Sacramento-San Joaquin Delta
Regional Ecosystem Restoration Implementation Plan

Life History Conceptual Model and Sub-Models

Longfin Smelt, San Francisco Estuary Population

Supporting Text

ERPP Species Designation:	Recovery "R"
Federal Status:	Candidate for ESA listing
State Status:	Candidate for ESA listing (receives protections afforded to listed species)
Recovery Plan(s):	U.S. Fish and Wildlife Service, 1996

FINAL

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Submitted: May 2010 for the Delta Regional Ecosystem Restoration Implementation Plan

Reviewed

PREFACE

This Conceptual Model is part of a suite of conceptual models which collectively articulate the current scientific understanding of important aspects of the Sacramento-San Joaquin River Delta ecosystem. The conceptual models are designed to aid in the identification and evaluation of ecosystem restoration actions in the Delta. These models are designed to structure scientific information such that it can be used to inform sound public policy.

The Delta Conceptual Models include both ecosystem element models (including process, habitat, and stressor models) and species life history models. The models were prepared by teams of experts using common guidance documents developed to promote consistency in the format and terminology of the models http://www.delta.dfg.ca.gov/erpdeltaplan/science_process.asp .

The Delta Conceptual Models are qualitative models which describe current understanding of how the system works. They are designed and intended to be used by experts to identify and evaluate potential restoration actions. They are not quantitative, numeric computer models that can be "run" to determine the effects of actions. Rather they are designed to facilitate informed discussions regarding expected outcomes resulting from restoration actions and the scientific basis for those expectations. The structure of many of the Delta Conceptual Models can serve as the basis for future development of quantitative models.

Each of the Delta Conceptual Models has been subject to a rigorous scientific peer review process.

The Delta Conceptual models will be updated and refined over time as new information is developed, and/or as the models are used and the need for further refinements or clarifications are identified.

CONTENTS

1. Introduction

This model describes the "Importance" of stressors on the life history of longfin smelt in the San Francisco Estuary. In addition, the model identifies the degree to which we understand the nature of a relationship between stressors and successful completion of the life cycle ("understanding") and the certainty surrounding how important a particular stressor is for a particular life stage ("certainty of impact").

2. Description

Longfin smelt (*Spirinchus thaleichthys*; LFS) are small (to ~140mm SL), euryhaline, anadromous, and semelparous fish with a life cycle of approximately 2 years (Table 1). Longfin smelt can be distinguished from other California smelts by their long pectoral fins, incomplete lateral line, weak or absent striations on the opercular bones, low number of scales in the lateral series (54-65), and long maxillary bones. The lower jaw projects forward of the upper jaw when the mouth is closed. Small, fine teeth are present on both jaws, tongue, vomer and palatines. The sides of living fish appear translucent silver while the back has an olive to iridescent pinkish hue. Mature males are usually darker than females, with enlarged and stiffened dorsal and anal fins, a dilated lateral line region, and breeding tubercles on the paired fins and scales (Moyle 2002).

Populations occur along the Pacific Coast of North America north to Hinchinbrook Island, Prince William Sound, Alaska. The San Francisco Estuary (Estuary) represents the southernmost population (Lee et al. 1980) and the largest spawning population in California. Individual LFS have been caught in Monterey Bay (Moyle 2002) but there is no evidence of a spawning population south of the Golden Gate. The existence of other spawning populations has been documented or suspected in Humboldt Bay, the Eel River estuary, the Klamath River estuary, the Van Duzen River, the Eel River drainage, and the Russian River (Moyle 2002, Pinnix et al. 2004; CDFG 2009). Most of these populations are small and perhaps ephemeral, if they exist at all; as a result, data from these estuaries (other than presence/absence) are largely unavailable (CDFG 2009).

Local population -- Longfin smelt are widespread within the San Francisco Estuary and, historically, they were found seasonally in all of its major openwater habitats and Suisun Marsh (Fig. 1). Longfin smelt are periodically caught in nearshore ocean surveys (CH2M Hill 1985). Because of their former abundance and broad distribution, LFS are believed to be an important integrator of the estuarine food web and a valuable indicator of ecosystem function (USFWS 1996; Moyle 2002).

A petition to list the San Francisco Estuary population as a threatened species under the Endangered Species Act was denied in 1994 (US Fish and Wildlife Service 1994) because the degree of reproductive and genetic isolation was unknown. Whereas, it is conceivable that successful migration (demographic and genetic exchange) occurs between the San Francisco Estuary and populations to the north, such exchange has not been documented. Given their small size and short life span, it is not likely that the San Francisco Estuary's population size or genetic diversity are supported by regular emigration from other California coastal populations which are all ephemeral, small, or distant (CDFG 2009). A new petition to protect this population under the state and federal Endangered Species Acts (ESA) was submitted in the summer of 2007. The State found that the petition presented sufficient cause to designate the species as a candidate for state ESA protection (a preliminary step to listing) – candidate species receive full protection under the state ESA. The federal ESA petition was pending as this model was prepared for publication.

Five life stages are referred to in this life history conceptual model (*see also* Table 1):

- Eggs – LFS produce adhesive (demersal) eggs (Dryfoos 1965, Moyle 2002) that develop for approximately 25-42 days after fertilization (Wang 1986; CDFG 2009). Little is know about the developmental response to varying physical or chemical conditions.
- Larval – for purposes of this model, this phase begins after hatching (5mm SL Wang 1991) and ends when resorption of the yolk-sac and fin formation are nearly complete (~15-16 mm SL; Wang 1991; R. Baxter. CDFG, *personal communication*). Other authors mark the end of the larval period at the completion of the development of fin rays (Baxter 1999). The distinction has biological significance. As defined here, larvae feed endogenously and behave more or less as buoyant "particles" in a hydrodynamically complex environment. This developmental stage lasts for several weeks to three months, depending on growth rate (Emmet et al. 1991 in USFWS 1996; CDFG 2009).
- Juvenile – this phase begins when yolk-sac resorption and fin formation are nearly complete (>15m) and ends after the second winter of life (<~70mm SL). For purposes of this model, this phase begins when fish depend on exogenous food supplies as opposed to the yolk sac. New juveniles are poor swimmers (fin rays are not completely developed until fish reach ~20mm); however, fish may adjust their position in the water column and thus manipulate their position by using convective currents (Bennett et al. 2002). This stage includes fish in their first year of detectability by the Bay Study's net (ages 4 months to 15 months; Age Class 0+);
- Sub-Adult – this phase is arbitrarily defined because it is useful to distinguish juveniles from fish in their second year of life. The phase begins when fish enter their second year of detectability by the Bay Study's nets (ages 16 months to 27 months >~70mm, Age Class 1+) and, ends when fish become reproductively mature (typically 80mm-120mm).
- Sexually Mature Adult -- sexually mature adults occur in the same size range as Age 1+ fish, although they are expected to be larger, on average than sub-adults (~70mm-140mm SL, more typically 80mm-120mm). The distinction between these two groups is based on age, season, and gonad development.

Female LFS produce 1,900 to 18,000 adhesive eggs (CDFG 2009). This large range reflects intra- and inter-population variability as well as variance over time within populations. Analysis of gravid females from the San Francisco Estuary caught during the 1992-1994 spawning seasons by CDFG sampling programs determined a strong relationship between female body size and fecundity (Fig. 2). Length explained ~75% of variation in fecundity. Much of the remaining variation in LFS fecundity is probably related to female condition (e.g., mass:length, % lipid content) although this relationship has not been studied.

Factors impacting these life history stages are described in three sub-models.

- Egg incubation through larval development and dispersal to the juvenile life stage (birth to Age 0+; Fig. 3);
- Growth, development, and migration of Age Class 0+ through sub-adult (Age 1+) LFS to sexual maturity (Fig. 4);
- Spawning of sexually mature adults to produce a population of eggs (Fig. 5).

3. Spatial and Temporal Distribution

Spawning and eggs -- The conditions experienced by LFS embryos and larvae are affected by the timing and location of spawning. For example, water temperatures, flow rates, and salinity are important factors that influence developmental rates and success in many demersal fish eggs; although the tolerances and responses of LFS to these conditions are unknown. These conditions vary over time and space in the Estuary.

The exact location of spawning sites and the factors that determine the rate and success of LFS embryogenesis are not well understood in this Estuary. Longfin smelt eggs are adhesive and are probably deposited on the same type of sandy substrates used by other osmerid species (Moulton 1974; Martin and Swiderski 2001; CDFG 2009). Although juvenile and sub-adult LFS aggregate in deep water (Rosenfield and Baxter 2007) it is not clear that spawning occurs in deep water habitats; sexually mature LFS may migrate to shallower locations briefly to spawn.

Longfin smelt are believed to spawn at or near the mixing zone between fresh and brackish water in this Estuary (Wang 1991; CDFG 2009). Based on the distribution of gravid adults, spawning habitat for LFS probably includes freshwater sections of the lower Sacramento River, eastern Suisun Bay, and Suisun Marsh (Wang 1991; Fig. 1, Table 1). In recent times, adult LFS have been detected in the San Joaquin River only rarely. When they are caught, this usually occurs below Twitchell Island (Moyle 2002). Longfin smelt have been detected as far up the San Joaquin River drainage as the Tuolumne River (i.e., in a sample from 1999, B. May, UC Davis, *unpublished data*) suggesting that the San Joaquin River may also provide spawning habitat in some years. LFS larvae are detected above Rio Vista on the Sacramento River near Cache Slough, in particular during years with low winter-spring outflow from the Delta (Wang 1991; CDFG 2009). The CDFG 20mm survey catches relatively large numbers of LFS larvae in the Napa River estuary, especially during wet winters (CDFG 20mm Survey database), indicating that spawning habitat may be periodically available in that area as well. Finally, some maturing LFS migrate into the South Bay during the fall and winter suggesting that spawning may occur in tributaries to the South Bay (*e.g.,* Coyote Creek).

Larvae -- Larvae are distributed near the surface of the water column in fresh and brackish waters (Wang 1986); the center of larval distribution is closely associated with the position of the 2ppt isohaline ("X2") regardless of outflow conditions (Dege and Brown 2004). Larvae are detected each year in the western Delta, Suisun Bay, Suisun Marsh; and the southern Delta (Baxter 1999; CDFG 2009; Fig 6) and less commonly in the eastern Delta; larvae are also frequently caught in San Pablo Bay and during high outflow years, larvae appear in the Central and South Bays (Wang 1991, Baxter 1999; Dege and Brown 2004; CDFG 20 mm survey *unpublished data*). In many years, LFS larvae are caught in the Napa River estuary as well. Larval sampling in the South Bay is not extensive enough to adequately characterize the presence or abundance (if any) of larval LFS in this area of the Estuary.

In this Estuary, larval LFS are detected over a protracted period; they are most common in the winter and early spring (Table 1). The CDFG 20mm survey detects larval LFS as late as the end of July (the end of its sampling period). Between 1980 and 1989, CDFG's Bay Study plankton net detected larval LFS in all but three months of the year (Aug-Oct) and, in most years LFS larvae were detected by this net for 7 months. Metamorphosis into the juvenile form may begin as quickly as ~15 days post-hatch but more commonly requires 3 months to complete (Emmet et al. 1991 in USFWS 1996; CDFG 2009). Water temperature has a large influence on these developmental rates.

Juvenile and sub-adult -- The location of LFS when they develop the ability to swim (i.e. when they enter the juvenile phase) depends largely on the distribution of larvae, a function of spawning location, freshwater outflow from the Delta, and tides during the late-spring. Early stage juveniles may adjust position in the water column and so use tidal fluctuations to maintain or change geographic position (Bennett et al. 2002). After fin rays are completely developed (~20mm SL; Table 1), longfin are able to swim to adjust their position in the water column and pursue prey.

Juvenile and sub-adult longfin are widely distributed throughout the year in brackish and marine environments inside the Golden Gate (Baxter 1999; Rosenfield and Baxter 2007; Fig. 7). Both of these age groups are found at greater densities in deep habitats (>7m) than in shallower habitats (Rosenfield and Baxter 2007). Juveniles (Age 0+) and sub-adult LFS (Age 1+) appear to migrate seasonally, downstream during summer months and upstream in the late-fall and winter; their wide distribution in the Estuary suggests a fair amount of plasticity in this behavior (Fig. 7). Marine migrations are suggested by a persistent seasonal decline in LFS abundance throughout the Estuary during the summer that is followed by a “re-appearance” of part of the population during the fall and winter (Fig. 8). That populations of LFS in their second winter of life (ages 22-24 months) are consistently greater than populations of LFS in the preceding fall (ages 19-21 months) strongly suggests that these fish migrate outside of the Estuary during the summer and return during the fall. The extent and duration of migrations into marine environments has received little study but it appears to be one of several life history tactics that may be employed by LFS from this Estuary (Rosenfield and Baxter 2007).

Sexually mature adult -- Sub-adults probably mature sexually as they migrate towards spawning locations. A shift in LFS distribution towards freshwater begins in late-fall and continues into the spring. Gravid females are commonly detected in trawling at Chipps Island (R. Baxter, CDFG, *personal communication*) and historically, a small number of sexually mature adults were detected in Suisun Marsh during winter months (Rosenfield and Baxter 2007). Similarly, a small number of Age Class 1+ adults are found in the southern end of the South Bay, particularly during wet years; this suggests that LFS may spawn in freshwater tributaries to the South Bay.

Substantial variation in the timing of all life cycle events can be seen within and across cohorts (Rosenfield and Baxter 2007; Figs. 6, 7; Table 1). The Suisun Marsh Survey has detected small juvenile LFS in every month of the year except December and January (UC Davis Suisun Marsh Survey *unpublished data*). Similarly, gravid females are detected over many months between late-fall and winter and larval LFS are caught in numerous months each year. This suggests that the spawning period is long and/or that developmental schedules vary substantially.

4. Life history and ecology

Egg-Larvae Transition

Longfin smelt are generally semelparous, although it is possible that some survive to spawn more than once. Semelparity is strong evidence that LFS evolved in environments where egg incubation conditions were historically reliable (i.e. once eggs are deposited, they have a high likelihood of successful development relative to adult survival; Charnov and Schaffer 1973). Life-history tactics that rely on predictable incubation conditions make LFS extremely vulnerable to changes in the physical, biological, and chemical conditions of their spawning grounds. Impairment or limitation of these oviposition and incubation conditions threatens success in this part of their life cycle.

Physical constraints on the successful incubation of LFS eggs have not been studied in this Estuary or elsewhere. The effect of salinity on developing LFS eggs is not known, although the distribution of sexually mature LFS suggests that preferred spawning locations are located in or close to fresh water (CDFG 2009; Fig. 7; Table 1). They are clearly capable of spawning in freshwater (the most-studied LFS population occurs in Lake Washington); however, LFS are close relatives of smelt that spawn in saline waters and spawning in brackish water may also be an option for these fish. Sexually mature fish are found in great numbers in Suisun Bay and it is possible that that spawning occurs in the brackish waters of that Bay (Wang 1991).

The microhabitat requirements of incubating LFS embryos are unknown. Juveniles, sub-adults, and sexually mature adults tend to aggregate in deep water, high-velocity environments but, it is possible that LFS aggregate ("stage") in these environments before making brief (perhaps nocturnal) migrations to spawning habitats, a behavior seen among other osmerids. It is not known whether sexually mature fish caught in brackish waters (Suisun Bay) or marsh environments (Suisun Marsh) were preparing to migrate to freshwater or whether either group spawned near where they were captured.

Eggs are deposited from late-fall to early-spring and can incubate in water temperatures of 7.0°-14.5°C (Emmett *et al.* 1991 *in* CALFED 1999). Wang (1986) proposed that LFS from this Estuary spawn at water temperatures of 8.33°-14.44°C (Wang 1986 *in* CALFED 1999). However, this range (to say nothing of "optima") is not well documented; LFS in this Estuary may have broader temperature tolerances (Table 1). The only known study on developmental rates (from the Lake Washington population) found that LFS eggs hatched in approximately 42 days at 7°C (Dryfoos 1965). Due to warmer temperatures in this Estuary, egg incubation may occur much more rapidly – in the vicinity of 4 weeks (R. Baxter CDFG *personal communication*).

In this Estuary, spawning appears to occur near the mixing zone between fresh and salt water. Salinity and temperature are almost certainly important factors in determining where LFS spawn; however, it is possible that the driving force behind selection of spawning sites is the transport of emergent larvae to areas where they will be most successful. For example, transport of larvae into the fresh–salt water mixing zone (a productive and turbid area in the Estuary) might result in reduced predation from visual predators. In addition, early-stage juveniles may benefit from transport into the mixing zone because of the relatively high densities of food items found there in the winter and spring (Kimmerer 2002, 2004). The location of the salt-fresh water mixing zone depends principally on the net volume of fresh water outflows from the Delta. Historically, these phenomena represented an interaction between winter snowpack and snowmelt conditions. Currently, the location of the mixing zone is at least partially controlled by operation of the hydrosystem (releases from dams upstream and pumping operations in the Delta).

If LFS choose spawning sites soley based on physical characteristics of the substrate (e.g. grain/cobble size, depth, vegetation, etc.), then spawning locations may not change much from year-to-year. If, as seems more likely, spawning locations represent the overlap of acceptable hydrological, chemical (e.g salinity), and physical conditions (e.g. substrate grain size), and proximity to high-productivity mixing zones in the Delta, then spawning location would, historically, have shifted depending on freshwater outflow conditions in a particular year. The distribution of young LFS larvae provide support for the latter option (CDFG 2009). Because the natural hydrology of the Delta was much more variable in the past than it is today, the geographic distribution of potential spawning habitat may have been more extensive in the past than it is currently.

Larvae – Juvenile Transition

In stark contrast to the predictability of incubation conditions that is implied by their semelparous spawning behavior, the wide spatial and temporal distribution of LFS larvae suggests that survival and success in this life stage were spatially and temporally unpredictable. In other words, no particular location always displayed environmental conditions suitable for successful development and the physical conditions that support successful development in any particular year were spatially variable (Table 1). During the larval phase (as defined in this model), LFS are expected to behave as neutral particles whose distribution is controlled by local hydrodynamics. High outflows increase overall distribution of larvae and push the center of their distribution towards San Pablo Bay (Dege and Brown 2004), whereas lower flow conditions produce a center of distribution in Suisun Bay and larval distribution that is restricted to the Estuary's northern embayments (Baxter 1999; Fig. 6).

The correlation between juvenile LFS production and freshwater flow through the Delta is well-documented, high magnitude, and statistically significant (Stevens & Miller 1983; Jassby et al. 1995; Meng & Matern 2001), features that persist despite a poorly understood step-change in the relationship that occurred in the mid-to late 1980's (Kimmerer 2002; Rosenfield and Baxter 2007; CDFG 2009). The mechanism behind this relationship is not completely understood and it is quite likely that more than one mechanism is behind the overall effect. High flows may increase available spawning habitat, increase hatching success, decrease predation on LFS larvae, increase success of the larval-juvenile transformation (e.g. by increasing food sources), or some combination of these factors. Baxter (1999) and Dege and Brown (2004) observed that larval densities did not respond significantly to freshwater flow conditions. This argues against mechanisms that produce a positive correlation between egg-larval production and freshwater flow rates (e.g., an increase in available spawning territories or improved egg hatching success) and for mechanisms that increase success of the larvae-juvenile transition.

High flow rates through the Delta correspond to increased abundance and spatial distribution of numerous LFS prey items (Kimmerer 2002, 2004), both of which could increase LFS success in early life history stages. The success of the transition from endogenously-fed, non-swimming larvae to exogenously-fed, free swimming juvenile is likely to be limited by food resources. After LFS larvae have depleted their yolk reserves and before juveniles become capable swimmers, they probably rely on chance encounters with small prey items to accomplish the critical "first feeding". This critical transition occurs sometime between January and April for most young-of-year LFS.

High flow rates may also decrease the success of LFS predators by increasing turbidity throughout their rearing grounds. Larval LFS and early stage juveniles are not strong swimmers (Wang 1986) and are thus vulnerable to predation. Also, since they become widely distributed throughout the Estuary in the top of the water column, they are exposed to a number of different predators including both fish and birds (e.g. terns, gulls, and cormorants). Striped bass (*Morone saxitalis*) are probably major predators on LFS larvae in brackish environments; however, the recent declines in longfin smelt populations have tracked similar declines in productivity of striped bass (Sommer et al. 2007), arguing against striped bass predation as a driver of the population decline. LFS larvae that drift into shallow fresh water environments may be preyed upon by inland silverside (*Menidia beryllina*), an invasive species whose population has increased substantially in recent years.

Kimmerer et al. (2009) investigated the hypothesis that the longfin smelt population response to high winter-spring Delta outflows might be related to an increase in the habitat volume usable by juvenile LFS. Their simple model equated "habitat" with salinity and depth, but did not include temperature, turbidity, or other physical factors. Their modeling indicated that, whereas LFS habitat increased with increases in Delta outflow, the magnitude of that increase was less than the magnitude of the population response; thus, they concluded that the flow-habitat mechanism was not the only factor driving the flow-population response for LFS.

Flow rate and larval transport also interact with the entrainment of LFS larvae. As the center of larval distribution moves eastward (a consequence of low Delta outflow; Dege and Brown 2004), the likelihood of larval transport into the southern Delta and subsequent entrainment at the south Delta export pumps increases (Grimaldo et al. 2009; Fig 6; Fig. 9).

Juvenile-Sub-adult – Sexually Mature Adult Transitions

Juvenile and sub-adult LFS are widely distributed throughout the Estuary (Table 1; Fig. 7). These fish tend to aggregate in deep water habitats and there appear to be diffuse seasonal migrations (described below). However, their use of multiple habitats throughout the year implies that the suite of characteristics that promote survival and reproductive success was not narrowly defined geographically in the past.

During their life cycle, LFS must assimilate enough energy to survive and grow to a point where they can reproduce successfully. Most of this somatic growth and energy consumption occurs during the juvenile and sub-adult life stages, each of which lasts ~1 year. Larger Age 0+ and Age Class 1+ LFS feed primarily on shrimp, including *Neomysis mercedis* (Dryfoos 1965, Chigbu and Sibley 1994, Moyle 2002). Populations of *Neomysis* and certain copepods are correlated with fresh water outflow through the Delta (Kimmerer 2004); thus, fluctuations in climate and water management may impact prey availability for LFS populations.

In summer months, Age 1+ LFS populations in the Estuary decline significantly and then rebound in the late-fall and winter (Rosenfield and Baxter 2007; Fig. 8). This strongly suggests that some Age 1+ LFS emigrate from the Estuary during summer months into the nearshore ocean. Supporting this inference is the fact that LFS are caught in infrequent sampling off the coast of San Francisco (CH2M Hill 1985) and spawning-aged LFS sometimes display marine ectoparasites (*personal observation*). The timing of the LFS migration (and perhaps the portion of the population following this life history path) may vary from year-to-year.

The benefits of migration from fresh water to marine environments (anadromy) usually relate to increased growth opportunities in the marine environment (Charnov and Schaeffer 1973; Quinn 2005). This behavior may also reflect an effort to avoid inhospitable physical conditions during some phase of the life cycle. These two possibilities are not mutually exclusive. Longfin smelt migration patterns suggest that high temperatures in this Estuary may stress juveniles and sub-adults as these life stages are not common in warmer and shallower sections of the Estuary during the summer months (Fig. 8). Also, LFS geography and ecology suggest that temperatures in the Estuary are at the extreme of those encountered during this species' evolutionary history -- the San Francisco Estuary represents the southern extreme of the species range (the nearest large population is found in Washington State) and the species is closely related to marine smelts.

Sexually Mature Adult – Egg Transition

Longfin smelt generally spawn after their second year. Because they are semelparous (die after spawning), anything that prevents reproduction of a sexually mature adult results in the loss of that individual's reproductive potential. Unless spawning habitats or mates are extremely limited, mortality at this phase translates directly to reduced population growth as there is no opportunity for density-dependent compensation and no discounting for mortality in future life stages. It has been suggested that some fish spawn after one year and others may spawn in their 3rd year (Moyle 2002; CDFG 2009); but the existence and frequency of these alternate life-histories is not documented. In Lake Washington (WA), odd and even year classes display different population characteristics (Chigbu and Sibley 1994; Chigbu 2000).

Competition for reproductive opportunities and "fit" mates are the central feature of most vertebrate reproductive systems. The contribution of individual females to overall reproductive effort may be approximated by their relative size and fecundity (Fig 2). The factors that determine LFS male reproductive success and variation in that success are not known; variation in male reproductive success can impact genetic diversity and effective population size (N_e).

Because our knowledge of LFS spawning behavior is poor, the nature of competition for mates and spawning sites among LFS is unknown. For example, if there is competition for spawning sites or reproductive partners, how is that competition mediated? Determining threshold densities beneath which the LFS mating system fails to function (depensatory mechanisms or "Allee effects") will require an understanding of LFS spawning behavior, including the environmental cues and sexual signals that trigger spawning and allow LFS to locate mates.

5. Stressors by life-history stage

Egg – Larval

Rosenfield and Baxter (2007) documented a decrease in juvenile (Age 0+) LFS production following the 1987-1992 drought after accounting for the effect of freshwater flow through the Delta (Fig. 10) – this finding is consistent with that detected in an earlier data set where both age classes were combined (Kimmerer 2002) . This indicates that conditions in the Estuary changed following the drought. Some have attributed this change to sequestration of a large portion of estuarine primary productivity by introduced filter feeders (Alpine and Cloern 1992; Kimmerer 2002). Introduced fish species may also prey upon LFS larvae (e.g. inland silverside may prey on larvae that drift into shoreline environments; Moyle 2002). Direct mortality of later life stages at the south Delta pumping plants has increased in recent years (Fig. 9) and this suggests increased mortality of larval LFS (larval entrainment is not enumerated). In addition, there is increasing concern about new classes of potentially toxic compounds and increasing concentrations of known toxins in the Delta near presumed LFS spawning areas. Little is known about LFS egg-larvae physical tolerances, incubation optima, or the biological stressors that limit successful production of LFS juveniles. Stressors impacting the egg-larval transition are depicted in Figure 3.

Flow rates, abundance and larval distribution Flow rates impact a variety of other important variables that contribute to the abundance and quality of incubation habitat, including the abundance and diversity of toxins, local sedimentation rates, and the location of the salt-fresh water transition zone. Through its relationship with these variables, flow rate may have an indirect impact on LFS incubation success. Flow rates may also impact LFS larval distribution (and that of subsequent life stages) by affecting transport to other parts of the Estuary and beyond.

Assessment: A strong positive relationship between LFS young-of-year class size and freshwater flow through the Estuary has been documented repeatedly (Stevens & Miller 1983; Jassby et al. 1995; Meng & Matern 2001; Kimmerer 2002; Rosenfield and Baxter 2007; CDFG 2009). The relationship may be due to improved conditions for oviposition, incubation, or larvae (Tables 2, 3). Baxter (1999) and Dege and Brown (2004) found little correlation between freshwater inflow and larval abundance, which hints that freshwater flow impacts larval survival to the juvenile life stage more than it influences spawning habitat availability or hatching success.

A strong positive correlation between the extent of LFS larval distribution and average winter-spring outflow has been documented (USF&WS 1995; Baxter 1999; Fig. 6). The wide distribution of LFS juveniles and sub-adults suggests that larval success in this Estuary is spatio-temporally unpredictable and that wide distribution increases the opportunities for successful growth and reproduction. All else being equal, wide distribution of LFS larvae insulates the population from the potentially devastating effects of localized catastrophes, predator aggregations, or disease outbreaks. The eventual fate of longfin smelt larvae that are transported to different areas of the Estuary is unknown – some of these areas may be population sinks for longfin smelt larvae. Information on relative success in different larval rearing habitats (e.g. through otolith micro-geochemical studies) would reveal whether and how breadth of larval distributions translate into improved recruitment of longfin smelt sub-adults.

Water Quality – Salinity, Temperature, Dissolved Oxygen

Fish eggs are very sensitive to physical and chemical properties of the waters in which they incubate. The location of oviposition sites determines the physical environment experienced by developing embryos. Temperature and dissolved oxygen levels exert a strong influence on developmental rates and mortality increases rapidly beyond species-specific thresholds. Also, developing eggs may have a relatively narrow range of tolerances for salinity.

Assessment: Longfin smelt oviposition site location and incubation microhabitat requirements are not known in this Estuary. Thus, it is difficult to assess whether impairment of incubation habitat currently limits LFS populations. Major modifications to the substrate in probable LFS spawning areas that correspond with the rapid decline of LFS during the early should be investigated.

Undoubtedly, developing LFS eggs and larvae respond to changes in temperature, dissolved oxygen, and salinity beyond certain thresholds (Table 2). No published studies document the relationship between hatching success/developmental rate and water temperature, dissolved oxygen, or salinity for the LFS population of this Estuary (Fig. 3; Table 3). Questions regarding LFS embryo physical tolerances and optima warrant further investigation.

Generally speaking, temperature correlates positively with growth rate up to a threshold and beyond that threshold, temperature and egg mortality would be positively correlated. Given the northern distribution of this species and most of the family Osmeridae, it is unlikely that LFS encounter critically low temperatures in the San Francisco Estuary. Indeed, because the San Francisco Estuary population is at the southern edge of the species' range, it is possible that eggs and larvae in this population are stressed by warm temeperatures.

Little is known about how LFS eggs develop under different salinity conditions. It is possible that the strong correlation between freshwater flow through the Delta and juvenile production reflects increased incubation success in fresh water; Baxter's (1999) finding that flow was not well-correlated with larval population size argues against this hypothesis. Analysis of data from additional years is necessary to establish the persistence of Baxter's observation.

Longfin smelt are related to fish that spawn in surf environments (Martin and Swiderski. 2001). Thus, their demersal eggs are not expected to tolerate conditions with low dissolved oxygen

(DO). The extent of exposure of LFS eggs to low dissolved oxygen conditions is not known. Given the location of adults just prior to spawning and the spawning behaviors of their close relatives, it is unlikely that spawning occurs in environments with low DO conditions.

Diversions When water is removed from emigration corridors, LFS larvae may be diverted as well. Because eggs are demersal, water diversions are unlikely to affect egg development directly. Longfin smelt larvae that become entrained in diversions almost certainly die – these fish are not successfully screened from most current diversions and would probably not survive "salvage" operations even if they were screened effectively. Indirect mortality may occur because water diversions affect habitat quantity and quality. Also, water diversions modify hydrodynamics in ways that may transport larval LFS to sub-optimal habitats within the Delta.

Assessment: Human water development (for agricultural, municipal, or industrial purposes) may represent a significant source of mortality for LFS larvae in some years (Fig. 3; Tables 2, 3). Diversions are small and large, have a variety of different purposes and operational regimes, and may be screened or unscreened. As a result, generalizations about mortality resulting from water diversions are difficult to make.

The largest diversions near LFS habitat are those made by pumps of the Central Valley Project (CVP) and State Water Project (SWP), which are both located in the southern Delta. Because entrainment data for other diversions is generally lacking (Moyle and Israel 2005), this conceptual model addresses diversion-related mortality arising from CVP/SWP pumping only. However, LFS mortality at other diversion facilities (e.g., power plant intakes) is potentially significant.

Water export operations of the CVP and SWP are highly likely to entrain larval LFS; larval LFS are not enumerated at the pumps. The problem is potentially serious during years when Delta outflows are low during the spawning period or following the hatching period for LFS (late-winter and early spring). Low outflows result in reduced transport of larval LFS larvae out of the Delta and (Dege and Brown 2004) the resulting easterly distribution places them closer to the export facilities. Also, low Delta outflows during the spawning period may cause sexually mature adults to spawn further upstream than they would if outflow rates were high. Larvae (and spawning adults) may be placed at greater risk of entrainment at the south Delta export pumps by this shift of spawning location to the east.

Export pumping by the CVP and SWP export facilities significantly alter the hydrodynamics of the upper Estuary and often cause the lower San Joaquin River to reverse flow towards the pumps. Even if LFS larvae were not entrained at the pumping facilities, this change in Delta outflow patterns probably draws LFS larvae into the interior and southern Delta where water quality conditions (e.g., temperature, salinity, turbidity) are not conducive to survival or optimal development. Entrainment levels are only a proxy for the full impact of water diversions; mortality that occurs as fish migrate through inhospitable portions of the Delta may exceed that which occurs at the pumping facilities themselves.

Toxins Aquatic eggs and larvae of many species are sensitive to pesticides, metals, disinfection-by-products, or other classes of anthropogenic chemicals in water. Lethal and negative sub-lethal effects of some chemicals may occur even at seemingly low levels of exposure. Pesticides applied to agricultural crops, suburban lawns, or nuisance aquatic species may have deleterious effects on developing LFS embryos as they do on other species in the Sacramento-San Joaquin watershed (e.g.

Wheelock et al. 2005; Viant et al. 2006), including Delta smelt (Kuivila and Moon 2004). Substances of particular concern include:

- pyrethroid-based pesticides whose toxicity and longevity in aquatic environments are poorly-understood and the subject of intense study (Weston et al. 2004, 2006; Amweg et al 2005);
- irrigation return flows which may contain a variety of metals and salts (e.g. selenium, molybdenum, etc.) and the by-products of industrial agriculture, and
- estrogen mimicking compounds (EMC's) that impair development of embryonic fish (e.g. Jobling et al. 2004).

Many of these compounds are known to have synergistic effects with other stressors (e.g. Stead et al. 2005; Clifford et al. 2005). Studies of these synergies are case-by-case – no general principles regarding stressor interactions have been developed.

Assessment: At this time, there are no studies of the effect of water chemistry on the development, growth, or survival of LFS eggs or larvae. Studies of other fish species suggest that the potential for widespread effects of toxic compounds (including sublethal impacts) on both LFS eggs and larvae may be important (Fig. 3; Tables 2, 3). For example, Viant et al. (2006) found significant developmental abnormalities and mortality in Central Valley Chinook salmon eggs or alevins exposed separately to three different types of pesticides (larvae were more sensitive to these compounds than eggs). They also reviewed other studies which indicated a synergistically negative effect of these pesticides in combination.

Understanding the impacts of toxins on LFS requires knowledge of the effect of toxins on different life stages, the expected exposure pathway for those life stages, concentrations of toxins, and interactions among toxins. A recent short-term investigation found no evidence of major or minor health problems due to bacteria, viruses, or toxic exposure among LFS larvae and juveniles sampled (Foott and Stone 2007). The geography and timing of LFS spawning probably affects the level of egg and larval exposure to different toxins. Cross-taxa comparisons may be useful. For example, there has been some speculation that ammonium concentrations in the Delta are responsible for the recent step-decline in the longfin smelt flow-abundance relationship (J. Johns, March 2010; Department of Water Resources, *personal communication*); however, several Delta fish species that live in freshwater (closer to the wastewater treatment plants that are the presumed source of the ammonium pollution), including Delta smelt, do not show a population response consistent with a direct effect of ammonium toxicity.

Descriptions of individual toxins, their distribution, mode of action, and impacts on LFS eggs and larvae are beyond the scope of this conceptual model; they are also completely unstudied. In general, actions that eliminate reduce, or dilute these contaminants in waters of the Central Valley are expected to benefit LFS and other fishes in the Estuary.

Predation Predation is a source of direct mortality to eggs and larvae. Some fish species (e.g. suckers, splittail, sturgeon) may feed on LFS eggs. Larval LFS are not strong swimmers (Wang 1986) and are thus highly vulnerable to predation. Also, since they become widely distributed throughout the Estuary in the top of the water column, larvae are exposed to a number of different predators including both fish and birds. Striped bass and inland silverside are probably major predators on LFS larvae. Terns, gulls, and cormorants may also prey on this life stage.

Assessment: Predation-related LFS mortality during the egg stage is not well documented. Since little is known about egg deposition locations, microhabitats, or incubation periods, the lack of information regarding egg predation rates is not surprising. New species are constantly being introduced to the San Francisco Estuary (Moyle 2002). Introduction of a major egg predator could have devastating impacts on LFS populations.

Little information regarding the impact of predation on larval LFS is available. The positive relationship between freshwater flow in the Estuary and young-of-year (juvenile) class size of LFS may arise, at least in part, because high fresh water flow rates increase the volume of LFS rearing habitat with relatively high-turbidity and thereby reduce exposure of LFS to visually-oriented predators. Similarly, low fresh water flow rates appear to result in an eastward shift of the LFS larval distribution (Dege and Brown 2004; CDFG 2009); this places a greater portion of the larval LFS population in the Delta, an area with high populations of introduced predatory fish species.

Populations of some potential predators (e.g. Striped bass (*Morone saxitalis*)) have declined in recent years (Sommer et al. 2007). However, the diversity and populations of other invasive predator species have increased in recent decades. For example, populations of inland silverside (*Menidia beryllina*) have increased. Inland silversides are voracious predators in shallow water habitats around the Delta's margins. Shallow freshwater habitats in the Delta also support large populations of a suite of predatory fish including several species of bass and sunfish (family Centrarchidae). Larval LFS may be transported to these predator-infested tidal and shallow sub-tidal areas in the Delta before their swimming abilities develop fully, particularly when Delta outflow is relatively low. Moyle (2002) suggested that the invasion of this Estuary by inland silverside may have accelerated the decline in LFS productivity that occurred about the same time.

Egg/Larval Parasitism: Eggs and larvae of some fish species are susceptible to infection and or parasitism ("disease"). Some parasites and diseases may be transmitted in a density-dependant fashion with potentially catastrophic outcomes.

Assessment: A recent short-term investigation found no evidence of major or minor health problems due to bacteria, viruses, or toxic exposure among LFS larvae and juveniles sampled (Foott and Stone 2007). LFS spawn during the winter and spring run-off period, when water temperatures are at annual lows, thus, they are not likely to suffer high mortality due to bacterial or parasitic infections of eggs. Because the San Francisco Estuary is at the southern extreme of the species' range, negative impacts of high temperatures (including indirect impacts) are a concern for this population (Tables 2, 3). Also, global climate trends and the rate of species introductions (including potential pathogens) in this ecosystem increase the potential threat from egg and larval parasites.

Juvenile – Sub-Adult

Rosenfield and Baxter (2007) documented decreased production of Age 1+ LFS production following the 1987-1992 drought even after accounting for the population of Age 0+ LFS in the previous year (Fig. 10). This indicates that conditions in the Estuary changed following the mid- to late-1980's such that transition from juvenile to sub-adult LFS was less likely. Stressors impacting survival from the juvenile to sub-adult life stages are documented in Figure 4. Diversion of primary productivity out of historical trophic pathways by introduced fish and mollusks and by export pumping may contribute to food limitations and a decline in LFS productivity. Increased predation may also impact this life stage although there has not been a major invasion by a potential LFS predator in the brackish and marine portions of the Estuary that corresponds to the decline in production of Age 1+ fish. Entrainment at water diversions may be a significant source of mortality limiting successful transition of juveniles and sub-adults into sexually mature LFS. Potentially toxic compounds may be responsible for the decline in LFS productivity; little is know about the effect of these compounds on juvenile LFS.

Food production and competitors Primary productivity decline in the Estuary is a suspected driver of declines in numerous pelagic fish species in this Estuary (Sommer et al. 2007) though there is little evidence of this effect for most species that have been studied (Kimmerer 2002). Production of LFS food items is positively correlated with the flow of fresh water through the Delta (Jassby et al. 1995; Kimmerer 2002; Kimmerer et al. 2009); this is particularly true for food items important to young juveniles that are just beginning to feed. Since the late-1980's, productivity of typical LFS prey items has declined in this Estuary even after accounting for the effect of fresh water flow through the Delta (e.g. Jassby et al 2002; Kimmerer 2004) In addition, major prey items of early stage LFS juveniles (copepods) and late-stage juveniles (e.g. mysid shrimp) have declined and/or been replaced by invasive organisms.

Assessment: Competition is expected to increase with density of conspecifics. Given the recent and substantial decline of LFS, it is unlikely that intra-specific competition is the fundamental limit on current LFS populations. In other words, although there may be competition among LFS for food resources, that competition (if it exists) is fundamentally driven by a reduction in productivity of LFS prey species, not an increase in LFS competing for that prey.

Interspecific competition for food resources may play a role in the recent decline in LFS populations. Many interspecific competitors for LFS prey have also experienced recent pronounced population declines (e.g., Delta smelt, striped bass; Sommer et al. 2007). The constant influx of other species that feed primarily on zooplankton and small macro-invertebrates probably increases competition and associated food limitation-related mortality for LFS. Competition with these non-natives may occur even though their populations do not overlap geographically or bathymetrically with those of LFS. For example, inland silverside are more common in shallow fresh and brackish water areas of the Delta; early stage LFS juveniles may occur in these areas but older juveniles and sub-adults aggregate in deeper more saline waters closer. Nevertheless, potential LFS food items consumed by inland silverside and other invasive species in the Delta are unavailable to LFS (or their prey items) elsewhere in the Estuary.

Declines in the LFS population may result from reduced production of food items. Early stage LFS juveniles (i.e. those that have only recently begun exogenous feeding) probably rely on *Eurytemora affinis* as a prey item during April and May (R. Baxter, CDFG, *personal communication*). The density of *Euytemora* has declined substantially since 1987, particularly during summer months (Kimmerer 2002). As a result, early stage LFS juveniles may have a lower encounter rate with prey items, making successful first-feeding less likely. Furthermore, the summertime decline in *Eurytemora* may create a period of low food availability prior to availability of other food items like calanoid copepods (R. Baxter CDFG *personal communication*).

By June, LFS feeding has transitioned to other copepods (Hobbs et al. 2006). Some copepod populations are also correlated with freshwater flows through the Delta (Kimmerer 2002). Also, the copepod assemblage in this Estuary has been reorganized and invaded by non-native species. Common early-juvenile food items include non-native copepods *Pseudodiaptomus forbesi* and *Acanthocyclops vernalis*; there is some evidence of a preference for the latter species (Hobbs et al. 2006). Because these are non-native species, their nutritional and net-caloric value as LFS food items cannot be assumed. For example, Hobbs et al (2006) detected a decline in condition between LFS rearing in northern Suisun Bay (where the primary food item was *A. vernalis*) and southern Suisun

Bay (where *P. forbesi* was the number one prey item in the diet) even though LFS population density and gut content mass were similar for both areas.

Invasive species at lower trophic levels sequester a large fraction of the energy and nutrient flow in this ecosystem. These invasive species may exert an indirect, bottom-up control on the LFS population by reducing populations of the LFS prey species. Introduced mollusks, such as *Corbicula fluminea* and *Corbula amurensis*, filter large amounts of phytoplankton out of estuarine water and are implicated in the decline of primary and secondary productivity in this system (e.g. Alpine and Cloern 1992; Kimmerer 2004). Certain formerly abundant copepods species (e.g., *Eurytemora affinis*) have declined substantially since the mid-1980's, following the introduction of the Amur Clam. Kimmerer (2002) found evidence of bottom-up trophic limitations on LFS productivity in this Estuary, a relationship that was not supported for other pelagic fish species.

Larger Age 0+ and Age Class 1+ LFS feed primarily on shrimp (Dryfoos 1965, Chigbu and Sibley 1994, Moyle 2002). Populations of the main juvenile and sub-adult LFS prey species, *Neomysis mercedis*, have dropped dramatically in recent years in the Estuary (Orsi & Mecum 1996) and they have been partially replaced by invasive shrimp species (e.g. *Acanthomysis bowmani*). The biomass of the invasive species is substantially less than historical levels of the native species (M. Nobriga, Calfed Science Program, *personal communication*) and the value of these invasive shrimp as LFS prey is unknown.

Longfin smelt marine migrations may be an important part of the LFS life-cycle. The diet of LFS in the nearshore marine environment is completely unstudied. As a result, the impact on the LFS population of long-term trends in productivity of the nearshore ocean environment is unknown.

Temperature Temperature affects the metabolic requirements and physiological processes of LFS. Beyond a certain threshold, temperature increases are expected to increase LFS mortality. Temperatures near the LFS's lower threshold are not likely to occur in this ecosystem.

Assessment: The temperature limitations and sub-lethal impacts of temperature variation on LFS are unknown. Given the northerly distribution of LFS and their probable derivation from a marine ancestor, it is possible that LFS distribution and abundance in the Estuary are limited by high temperatures, particularly during summer months. Rosenfield and Baxter (2007) noted aspects of LFS distribution patterns that would be consistent with temperature-limitation, including the apparent summer emigration from the Estuary (Fig. 8). The relatively low densities of LFS in embayments with mean monthly water temperatures >20.5°C may indicate an intolerance for daily exposure to higher water temperatures in the >21-22 °C (Fig. 7). Temperatures below the LFS minimum temperature threshold are not likely to occur in this estuary.

Toxins Fish are very sensitive to the chemical composition of their environment. They can absorb toxins through their gills or skin or through the food that they consume. When pesticides applied to agricultural crops, suburban lawns, or nuisance aquatic species are transported to aquatic environments, deleterious effects on aquatic species may result (Kuivila and Moon 2004; Wheelock et al. 2005; Viant et al. 2006). Even sub-lethal concentrations of toxic chemicals can lead to severe population-level consequences. Fish exposed to sub-lethal levels of a toxin may be more susceptible to infection, predation, or abnormal behaviors that limit reproductive success (e.g. Scholz et al 2000; Clifford et al. 2005). The problem is further complicated by the potential synergistic negative impacts of multiple chemical compounds (e.g., Stead et al. 2005).

In the Central Valley and San Francisco Estuary, the impacts of pyrethroid-based pesticides on aquatic environments are the subject of intense study (Amweg et al. 2005, Weston et al. 2004, 2006). Organophosphate compounds, an older but still widely used class of pesticides, also produce lethal and adverse sub-lethal effects, even at seemingly low concentrations (e.g. Scholz et al. 2000; Wheelock et al. 2005). Urban stormwater runoff, disinfection byproducts in treated wastewater, and irrigation return flows each contain a variety of chemical compounds whose impact on LFS is unstudied.

There are too many compounds, applications, impact mechanisms, toxicity levels, and vectors to allow for a thorough review here.

Assessment: The impact of anthropogenic chemical inputs on LFS habitat use, survival, and reproduction is almost completely unstudied; however, chemical toxins are a leading suspect in the general decline of pelagic species in the San Francisco Estuary (Sommer et al. 2007). Foott and Stone (2007) found high rates of hepatocyte vacuolation (25-75%) in small samples of LFS juveniles caught in 2006 and 2007, but, the cause and meaning of this phenomenon cannot be determined without comparisons to known healthy LFS and those known to be exposed to toxins. The hepatocyte vacuolation did not appear to have a major health impact on the LFS juveniles studied.

The impact of toxins may be reduced by dilution if the diluting waters are free of toxic substances. Thus, high flows resulting from snowmelt (or reservoir releases) would tend to reduce the toxin stressors whereas increased flows due to stormwater runoff or agricultural irrigation returns may increase the toxin stressor. Because juvenile and sub-adult LFS are pelagic fish occupying deep, fast-flowing channel environments, significant direct exposure to toxins seem unlikely. However, LFS may ingest and accumulate toxins over the course of their lives with potentially negative consequences.

Research on the response of Delta smelt to toxics exposure is underway (e.g., Kuivila and Moon 2004). These results may have some relevance to LFS, but, the two species are only distantly related and have different ecologies so LFS-specific toxicological studies are warranted.

Predation Juvenile and sub-adult LFS are probably eaten by a variety of predatory fishes and marine mammals. The importance of LFS to the aquatic food web has been studied and documented in Lake Washington (e.g. Nowak et al. 2004); similar studies have not been performed in the San Francisco Estuary. Just as introduced species have probably negatively impacted the LFS prey base, exotic predators may limit LFS populations as well.

Assessment: Increases in predation on juvenile and sub-adult LFS are unlikely to be responsible for the most recent decline in the LFS population. Striped bass are probably the major predators of LFS juveniles and sub-adults, but their populations have declined substantially in recent years and any impact they have on LFS populations is also expected to have declined.

Based on timing of arrival in the Estuary and subsequent LFS population response, Moyle (2002) suggested that inland silverside (*Menidia beryllina*) might have had a major impact on LFS population dynamics. Inland silversides are predatory, however, they prefer shallow water habitats where juvenile and sub-adult LFS are rare, thus, their impact as predators of juvenile and sub-adult LFS is probably slight.

Diversions Longfin smelt juveniles and sub-adults may be entrained and experience high mortality at water diversions. Water diversions modify hydrodynamics in ways that may transport juvenile LFS to sub-optimal habitats within the Delta. Indirect mortality may occur because water diversions affect habitat quantity and quality. Also, water diversions may impact the abundance and distribution of LFS prey, predators, and competitors.

Again, because of the number and variety of diversions in the Delta, this conceptual model focuses only on impacts of the CVP and SWP water export facilities located in the southern Delta. These pumps alter the hydrodynamics of the upper Estuary and often cause the lower San Joaquin River to reverse flow towards the pumps. Furthermore, CVP/SWP pumping has the potential to draw juvenile LFS into the interior and southern delta where survival is probably low (because of the pumps and other sources of mortality). Entrainment levels are only a proxy for the full impact of water diversions; mortality that occurs as fish migrate through inhospitable portions of the Delta may exceed that which occurs at the pumping facilities themselves.

Assessment: Mortality of juvenile LFS at water diversions may represent a significant impact on the LFS population in some years. Longfin smelt entrainment (and probable mortality) at the South Delta pumps is greatest during low outflow years (Fig. 11). A strong negative correlation between flows in the Old and Middle San Joaquin River and LFS entrainment has been observed (Grimaldo et al. 2009). The proportion [Delta exports:Delta outflow] from January through March explains a significant fraction of the variation in total LFS entrainment (arcsin(sqrt %export)):ln (entrainment)): $R^2 = 0.384$; $p < 0.001$) – most of these fish are Age 0+. This relationship is not an artifact of a correlation between entrainment rates and population size – quite the opposite, entrainment is negatively correlated with the overall abundance of both Age 0+ and Age 1+ LFS (Sommer et al 2007), the relationship is highly significant for the older (spawning) age class.

Most Age 0+ fish are entrained in May, probably because this is when most young-of-year LFS reach a size where they can be screened by the technology at the CVP and SWP pumps – the screening technology at those diversions does not effectively screen smaller (larval) fish. Age 0+ LFS migrate towards freshwater in the winter, however, they do not tend to migrate into freshwater as far as Age 1+ (sexually mature) fish do in that season (Fig. 7); thus they are less susceptible (in relation to age class abundance) to entrainment than Age 1+ fish in the winter.

Sexually Mature Adult – Egg Deposition

As noted above, the decline in LFS productivity in the San Francisco Estuary is well documented (e.g., Rosenfield and Baxter 2007; Fig. 10). The transition between gravid adults and incubating eggs is not well-studied for this species in this Estuary. Potential causes of a decline in LFS reproduction are depicted in Figure 5 and they include: reduced fecundity or egg conditions in response to poor growth in previous life stages; declines in the quality or quantity, or availability of oviposition/incubation habitat; mortality of gravid LFS; or inefficient operation of the LFS breeding system resulting from low population densities. Factors that cause mortality or failure to spawn can have particularly strong leverage over population dynamics because there are fewer opportunities for a density-dependent compensatory response to such mortality and because failure at this stage is not discounted by mortality rates in subsequent life stages.

Fecundity Among fishes, fecundity is usually dependent on the size of females and LFS are no exception (Fig. 2). Fish also display indeterminate growth – meaning size at reproduction and maximum size are somewhat plastic; both may be reduced due to limitations on habitat size or food availability (Moyle and Cech 2004). Reduction in the body size or condition of gravid females could be caused by the food limitation that is believed to have intensified recently in this ecosystem (*see above*). Indeed, Chigbu and Sibley (1994) documented a long-term decline in LFS size and fecundity in the Lake Washington longfin smelt population. They attributed the decrease in growth and fecundity to a decline in LFS' primary food source, mysid shrimp.

Assessment: If LFS in this Estuary are experiencing greater food limitation than they have historically, it is likely that both size at maturity and fecundity have declined as well. This question could be assessed using longitudinal data on length and fecundity taken from gravid fish over a range of years. Records from sampling programs, such as the USFWS' Chipps Island Trawl, should be explored to determine whether there is sufficient long-term data on gravid female size and fecundity that can be used to determine whether a long-term decline in fecundity has occurred.

Spawning substrate distribution, abundance, and quality To be of use for LFS, spawning substrate must be: (1) accessible, (2) of a condition (e.g. grain size) that facilitate egg deposition, retention, and development, and (3) positioned in a waterbody such that incubating eggs will remain immersed in a flow sufficient to support embryogensis. As a result, only a fraction of any particular waterbody may be useful for LFS spawning and incubation. Hydrology and stream geomorphology determine the accessibility and suitability of oviposition habitat.

The only information on location and distribution of LFS spawning habitat is inferred from the relative distribution of sexually mature-adults in the winter and that of larvae in the winter and early spring. The spatial distribution of spawning areas is important because (among other reasons) the probability of extirpation increases as the geographic extent of spawning locations decreases (Rosenfield 2002).

Assessment: Beyond some simple generalizations, the flow rates, water quality, and substrate conditions required for successful LFS spawning are unknown as are the distribution of spawning habitat throughout the San Francisco Estuary. The requirements for and distribution of LFS spawning areas and potential spawning areas in the San Francisco Estuary must be documented.

Longfin smelt are believed to spawn in the mainstem of the Sacramento River near and below Rio Vista during years with moderate to high outflow; some spawning appears to occur upstream of Rio Vista in years with low outflow . Spawning may also occur in tributaries to Suisun Marsh, the Napa River Estuary, and tributaries to the South and Central Bays. There is no reason to believe that sections of the lower San Joaquin River with suitable hydrodynamics and water quality conditions were not also historically important spawning grounds – the San Joaquin River does not appear to support much spawning currently.

Diversions Sexually mature LFS may be particularly susceptible to entrainment and mortality at water diversions because these fish tend to swim into freshwater prior to spawning and physiological preparations for spawning may leave them in a weakened state. Indirect mortality may occur because water diversions affect habitat quantity and quality. Water diversions modify hydrodynamics in ways that may transport adult LFS to sub-optimal habitats within the Delta.

As above, export operations of the CVP and SWP are the only diversions analyzed in this conceptual model – other diversions are likely to have impacts as well but little data exists with which to study those impacts (Moyle and Israel 2005). Direct mortality of spawning age LFS via entrainment at the pumps is known to occur, although the number of sexually mature adults entrained is usually one or two orders of magnitude lower than the number of age 0+ fish

(Grimaldo et al. 2009). Still, the population consequences of losing reproductively mature fish are much greater than that of younger fish that will require a year or more before they are ready to spawn. Furthermore, CVP/SWP pumping has the potential to draw mature LFS into the interior and southern delta where their survival (and that of subsequent life history stages) is probably low due to high predator densities and poor water quality conditions; mortality that occurs as fish migrate through inhospitable portions of the Delta may exceed that which occurs at the pumping facilities themselves.

Assessment: Mortality of sexually mature adult LFS at water diversions may represent a significant impact on the LFS population in some years (Tables 2, 3). Size-specific salvage data for LFS were recorded from 1993 onward; these data allow discrimination of LFS Age classes. Although overall entrainment (which largely reflects entrainment of Age 0+ fish) is significantly and negatively correlated with outflow (*see above*), entrainment of sexually mature Age 1+ LFS is significantly and positively correlated with fresh water export rates at the south Delta pumping facilities (ln(SWP+CVP exports):ln(age 1+ salvage)): $R^2 = 0.418$; $p < 0.01$; Fig 11). This result is consistent with that of Grimaldo et al. (2009) who studied the relationship between Old and Middle River flows (that are heavily impacted by export rates) and longfin smelt entrainment. This relationship is not an artifact of a correlation between entrainment and Age 1+ population size Sommer et al. 2007). Age 1+ LFS entrainment is significantly negatively correlated with the Age 1+ LFS population size as measured by the FMWT index (Fig. 12). Entrainment has increased in recent years as the population declined.

Spawning (Age 1+) LFS migrate eastwards, towards the Delta (Fig. 7). Their migration patterns expose these spawning fish (and their subsequent offspring) to entrainment at the CVP/SWP pumps. Significant Age 1+ LFS entrainment at CVP/SWP facilities has occurred in months between December and June. Between 1993 and 2007, longfin smelt entrainment was recorded in 12 years; in 7 of those years, the annual maximum entrainment occurred in January whereas December produced the maximum entrainment in three years.

Water export operations in the southern Delta may be responsible for the near-absence of spawning LFS in the lower San Joaquin River. The CVP/SWP pumps are located near where one would expect LFS to spawn in the lower San Joaquin River. If LFS spawned historically in areas of the San Joaquin River that were similar to those currently used in the lower Sacramento River, it is likely that CVP/SWP export operations entrained large numbers of spawning adults and recently-hatched larvae in this area. Deterioration of water quality in the lower San Joaquin River (a product of water exports and agricultural operations supported by those exports) could also be responsible for the absence of LFS spawning in this area if San Joaquin flows were toxic to developing eggs or prohibit spawning in this area. Furthermore, the low freshwater outflow rates from the San Joaquin River that result from operation of the larger hydrosystem may make this area unsuitable for spawning and/or incubation.

Spawning Behavior and Opportunities Competition for nest sites is common among fishes with demersal eggs. In addition, it is very common for males and females to compete for access to the most attractive members of the opposite sex. As a result of this competition, sexual selection produces differential reproductive success and reduces the effective population size (i.e. breeding population size) of natural populations. Limited breeding territories may ultimately limit population size and growth rate. Alternatively, if LFS density on the spawning grounds drops below some critical threshold, then reproductive success may drop precipitously as a result of disruptions to the mating system structure (Allee 1938). At very low densities, sexually mature LFS may have trouble simply finding mates in the right place at the right time. Such “density depensation” phenomena can result in negative population growth and chaotic population dynamics even when conditions are otherwise suitable for reproduction.

Assessment: The degree to which population density affects reproductive success, operation of the mating system, and population growth rates for LFS in this Estuary are unknown. This species’ breeding system has not been studied and the distribution and abundance of spawning habitat (under any hydrological conditions) is unknown. If spawning locations are limiting, then restoring spawning habitat (which might mean restoring substrate or restoring appropriate hydrological conditions) would alleviate the lack of breeding opportunities. If, on the other hand, spawning is limited by low density of available spawning partners, the only solution is to increase production and survival of LFS through earlier life-history stages.

6. Future research

Clearly there is much to left to know about the basic ecology and life history of LFS in this Estuary and the forces that constrain their population dynamics. Data from the once-sizeable population of longfin smelt in Humboldt Bay should be studied for comparison with patterns from the San Francisco Estuary. Unfortunately, historic records from the Humboldt Bay ecosystem are believed to be scant and comparisons between the two systems are not likely to produce definitive insights into the causes of decline in the San Francisco Estuary because (a) it is very different (biotically and physically) from the Humboldt Bay ecosystem and (b) because the comparison cannot produce much in the statistical sense (there are only two systems being compared). Still, comparing the two systems might allow greater prioritization of probable causes and investigations into those mechanisms in the SF Estuary

Listed below are questions that underlie several critical studies that would contribute to a better understanding of these fish and their stressors in this ecosystem. Results of these studies would clarify important unknowns and allow for more targeted and effective population restoration activities.

Studies are needed to answer the following questions:

Egg- Larvae

What are the specific characteristics/requirements of LFS spawning habitat? The Napa River estuary is a potential site for study of longfin smelt spawning requirements because it is a smaller area and less complex hydrodynamically than the Delta.

How is this habitat distributed throughout the Estuary and across years with different hydrologic characteristics?
What cues/mechanisms release spawning behavior in this fish? Again, field studies of this sort are more likely to succeed in the Napa River Estuary than they are in an environment as complex as the Delta.

What are the physical limits, optima, and survival/development response curves for incubating LFS eggs and developing larvae?

What is the extent of predation pressure on LFS larvae by non-native and native predators?

What concentrations of pesticides, EMC's, and metals are LFS egg and larvae exposed to and what is their response to this exposure?

Are parasites and diseases (fungi, bacteria, viruses, and/or protozoa) common among LFS eggs and larvae? If so, what are their impacts? (Such studies can and should accompany more general investigations of this species' spawning, incubation, and early development periods).

Juvenile-Sub-Adult

What is (are) the mechanism(s) by which increased Delta outflow increases Age 0+ LFS production? Is there a mechanistic relationship between Delta outflow and transition success of Age 0+ to Age 1+ LFS?

How does the spatial extent and severity of food limitation (e.g. as documented by Hobbs et al. 2006) vary with Delta outflow conditions?

How common is ocean migration? How long (in time and space) are these migrations? What are the impacts of ocean migrations on LFS survival, condition, and reproductive success?

What is the extent of predation pressure on LFS juveniles and sub-adults by non-native and native predators?

What are the physical limits, optima, and response curves for LFS juveniles and sub-adults?

Mature Adult -Egg

Where do LFS spawn and what characterizes good spawning habitat? Do these locations and microhabitats change across years, between seasons, and under different outflow conditions? To what extent are these habitats, or access to them, limiting in the Delta?

What is the relationship between LFS fecundity and somatic condition in this ecosystem?

Are long-term trends in size and fecundity evident among spawning LFS?

What is the effect on egg production, condition, and oviposition success of toxins encountered in the adult life stage and those that come earlier?

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Table 1. Location and timing of longfin smelt throughout their life cycle in the San Francisco Estuary.

Habitat (*life stage*)	**Dates**	**Age (Days post oviposition)**	**Length (U)**	**Approximate Temperature range**	**Approximate Salinity range**
Delta (*Egg*)	December-April	0 - ~42 (varies significantly with temperature)	0.5 - 1.5	**8-12^{o}C**	**Range unknown. Typically 0.0 - <2ppt bottom salinity**
Delta and Bays (*Larvae*)	January-June	~26-120 (probably varies significantly with temperature)	1.5 - <4.0	**9-14^{o}C**	Widespread, densest populations found in and around 2ppt bottom salinity
Delta and Bays (*Juveniles*)	May of Year 0 in most years, sometimes as early as April	~50 - 404	4.0 - < 7.0	**9-20^{o}C**	Complete range of salinities found in Estuary. Most typically >5ppt
Bay (*Adults*)	April of Year 1 (by definition for this model)	~405 - 709	7.0 - 12.0	**9-20^{o}C**	Complete range of salinities found in Estuary. Most typically >5ppt
Coastal Ocean (*Adult*) *May not be part of all individual LFS life cycles	Mainly in summer months (migration may begin earlier); Unknown duration and fequency		7.0 – 12.0	14-16^{o}C	Marine
Delta (*Spawner*)	November-March	~710 - 770	typically 8.0 – 12.0 (range 7.0 – 14.0)	**8-12^{o}C**	Wide range of salinities; aggregate in or near 2ppt bottom salinity
River (*Post-spawn*)	Semelparous (post-spawn period believed to be insignificant)	Semelparous (post-spawn period believed to be insignificant)	Semelparous (post-spawn period believed to be insignificant)	Semelparous (post-spawn period believed to be insignificant)	Semelparous (post-spawn period believed to be insignificant)

Table 2. Life-stage-by-stressor matrix identifying mechanisms affecting longfin smelt life stage transitions (in terms of growth, survival and timing) in the San Francisco Estuary.

Habitat (*life stage*)	**Entrainment**	**Outflow**	**Habitat loss**	**Water quality (Salinity and Temperature)**	**Food Availability**	**Predation**	**Toxics**	**Climate change**
Delta (*Egg*)	-----	May increase incubation habitat; may increase incubation success	Suitable incubation conditions unknown	Temp, DO, and salinity all affect incubation rate and success but relationships are unstudied	-----	Egg predators unstudied and unnknown	Potential impacts from Pyrethroids Mercury; Endocrine disrupters	Warming water temps and alterations in outflow patterns potentially damaging
Delta & Bays (*Larvae)*	Small Ag Power Plant SWP/CVP; may effectively limit “habitat” to areas outside “zone of impact”	Increases distribution and success of larvae (probably through multiple mechanisms); outflow negatively correlated with entrainment	Habitat “loss” occurs when low salinity zone is restricted due to low Delta outflow. No known beneficial use of habitats at terrestrial/ aquatic interface	Temp, DO, and salinity all affect development rate and success. Relationship of position of low salinity zone to larval success and distribution is well documented.	For purposes of this model, external feeding begins in earnest at the end of the larval-juvenile transition	Larval predators probably abundant (greatest impact likely from striped bass and inland silverside in shallow areas where larvae may be dispersed)	Potential impacts from Pyrethroids Mercury; Endocrine disrupters	Warming water temps and alterations in outflow patterns potentially damaging

Habitat (*life stage*)	**Entrainment**	**Outflow**	**Habitat loss**	**Water quality (Salinity and Temperature)**	**Food Availability**	**Predation**	**Toxics**	**Climate change**
Delta & Bays *(Juveniles)*	Small Ag Power Plant SWP/CVP; may effectively limit "habitat" to areas outside "zone of impact"	Increases distribution and success of juveniles; outflow negatively correlated with entrainment; outflow also correlated with prey production	-----	Occur at wide range of temperatures and salinities. High temperatures may represent a limit to distribution	Early juvenile period may be affected by abundance and distribution of *Eurytemora* and other small food items. Later juveniles impacted by loss of *Mysid* shrimp and invasion by non-native shrimp	Predation rates unstudied. No commercial harvest.	Impacts from Pyrethroids Mercury; Endocrine disrupters less likely	Warming water temps and alterations in outflow patterns potentially damaging
Bay *(Adults)*	-----	-----	-----	Occur at wide range of temperatures and salinities. High temperatures may represent a limit to distribution	Unknown impacts	Predation rates unstudied. No commercial harvest.	Impacts from Pyrethroids Mercury; Endocrine disrupters less likely	Warming water temps potentially damaging
Coastal Ocean (*Adult*)	-----	-----	-----	-----	Unknown impacts	Predation rates unstudied. No commercial harvest.	Encounters with Pyrethroids Mercury; Endocrine disrupters less likely	

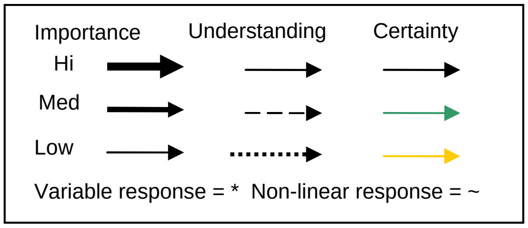
Habitat (*life stage*)	**Entrainment**	**Outflow**	**Habitat loss**	**Water quality (Salinity and Temperature)**	**Food Availability**	**Predation**	**Toxics**	**Climate change**
Delta (*Spawner*)	Small Ag Power Plant SWP/CVP; Exports strongly correlated with entrainment; entrainment may make lower SJR inhospitable to spawning adults and larvae	Affects spawning location – lower flow results in more easterly spawning	Loss of lower SJR (near confluence) as spawning habitat	Occur in fresh to low salinity water. Temperatures do not appear to limit distribution during spawning period (winter – spring)	-----	Predation rates unstudied., but believed to be high at certain locations (e.g. Clifton Court Forebay) within freshwater Delta. No commercial harvest.	Impacts from Pyrethroids Mercury; Endocrine disrupters less likely at this stage.	Warming water temps and alterations in outflow patterns potentially damaging

Table 3. Stressor matrix. Stressors are characterized by importance (I), understanding (U), and certainty of impact (CI) on LFS success in the San Francisco Estuary. “Importance” measures the likely impact of a stressor on the transition probability of one life stage to the next. “Understanding” reflects the state of knowledge regarding the relationship between the stressor and life stage success (e.g., can it be quantified) whereas “Certainty of Impact” indicates the extent of scientific support for the “Importance” score. Scores are : 1= high, 2=medium, 3= low, and *= varies.

Habitat (*life stage*)	**Entrainment**	**Outflow**	**Salinity**	**Temp.**	**Habitat loss**	**Food Availability**	**Predation**	**Toxics**
Delta (*Egg*)	**Eggs unlikely to be entrained**	I =1 U = * CI = 1	I = 1 U = 1 CI = 1	I = 3 U =2 CI = 2	*Spawning Habitat* I = 2 U = 2 CI = 3	**Life stage does not feed**	I = 2 U = 3 CI = 3	I = 2 U = 3 CI = 3
Delta and Bays (*Larvae*)	I = 1 (varies inversely with ouflow) U = 2 CI = 3	I = 1 U = * CI = 1	I = 1 U = 2 CI = 1	I = 2 U = 2 CI = 2	*Estuarine Habitat* I = 2 U = 1 CI = 2	**As defined here, life stage does not feed externally to a significant degree**	I = 2 U = 2 CI = 3	I = 2 U = 3 CI = 3
Delta and Bays (*Juveniles*)	I = 1 (varies inversely with ouflow) U = 1 CI = 3	I = 1 U = * CI = 1	I = 2 U = 1 CI = 2	I = 2 U = 2 CI = 3	*Estuarine Habitat* I = 2 U = 1 CI = 2	I = 1 U = 1 CI = 2	I = 2 U =2 CI = 2	I = 3 U = 3 CI = 3
Bay (*Adults*)	I = 3 U = 1 CI = 1	I = 2 U = * CI = 2	(see “food avail.”)	I = 2 U = 2 CI = 3	*Estuarine Habitat* I = 2 U = 1 CI = 2	I = 1 U = 2 CI = 2	I = 2 U = 2 CI = 3	I = 3 U = 3 CI = 2
Coastal Ocean (*Adult*)	Very little is known about the extent (duration) and frequency (proportion of the population) of marine migrations in this population. Stressors are unstudied in this life-stage.							
Delta (*Spawner*)	I = 2 U = 2 CI = 2	I = 1 U = * CI = 2	I = 1 U = 2 CI = 1	I = 3 U = 2 CI = 2	*Spawning Habitat* (in particular, loss of SJR habitat) I = 1 U = 2 CI = 1	I =3 U = 3 CI = 3	I = 2 U = 3 CI = 2	I = 3 U = 3 CI = 3

8. Figures

Figures 3, 4, 5 Matrices showing transitions from one life stage to another. Negative and positive effects of processes are designated by (-) and (+). Levels of importance, understanding and certainty of each process are given in the key below.



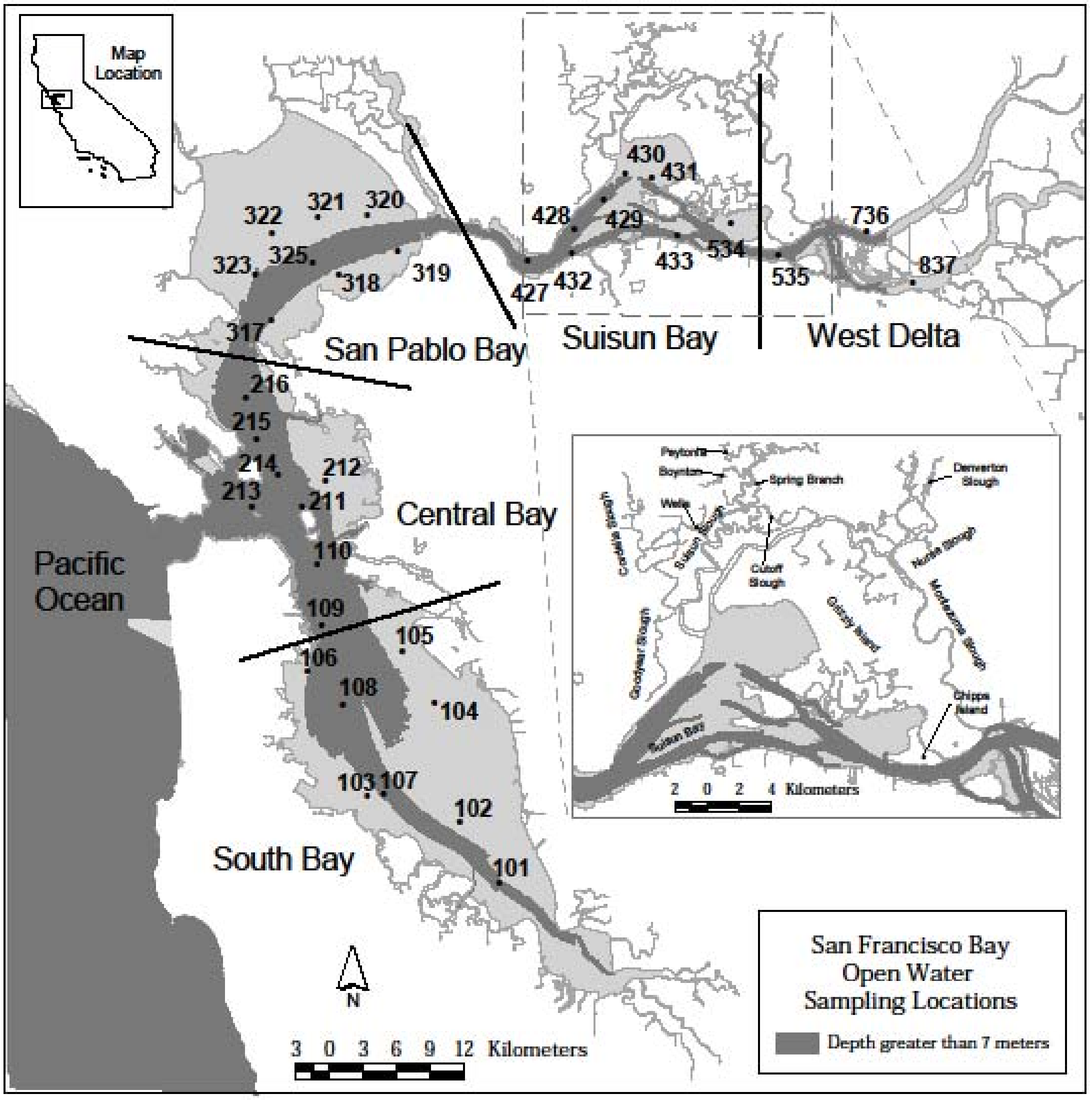


Fig. 1. Map of the San Francisco Estuary showing sampling station localities for the California Department of Fish and Game's Bay Study estuarine survey program. Inset shows sloughs surveyed by the UC Davis Suisun Marsh Survey Program. Longfin smelt are detected throughout the aquatic habitats displayed here. Map reprinted from Rosenfield and Baxter (2007).

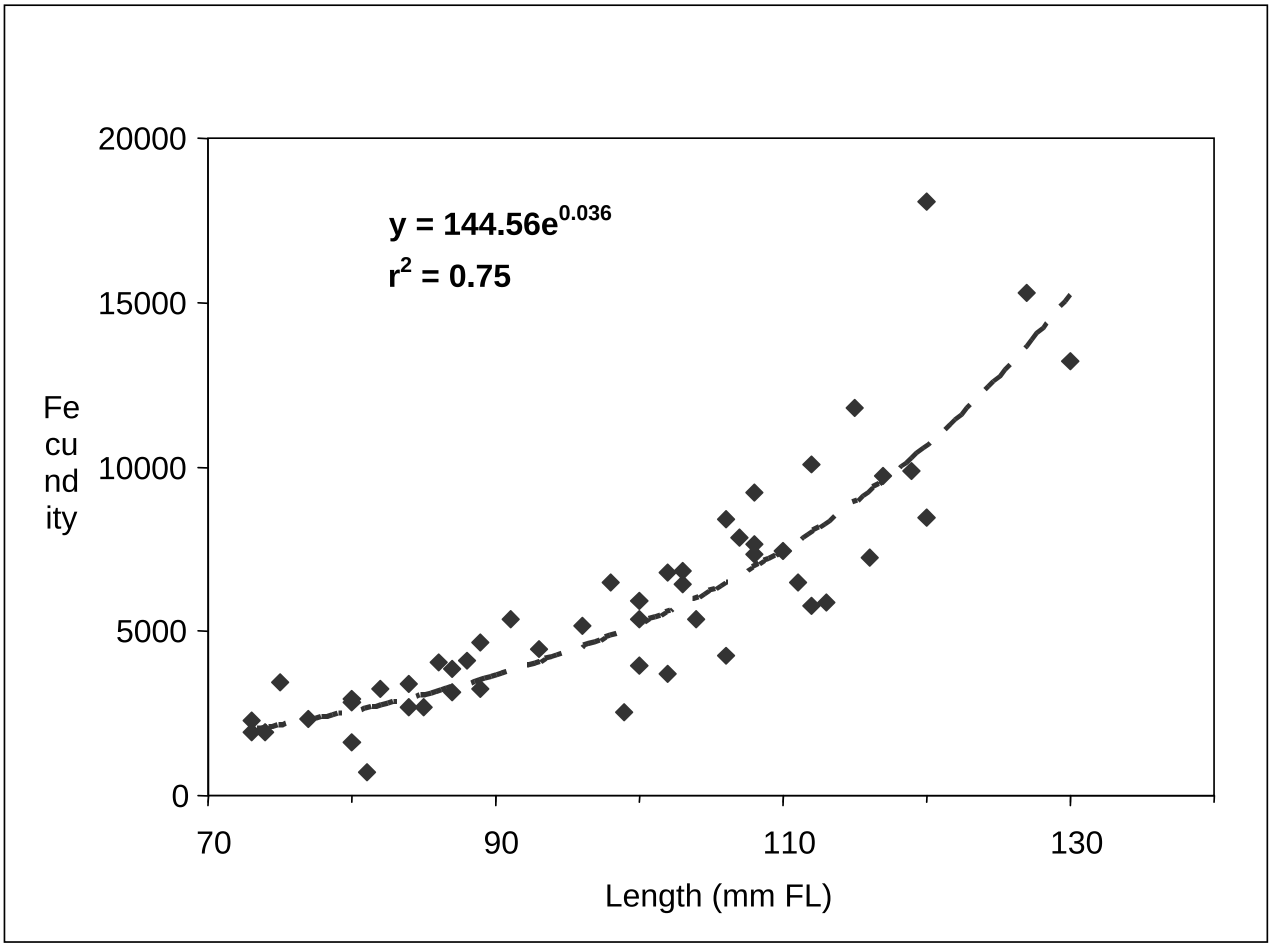
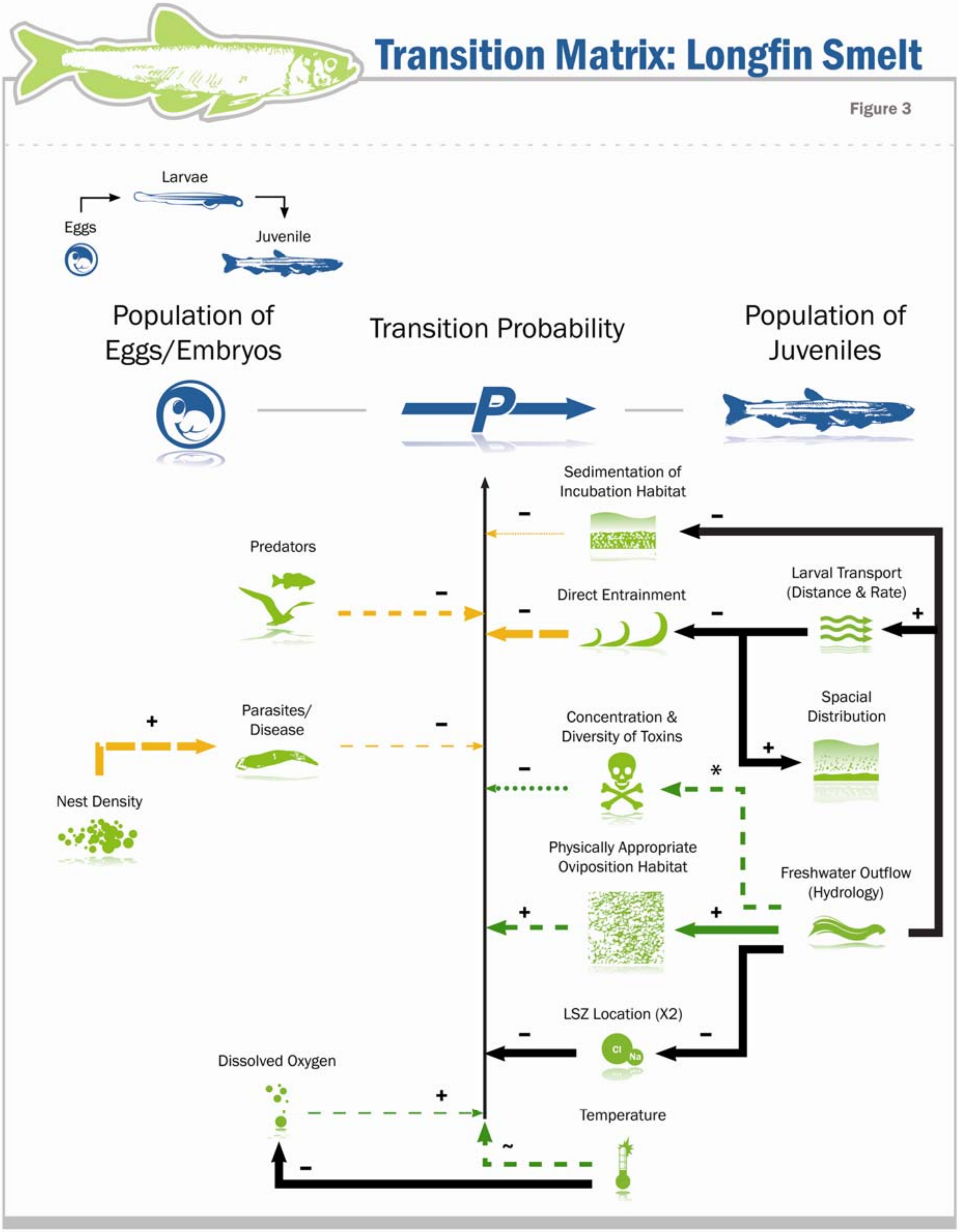
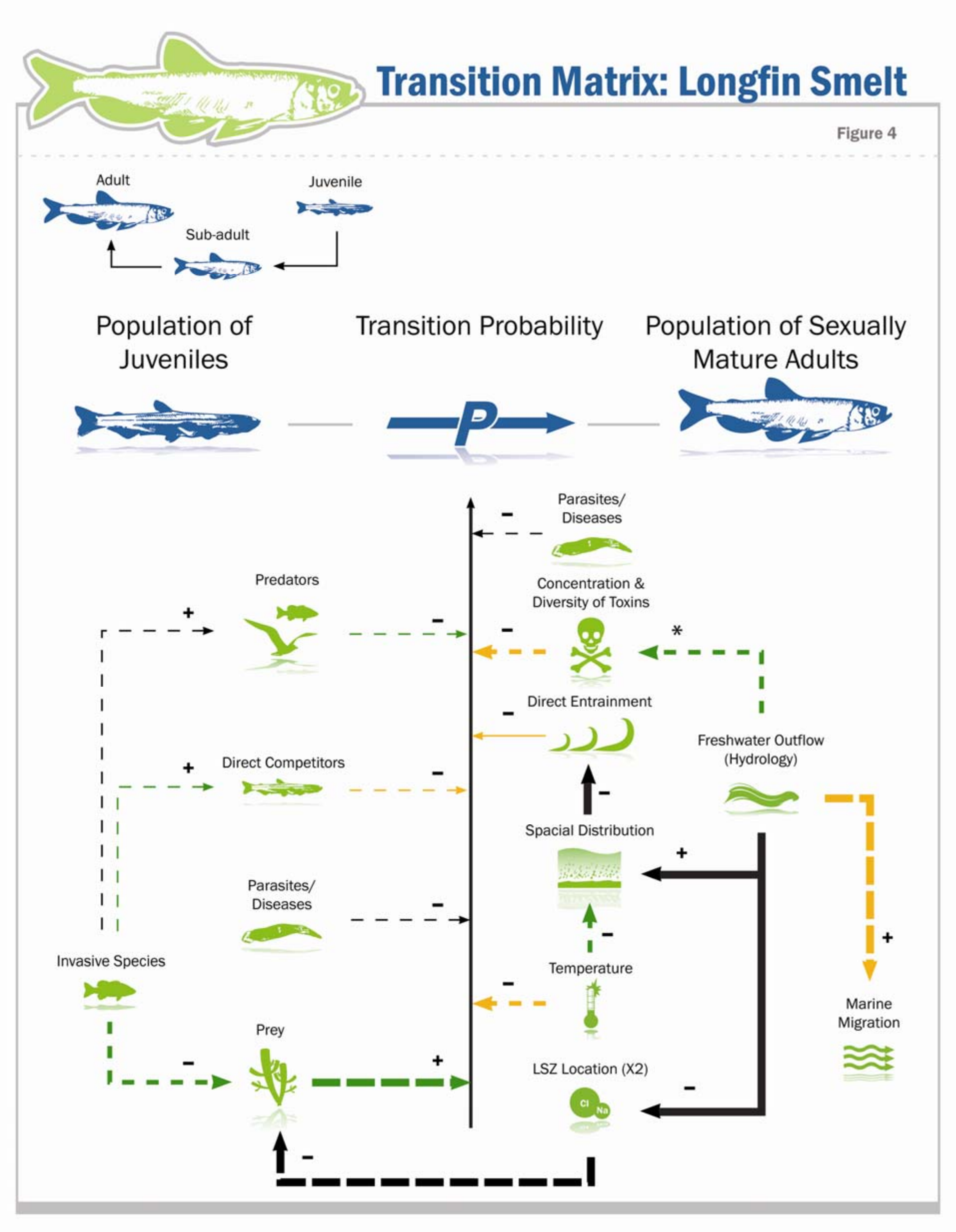
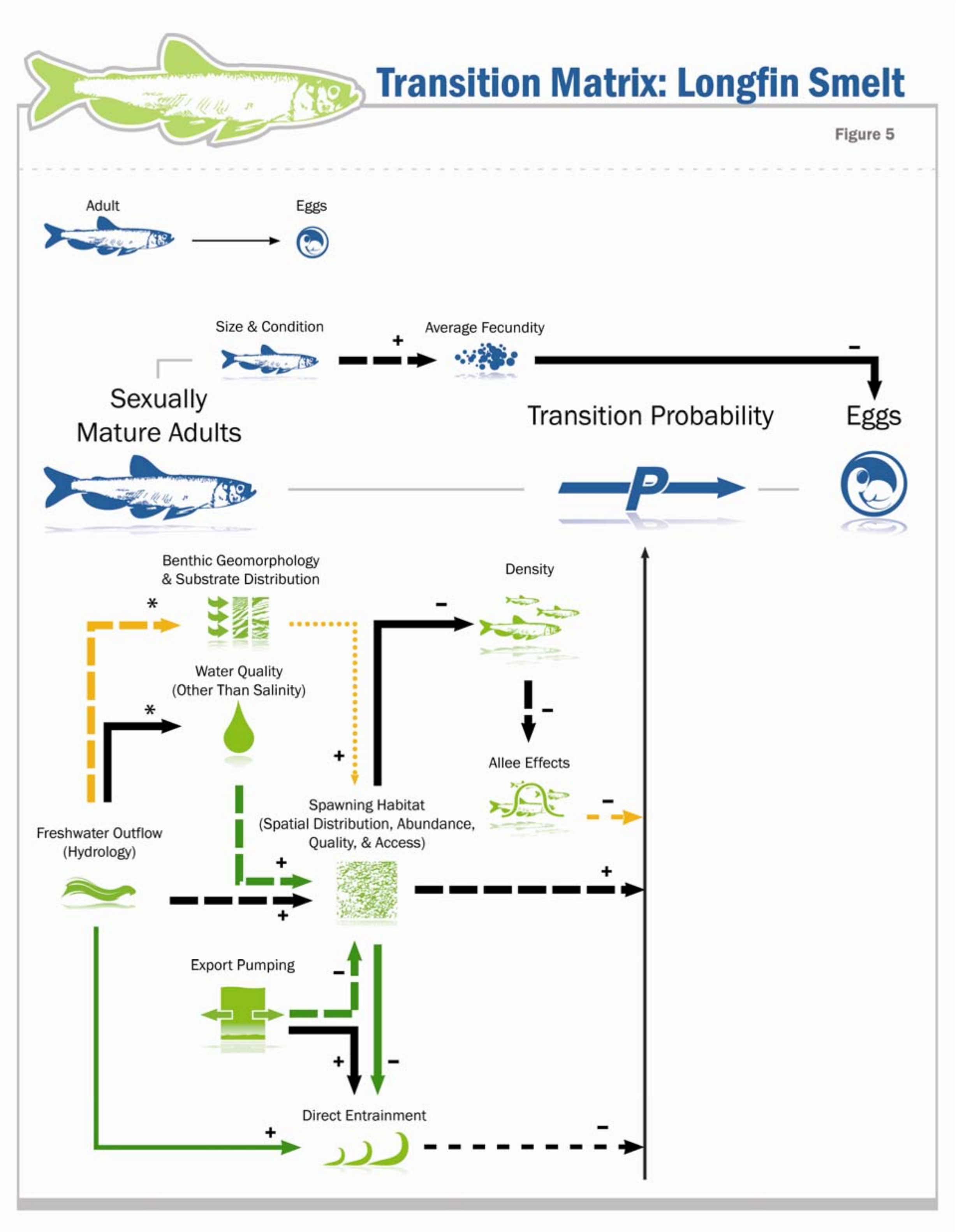


Figure 2. Longfin smelt length (mm FL) fecundity relationship for females captured from November 1992 to January 1994 by Bay Study midwater and otter trawls, Fall Midwater trawl and Chipps Island trawl in the Sacramento-San Joaquin Estuary. (Source: R. Baxter, CDFG, unpublished data).


Transition Matrix: Longfin Smelt
Figure 3
Larvae
Eggs
Juvenile
Population of Eggs/Embryos
Transition Probability
P
Population of Juveniles
Sedimentation of Incubation Habitat
Predators
Direct Entrainment
Larval Transport (Distance & Rate)
Parasites/ Disease
Spacial Distribution
Concentration & Diversity of Toxins
Nest Density
Physically Appropriate Oviposition Habitat
Freshwater Outflow (Hydrology)
LSZ Location (X2)
Cl
Na
Dissolved Oxygen
Temperature
+
−
*
~


Transition Matrix: Longfin Smelt
Figure 4
Adult
Juvenile
Sub-adult
Population of Juveniles
Transition Probability
Population of Sexually Mature Adults
P
Parasites/ Diseases
Predators
Concentration & Diversity of Toxins
Direct Entrainment
Freshwater Outflow (Hydrology)
Direct Competitors
Spacial Distribution
Parasites/ Diseases
Invasive Species
Temperature
Marine Migration
Prey
LSZ Location (X2)
Cl
Na


Transition Matrix: Longfin Smelt
Figure 5
Adult
Eggs
Size & Condition
+
Average Fecundity
–
Sexually Mature Adults
Transition Probability
Eggs
P
Benthic Geomorphology & Substrate Distribution
*
Density
–
Water Quality (Other Than Salinity)
*
–
+
Allee Effects
Spawning Habitat (Spatial Distribution, Abundance, Quality, & Access)
–
Freshwater Outflow (Hydrology)
+
+
+
Export Pumping
–
+
–
Direct Entrainment
+
–

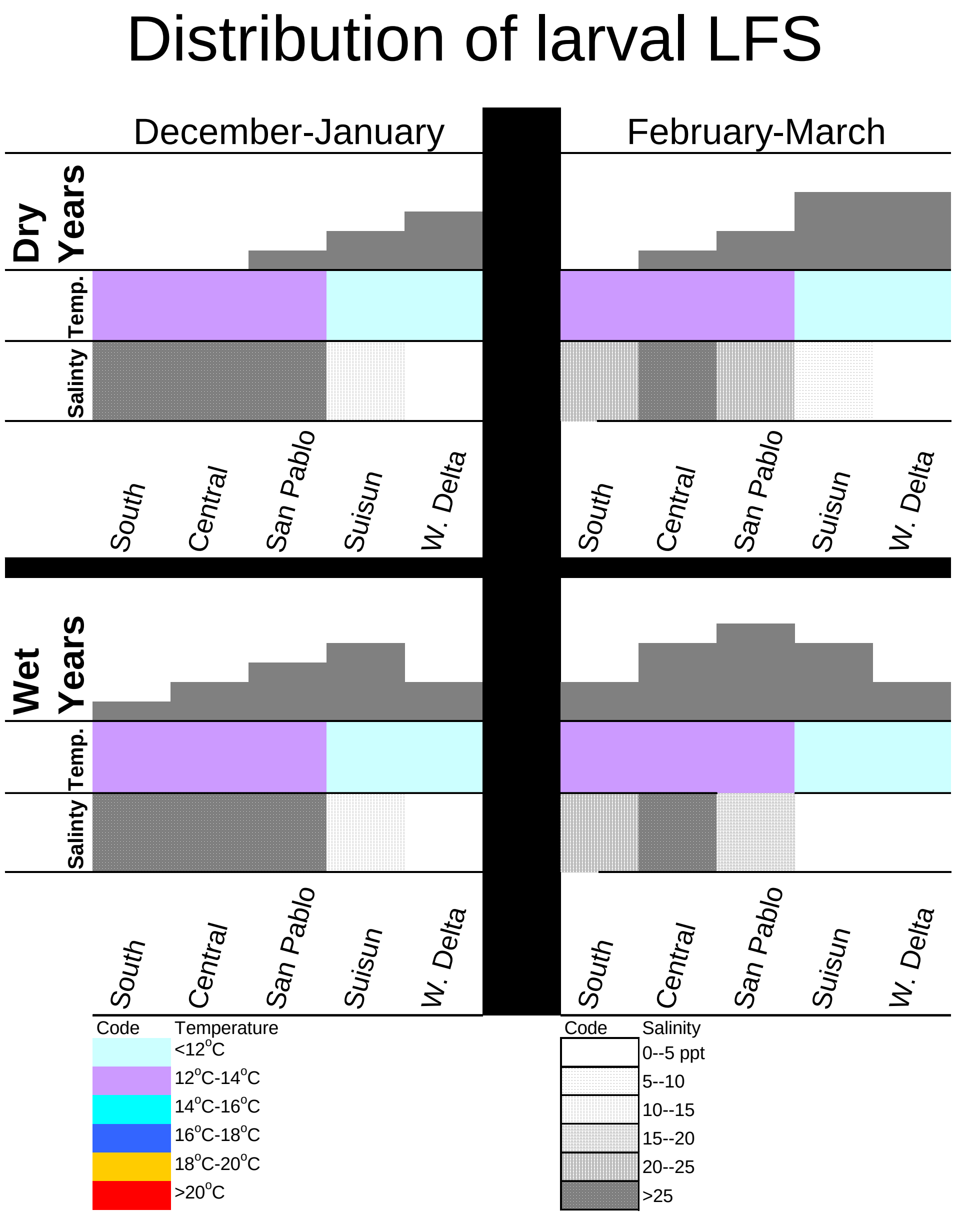


Figure 6: Relative distribution of longfin smelt larvae through the San Francsico Estuary under different hydrological conditions. Height of solid grey bars represent relative abundance within a two month time period in different embayments of the Estuary. The center of longfin smelt larval distribution appears to be controlled by the position of the low salinity zone (Dege and Brown 2004). In years with high freshwater outflow through the Delta, longfin smelt larvae are distributed further down the axis of the Estuary than in dry years.

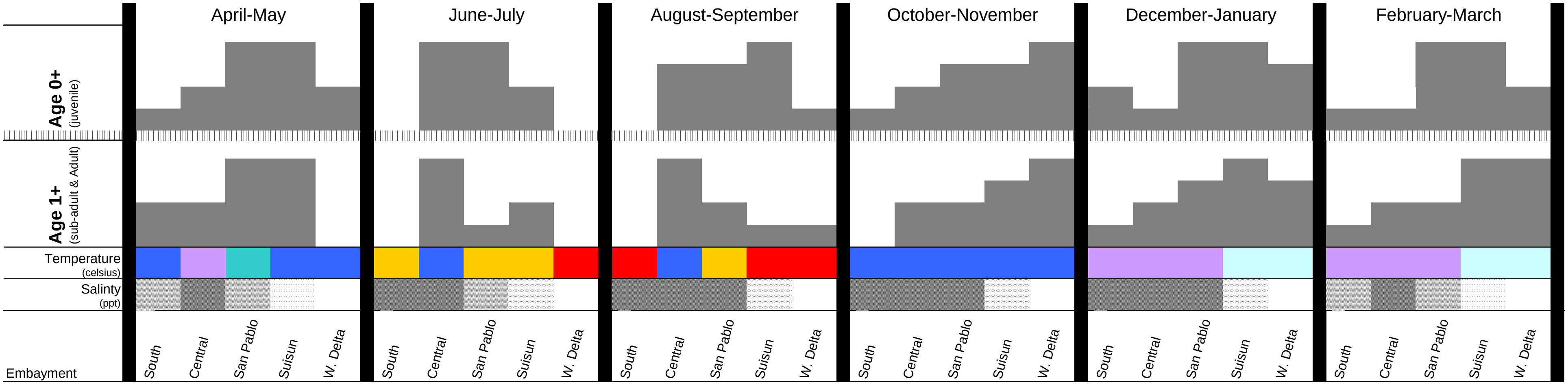


Figure 7: Approximate distribution during their free-swimming life-cycle of two age classes of longfin smelt in the San Francisco Estuary. Height of solid grey bars represent relative abundance within a two month time period in different embayments of the Estuary. This pattern reveals (a) that longfin smelt have a broad distribution that becomes more constrained during summer and (b) migrate seasonally towards Central Bay in summer and towards the West Delta in winter. Colors indicate approximate mean bottom temperatures and shading indicates approximate bottom salinity during the two months; longfin smelt larvae may be limited by temperatures >20oC their distribution does not appear to be limited by salinity.

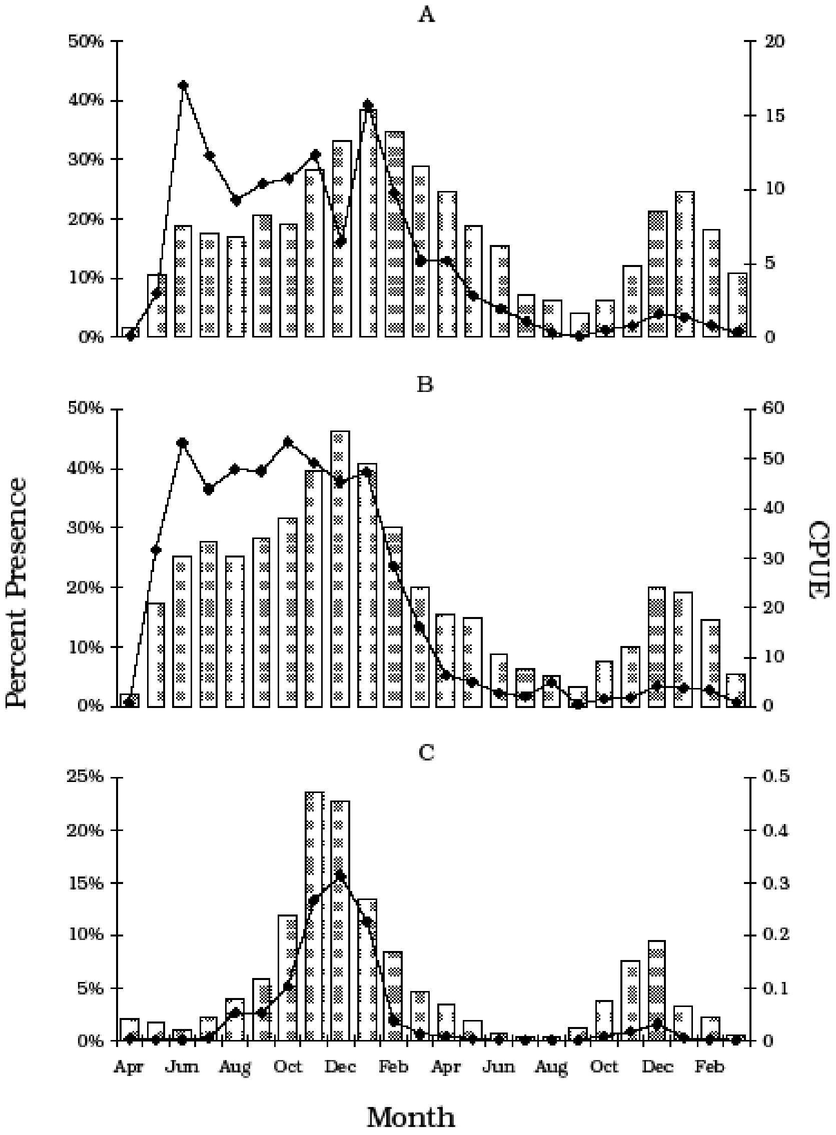


Figure 8: Mean percent of sites present (bars) and catch-per-unit-effort (lines) across years (from 1980-2004) throughout the longfin smelt life cycle as portrayed by the (A) the Bay Study's Mid-water Trawl; (B) Bay Study's Otter Trawl; and (C) the Suisun Marsh Survey. Calendar months in the longfin smelt life cycle are represented along the abscissa. The number of years contributing to the mean varied among months as a result of changes in the sampling programs. The relative decline in LFS abundance and distribution seen between the first winter and second summer of life cannot be attributed to mortality alone; migration out of the Estuary into the Pacific Ocean during summer and a subsequent return in the fall is the most likely explanation. This pattern is consistent across years (Rosenfield and Baxter 2007). (Figure from Rosenfield and Baxter 2007).

Total Entrainment v. Outflow

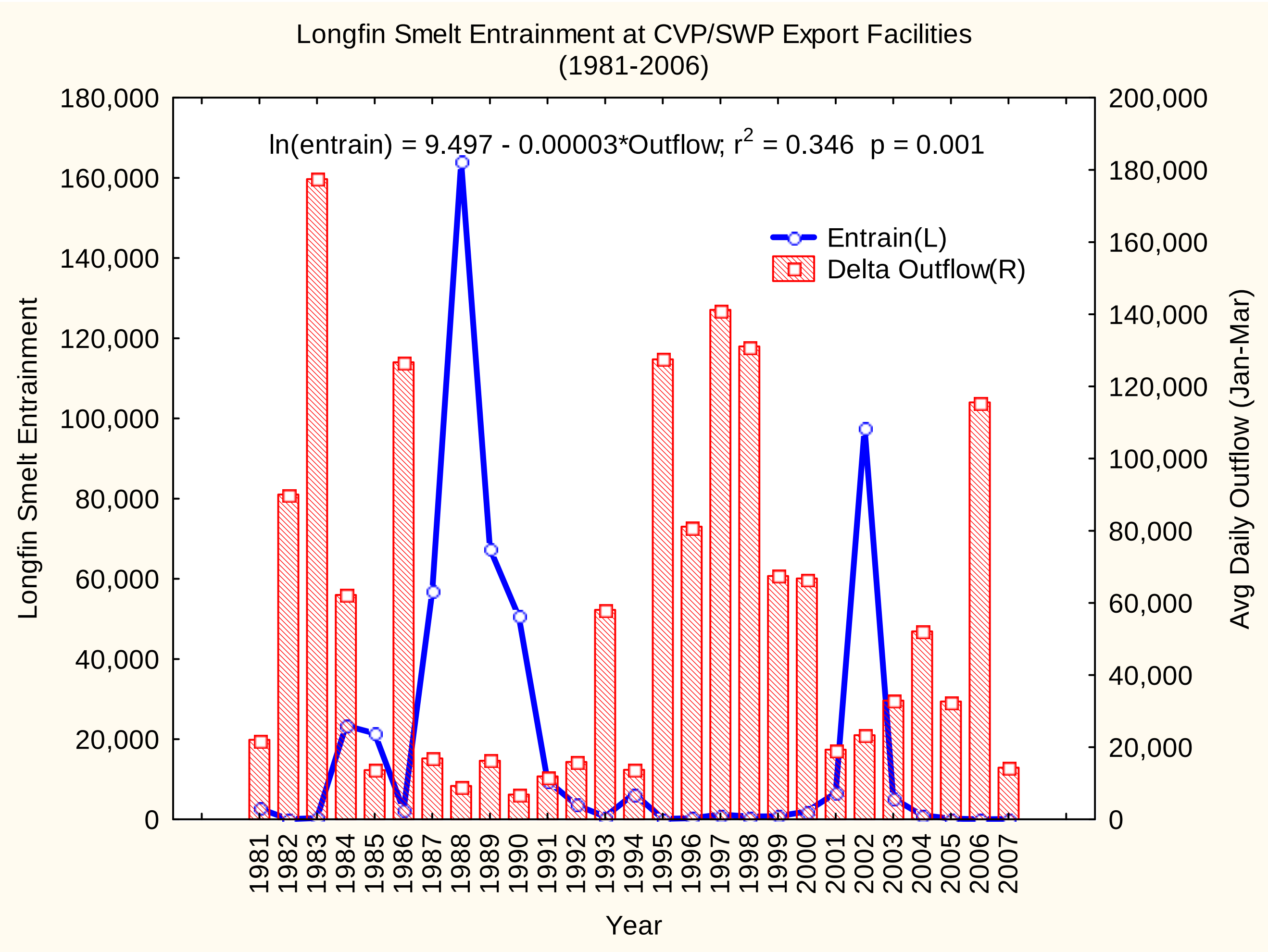


Figure 9: Annual entrainment of longfin smelt at SWP and CVP south delta export facilities compared with outflow from the Delta (Jan-March). In each year, entrainment numbers are dominated by Age 0+ juveniles – larvae are not enumerated at salvage facilities.

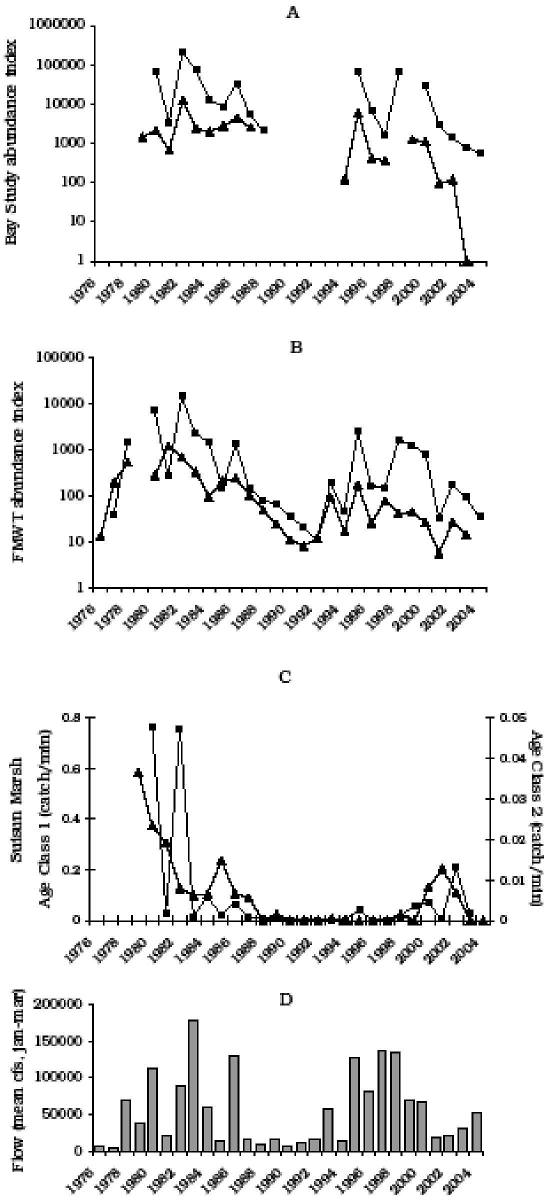


Figure 10: Abundance of longfin smelt as measured by (A) the Bay Study, (B) the FMWT, and (C) the Suisun Marsh Survey compared with (D) winter-spring freshwater outflow from the San Joaquin-Sacramento Delta. Squares represent abundance indices for Age Class 1 fish, triangles represent Age Class 2 indices. In (A) and (B) ordinal scales are logarithmic. In (C), the ordinal scale to the left represents catch-per-minute of Age Class 1 longfin smelt whereas the ordinal scale to the right represents catch-per-minute of Age Class 2 longfin smelt. Values for Age Class 2 longfin smelt are plotted in the year they were spawned (one year before they were sampled) directly underneath the Age Class 1 population from which they were derived. Statistically significant decline in Age Class 1 and Age Class 2 fish have been detected (Rosenfield and Baxter in press). (Figure from Rosenfield and Baxter 2007).

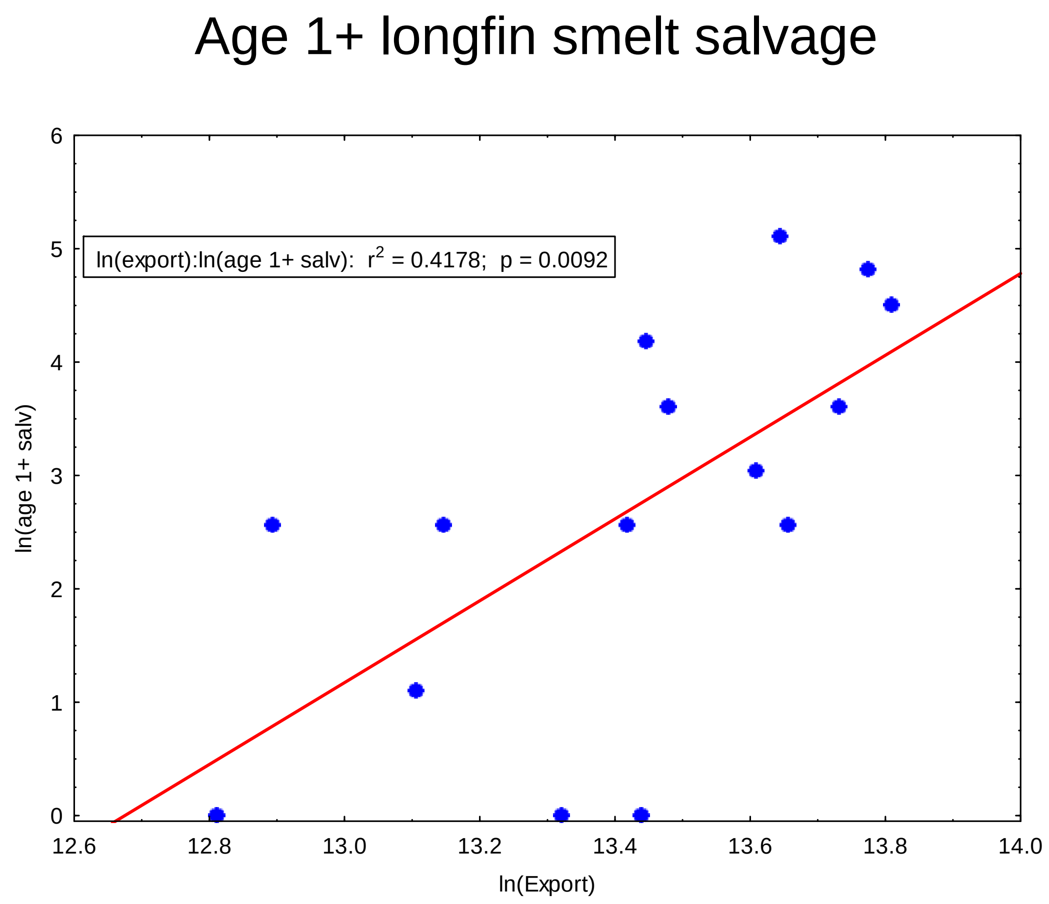


Figure 11: Salvage of Age 1+ (“mature”) longfin smelt at CVP and SWP water export facilities as a function of export rates.

Age 1+ longfin smelt salvage vs. total population

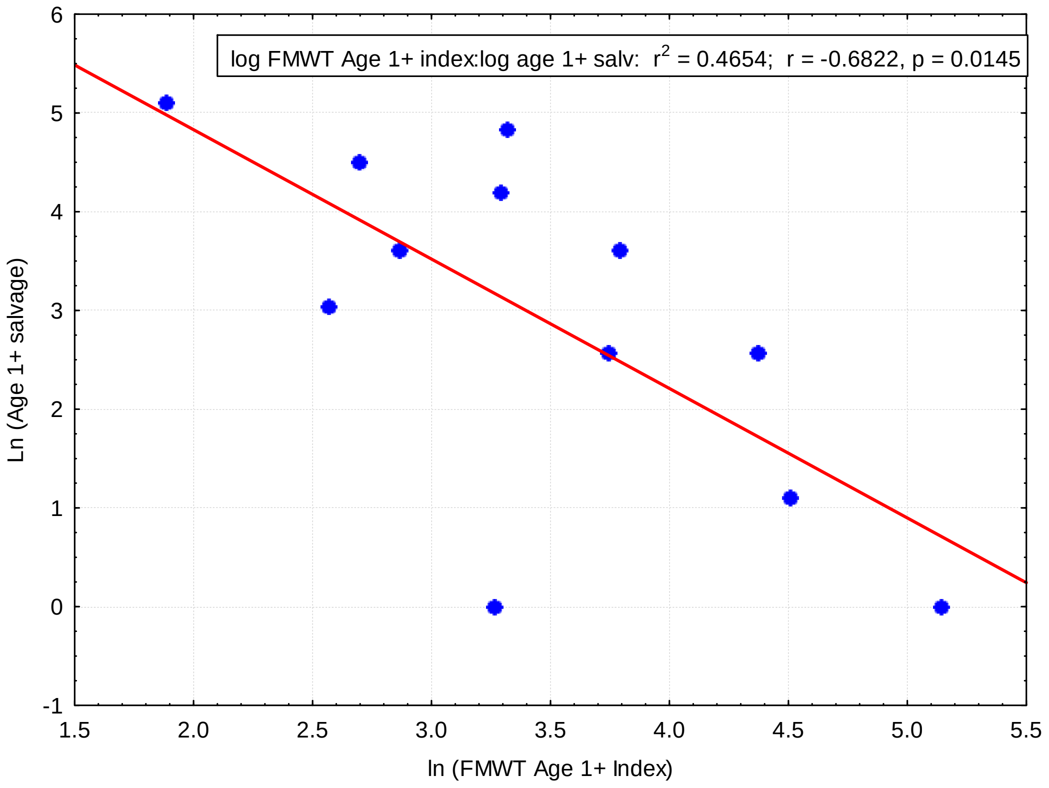


Figure 12: Salvage of Age 1+ (“mature”) longfin smelt at CVP and SWP water export facilities as a function of total population size measured in the previous fall. The inverse relationship shows that increases in salvage are not a result of increases in longfin smelt population size.