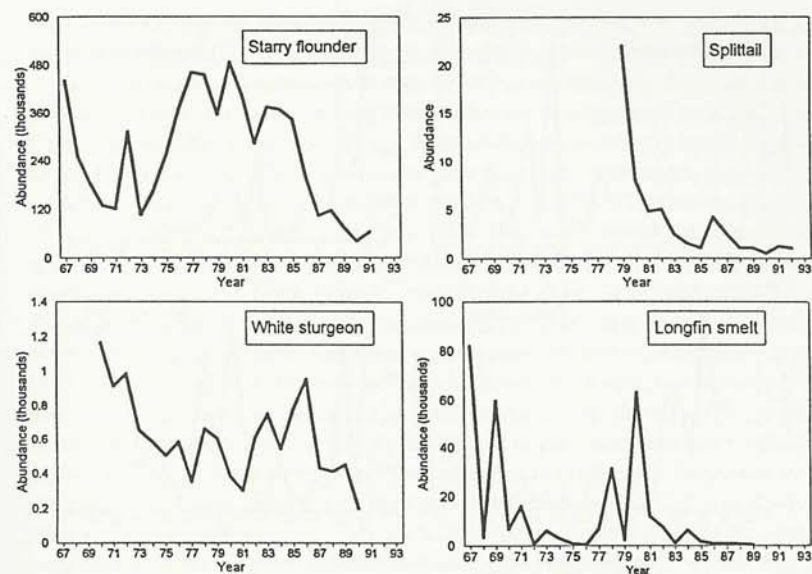


FIGURE 5. Change in abundance of selected native fishes from the Sacramento-San Joaquin estuary. Data for starry flounder (thousands of pounds) and white sturgeon (thousands of fish) are landings from commercial passenger fishing vessels. Data for Sacramento splittail are catch-per-otter trawl estimates from Moyle's Suisun Marsh survey, beginning in 1979. Data for longfin smelt are abundance indices derived from fall mid-water trawl surveys weighted by the volume of water at each site (by CDFG).

which quickly became the dominant filter-feeding organism in the estuary, with drastic effects on the plankton (Kimmerer *et al.* 1995; Kimmerer & Orsi, this volume). Other post-1986 invaders include a number of crustacean species (Carlton & Geller 1993; Hedgpeth 1993; Kimmerer & Orsi, this volume). The most recent fish invader is the shimofuri goby (*Tridentiger bifasciatus*) which arrived around 1986 (Matern & Fleming, in press), and is now one of the most abundant fish in the system (Meng *et al.* 1994; see Fig. 6). Therefore, the rate at which exotic species have become established in the estuary has increased dramatically in recent years, concurrent with and perhaps facilitated by, the maintenance of low outflow conditions by drought and diversions.

In addition to flow regulation, the high invasibility of the estuary appears to be the result of a number of interacting factors: (1) the young geologic age of the estuary and the consequent comparative lack of species specifically adapted for estuarine conditions; (2) the depauperate nature of the estuarine biota; (3) the high degree of alteration of estuarine habitats by humans; (4) the enormous extent to which introductions, both deliberate and accidental, have been made; and (5) the changing nature of estuarine conditions. As a consequence of these factors, many of the organisms that appear to dominate ecosystem processes are non-native species, new invaders appear on a regular basis, and assemblages of organisms

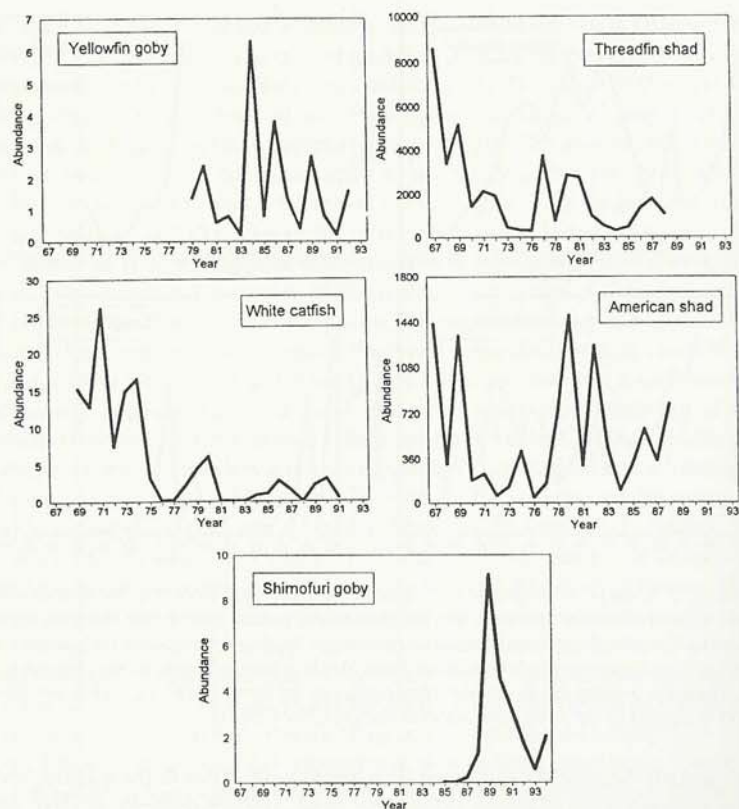


FIGURE 6. Change in abundance of selected introduced fishes from the Sacramento-San Joaquin estuary. Data for yellowfin goby (introduced about 1960, Moyle 1976) and shimofuri goby (introduced about 1986, Matern & Fleming, in press) are catch-per-otter trawl estimates from Moyle's Suisun Marsh survey, beginning in 1979. Data for American shad (introduced in 1871, Moyle 1976) and threadfin shad (introduced in 1953, Moyle 1976) are annual catches from fall mid-water trawl surveys (by CDFG). Data for white catfish (introduced in 1874, Moyle 1976) are catch-per-tow estimates from CDFG's summer tow-net survey.

have developed that are made up of mixtures of native and non-native species (Herbold & Moyle 1989). Surprisingly, extinctions of native organisms have been few (e.g., thicktail chub, *Gila crassicauda*, last seen in 1958, Moyle 1976), although many are greatly diminished in numbers and may face extinction in the future.

One consequence of an invasion prone food web is that the abundance and composition of prey items, competitors, and predators can change contemporaneously (Drake 1991). For the most part, fishes in this system seem to be able to quickly switch to new prey. Delta smelt and larval striped bass, for example, both began preying on non-native zooplankton when the native species declined (Meng & Orsi 1991; Moyle *et al.* 1992; see Path 3 above). However, when an invading

species both competes with and preys on established species, *i.e.*, is an intraguild predator (Polis *et al.* 1989), it can produce major negative effects (Race 1982).

Such an intraguild relationship may be occurring between the exotic inland silverside and delta smelt. Inland silversides were introduced to Clear Lake, California, in 1966 to control the gnat population, and eventually made their way to the Delta (Moyle 1974, 1976). Like many successful invaders, they became established in the estuary during drought conditions (1976-1977) (Meinz & Mecum 1977), and increased sharply after 1981-1982, concurrent with the decline of delta smelt (Fig. 4). Gut content analyses indicate considerable diet overlap between silversides and delta smelt (Moyle, unpublished data), and field experiments indicated silversides are very efficient predators on fish larvae (see Path 3 above; Bennett & Rogers-Bennett, submitted manuscript). Moreover, silversides appear to be highly abundant in the shoal habitats of the western Delta (lower Sacramento River) where delta smelt spawn in low outflow years. In high outflow years, delta smelt larvae appear to be more evenly distributed in the estuary and more abundant in Suisun Bay, and thus away from shoreline areas, possibly reducing contact with silversides (Bennett, unpublished manuscript). The abundances of inland silversides and delta smelt are negatively associated in low outflow (dry) years, using a reduced major axis (Model II Sokal & Rohlf 1981) regression ($P < 0.05$, Fig. 7), supporting this hypothesis. Therefore, while the silverside-delta smelt relationship requires more study, it illustrates how freshwater outflow may regulate invasion success as well as the impact of an exotic species.

Path 5. Dilution and Flushing of Pollutants. — Pollution has been a problem in the estuary starting in the 1860s when sediments and mercury poured in from upstream mining. When mining sources of pollution diminished, urban, industrial, and agricultural sources increased. The most obvious pollutants were the domestic sewage and industrial waste which was dumped directly into the estuary with minimal treatment. In 1972, however, the federal Clean Water Act was passed, followed by the passage of the state Porter-Cologne Act. The gradual but dramatic increase in water quality that followed the decrease in sewage input in the next 20 years revealed that many problems exist, including pesticides, heavy metals, and petroleum compounds in the estuary. In 1990, the State Water Resources Control Board identified human and ecosystem health problems as cumulative pesticide loads were found in organisms as well as concentrations of arsenic, cadmium, chromium, copper, chlorinated dibenzodioxins and dibenzofurans, hydrocarbons, lead, mercury, nickel, organochlorines, selenium, silver, tributyltin, and zinc (Nichols *et al.* 1986; Setzler-Hamilton *et al.* 1988). Human health warnings have been posted against the regular human consumption of striped bass and other Delta fishes, especially those from the San Joaquin River (Setzler-Hamilton *et al.* 1988).

The effects of some pollutants are associated with the amount of freshwater outflow (Cornaccia *et al.* 1984; Foe & Connor 1989; Bailey *et al.* 1994). For example, most of the area surrounding the striped bass spawning habitat in the Sacramento River is used for rice cultivation, and consequently discharges of irrigation water containing pesticides can contribute up to 30% of the river volume, depending on the amount of outflow (Cornaccia *et al.* 1984). Bioassays indicate

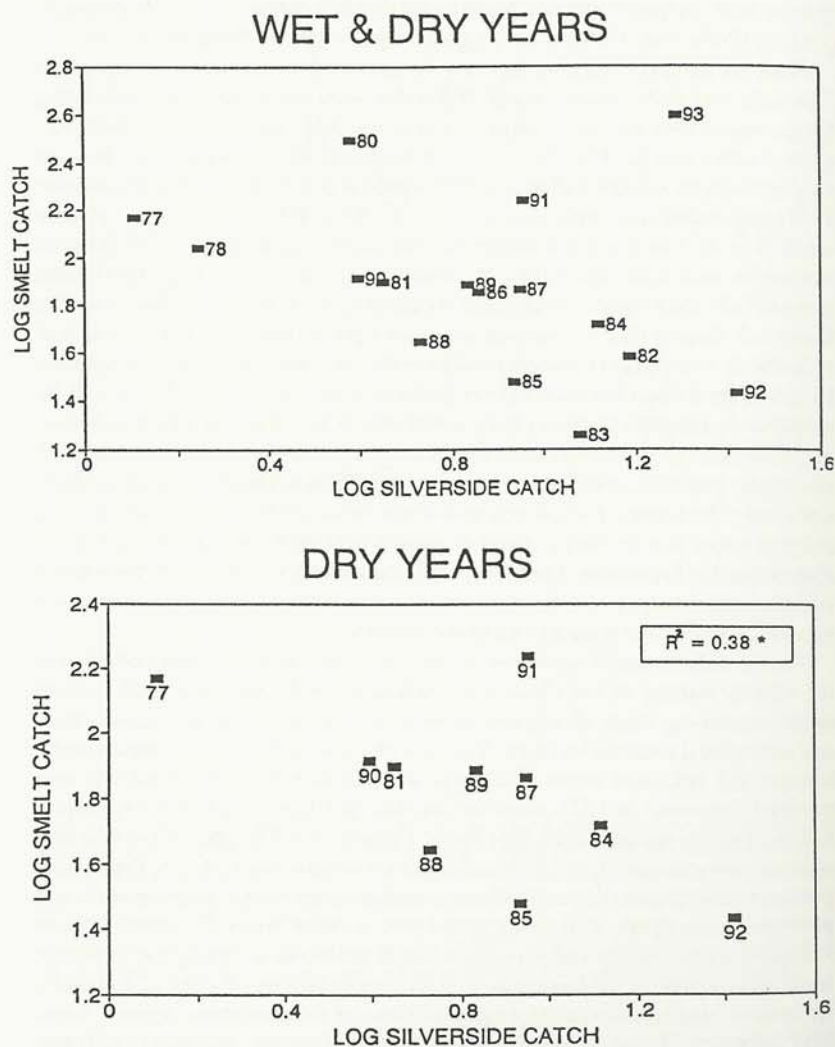


FIGURE 7. Association of delta smelt catch in CDFG's fall mid-water trawl survey with catch of inland silversides per haul in USFWS's salmon smolt beach seine survey in "wet and dry years" and in "dry years" (using DWR criteria for water year type) since 1977. Reduced major axis (Model II, Sokal & Rohlf 1981) regression is significant in "dry years" ($P < 0.05$, $R^2 = 0.38$).

that the runoff produced sublethal and lethal effects on invertebrates and striped bass larvae (Foe & Connor 1989; Heath *et al.* 1993; Bailey *et al.* 1994). In addition, histopathological evaluation of field-caught striped bass larvae during the recent

drought (1988-1990) indicated that 26-30% had liver alterations consistent with exposure to rice pesticides that would slow larval growth, enhancing mortality (Bennett *et al.* 1995). In 1991, the toxicity of rice runoff in bioassays and the proportion of afflicted larvae decreased by about 50%, as a result of changes in the application of rice pesticides (Bennett *et al.* 1995). However, while the incidence of affected larvae declined by 50%, striped bass year-class success remained poor. In addition, pesticides from other agricultural activities are regularly detected in Delta water particularly during critical spawning seasons in low outflow years (C. Foe, pers. commun.), suggesting they will remain an important concern.

Path 6. Habitat Alterations. — The estuarine habitats have been experiencing considerable alteration since 1850 with the advent of hydraulic mining, which pushed millions of tons of sediment downstream. The diking of islands in the Delta for farmland began about the same time (1852) and the vast wetland system that once existed became 90% dry land, intersected with deep, narrow channels. Only 3% of the Delta still resembles its original shallow-water habitat (Herbold & Moyle 1989; Herbold *et al.* 1992). Similar kinds of diking operations occurred in lower parts of the estuary as well (*e.g.*, Suisun Marsh) although some of that area has been restored to wetland. Dredging of channels and filling in of shallow areas has also caused significant alteration of estuarine habitats. While habitat alteration in the estuary has been drastic and is still ongoing, most of the activity took place before the present precipitous declines of fish abundances. Presumably habitat alteration had equally drastic effects when it occurred in the 19th century, but there was no monitoring of fish populations at the time. Many resident native species may have started to decline in this early period because the loss of wetlands and shallow water habitat may have reduced estuarine productivity, as well as decreased residence time of water in the Delta, reducing the suitable habitat available to larval and juvenile fish. In recent times substantial shallow water habitat is created only in extremely wet years during spring, when large areas become flooded. The recruitment success of native species (*e.g.*, Sacramento splittail) is highly associated with the creation of such habitat (T. Sommer, DWR, pers. commun.), possibly due to adequate spawning substrate for their adhesive eggs and nursery habitat for young fish (Daniels & Moyle 1983).

Harvesting. — While not directly influenced by outflow (and thus not included in our model, Fig. 2), overharvesting is often cited as the primary cause of collapse in many of the world's fish populations (Rothschild 1986). However, the current role of fishing on populations in the estuary is unclear. In the 19th century, overharvesting of chinook salmon and white sturgeon was a major factor contributing to their declines and reduction of the fisheries led to a recovery (Smith & Kato 1979). Because of critically low abundance, it is likely that commercial and sport fishing for naturally spawned chinook salmon is now contributing to their decline, or at least making recovery more difficult. Depleted populations of wild fish, with relatively low levels of juvenile survival in freshwater, presumably cannot withstand even moderate levels of exploitation. Likewise, it is possible that the removal of large female striped bass by legal or illegal fishing has contributed to the downward spiral of the bass population. The largest females have the highest

fecundities and can contribute a high proportion of the new recruits to the population each year (Cowan *et al.* 1993). When survival rates of larvae and juveniles are low, high production rates of young may partially compensate for the reduced survival rates. In addition, sampling of severely depressed/ endangered populations has been shown to increase substantially the risk of extinction (Harrison *et al.* 1991).

DISCUSSION

Multiple Pathway Effects and Recruitment Success. — We have reviewed work indicating that several pathways can act simultaneously to affect survival of young fish. However, the relative importance of various pathways can differ among years and species. In this light, we highlight differences among pathway functions in order to provide a better understanding of their relative importance. Our discussion will focus on the problems of young striped bass (see Fig. 2 pathways 1,3,5), because we know the most about the species.

Without human intervention, fish eggs and larvae naturally experience very high mortality. A large portion of this mortality may be produced by inherent variability among larvae, leading to differential survival. Among the many factors that can affect survival of eggs and larvae, individual growth and size variation have recently been emphasized as important factors determining recruitment success (Houde 1987; Crowder *et al.* 1992; Rice *et al.* 1993). This is partly due to the diversity of factors that can influence growth and size variability (*e.g.*, parental/egg size, inherent developmental processes, food abundance, temperature, competition, parasitism), and partly to the frustration of trying to assign single factor explanations for recruitment variability (Sissenwine 1984; Leggett 1986; Lawrence 1991).

Slower growth influences recruitment success by increasing the cumulative impact of predation on a cohort (Houde 1987; Lawrence 1991). Traditionally, this has been considered to be a density-dependent process with compensatory effects, because low spawner abundance translates into reduced competition for food or habitat. This in turn produces higher larval growth rates than would occur during times of very high spawner/larval abundance (Shepherd & Cushing 1980; Sissenwine 1984; Rothschild 1986). In the Sacramento-San Joaquin estuary, however, abundance of spawning striped bass is low enough such that mortality of larvae from slower growth is density-independent, or density vague (Strong 1986), acting in a stochastic fashion (Lawrence 1991). This is because larvae are typically at low densities, thus they should not impact their food resources and they are presumably an incidental rather than sought-after prey item. This implies that finding food and being eaten can be stochastic or density-independent events, when populations are at intermediate to low abundance.

Entrainment and lethal exposure to contaminants also act in a density independent manner. Various environmental or human interventions affecting larval growth (*e.g.*, temperature, sublethal toxic exposure) become superimposed on the natural growth pattern in a stochastic fashion. This suggests that food limitation, toxic exposure, and entrainment all produce mortality in a stochastic fashion, and thus they can work simultaneously to limit recruitment in low outflow years. This

is consistent with the idea that recruitment failure or success is often the product of at least 2 factors acting synergistically (Lasker 1981; Cohen *et al.* 1988; Cowan *et al.* 1993). Low outflow conditions promote these interactions.

The altered estuarine hydrodynamics in low outflow years may produce a gauntlet of stochastic effects for young striped bass. In low outflow years, water flow is typically altered and drawn south across the Delta towards the state and federal pumping facilities (Fig. 1, Moyle *et al.* 1992; Arthur *et al.*, this volume). Toxic runoff enters the main striped bass spawning areas in the upper Sacramento river, and throughout the Delta. Thus, the probability of exposure begins at the time of spawning (or before, by maternal gift of toxins accumulated in eggs). Food limitation/stage duration problems arise after about 1 week of egg and larval transport, and thus may occur most often in the central and western Delta. While the magnitude of entrainment losses in the 1,800 or so small water diversions throughout the Delta is uncertain, clearly large numbers of young fish are lost from the combined effects of predation in Clifton Court Forebay and in the pumping facilities (Fig. 1). Therefore, young striped bass must run a gauntlet of stochastic effects beginning with toxic exposure and food limitation, even before entrainment affects them. Therefore, the probabilities of mortality from toxic exposure and food limitation operate before entrainment. Essentially, if one pathway doesn't kill you, odds are the other ones will.

This simple scenario is supported by the larval condition study (Bennett *et al.* 1995). Histopathological evaluations indicated the proportion of larvae with damaged livers dropped by 50% in 1991, concurrent with an approximately equal reduction in the toxicity of rice-field runoff. However, the 1991 young-of-the-year (38mm) recruitment index remained very low (Fig. 3). This indicates that larvae spared by the cleaner effluent were killed by other factors (*e.g.*, slower growth, entrainment), such that various pathways act in concert to regulate recruitment. Therefore, we suggest that the high degree with which pathways interact, indicates the futility of determining the relative importance of single factors. Moreover, factors may alternate in importance within and among years, as well as among species.

Indeed, the transport/entrainment pathway clearly has an important impact. Simulation models indicate that high entrainment rates can severely limit young-of-the-year success of Hudson River striped bass (Christensen *et al.* 1977). Other modeling studies indicate constant harvesting (entrainment) in a variable environment that undergoes sequences of adverse conditions (*e.g.*, prolonged drought) will exacerbate greatly the harvest effects (Beddington & May 1977; Fogarty *et al.* 1991). We are, however, emphasizing the importance of interacting pathways that occur in the Delta region during times of low outflow, and in a transport sense, have the potential to affect fish even before they are entrained. This suggests that if entrainment was curtailed entirely, yet outflow remained low, recruitment may also remain low. However, because species exhibit differences in their susceptibility to entrainment and in their relationships with outflow (Jassby *et al.* 1995), elimination of entrainment could improve the recruitment of highly susceptible species (*e.g.*, striped bass, salmon).

The implication of so many pathways acting simultaneously is that the estuarine habitat has been degraded to such an extent that the potential carrying capacity (K) has been reduced significantly for many fishes. The degree of reduction may have been severe enough to have pushed many populations to alternative states of low abundance (May 1977; Peterman *et al.* 1979). An unfortunate consequence of this, however, is that a population's abundance may remain in the lower state for an indefinite period even after perturbations are removed (*e.g.*, outflow is not diverted), because ecologically similar species may acquire numerical dominance during the perturbation period and maintain dominance subsequent to its removal (Peterman *et al.* 1979; Botsford 1981). This could occur in the Sacramento-San Joaquin estuary if abundant exotic species (*e.g.*, shimofuri goby, inland silverside) can effectively reduce the recruitment success of formally dominant species (*e.g.*, delta smelt, white catfish) by competition and/or predation, precluding their return to pre-perturbation levels of abundance.

Life History and Recruitment of Less Studied Species.— While striped bass have been well studied, they differ considerably in several key life history characteristics from native fishes. This suggests they may be a poor model organism for understanding declines in other species. For example, striped bass are long-lived (20-40 years), but reproduce at about age 3, whereas most native species live less than 5 years (Table 1). This high degree of generation overlap complicates evaluations of striped bass population dynamics. In addition, larval striped bass are highly resistant to starvation (Houde 1987), and several studies indicate they can survive without food for 30 days (Eldridge *et al.* 1981; Chesney 1989; Bennett *et al.* 1995). This period for striped bass, is about twice as long as for most similarly sized fish larvae (Miller *et al.* 1988).

By comparison, delta smelt larvae are more susceptible to starvation and have recently been shown to starve in 10-14 days post-hatch (R. Mager, UCD, pers. commun.). The importance of this for delta smelt is underscored, because rotifers, a preferred food item of first-feeding larvae, have declined dramatically throughout the estuary in recent years (Kimmerer & Orsi, this volume). While estimates of larval susceptibility to starvation (point-of-no-return) have not been conducted on other larval fishes residing in the upper estuary, several studies (Table 1.) using various methods indicate many are sensitive to low food and/or susceptible to slow growth.

Overall, species in decline (see Fig. 3-6) with the exception of striped bass, tend to be pelagic, reside in the Delta, exhibit some degree of food sensitivity, and require suitable spawning substrate. This implies that they are susceptible to all pathways in Figure 2. For example, pelagic and Delta resident fishes are susceptible to transport/entrainment and toxic runoff events. Most native species (*e.g.*, delta smelt, longfin smelt, splittail, see Table 1) require suitable spawning substrate (submerged vegetation, fallen trees), because they have benthic or adhesive eggs. For example, lack of suitable substrate may preclude spawning by splittail in low outflow years (Caywood 1974; Daniels & Moyle 1983).

An alternative way to identify factors that produce fish declines is to examine the characteristics of the few species that are either not in dramatic decline (*e.g.*,

TABLE 1. Life history characteristics of selected Bay/Delta fishes.

Species	Life Span (years)	Spawning Season	Egg Type	Size at Hatch (mm)	Starvation Sensitive	Nursery Habitat	
						Pelagic/Benthic	Delta Dependent?
Striped bass <i>Morone saxatilis</i>	20-40	April-June	semi-boyant	3-5	No (25-30 dph ¹)	pelagic	Yes
American shad <i>Alosa sapidissima</i>	3-4	April-July	semi-boyant	7-10	Yes (Creco & Savoy 1987)	pelagic	No
Threadfin shad <i>Dorosoma petenense</i>	2	April-Sept.	benthic	3-4	Yes (Kashuba & Matthews 1984)	pelagic	No
Delta smelt <i>Hypomesus transpacificus</i>	1	April-May	benthic	4-5	Yes (10-14 dph, R. Mager, UCD)	pelagic	Yes
Longfin smelt <i>Spirincheilus thaleichthys</i>	2	Feb.-April	benthic	5-7	?	pelagic	Yes
Splittail <i>Pogonichthys macrolepidotus</i>	5-7	March-July	benthic	4-6	?	pelagic	Yes
Starry flounder <i>Platichthys stellatus</i>	4+	Nov.-Feb.	buoyant	2-3	Yes (Policanski & Sieswerda 1979)	pelagic/ benthic (7mm)	No
Yellowfin goby <i>Acanthogobius flavimanus</i>	3-4	Nov.-March	benthic/ protected	4-5	?	pelagic/ benthic (13mm)	No
Shimofuri goby <i>Tridentiger bifasciatus</i>	2-3	April-Sept.	benthic/ protected	2-3	?	pelagic/ benthic (14mm)	No
White catfish <i>Ictalurus catus</i>	10?	June-Sept.	benthic/ protected	9-10	?	benthic	Yes
White sturgeon <i>Acipenser transmontanus</i>	50-100	Feb.-May	benthic	10-11	Yes (12-17 dph, K. Kroil, UCD)	benthic	Yes
Inland silverside <i>Menidia beryllina</i>	1	April-Sept.	benthic	4-5	?	pelagic	No

¹ Days post-hatch

yellowfin goby, white sturgeon) or are actually increasing in abundance (shimofuri goby). It is significant that most of these species are benthic predators with life histories that avoid many of the problems faced by fish with a prolonged pelagic existence (pathways 1-6, Fig. 2). One advantage of benthic foraging is that benthic food organisms have generally remained abundant, despite major changes in species composition in recent years (Hymanson *et al.* 1994). The reasons for this are not clear, but reduced predation by benthic foragers that have declined (*e.g.*, splittail, white catfish) may play a role. In particular, the white sturgeon may have benefited from the abundance of benthic prey, including exotic clams, although its long life span and reliance on episodic reproduction events during extremely high outflow years (Kolhorst *et al.* 1991) also offer it a high degree of immunity from estuarine problems. The two goby species (Fig. 3) appear to be able to take advantage of the immense amount of spawning habitat created by the extensive rip-rap (concrete rubble) used to reinforce the sides of Delta channels. In addition, they have long or multi-clutch spawning seasons and begin their benthic life style early, spending a comparatively short time in the plankton as larvae (Table 1). The only pelagic fish that does not appear to have declined is the inland silverside. Its successful invasion of the estuary can probably be attributed to three factors: (1) it is primarily an inshore species, rather than a true pelagic species, (2) it is a fractional spawner, producing eggs all summer long (Table 1), and (3) it is present in large numbers in areas upstream of the estuary (Moyle 1976; Bennett, unpublished manuscript).

CONCLUSIONS

The presence of a critical pelagic stage in the early life histories of most of the declining fishes in the estuary suggests that the declines are related to repeated recruitment failure. Clearly, the factors producing failure can be multiple and/or synergistic pathways for each species (Fig. 2). The relative importance of pathways may also differ among species; pesticides, for example, may be more likely to affect striped bass than white catfish, because of their relative spawning times (Table 1). However, the best evidence available to date indicates that the single most important factor associated with recruitment failure in fishes of the upper Sacramento-San Joaquin estuary is the reduction of outflowing freshwater through the estuary (Fig. 2). This is produced by water diversions both within and upstream of the Delta and exacerbated by drought. Unfortunately, even in the unlikely case that the diversion problems were solved soon, fish populations may not exhibit an immediate resurgence as might be predicted. Solving the outflow problem may quite likely reveal additional limiting factors as the estuarine food web reshapes itself under a different hydrodynamic regime. This is suggested by the apparent lack of response in striped bass recruitment after the reduction in the toxicity of pesticide runoff into the spawning habitat in the Sacramento River. All of this indicates that we need a much better understanding of the early life stages of the estuary's fishes if their declines are to be permanently reversed. Even with the volumes of information on striped bass, we are only now beginning to understand its recruitment problems. This understanding is being facilitated by an integrated approach

in which field studies (especially long-term monitoring) are used to design experiments to test process-oriented hypotheses. Particularly important in this approach have been the development of hydrodynamic and individual-based simulation models (Cowan *et al.* 1993; Rose *et al.*, unpublished manuscript). However, while such models are shedding considerable light on the highly interactive nature of mortality pathways affecting striped bass, there is too little information available to apply them to native fishes. Currently, we have to hope that the depressed populations of native fishes can persist until a better understanding of their life histories is developed.

This pessimistic statement does not mean that we are without options until more research is completed. Clearly, improving estuarine hydrodynamics, reducing entrainment, decreasing pesticide runoff, and increasing the amount of shallow-water spawning habitat, as well as other actions to ameliorate the pathways identified here (Fig. 2) will improve conditions for fishes in the estuary. Better knowledge of early life histories, however, should tell us why various actions work. If we understand why actions work, then management policies can be refined to target problem species. Ideally, more sophisticated management of fish populations could increase the amount of water for other beneficial uses as well as improve conditions in the entire estuarine ecosystem.

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SAN FRANCISCO BAY: THE ECOSYSTEM

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