

**Sacramento-San Joaquin Delta
Regional Ecosystem Restoration Implementation Plan**

**The Little Fish in California's Water Supply: a Literature Review and
Life-History Conceptual Model for delta smelt (*Hypomesus transpacificus*)
for the Delta Regional Ecosystem Restoration and Implementation Plan
(DRERIP)**

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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, or is currently being subject to a rigorous scientific peer review process. The peer review status of each model is indicated on the title page of the model.

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.

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I. Introduction

A. DRERIP background

This document is a qualitative (conceptual) model of the life history and population drivers of delta smelt, *Hypomesus transpacificus*. The model was developed for the Delta Regional Ecosystem Restoration and Implementation Plan (DRERIP). The DRERIP is developing a suite of conceptual models to articulate the state of scientific understanding of the Bay-Delta ecosystem. The delta smelt model provides the authors' understanding of how current drivers and stressors acting on delta smelt in the Bay-Delta *presently* influence this fish's population dynamics. We contrast this snapshot of the current ecology of delta smelt with its likely pre-colonial ecology. Note however that there are no quantitative historical data prior to 1950 (Erkkila et al. 1950). Thus, our characterizations of 'ancestral' delta smelt ecology are a mixture of best professional judgement, generalizations from fish ecology, and generalizations from similar species.

Delta smelt is endemic to the San Francisco Estuary ([Figure 1](#); Moyle 2002). Following about a decade of abundance decline, delta smelt were listed under the State of California and federal Endangered Species Acts as a threatened species in 1993. Although delta smelt abundance does not respond to flow variation on a year by year basis, population numbers rebounded during conditions of sustained above average Delta outflow between 1993 and 2000. Thereafter, the population declined quickly, and has remained at or near record low levels since 2004 (Sommer et al. 2007; [Figure 2](#)). In 2009, delta smelt was reclassified as an endangered species under the California Endangered Species Act. The delta smelt decline has been attributed to an interactive mixture of water project impacts, invasive species impacts, and contaminant impacts that vary in their relative importance through time (Moyle et al. 1992; Bennett and Moyle 1996; Bennett 2005; Sommer et al. 2007). This conceptual model compiles previous work and adds some recent results and a few new observations. Throughout the model we have tried to place conceptual model details in Tables and reserve the Figures for the communication of "big picture" concepts.

B. Regional definitions:

The San Francisco Estuary extends from the Golden Gate Bridge to the eastern limit of tidal influence on the Sacramento River (at Sacramento) and the San Joaquin River (at Mossdale, [Figure 1](#)). The San Francisco Estuary has a full freshwater to seawater salinity gradient under all but the highest river flow conditions. River flows vary greatly both seasonally and interannually. Wet season (Dec-May) outflows often range from 10,000-50,000 cfs, whereas dry season outflows seldom range beyond 3500-15,000 cfs.

The Sacramento-San Joaquin Delta is the part of San Francisco Estuary that extends eastward from Chipps Island to the limit of tidal influence. The Sacramento-San Joaquin Delta is predominantly a tidal freshwater region (0-2 psu), though salinity is frequently higher than 2 psu between Collinsville and Chipps Island in summer and fall. Suisun Bay is a large embayment between San Pablo Bay and the Delta where salinity usually varies between 0-20 psu. Suisun Marsh is a wetland complex north of Suisun Bay. This former tidal marsh is now mostly diked managed wetlands and channels. The Cache Slough

region is part of the tidally-influenced lower Sacramento River. It includes the tidally-influenced part of Yolo Bypass, a seasonal floodplain that drains into the Sacramento River via Cache Slough. The South Delta includes the San Joaquin River from Mossdale to Franks Tract, Old and Middle rivers, and all of the channels that connect the San Joaquin River to Old and Middle rivers.

The Delta is the home of two large water diversions: the Banks Pumping Plant of the State Water Project (SWP) and the Jones Pumping Plant of the Central Valley Project (CVP) ([Figure 1](#)). Their maximum combined diversion rates have been as high as 11,500 cfs. These diversions export Delta water from Old River to agricultural and municipal users to the south. The SWP's North Bay Aqueduct (maximum export rate of 175 cfs) is a second SWP diversion, located in the Cache Slough region. The Contra Costa Water District diversion on Old River (maximum export rate of 250 cfs) is part of the CVP. The North Bay Aqueduct and Contra Costa Water District diversions are not considered significant drivers of delta smelt distribution and abundance. The former has a positive barrier fish screen designed to protect delta smelt. The latter monitored their entrainment of delta smelt, but very low levels of entrainment were reported (<http://www.delta.dfg.ca.gov/data/nba/catchsummary.asp>). The North Bay and Contra Costa diversions are not discussed further in this model. There are approximately 2200 small, (<50 cfs), unscreened agricultural diversions reported from the Delta (Herren and Kawasaki 2001). These are also considered of minor if any significance to delta smelt population dynamics.

This conceptual model uses some habitat-based terms that do not have static locations. The low-salinity zone (LSZ) is where freshwater transitions into brackish water; the LSZ is defined as 0.5-6.0 psu (parts per thousand salinity; Kimmerer 2004). The 2 psu isohaline is a specific point within the LSZ where the average daily salinity at the bottom of the water is 2 psu (Jassby et al. 1995). By local convention the location of the LSZ is described in terms of the distance from the 2 psu isohaline to the Golden Gate Bridge (X_2); X_2 is an indicator of habitat suitability for many San Francisco Estuary organisms and is associated with variance in abundance of diverse components of the ecosystem (Jassby et al. 1995; Kimmerer 2002; Kimmerer et al. 2009). The LSZ expands and moves downstream when river flows into the estuary are high. Similarly, it contracts and moves upstream when river flows are low. During the past 40 years, monthly average X_2 has varied from as far downstream as San Pablo Bay (45 km) to as far upstream as Rio Vista on the Sacramento River (95 km) ([Figure 1](#)).

II. Delta Smelt Biology

Delta smelt live their entire life in the tidally-influenced fresh- and brackish waters of the San Francisco Estuary (Moyle 2002; [Table 1](#)). Delta smelt are an open-water, or pelagic, species. They do not associate with structures. They may use nearshore habitats for spawning, but free-swimming life stages mainly occupy offshore waters. Thus, the distribution of the population is strongly influenced by river flows through the estuary because the quantity of fresh water flowing through the estuary changes the amount and location of suitable low-salinity, open-water habitat (Kimmerer et al. 2009; Feyrer et al.

in review). This is true for all life stages. During periods of high river flow through the estuary, delta smelt distribution can transiently extend as far west as the Napa River and San Pablo Bay (Sweetnam 1999; Hobbs et al. 2007). Delta smelt distribution is highly constricted near the Sacramento-San Joaquin river confluence during periods of low river flow into the estuary (Feyrer et al. 2007).

A. Spawning

Mature delta smelt migrate from brackish water into fresh water to spawn. Typically, delta smelt migrate upstream to spawning habitats in the Delta (Moyle 2002). However, spawning migrations are not always upstream. During occasional periods of high river flows that spread freshwater habitat throughout much of the estuary, delta smelt may migrate “downstream” from rearing habitats in Suisun Bay and the Sacramento-San Joaquin river confluence to freshwater spawning habitats in the Napa River (Hobbs et al. 2007). Also under high flow conditions, some delta smelt may not migrate in any direction; if their brackish rearing habitat becomes fresh, they can spawn in suitable microhabitats nearby.

Delta smelt fecundity varies from about 1,000-12,000 eggs per female and is related to female size; larger and older females are often more fecund (Bennett 2005). There is a large increase in fecundity for fish that grow to 90 or more mm in length, but few wild fish grow this large. Delta smelt can spawn at water temperatures between about 10°C-20°C, but optimum temperature for larval hatching success is about 15°C ([Table 1](#)). In years when temperatures warm rapidly during spring, the delta smelt spawning season is shortened and opportunities to spawn are limited. When this happens, there is usually one larval cohort (Bennett 2005). Conversely, in years where spring temperatures warm slowly, multiple larval cohorts are produced because adults have more time to ripen and spawn (Bennett 2005); some likely spawn more than once (Wang 2007). Different cohorts experience different environmental conditions. Thus, a long spawning season decreases the likelihood that any given environmental factor will cause catastrophic loss of the larval population (Bennett 2005).

The spawning behavior of delta smelt has only been observed in captivity (Bennett 2005; Wang 2007), so our characterization of spawning habitat is speculative, though there is a growing body of evidence to support it. Unpublished studies have indicated captive delta smelt preferentially spawn at night in current on sand or gravel. These results led Bennett (2005) to hypothesize that delta smelt, like its nearest relative the surf smelt *Hypomesus pretiosus*, spawn on shallow beaches rather than the marsh/riparian plants sometimes assumed to represent spawning substrata previously. The CALFED Science Program hosted a workshop on smelt spawning biology on November 15, 2007. Presentations included speakers who have studied the biology of other smelt species in the Pacific Northwest. Based on the presentations and discussion at this workshop, the following general conceptual model of smelt spawning emerged:

1. Smelts generally spawn in shallow water. This includes beaches for marine species and river edges or small streams for estuarine/freshwater populations.

2. Smelts spawn most often on sand or gravel. This conclusion is further supported by several gray literature and book references cited within the delta smelt, longfin smelt (*Spirinchus thaleichthys*), wakasagi (*Hypomesus nipponensis*), and eulachon (*Thaleichthys pacificus*) chapters in Moyle (2002). The correlation of substrate choice is also consistent with fish choosing spawning microhabitats where water velocity keeps the eggs from being smothered by fine sediments.
3. Smelts are nocturnal spawners, making overnight forays into spawning microhabitats and leaving them before dawn. This appears to be true for marine beach spawners, estuarine populations and the landlocked Lake Washington longfin smelt. A key potential lesson from this is that delta smelt distributions in the IEP Kodiak Trawl Survey (<http://www.delta.dfg.ca.gov/data/skt/>), which is conducted during daylight in offshore habitats likely reflects general regions of spawning activity, but does not pinpoint the actual spawning sites.

A final possibility is that osmerid eggs may “tumble incubate” (phrase attributed to Doug Hay, Department of Fisheries and Oceans, Canada). Delta smelt, like other members of its family (Osmeridae) have adhesive eggs. It has been assumed that eggs are affixed to immobile substrates (Moyle 2002). Dr. Hay suggested the eggs of another smelt, the eulachon, attach to sand particles which keep them negatively buoyant, but not immobile. This is analogous to what has been observed in the marine surf smelt (Hirose and Kawaguchi 1998). The benefits include dispersal of eggs so that they are not exposed to air during very low tides and not so highly aggregated that they attract predators, but not so broadly dispersed that they hatch in conditions very different from those in which they were spawned. The ‘tumble incubation’ hypothesis is highly speculative for delta smelt, but we think it should be considered in discussions of habitat restoration needs of this species.

B. Larval biology

Delta smelt can have a lengthy larval phase (sometimes lasting more than two months). The currently available details of larval stage transitions and their temperature-dependence are summarized in [Table 1](#) and [Figure 3](#). Briefly, delta smelt hatch into pelagic larvae during February-June. Peak larval abundance typically occurs in April or early May. The newly hatched embryos disperse from spawning areas downstream toward the low-salinity zone. However, the center of distribution of 30-40 day old larvae transitioning to the juvenile stage typically remains in the Delta, often 5-20 km upstream of the 2 psu isohaline (Dege and Brown 2004).

After hatching, delta smelt larvae are nourished from a yolk-sac for up to 12 days before they need to start capturing prey (Bennett 2005). The success of larval feeding is a function of larval size and prey density (Nobriga 2002) and turbidity (Baskerville-Bridges et al. 2004) ([Table 1](#)). Turbidity (either from sediment or algae suspended in the water) is thought to help delta smelt larvae see their prey by increasing its visual contrast in the water. Larvae with developing fins and swim bladders can actively maintain position within areas of suitable low-salinity habitat (Bennett et al. 2002). It is not known whether yolk-sac larvae can effectively maintain desired geographic position, but

it is likely they can since smaller crustacean zooplankton are able to do so (Kimmerer et al. 2002). Larvae can also move quickly away from habitat that becomes unsuitable (Hobbs et al. 2007).

Growth rates of wild-caught delta smelt larvae are faster than laboratory-cultured individuals. Mager et al. (2004) reported growth rates of captive-raised delta smelt reared at near-optimum temperatures (16°C-17°C). Their fish were about 12 mm long after 40 d and about 20 mm long after 70 d. In contrast, analyses of otoliths indicated that wild delta smelt larvae were 15-25 mm, or up to twice as long at 40 d of age (Bennett 2005; [Figure 3](#)). By 70 d, most wild fish were 30-40 mm long and beyond the larval stage. This suggests there is strong selective pressure for rapid larval growth in nature, a situation that is typical for fish in general (Houde 1987).

The food available to larval fishes is constrained by mouth gape and fin development. Larval delta smelt cannot capture as many kinds of prey as larger individuals, but all life stages have small gapes that limit their range of potential prey. Prey availability is also constrained by habitat use, which affects what types of prey are encountered. Larval delta smelt are visual feeders. They find and select individual prey organisms and their ability to see prey in the water is enhanced by turbidity (Baskerville-Bridges et al. 2004). Thus, delta smelt diets are largely comprised of small crustacea that inhabit the estuary's turbid, low-salinity, open-water habitats (i.e., zooplankton). Larval delta smelt have particularly restricted diets (Nobriga 2002). They do not feed on the full array of zooplankton with which they co-occur; they mainly consume three copepods, *Eurytemora affinis*, *Pseudodiaptomus forbesi*, and freshwater species of the family Cyclopidae. Further, the diets of first-feeding delta smelt larvae are largely restricted to the larval stages of these copepods; older life stages of the copepods are increasingly targeted as the delta smelt larvae grow, their gape increases, and they become stronger swimmers.

Laboratory-cultured delta smelt larvae have generally been fed rotifers at first-feeding (Baskerville-Bridges et al. 2004; Mager et al. 2004). However, rotifers rarely occur in the guts of wild delta smelt larvae (Nobriga 2002). As stated above, the most common first prey of wild delta smelt larvae is the larval stages of several copepod species. These copepod 'nauplii' are larger and have more calories than rotifers. This difference in diet may contribute to the faster growth rates observed in wild-caught larvae.

Table 1. Summary of biological measures by life stage for delta smelt. UNK = unknown

Habitat (life stage)	Dates	Days post spawn	Weight (mg)	Length (mm)	Acclimation temperature (°C)	Optimum temperature (°C)	Min/Max Critical temperature (°C)	Common salinity	Critical salinity	Common water transparency (cm)	Citations
Sandy-gravel channel edge (egg/embryo)	Feb-Jun	17 10 7		5.4 5.2 4.9	10 15 20	15	10/20	< 1 psu	UNK	UNK	Bennett (2005)
Offshore tidal freshwater (yolk-sac larvae)	Feb-Jun	25 16 11		5.4-6.8 5.2-6.3 4.9-5.8	10 15 20	15	10/20	< 1 psu	UNK	UNK	Bennett (2005)
Offshore tidal freshwater (first-feeding larvae)	Feb-Jun	25+ 16+ 11+		6.8 ^a 6.3 ^b 5.8 ^c	10 15 20	15	10/20	< 1 psu	UNK	≥ 2 million algal cells/mL	Baskerville-Bridges et al. (2004); Bennett (2005)
Offshore tidal freshwater (fin-fold larvae)	Mar-Jul	30-60		10-12 ^d	15-16	15	UNK	< 1 psu	UNK	UNK	Mager et al. (2004)
Offshore tidal freshwater and LSZ (metamorphosing larvae)	Apr-Jul	40-130		19-35	15-16	20	UNK/25	< 2 psu	Similar to juveniles	< 100	Dege and Brown (2004); CDFG unpublished data
Offshore tidal freshwater and LSZ (juveniles)	May-Dec	~ 60-300	Wt = 0.0018 * L ^{3.38}	35-60	17	20	7.5/25.4	< 3 psu	19	< 50	Swanson et al. (2000); Mager et al. (2004); Kimmerer et al. (2005); Feyrer et al. (2007); Nobriga et al. (2008)
Offshore tidal freshwater (migrating adult)	Dec-Apr	> 200	Wt = 0.0018 * L ^{3.38}	60-110	17	20	7.5/25.4	< 1 psu	19	< 50	Swanson et al. (2000); Bennett (2005); Kimmerer et al. (2005); Feyrer et al. (2007)
Tidal freshwater (spawner)	Feb-Jun	> 200	UNK ^e	60-110	NA	15	10/20	< 1 psu	UNK	< 50	Bennett (2005)

^aFeeding incidence of field-caught larvae of this size ~ 30%-60% (Nobriga 2002)

^bFeeding incidence of field-caught larvae of this size ~ 20%-25% (Nobriga 2002)

^cFeeding incidence of field-caught larvae of this size ~ 5%-10% (Nobriga 2002)

^dFeeding incidence of 10-20 mm field-caught larvae ~ 80%-95% (Nobriga 2002)

^eFecundity ranges from about 1,000-4,000 eggs per 60-85 mm female and about 2,000-12,000 eggs per 90-110 mm female (Bennett 2005)

C. Juvenile biology

Most delta smelt live one year and spend about half of their lives as juvenile fish rearing in the turbid open waters of the San Francisco Estuary low-salinity zone. The physiological tolerances of juvenile delta smelt for salinity and water temperature have been determined (Swanson et al. 2000). Similarly, the multivariate distributions of juvenile delta smelt along gradients of salinity, water temperature, and water transparency have recently been described (Feyrer et al. 2007; Nobriga et al. 2008; Kimmerer et al. 2009; [Figure 4](#)). Delta smelt is sometimes characterized as a weak swimmer. However, the maximum swimming speed of juvenile delta smelt is $28 \text{ cm} \cdot \text{sec}^{-1}$, comparable to other fishes of similar size (Swanson et al. 1998).

Salinity: Ocean salinity is usually about 33 psu, but the highest salinity in which juvenile delta smelt can survive is about 19 psu (Swanson et al. 2000). Thus, salinity provides the primary constraint on delta smelt distribution. In captivity, delta smelt can tolerate salinities as high as 10 psu for extended periods (Swanson et al. 2000), but long-term monitoring shows that most juvenile delta smelt reside where specific conductance is about 1,000-5,000 microsiemens per centimeter, (about 0.6-3.0 psu) (Feyrer et al. 2007; Nobriga et al. 2008; Kimmerer et al. 2009; [Figure 4](#)). This may represent a physiologic optimum or a trade-off between physiology and biotic constraints such as predator avoidance or minimization of competition with other more abundant fishes, or both. Because of this association with a particularly narrow range of salinity, the geographic distribution of the juvenile delta smelt population also changes with river flow (Moyle et al. 1992; Sweetnam 1999).

Turbidity: Sediment and algal blooms lower water transparency. Long-term monitoring shows the distribution of juvenile delta smelt is strongly influenced by water transparency; delta smelt seldom occur in water where a Secchi disk can be seen more than about 50 cm (20 inches) from the surface during daylight (Feyrer et al. 2007; Nobriga et al. 2008; [Figure 4](#)). One explanation for this pattern is that delta smelt use turbidity to conceal themselves from predators. This is a hypothesis based on 1) laboratory observations that found delta smelt dislike well-lighted tanks (Joan Lindberg, UC Davis, pers. comm.), 2) a laboratory study indicating that pelagic gizzard shad (*Dorosoma cepedianum*) effectively avoid predation by a visual predator, largemouth bass (*Micropterus salmoides*), given any amount of turbidity in the water (Shoup and Wahl 2009), and 3) studies of predation risk to small pelagic fishes in other river systems (Gregory and Levings 1998; Quist et al. 2004). Turbidity throughout the Delta is lower than it was 30-40 years ago (Jassby et al. 2002) because sediment supply is lower (Wright and Schoellhamer 2004). Decreasing turbidity in the Delta has constrained the distribution of juvenile delta smelt (Feyrer et al. 2007; Nobriga et al. 2008).

Water temperature: Some locations in the estuary exceed the thermal limits of delta smelt during winter and summer. The laboratory-derived lower and upper temperature tolerances of juvenile delta smelt are 7.5°C (46°F) and 25.4°C (78°F), respectively (Swanson et al. 2000). Careful acclimation can extend these boundaries slightly (Tina Swanson, The Bay Institute, pers. comm.). Long-term monitoring data do not strongly

support the lower limit, but do support the upper one. Autumn capture probabilities of delta smelt do not taper off at temperatures less than 10°C (50°F; Feyrer et al. 2007). However, winter water temperatures less than 10°C are uncommon in the estuary (Kimmerer 2004). For metamorphosing and juvenile delta smelt collected in the summer, there seems to be a thermal optimum near 20°C (68°F) ([Figure 4](#)). Capture probabilities decline rapidly at higher temperatures, and based on historical sampling are near zero at temperatures $\geq 25^{\circ}\text{C}$ (77°F).

In addition to lethal limits, water temperatures increase the stress associated with food limitation, exposure to contaminants, and low dissolved oxygen concentrations, causing mortality at levels below laboratory-derived lethal limits (e.g. Kumaraguru and Beamish 1981; Marine and Cech 2004; Bennett et al. 2008). The combination of multiple stressors and seasonally stressful temperatures strongly suggest water temperature increases associated with a warming climate (Dettinger 2005) will be a major impediment to delta smelt recovery in coming decades.

Food: Like the larvae, juvenile and adult delta smelt are visual feeders that select prey individually rather than by filtering mouthfuls of water. Juvenile and adult delta smelt eat zooplankton, but they can capture larger varieties than larval stages including cladocerans, mysids, amphipods, and larval fish (Moyle et al. 1992; Lott 1998). During the 1970s and early 1980s, juvenile and adult delta smelt diets were dominated by the copepod *Eurytemora affinis*, the mysid shrimp *Neomysis mercedis*, and the cladoceran *Bosmina longirostris* (Moyle et al. 1992; Feyrer et al. 2003). None of these are important prey now. When delta smelt diets were examined between 1988 and 1996, they were consistently dominated by the copepod *Pseudodiaptomus forbesi*, which was introduced and became abundant following the overbite clam invasion (Lott 1998). Recent diet studies have shown that *P. forbesi* remains an important prey for juvenile delta smelt during summer, but that several other copepods introduced into the system in the mid-1990s, are also frequently eaten (Steve Slater, Department of Fish and Game, unpublished data). Current analyses of adult delta smelt diets suggest amphipods and cladocerans are important in addition to copepods.

There have been numerous analytical attempts to document food limitation in delta smelt. However, food limitation cannot be readily separated from the stress of high water temperature (Bennett et al. 2008). When water temperatures are low (e.g., $< 20^{\circ}\text{C}$), a lower metabolic rate allows delta smelt to survive and grow in areas of low prey density. When water temperatures exceed the optimum, delta smelt metabolism rapidly begins to be stressed. When this happens, delta smelt may have trouble assimilating prey no matter how abundant it is. Low prey density at high temperatures worsens the metabolic stress.

Unpublished histopathologic evaluations of juvenile delta smelt collected during summer-fall 2005 showed severe glycogen depletion, which is evidence of food limitation or other water-temperature related bioenergetic stress (Bennett et al. 2008). These mechanisms cannot be readily differentiated. This recent work adds to the histopathologic evidence for food limitation or thermal stress of juvenile delta smelt reported previously from samples collected in summer 1999 (Bennett 2005). In seeming

contrast, adult delta smelt collected during winter in 2005 and 2006 did not have a high incidence of glycogen depletion (Baxter et al. 2008). However, the 2005 delta smelt cohort suffered considerable size-selective mortality during late summer and early autumn (Bennett et al. 2008), so the likely explanation is that the fish that survived to adulthood had acquired enough food to build back glycogen reserves as water temperatures cooled during the autumn.

III. Delta Smelt Distribution

A. Habitat connectivity

Delta smelt live only in the San Francisco Estuary and have a very short life cycle (1-2 years; Bennett 2005). This means, that low or high flow, the estuary always has to provide suitable habitat. At all life stages, delta smelt distribution is controlled by freshwater flow; small larvae are distributed furthest from the LSZ and juveniles and maturing adults are often distributed at the upstream edge of the LSZ. Delta smelt's geographic distribution can stretch from San Pablo Bay and the Napa River into Suisun Bay, Suisun Marsh, and the Delta (Moyle 2002). Thus, the northern estuary represents a habitat continuum; any part of which can be extremely important under certain conditions. Recent studies demonstrate this very clearly – different regions are used as spawning and rearing habitat as conditions allow (Hobbs et al. 2007; Nobriga et al. 2008). Through time, this continuum has become less suitable – at least during summer-fall (Feyrer et al. 2007; Nobriga et al. 2008). Climate change and human demand for freshwater are likely to further impact delta smelt habitat suitability in the coming decades (Feyrer et al. in review).

B. Long-term change, cumulative effects, and extinction risk

The DRERIP conceptual models were designed to aid management decisions including decisions regarding restoration strategies. Thus, it is appropriate to discuss habitat change over long time scales and the possible influence of these changes on extinction.

The San Francisco Estuary has been greatly changed in the past 160 years (Moyle 2002). The system was converted from a large tidal marsh-river floodplain system draining into estuarine embayments into the series of water delivery canals, shaped by dikes that protect adjacent cities and farms shown in *Figure 1*. The canals also protect drinking and agricultural water supplies from seawater intrusion. The Delta's canals highly connect all waters within the Delta, but the water is highly disconnected from the surrounding land.

Massive ecosystem conversions, like those that have occurred in the Delta, have been frequently associated with extinctions of native species. Further, extinctions often occur very distant in time from the ecosystem changes that set them in motion (Tilman et al. 1994; Unmack and Fagan 2004). For instance, it was more than 100 years after the start of California's Gold Rush, and the conversion of the Delta that came with it, that the first native fish went extinct. The last thicktail chub *Gila crassicauda*, was collected in 1957 (Moyle 2002). Most fish species native to California's Central Valley have undergone substantial long-term population declines (Moyle 2002; Brown and Moyle 2005). Thus,

from an ecological standpoint, it is likely that many native fishes are trending toward extinction due to system changes both past and present.

Delta smelt have a very high likelihood of extirpation in the near future (Bennett 2005). This has led to extensive planning to raise delta smelt in captivity to prevent its extinction (http://www.science.calwater.ca.gov/events/workshops/workshop_ap.html; Israel et al. in review). We can only track trends in delta smelt relative abundance (relative to themselves and relative to other pelagic fishes) over the period for which monitoring data are available (1959-present; *Figure 2*). It is very likely that delta smelt were much more abundant prior to the onset of routine monitoring (Moyle 2002). This makes it very difficult to determine whether population rebounds like that observed during the 1990s reflect true resilience or merely a temporary slowing of a background extinction rate during favorable environmental conditions. Certainly, the abundance decline to record lows in the past five years suggests an increase in the risk of extinction.

The record since 1959 provides an example of the difficulty in distinguishing between population resilience and changes in risk of extinction. Delta smelt have recently been described as an abundant fish in the 1970s (e.g., *Plaintiff's Declaration in Natural Resources Defense Council et al. v. Kempthorne et al. August 21, 2007: Case 1:05-cv-01207-OWW-NEW Document 421*). However, this is not well supported by the data and many of the factors that we identify as probably promoting abundance of the ancestral population were already substantially changed before quantitative data were gathered.

The Department of Fish and Game Summer Townet Survey is the sampling program showing the highest density of delta smelt relative to other pelagic fishes. Delta smelt have constituted 1%-45% of annual townet survey catches (mean = 11%), and delta smelt catches sporadically exceeded 20% of the total catch from 1959-1999. However, the townet survey is a temporally restricted survey (1-2 months), the timing of which happens to elevate the relative abundance of delta smelt by missing peak recruitment events of other much more abundant pelagic fishes like longfin smelt *Spirinchus thaleichthys*, American shad *Alosa sapidissima*, and threadfin shad *Dorosoma petenense*. It also has often skipped sampling higher salinity stations where northern anchovy *Engraulis mordax* catches can be very high (Kimmerer 2006).

DFG has also conducted the fall midwater trawl survey (FMWT) since 1967. Like the townet survey, the FMWT was designed to index the relative abundance of age-0 striped bass, but it is used to index delta smelt abundance as well (Moyle et al. 1992; Bennett 2005). The FMWT is conducted for four months of the year and samples many more stations than the TNS. Thus, it has fewer mismatches between fish size and net mesh size. Delta smelt catches have accounted for only 0.17%-8.9% (mean = 1.8%) in the FMWT (e.g., delta smelt is not even visible in *Figure 5*). Delta smelt catches have only exceeded 5% of the total fish catch in four years, two of which were about 35 years ago, but two of which are fairly recent: 1974, 1976, 1999, and 2000. There are several other shorter-term surveys that agree closely with the FMWT (*Table 3*). Thus, most of the available evidence suggests that delta smelt has been a comparatively rare species, at all life stages, in all habitats, for at least the past 40 years.

Table 2. The percent of total fish catch composed of delta smelt from selected fish monitoring programs in the upper San Francisco Estuary

Survey	Dates sampled	Habitat sampled	Delta smelt %
Suisun Marsh Otter Trawl	1979-1999 (Matern et al. 2002)	Marsh channels	1%
Suisun Marsh Larval Fish Survey	1994-1999 (Meng and Matern 2001)	Marsh channels	0.7%
Delta Beach Seine Survey	1994-2002 (Brown and May 2006)	Boat ramps and sandy beaches	0%-1.7% depending on region
20mm Survey	1995-2001 (Dege and Brown 2004)	Pelagic habitats	2%
Predator-Prey Dynamics Study	2001 and 2003 (Nobriga et al. 2005)	Sandy beaches	0.7%
SWP/CVP fish salvage	1993-2002 (Pat Coulston, CDFG, unpublished data)	Southern Delta	0.5%

C. Spawners

The distribution of maturing delta smelt depends on freshwater flow and turbidity. Adults are cued to move by freshets during winter-spring (Grimaldo et al. 2009). During low outflow conditions, delta smelt move into the Delta to spawn. During high outflow conditions, spawners are more widely distributed and ripe individuals have been found in the Delta, Suisun Marsh, and the Napa River (Bennett 2005; Hobbs et al. 2007).

Historically, adult delta smelt spawned throughout the Delta during winter-spring ([Figure 6](#)). Although the area was not sampled in the surveys shown in [Figure 6](#), the spawning distribution likely included the Sacramento River from Rio Vista to Sacramento. Stevens (1963) sampled striped bass stomach contents in this reach and concluded the following. Note that “freshwater smelt” was a name applied to delta smelt at the time.

...in the spring months when the seaward migration of fingerling salmon should be relatively heavy through the study area, analysis of striped bass stomach contents shows freshwater smelt to be the dominant food. Members of this species, apparently spawning in the area, are probably present in such numbers that they are more readily obtained than young salmon.

Presently, spawner distributions are often strongly skewed toward the Cache Slough region and away from the Sacramento River and south Delta ([Figure 6](#)). See <http://www.delta.dfg.ca.gov/data/skt/DisplayMaps.asp> for additional images of adult distribution. Thus, the distribution of suitable spawning habitat has moved or been constricted. It is not possible to determine which has occurred because there are no long-term spawner distribution data collected consistently in the same places. However, it is likely that increased water clarity and possibly water diversions have constricted the distribution of suitable spawning habitat because: 1) the sediment supply moving down the Sacramento River mainstem is lower now than it was in the early 1960s (wet year sediment loads are presently comparable to historical dry year sediment loads; Wright and Schoellhamer 2004); 2) water clarity has increased in the south Delta (Nobriga et al. 2008); 3) water diversions from the south Delta are much higher than they were in the early 1960s ([Figure 7](#)).

D. Larvae

The distribution of delta smelt larvae follows that of the spawners because larvae emerge near where they are spawned. Thus, larvae are distributed more widely during high outflow periods. Delta smelt larvae mainly inhabit tidal freshwater at temperatures between 10°C-20°C (Bennett 2005). The center of distribution for delta smelt larvae < 20 mm is usually 5-20 km upstream of the 2 ppt isohaline, but larvae move closer to 2 ppt as the spring progresses into summer (Dege and Brown 2004).

E. Juveniles

Juvenile delta smelt are most abundant where salinity is low (< 3 psu), water transparency is low (Secchi disk depth < 0.5 m), and water temperatures are cool (~ 20°C) ([Figures 5-6](#)). High springtime river flows move the low salinity zone well into Suisun Bay, but they are never sustained through the juvenile stage (July-December). Thus, many juvenile delta smelt rear near the Sacramento-San Joaquin river confluence (Feyrer et al. 2007; Nobriga et al. 2008). As with spawners, this reflects a long-term change in distribution. Currently, young delta smelt rear throughout the Delta into June or the first week of July, but thereafter, distribution shifts to the Sacramento-San Joaquin river confluence where water temperatures are comparatively cool and water transparencies are low (Feyrer et al. 2007; Nobriga et al. 2008). Note that this change in summertime distribution has often been mischaracterized as a migration into brackish water, but this is unlikely the case. During surveys in the latter 1940s, juvenile delta smelt reared throughout the Delta during summer (Erkkila 1950), and juvenile delta smelt were still routinely collected from the south Delta into the 1970s (Nobriga et al. 2008). However, the lack of a consistent sampling program makes it impossible to quantitatively evaluate distribution prior to 1959.

IV. Delta Smelt Ecology

A. Life History Strategy

Using the fish life history strategies of Winemiller and Rose (1992), Nobriga et al. (2005) determined that delta smelt had most of the traits associated with an opportunistic life-history. At the time, delta smelt appeared to be missing just one characteristic typical of opportunistic fishes – the ability to spawn more than once in a season. Since that time, laboratory studies have shown that delta smelt can spawn more than once if conditions remain suitable for a long enough time (Wang 2007). Thus, delta smelt fit the opportunistic species model very well.

Opportunistic fishes are small species that mature rapidly (Winemiller and Rose 1992). They often densely populate habitat regions called ecotones that are transitional between larger adjacent habitats, or habitats that have recently been disturbed by a natural process. The San Francisco Estuary's low-salinity zone is an ecotonal habitat sitting between freshwater and marine habitats. It is also 'disturbed' by annual winter-spring flooding of various magnitudes. Opportunistic fishes are adapted to sustain high mortality during the adult stage (Winemiller and Rose 1992). Predation mortality is typically high in

opportunistic species because they are small.

B. A hypothesis for the ancestral ecology of delta smelt

Delta smelt is one of the 16 species in the coldwater family Osmeridae, many of which occur in deep cold waters of the ocean, lakes or impoundments of the northern hemisphere. Delta smelt occur more southerly than most other members of the family; as described above, delta smelt can be sensitive to warm summer water temperatures in the estuary (Swanson et al. 2000; Bennett et al. 2008; Nobriga et al. 2008). However, it evolved for approximately 10,000 years in the Bay-Delta despite warm summers and occasional very long droughts. We hypothesize that this was made possible by at least three conditions (based on Moyle 2002): 1) summer snowmelt in the San Joaquin basin that cooled the Delta; 2) vast tidal marshes in the Delta and Suisun Marsh that cooled low-salinity zone water; and 3) the vast tidal marshes exported high prey densities into the open-water habitats, which allowed delta smelt to acquire large rations, to help offset the stress of high summer water temperature. None of these conditions characterize the modern-day Delta.

We hypothesize that ancestral delta smelt population dynamics were driven by two primary factors: water temperature and predation ([Figure 8](#)). Advection may have been a secondary driver. However, we consider advection less important because very high flows did not occur every year and because only larvae were likely affected. Predation rates are affected by water temperature. However, we considered these mechanisms separately because predation rates tend to be higher on smaller fish than larger fish, independent of temperature. The most likely ancestral delta smelt predators would have been piscivorous birds, salmonid fishes, and, secondarily, longfin smelt as a larval predator and predatory freshwater fishes like Sacramento pikeminnow *Ptychocheilus grandis*, Sacramento perch *Archoplites interruptus*, and thicktail chub *Gila crassicauda* (Moyle 2002). The introduction of striped bass *Morone saxatilis* in the 1870s likely greatly increased predation pressure on delta smelt by placing a resident low-salinity zone predator where there was not one historically (Moyle 2002).

The ancestral conceptual model posits that conditions differed for early-spawned and late-spawned larvae. For instance, increasing water temperature should have benefitted early-spawned larvae by keeping predator metabolisms low, while increasing the water temperature toward a physiological optimum as the larvae developed ([Figure 8](#)). In contrast, for late-spawned larvae, water temperatures could quickly rise to problem levels and predator metabolisms would be higher. We hypothesize that this water temperature effect was stronger on larvae than juveniles because larval hatch success is very low at 20°C (Bennett 2005), but 20°C is about the optimum water temperature for delta smelt \geq 20 mm ([Figure 4](#)).

We further hypothesize that early-spawned larvae became large juveniles and, thus, large adults and that most late-spawned larvae became small juveniles and, thus, small adults ([Table 3](#); [Figure 8](#)). Large adults are more fecund (Bennett 2005). They also would have spawned earlier in the season and more than once when spring temperatures warmed slowly. In contrast, we hypothesize that small adults tended to spawn later in the season,

but have a higher probability of living a second year because they would not have time to reproduce more than once in their first spawning season. Thus, both early- and late-spawned delta smelt could sometimes produce both early- and late-spawned offspring. We posit that this allowed delta smelt to thrive in its variable ecotonal environment.

Larvae spawned during late winter and early spring grow the largest in their first year of life because they have the longest time to do so ([Table 3](#); Bill Bennett, UC Davis, unpublished data). However, spawning early may have translated into a higher risk of advection ([Table 3](#)). Late winter flows can sometimes be very high and high flows are thought to advect many delta smelt larvae too far seaward for them to survive (Moyle et al. 1992). Prior to major water diversions and contaminant loading, early spawning may have been a successful strategy during low flow years when advection would have been low. Historically, zooplankton densities were probably higher under low flow conditions because the longer hydraulic residence times would have allowed more time for zooplankton populations to build up.

Currently during dry winters, water exports take a substantial fraction of Delta inflow (Baxter et al. 2008; [Figure 7](#)). This increases the entrainment risk for adults and early-spawned larvae (Kimmerer 2008). The combination of low flows, high entrainment and pulses of pesticides (e.g., Bergamaschi et al. 2001; Kuivila and Moon 2004), nutrients (Wilkerson et al. 2006; Dugdale et al. 2007; Van Nieuwenhuyse 2007), and other contaminants may suppress zooplankton productivity. Note that the highest abundance and feeding success of delta smelt larvae observed by Nobriga (2002) occurred in 1994 – a cool, dry spring with low exports. If low flow years historically produced relatively high abundance of large, early spawned fish, dry year survival would have been high, but human-caused changes to the system have interfered with that aspect of delta smelt's life-history strategy. Note however, that based on averages of Delta hydrodynamic variables, late-spawned larvae face the highest risk of entrainment ([Table 3](#)).

Table 3. Summary of hypothesized environmental influences on delta smelt larvae spawned early, in the middle, and late in the spawning season as defined by hatch timing and ambient water temperature.

Hatch Timing	Ambient Water Temp	Hatch Success	Larval vulnerability to seaward advection	Larval vulnerability to entrainment	Larval Bioenergetic environment around first-feeding	Survival to juvenile stage	Length of growing season	Fecundity at yr 1	Survival to spawn at year 2
Early (mid-Feb to early April)	Low (10°-13°C)	Intermediate ~ 50%	Highest	Lowest Avg X ₂ = 63 km (March) to 66 km (April); Avg EI = 20% (April) to 23% (February)	High (high feeding incidence and low metabolic demand)	Naturally high in low advection years due to large hatch size and size at first-feeding; no long-term trend in entrainment loss	Longest	Highest	Lowest
Middle (mid-April to mid-May) ~ VAMP	Intermediate (14°-20°C)	High ~ 80%	Intermediate	Low Intermediate Avg X ₂ = 66 km (April) to 70 km (May); Avg EI = 20% (April) to 23% (May)	Intermediate (intermediate; feeding incidence and metabolic demand)	Intermediate with lower entrainment loss 1993-2007	Intermediate	Intermediate	Intermediate
Late (mid-May to June)	High (>20°C)	Low ~ 25%	Lowest	Highest Avg X ₂ = 70 km (May) to 74 km (June); Avg EI = 23% (May) to 26% (June)	Low (low feeding incidence and high metabolic demand)	Low due to small hatch size and poorer bioenergetic environment; no long-term trend in entrainment loss	Shortest	Lowest	Highest

C. Contemporary Population Dynamics

Delta smelt mortality is still influenced by natural population drivers like water temperature and predation as outlined in section 4.2 and [Figure 8](#). However, the delta smelt life cycle is now superimposed on a highly managed freshwater hydrology flowing over a greatly altered landscape. Recently, there have been trends toward lower export to inflow ratios (EI) in April and May. This is due to the Vernalis Adaptive Management Program, an experiment using a one month flow pulse in the San Joaquin River and concurrent export reductions to better understand San Joaquin River Chinook salmon smolt survival through the Delta. However, both EI and the average position of X_2 have increased during the summer and autumn as SWP water diversions increased (Feyrer et al. in review; IEP unpublished data). The summer-autumn period has been considered a less environmentally sensitive time for diverting water because entrainment of delta smelt and Chinook salmon is low ([Figure 9](#); historical management model). Collectively, the available data suggest factors occurring throughout delta smelt's short life cycle are contributing to low population resilience ([Figures 9-10](#)).

Here, we summarize key statistical clues about delta smelt population responses that have resulted from extensive data mining of the Department of Fish and Game's two longest running delta smelt relative abundance metrics, the Summer Towntnet Survey and Fall Midwater Trawl indices ([Figure 2](#)).

Kimmerer (2008) evaluated a food web related hypothesis on delta smelt population dynamics using a summer survival ratio. The ratio was the base ten logarithm of the FMWT index divided by the previous summer townet index. [Figure 12](#) shows the time series of this summer survival index as well as a similar index for the remaining longer fraction of the life cycle – the summer townet index divided by the FMWT index that preceded it. The latter is a metric of recruits per adult. These ratio indices show when population dynamics have been driven by summertime factors (higher than average loss of adults per juvenile) versus when they have been driven by factors occurring between fall and the subsequent summer (higher than average loss of juveniles per adult).

The among-year variability of the index ratios has tended to decline through time ([Figure 12](#)) because the variability in the indices has declined as population abundance has decreased. Thus, we offer an interpretation based on binomial probabilities. If the long-term decline in delta smelt were caused by an equivalent mixture of summer and fall to next summer mortality, then about 50% of the data points should be above the zero line and 50% below.

The summer survival index was often below the long-term average during the 1970s and early 1980s. This suggests that the number of adults produced per juvenile used to be comparatively low. However, summer survival has tended to be above the long-term average since 1984 ([Figure 12](#); > 0 in 18 of 23 years from 1984-2007). This suggests that delta smelt population dynamics since the mid-1980s have not usually been driven by summer mortality.

In contrast, the index of delta smelt recruits per adult has frequently been below the long-term average since 1980 (dubbed ReproductiveOutput in *Figure 12*). The frequency of negative ratio values for the entire time series is less than expected if the initial assumption is a 50:50 ratio distribution ($P = 0.044$). This is driven by the high proportion of negative ratio values beginning in 1980 (20 of 28 values were negative; $P = 0.012$). This suggests the sources of mortality that have most strongly driven the delta smelt decline usually act during fall, winter, or spring, and thus, act on adults or early life stages.

There is some evidence that the recruitment of delta smelt may have sometimes responded to springtime flow variation (Herbold et al. 1992; Kimmerer 2002). However, the weight of evidence suggests that delta smelt abundance does not (statistically) respond to springtime flow like the abundance of several other local estuarine fishes (Stevens and Miller 1983; Jassby et al. 1995; Bennett 2005; Kimmerer et al. 2009). The number of days of suitable spawning temperature during spring is correlated with subsequent abundance indices in the autumn (Bennett 2005). This is evidence that cool springs, which allow for repeat spawning and multiple larval cohorts, can contribute to population resilience. However, these relationships do not explain a large proportion of variance in autumn abundance. Depending on which abundance index is used, the r^2 are 0.24-0.29.

Bennett (2005) also conducted extensive stock-recruit analyses using the summer townet and fall midwater trawl indices. He provided statistical evidence that survival from summer to fall is nonlinear (or density-dependent). He also noted that carrying capacity had declined. Bennett (2005) surmised that density-dependence and lower carrying capacity during the summer and fall could happen in a small population if habitat space was smaller than it was historically. This was recently demonstrated (Feyrer et al. 2007; Nobriga et al. 2008). Reduced Delta outflow during autumn has led to higher salinity in Suisun Bay and the western Delta while the proliferation of submerged vegetation has increased the rate that Delta waterways are clearing due to loss of Sacramento River sediment supply (DRERIP Sediment model). Together, these mechanisms have led to a long-term seasonal decline in habitat suitability for delta smelt. High summer water temperatures also limit delta smelt distribution (Nobriga et al. 2008) and impair their health (Bennett et al. 2008).

Since 2000, the stock-recruit relationship for delta smelt has been very strongly linear ($r^2 = 0.88$; Baxter et al. 2008). This has led to speculation about Allee effects. Allee effects occur when reproductive output per fish declines at low population levels (Allee 1931, Berec et al. 2006). Below a certain threshold the individuals in a population can no longer reproduce rapidly enough to replace themselves and the population spirals to extinction. For delta smelt, possible mechanisms for Allee effects include mechanisms directly related to reproduction such as difficulty finding enough males to maximize egg fertilization during spawning (e.g., Purchase et al. 2007) or compensatory egg predation (e.g., DeBlois and Leggett 1991). Genetic problems arising from small population sizes like inbreeding and genetic drift also can contribute to Allee effects, but genetic bottlenecks do not occur until after demographic problems like those listed above (Lande

1988). Other mechanisms related to survival such as increased vulnerability of one or more life-stages to predation are also possible, based on studies of other species (Courchamp et al. 1999).

Another possible contributing driver of reduced delta smelt survival, health, fecundity, and resilience that may occur during winter and early spring is the “Big Mama Hypothesis” (posited by Bill Bennett, UC Davis, pers. comm. and various oral presentations). As a result of his synthesis of a variety of studies, Bennett proposed that the largest delta smelt (whether the fastest growing age-1 fish or fish that manage to spawn at age-2) could have a large influence on population trends. We have speculated how spawn timing affects the relative importance of stressors on delta smelt larvae ([Table 3](#); [Figure 8](#)). Prior to major water diversions from the system, early-spawned fish are hypothesized to have had high survival in low flow years and late-spawned fish were “insurance” for the population during flood years when advection of early-spawned larvae was high.

Delta smelt larvae spawned in the south Delta have high risk of entrainment under most hydrologic conditions (Kimmerer 2008). Water temperatures often warm earlier in the south Delta than the Sacramento River ([Figure 11](#)). Thus, delta smelt spawning often can start and end earlier in the south Delta than elsewhere. This differential warming may contribute to the “Big Mama Hypothesis” by causing the earliest ripening females to spawn disproportionately in the south Delta, putting themselves and their offspring at high risk of entrainment. Although water diversion strategies have been changed to better protect the ‘average’ larva, the resilience historically provided by variable spawn timing may be reduced by water diversions and other factors ([Tables 3-4](#)).

D. Concise version of the conceptual model

The current evidence suggests that delta smelt population dynamics are driven by factors affecting the health, survival and viability of all life-stages, but that factors affecting either adults and/or early life stages have operated most frequently and most strongly ([Figure 12](#)). However, current data also suggest there is a strong bottleneck in the juvenile stage (Bennett 2005; Feyrer et al. 2007; in review; Bennett et al. 2008). There is sporadically high adult and larval entrainment (Kimmerer 2008). There is a detectable influence of spring water temperature through effects on spawning season duration (Bennett 2005). There appears to be a strong influence of summer-fall habitat suitability due to an interaction of warm water temperature, reduced abiotic habitat suitability and suppression of the food web supporting delta smelt (Bennett 2005; Feyrer et al. 2007; Bennett et al. 2008; Feyrer et al. in review). Lastly, there may also now be depensatory Allee effects operating on delta smelt (Baxter et al. 2008).

Thus, in some years migrating adults are subjected to high entrainment that removes potential spawners from the population. This may exacerbate depensatory predation (or be a primary mechanism for it because adult salvage is unrelated to adult abundance; Grimaldo et al. 2009) if such Allee effects are indeed occurring. In other years, losses of adults to entrainment are minimal, but losses of adults and eggs to predators are currently unquantifiable. If outflows are not sufficient to position the low salinity zone in Suisun

Bay before larvae hatch, they too can be subjected to high entrainment losses. If water does not remain cool during spring, the spawning season is short and impacts due to high entrainment, toxicity, or Allee effects affect the population more intensely than if there were more spawning opportunities under a wider variety of environmental conditions. If summer water temperatures in the LSZ remain above about 20°-22°C for too long, there is a high likelihood that low food densities, water toxicity, disease and predation will cull a large proportion of the fish and reduce the fecundity of survivors. Chronically low late summer-fall outflows since the mid-1980s exacerbate problems associated with low prey density, water toxicity, and predation.

The spatial and temporal variability in many of these stressors, superimposed over long-term trends in others, creates myriad stressor combinations that have likely been the primary reason for a general lack of strongly statistically significant, multi-year predictors of population response (e.g., Jassby et al. 1995; Bennett 2005; Thompson et al. in press). The short life span and highly restricted spatial distribution of delta smelt also may render the species more sensitive than other estuarine fishes to intra-annual changes in its low-salinity habitat (Bennett et al. 2008; Feyrer et al. in review).

V. Stressors by Life History Stage

Stressor overviews: There is a long list of stressors that have been hypothesized to have negative effects on delta smelt abundance ([Table 4](#)). For the purposes of simplifying this conceptual model, the stressors have been divided into categories ([Figure 13](#)). Primary drivers, or factors that modulate, influence, or control delta smelt habitat suitability. Secondary drivers, which are at least partly influenced by a primary driver, also modulate, influence, or control delta smelt habitat suitability. Primary stressors, may affect delta smelt population dynamics, but only because of variation in one or more of the primary and secondary drivers. Secondary stressors, also may affect delta smelt population dynamics, but only because of variation in one or more of the primary and secondary drivers, or primary stressors. The primary drivers affect all life stages. The primary and secondary stressors are often life-stage specific.

A. Primary and Secondary Drivers

Human Land Use (Primary Driver): A fundamental source of change in delta smelt habitat is human land use (Nichols et al. 1986; Moyle 2002). This stressor has been operating significantly since at least the Gold Rush. Human land use has changed the Delta into the channelized habitat that it is today. In addition to structural change, human land use affects water quality profoundly and it influences demand for freshwater.

Climate (Primary Driver): Variation in precipitation patterns affects the amount and timing of freshwater flow entering the estuary and demand for freshwater from the estuary. As described in Sections II.A, II.C and Tables 1 and 2, water temperature, which is mainly a function of air temperature (Kimmerer 2004) strongly influences delta smelt reproduction and health during spring and summer.

Contaminant loading (Secondary Driver): Contaminant loading into the Bay-Delta is a secondary driver because it is affected by human land use in the estuary watershed and climate through effects on freshwater inputs to the estuary.

Freshwater input to the estuary (Secondary Driver): Freshwater flow into the estuary is a secondary driver because it is affected by climatic influence on the amount, form and timing of precipitation and human land use within and beyond the Sacramento-San Joaquin river basins.

B. Primary and Secondary Stressors

1. Delta hydrodynamics

Delta hydrodynamics and resulting entrainment in water diversions are primary stressors that affect delta smelt mortality. The potential for major delta smelt mortality due to entrainment in water diversions has been recognized for many years (Erkkila 1950; Stevens and Miller 1983; Moyle et al. 1992; Kimmerer 2008); the indirect effect of export diversions on habitat suitability has been demonstrated more recently (Feyrer et al. 2007).

1.a Water export diversions: The SWP and CVP diversions are usually considered the largest source of entrainment mortality and habitat impact because of their very large hydrodynamic ‘footprint’ that by design, can extend for miles away from the points of diversion (Kimmerer and Nobriga 2008). However, the population-level effects of entrainment have often been overshadowed by other stressors; so, entrainment is an episodic, rather than chronic, source of significant delta smelt mortality (Kimmerer 2008).

Delta smelt are vulnerable to entrainment in the SWP and CVP diversions during winter-spring spawning migrations and during their larval and early juvenile periods in the spring-early summer, but the relationship between river flows and entrainment in the SWP and CVP diversions varies by life stage (Kimmerer 2008). Winter entrainment of migrating adult delta smelt commonly occurs during early wet season rain events that generate abrupt increases in river flow and turbidity. Such increases in inflow also trigger increased export pumping, historically producing net flows in Old and Middle rivers that were strongly negative (i.e., flowing “upstream” toward the diversions; Grimaldo et al. in press). These events usually occur in January-February, but adult entrainment events also sometimes occur after very high flows have subsided in March or April. Adult entrainment is correlated with X_2 in the month preceding the entrainment (Grimaldo et al. in press), but not with X_2 during the entrainment event (Kimmerer 2008). This differs from entrainment of larvae and juveniles, which is correlated with concurrent Delta inflows and export flows, including composite flow variables like X_2 and net Old and Middle river flows (Kimmerer 2008; USFWS 2008). Recent analyses have shown that young-of-year delta smelt entrainment events also co-occur with high zooplankton densities in the vicinity of the SWP and CVP diversions and cool water temperatures in the Delta (Kimmerer 2008; Grimaldo et al. in press). Entrainment of larvae and juveniles occurs in most years from March-June, sometimes extending into the first week of July.

From mid-July until mid-December, delta smelt entrainment at the SWP and CVP diversions declines to essentially zero. By June or early July entrainment ceases because habitat conditions in the vicinity of the SWP and CVP water diversions become unsuitable (Feyrer et al. 2007; Nobriga et al. 2008) so delta smelt do not inhabit this region (Kimmerer 2008). By autumn, delta smelt are usually confined to a small area at the Sacramento-San Joaquin river confluence pinned between unsuitably high water transparency in the south Delta and unsuitably high salinity in Suisun Bay (Feyrer et al. 2007). The main driver of the increasing autumn salinity in Suisun Bay is the increasing trend in August-December export to inflow ratio (USFWS 2008).

1.b. Delta Cross Channel: The Delta Cross Channel is part of the CVP that is used to divert Sacramento River water more directly into the south Delta, which reduces salinity and improves drinking and irrigation water quality (Monsen et al. 2007). There has been concern that opening the DCC and allowing more Sacramento River water into the south Delta could increase the entrainment risk of delta smelt in the south Delta, but this hypothesis is not supported by particle tracking modeling (Kimmerer and Nobriga 2008). To protect salmonid smolts, the DCC is kept closed most of the time from December-June and is now mandated by NMFS (2009) to be closed for this entire period. This closure decreases net downstream river flow in the San Joaquin River in the reach from Jersey Point to Antioch (also known as QWEST), but it has not been demonstrated that the increment of difference due to closing the DCC strongly affects delta smelt entrainment risk.

1.c. South Delta Barriers: The Department of Water Resources installs temporary barriers at four sites in the south Delta to improve San Joaquin River salmon survival and to improve south Delta water levels and water quality. These barriers have been put in place as early as April. The barrier at the head of Old River is intended to protect out-migrating salmon, but it decreases the net downstream river flow in Old and Middle rivers, which increases entrainment risk in the south Delta. The operation of these barriers has sometimes increased delta smelt entrainment (Nobriga et al. 2000). In recent years, the barriers were not fully operational until temperatures in the Delta were believed unsuitable for delta smelt and delta smelt concerns now keep them partially installed until late spring or even summer (USFWS 2008).

1.d. Suisun Marsh Salinity Control Gates: The SMSCG is an operable barrier on Montezuma Slough, the main channel into Suisun Marsh. It has been operational since 1988. It is used to lower the salinity of water in Suisun Marsh to assist waterfowl hunting clubs. It has been used less frequently through time, but is still used during autumn. Opening the SMSCS diverts Sacramento River water into Suisun Marsh, which lowers freshwater flow into Suisun Bay. This can cause X_2 to increase by up to 3 km (Dave Fullerton, Metropolitan Water District, unpublished data), which can exacerbate delta smelt's autumn habitat constriction. However, the SMSCS is typically operated fewer than 30 days per year and is thus a minor contributor to autumn habitat quality. Because the SMSCG is also an artificial structure located in the core habitat area used by delta smelt, it also may sometimes be a hindrance to natural movement through the region.

I.e. Mirant Power Plants: Delta smelt are entrained with water taken to cool the Mirant power plants. Some previous unpublished evaluations in the 1970s have suggested that delta smelt losses to the Mirant power plants were very high. The plants are located in the core area occupied by most delta smelt life stages. Currently the plants are operated infrequently, only to meet sporadic peak power needs, usually during summer (Carol Raifsnider, Tenera Associates, pers. comm.) when juvenile fish are rearing in the area. Thus, they take in little cooling water compared to their operations in the 1970s, so their entrainment of delta smelt is probably similarly reduced. Studies are underway to assess their current impacts.

I.f. Waterfowl management and private irrigation water diversions: Delta smelt are entrained into the diversions used for waterfowl management in Suisun Marsh (Pickard et al. 1982) and the private irrigation diversions scattered throughout the Delta (Hallock and Van Woert 1959; Nobriga et al. 2004). Collectively, these are reported to comprise > 2,500 mostly unscreened water diversions (Herren and Kawasaki 2001). The waterfowl diversions usually have a peak “flood-up” period in the fall. The Delta irrigation diversions take most of their water from April-October with a peak during the summer months.

Delta smelt entrainment into Suisun Marsh’s Roaring River Distribution System (RRDS) was high before the intakes were screened (Pickard et al. 1982). In contrast, a recent study of the Suisun Marsh’s Morrow Island Distribution System (MIDS), which is unscreened, entrained almost no delta smelt at all (one larva and no older delta smelt were collected during a two-year study; Enos et al. 2007). The RRDS is located on the eastern side of Suisun Marsh where salinities are typically appropriate for delta smelt rearing, whereas the MIDS intake is located where the salinity is often higher than delta smelt tend to occupy.

There are reportedly more than 2,200 mostly unscreened irrigation diversions in the Delta (Herren and Kawasaki 2001). However, the number may be notably smaller because Herren and Kawasaki were unable to differentiate intake pipes used to divert water, from outfall pipes used to drain water off of Delta islands. These diversions have been a fishery management concern for a long time (Hallock and Van Woert 1959; Moyle and Israel 2005). However, we do not consider the Delta’s small diversions a major stressor for delta smelt for four basic reasons. First, a recent study of one of them located in an area where delta smelt were aggregated found low loss rates (Nobriga et al. 2004). The loss of delta smelt into the Horseshoe Bend diversion was 1.5-3.4 fish per 10,000 m³ of water diverted while the densities estimated from trawling in nearby channels were 50-150 fish per 10,000 m³. The low loss rates were attributed to two factors: 1) the diversion took a small quantity of water relative to the volume of the channel it was in, so it had a very small hydrodynamic ‘footprint,’ and 2) delta smelt tend to occupy the offshore environment whereas the diversion was situated against a shoreline. These two factors apply to most Delta irrigation diversions. Second, many of the irrigation diversions in the Delta do not divert water every day. For instance, Nobriga et al. (2004) had to wait until peak irrigation water demand in July just to sample the diversion for two consecutive days. Third, many of the irrigation diversions are located in the south Delta where 1)

entrainment risk of young delta smelt is confounded by a high likelihood of SWP/CVP entrainment during spring and early summer, and 2) habitat conditions become unsuitable for delta smelt during summer-autumn (Feyrer et al. 2007; Nobriga et al. 2008), so delta smelt are not exposed to them. Fourth, agricultural water demand within the Delta has not changed appreciably since the 1930s (State Water Contractors presentation to the SWRCB, January 2008). This is in stark contrast to SWP/CVP water demand, which has steadily increased since the late 1960s. Lastly, the fish most vulnerable to the Delta's irrigation diversions are littoral species that spawn during summer because irrigation demand peaks during summer and small fish are more vulnerable than large fish (Nobriga et al. 2004). The Delta's fish fauna is currently dominated by species that should be at maximum risk of these effects, such as centrarchids and inland silverside, which are both doing comparatively well (Nobriga et al. 2005; Brown and May 2006; Brown and Michniuk 2007). Thus, it seems unlikely that the irrigation diversions collectively drive fish population dynamics in the Delta or have a significant cumulative effect on delta smelt.

2. *Food web*

The food web supporting delta smelt production is a primary component of habitat suitability (but still termed a 'stressor' for consistency) that affects delta smelt growth rates, health, fecundity, and mortality. The food web supporting delta smelt is based on the production of pelagic zooplankton. The production of pelagic zooplankton is affected by water diversions and water toxicity as described in other sections. This section focuses on the overbite clam, which has had a substantial and persistent influence on Bay-Delta zooplankton production since it was introduced in 1986.

The introduction of the overbite clam substantially reduced the estuary's pelagic productivity at all trophic levels from phytoplankton (Jassby et al. 2002) to fish (Kimmerer 2002; 2006). Note however, that not all fish species were affected and there is no evidence that delta smelt abundance was affected (Kimmerer 2002; Kimmerer et al. 2009). The overbite clam tolerates a wide range of salinity and has a high metabolism, so it has been able to graze much of the phytoplankton standing crop during late spring-autumn each year since its introduction (Jassby et al. 2002). Its grazing also exerts a strong predatory influence on copepod nauplii (Kimmerer et al. 1994). The feeding incidence of delta smelt larvae is correlated with calanoid copepod density (Nobriga 2002). Thus, the overbite clam directly competes with delta smelt for calanoid copepods and it grazes phytoplankton that helps support the production of copepods and other historically important delta smelt prey (e.g., mysid shrimp; See Section 2.3).

Despite its strong effect on the estuary's pelagic food web, evidence for direct linkages between the overbite clam and delta smelt is controvertible. The fork length of maturing delta smelt collected during autumn declined abruptly in 1990 and has stayed low since (Sweetnam 1999; Bennett 2005). However, it is uncertain that this was a direct result of overbite clam grazing because the overbite clam's impacts on the estuarine food web were visible by 1987 or 1988 (Kimmerer 2002), two to three years and as many delta smelt generations prior to the step-decline in fork lengths. Bill Bennett (UC Davis, unpublished data) has recently hypothesized that changed export schedules since about

1990 have unintentionally removed high proportions of early spawning fish and/or their larvae, effectively reducing the average length of the delta smelt growing season.

The impacts of overbite clams on the food web supporting delta smelt likely interact with other stressors to affect delta smelt viability. For instance, autumn habitat suitability has only been correlated with delta smelt population dynamics since the overbite clam invasion (Feyrer et al. 2007) and there are also correlations between indices of delta smelt food supply and their resultant survival as detailed in Section 5.3.18. Further, any significant effect of overbite clam grazing on summer calanoid copepod production can only exacerbate the bioenergetic stress on delta smelt caused by warm summer water temperatures (Bennett et al. 2008).

3. *Water toxicity*

Water toxicity is a primary stressor that affects growth rate, health, fecundity, and mortality. Water toxicity can act either directly through physiological impairment of the fish themselves or indirectly by suppressing the supporting food web.

3.a. Pesticides: Pesticide loading is a secondary driver because it is affected by human land use and X_2 (freshwater flow). Many pesticides enter the Delta from farms, orchards, and urban runoff during winter-spring storms (Bergamaschi et al. 2001). This can lead to high overlap of pesticide loading with delta smelt spawning and larval development (Kuivila and Moon 2004). The association of many pesticides with sediment is noteworthy given delta smelt's affinity for turbid water. Pesticides also enter the Delta in agricultural return water in the summer and autumn (see the DRERIP Contaminants Model). This timing overlaps the chronic low autumn outflows that have affected delta smelt habitat suitability (Feyrer et al. 2007).

There is high concern about the effects of pyrethroid pesticides on aquatic life in the Delta. Pyrethroid pesticides are highly toxic to zooplankton and fish at very low environmental concentrations and the recent trend has been for users to shift to more toxic varieties (Oros et al. 2005; DRERIP [Pyrethroids Model](#)). Pyrethroid pesticides are a likely source of zooplankton mortality (Werner et al. 2008), and a factor influencing fish health and survival (Floyd et al. 2008). Their use in the Delta watershed increased substantially during the 1990s and early 2000s because they are less toxic to mammals than the previous generation of organophosphate pesticides. Like other pesticides (Bergamaschi et al. 2001; Kuivila and Moon 2004), pyrethroids are associated with sediment and mainly transported into the system during runoff events, so there is high probability of exposure to spawning delta smelt and the early life stages of their progeny, as well as to their co-occurring prey.

During 2006 and 2007, the toxicity of Delta water was evaluated with 10-day bioassays involving the standard toxicity test amphipod *Hyallela azteca* (Werner et al. 2008). Water samples were taken twice per month at 10 sites from the Napa River, Suisun Bay, and the Delta. Toxicity was rarely observed. Of 693 samples tested, only 2.2% caused significant mortality to the test amphipod. However, all but one of these toxic samples occurred in the July-December 2007 collections. Note that spring 2006 had a very high

outflow, whereas 2007 did not. The causal agents of these toxic “hits” were not determined, but both organophosphate and pyrethroid pesticides were suspected. Thus, the limited data currently available suggest that pesticides have sporadic impacts on the food web supporting delta smelt during summer and that low river flows may exacerbate toxicity.

3.b. Copper: Copper enters the aquatic environment from urban stormwater runoff (winter-spring), agricultural applications, herbicide treatments of SAV (mainly summer), and as a heritage contaminant from mining activities, so copper toxicity is a secondary driver influenced by human land use and X_2 (freshwater flow). Delta smelt can reasonably be expected to be exposed to a variety of copper concentrations. Copper has been found at dissolved concentrations of $6\mu\text{g Cu}^+ \cdot \text{L}^{-1}$ in Delta waterways (USGS 1998), but near effluents from agricultural discharges concentrations in excess of $500\mu\text{g Cu}^+ \cdot \text{L}^{-1}$ have been reported (DFG 1998). Delta smelt are rather sensitive to copper with an LC_{10} of 45 (19-55) $\mu\text{g Cu}^+ \cdot \text{L}^{-1}$ and an LC_{50} of 85 (76-95) $\mu\text{g Cu}^+ \cdot \text{L}^{-1}$ (Werner et al. 2008).

Copper affects delta smelt by disrupting neuromuscular activity, respiration, immune response and metabolism. However, in identifying the sources of toxicity in samples of Delta water, copper and other metals were not believed to be as important as organic chemicals (Werner et al. 2008). Very short-term exposures to copper intended to simulate stormwater runoff events have been shown to affect the ability of coho salmon to detect dissolved chemicals (Baldwin et al. 2003). Thus, it is possible that similar short-term exposures to copper might affect delta smelt’s ability to migrate and aggregate effectively, but this is speculation.

3.c. Methyl Mercury and Selenium: Methyl mercury and selenium toxicity are secondary drivers because they respond to human land use and X_2 (freshwater flow). Methyl mercury concentrations in the Delta, as indexed by inland silverside body burden, increase when freshwater flow increases – particularly where sediments have an opportunity to dry between flood events (e.g., floodplains and high tidal marsh; DRERIP Mercury Model). However, delta smelt do not use floodplain or high marsh habitats, so they rarely occur in “hot spots” for MeHg accumulation like Yolo Bypass, the Cosumnes River floodplain, and the San Joaquin River upstream of tidal influence. Further, they are not apex predators, which have the highest MeHg bioaccumulation (Davis et al. 2008). Finally, their short life spans do not allow much time for MeHg bio-accumulation. Thus, we do not consider methyl mercury a significant stressor of delta smelt viability.

There are two primary sources of selenium including effluents from Bay Area oil refineries and agricultural drainage from the San Joaquin Valley. The major toxic effect of selenium is abnormal early development (Beckon and Maurer 2008). Selenium may occur in concentrations high enough to impair reproduction in some San Francisco Estuary organisms; predators of overbite clams are at the highest risk of significant selenium bioaccumulation (Stewart et al. 2004). Delta smelt do not eat overbite clams and have comparatively low selenium body burdens (Beckon and Maurer 2008). As noted above for mercury, the short life of delta smelt is unlikely to provide them with

adequate time to accumulate high loads of selenium. However, delta smelt are evolutionarily allied with salmonid fishes and salmonid fishes are more sensitive than most to selenium toxicity (Beckon and Maurer 2008). Thus, it is possible that delta smelt have some reproductive impairment attributable to selenium exposure. Note it is unlikely that exposure of delta smelt to selenium has increased recently, so selenium-related reproductive impairment should be viewed as a possible, but unproven long-term chronic stressor.

3.d. Toxicity originating from urban wastewater treatment (Secondary Driver): Toxicity originating from urban wastewater treatment is a secondary driver because inputs are influenced by human land use and X_2 (precipitation and freshwater flow) that both causes and dilutes wastewater inputs. This section briefly discusses nutrients and endocrine-disrupting chemicals. See the Contaminants model for additional details. Ammonia is a component of treated sewage that can be highly toxic to fish (Passell et al. 2007). Preliminary toxicity work has indicated that delta smelt may be exceptionally sensitive to ammonia toxicity (Werner et al. 2008). Further, ammonium ion may inhibit phytoplankton blooms (Wilkerson et al. 2006; Dugdale et al. 2007). Ammonium ion also may provide a competitive edge to toxic *Microcystis aeruginosa* over diatoms that are more edible to zooplankton (Takamura et al. 1987), possibly leading to lower zooplankton productivity (Ger et al. 2009).

The Sacramento Regional Wastewater Treatment Plant (SRWWTP) is currently the largest discharger of ammonia into the Delta (Jassby 2008). The Stockton treatment plant has sometimes been another significant source. The Stockton plant began incorporating advanced secondary treatment in 2007, so its ammonia loading is expected to decrease. The ammonia loading from the SRWWTP has increased steadily since 1985 and accounts for about 90% of the ammonia entering the Delta at Freeport. It has also been shown recently that reduced phosphorus loading in the Sacramento River was associated with an abrupt decline in phytoplankton in the Delta (Van Nieuwenhuysse 2007). Thus, recent trends in nutrient inputs may have had a strong negative effect on the base of the food web that supports delta smelt.

Endocrine-disrupting chemicals (EDC) present in treated wastewater can interfere with fish maturation and reproduction (Jobling et al. 1998). A recent study in a Canadian lake showed that very low concentrations of EDCs caused rapid population failure of fathead minnow *Pimephales promelas* (Kidd et al. 2007). One of the biomarkers of EDCs is intersex fish – fish with both male and female reproductive organs. A recent histopathologic evaluation of delta smelt for the pelagic organism decline study found 9 of 144 maturing delta smelt (6%) collected in the fall were intersex males (Baxter et al. 2008). This is evidence that delta smelt are being exposed to EDCs. However, there are no long-term data to compare this data point to, so its significance is unknown. Note that large stochastic changes in population sex ratios are a known mechanism for Allee effects in insects that has been exploited for biocontrol (Courchamp et al. 1999). Thus, it seems possible that EDCs could cause similar compensatory effects by changing sex ratios in fish populations.

4. *Water turbidity*

Water turbidity is a primary stressor that is also a component of delta smelt habitat. Delta smelt distribution is strongly associated with turbid water (Nobriga et al. 2005; Feyrer et al. 2007; Nobriga et al. 2008). Larval feeding success is also enhanced by turbidity (Baskerville-Bridges et al. 2004). The turbidity of San Francisco Estuary water is affected by land use and river flows; turbidity increases when inflows are high (Kimmerer 2004). Turbidity is also affected by tidal currents, wind events and bathymetry (Ruhl et al. 2001). Turbidity in the Delta has decreased through time (Jassby et al. 2002). The primary hypotheses to explain the turbidity decrease are (1) reduced sediment supply due to dams and levee construction in the watershed (Wright and Schoellhamer 2004), (2) sediment washout from very high inflows during the 1982-1983 El Nino (Jassby et al. 2005), and (3) biological filtering by submerged aquatic vegetation (Brown and Michniuk 2007).

5. *Low Dissolved Oxygen (Secondary stressor)*

Low dissolved oxygen is a symptom of habitat degradation that arises from high nutrient loading into low flow habitats (Jassby and Van Nieuwenhuysen 2006). Low dissolved oxygen concentrations occur during late spring through autumn in the San Joaquin River near Stockton (Jassby and Van Nieuwenhuysen 2006) and in Suisun Marsh during autumn. Neither of these locations is used extensively, if at all, by delta smelt during these times of year so low dissolved oxygen is currently considered a minor problem for pelagic estuarine fishes (Kimmerer 2004).

6. *Proliferation of Submerged Aquatic Vegetation (Secondary stressor)*

The proliferation of submerged vegetation is a symptom of nutrient input changes (e.g., increased ammonia), habitat simplification, and possibly the reduced Sacramento River sediment supply described above. The extensive proliferation of SAV has occurred mainly since the 1980s and has profoundly changed the fish assemblages inhabiting nearshore habitats in the Delta (Nobriga et al. 2005; Brown and Michniuk 2007). The proliferation of SAV has also decreased turbidity, particularly in the south Delta (Feyrer et al. 2007; Nobriga et al. 2008). This has substantially decreased seasonal habitat suitability for delta smelt (see Section 2.3).

7. *Microcystis Blooms (Secondary stressor)*

There are now annual summertime blooms of *Microcystis aeruginosa*, a nuisance cyanobacterium that produces toxic metabolites (Lehman et al. 2005; in revision). *Microcystis* blooms are a symptom of low river flow and water quality changes (Lehman et al. 2008). *Microcystis* has bloomed each summer in the Delta since about 1999. The intensity of the bloom, and thus its potential toxicity, may be increasing (Peggy Lehman, presentation at the 2008 CALFED Science Conference). *Microcystis* growth is inhibited at ~ 7 psu salinity (Robson and Hamilton 2003). Thus, *Microcystis* can extend nearly as far seaward as delta smelt, so salinity does not strongly limit the overlap of *Microcystis* and delta smelt. Lysing (dying) *Microcystis* cells may create a zone of comparatively high toxicity in the low-salinity zone as they reach intolerable salinities (Peggy Lehman, presentation at the 2008 CALFED Science Conference). This lysing zone likely overlaps with the distributions of delta smelt and their prey. *Microcystis* is highly toxic to

Pseudodiaptomus forbesi, the primary prey copepod of delta smelt during summer (Ger et al. 2009). Therefore, *Microcystis* blooms plausibly exacerbate the bioenergetic problems that delta smelt have during summer and early fall (see Section 2.3).

8. *Altered Co-occurrence with Prey (Secondary stressor)*

Fish need food to survive and grow. There are strong correlations between the apparent spatial-temporal “co-occurrence” of early life stage delta smelt with their prey and abundance of maturing adults in the subsequent autumn ($r^2 > 0.90$ for larvae and > 0.70 for juveniles; BJ Miller and Tom Mongan, San Luis and Delta Mendota Water Authority, unpublished data). Similarly, Kimmerer (2008) recently published a statistically significant correlation between summer biomass of calanoid copepods in the low-salinity zone and an index of delta smelt survival from summer-autumn. This version of the analysis explains about one-third of the variability in summer-autumn survival. The difference in variance explained between these analyses may be due to the inclusion of the spatial terms in the unpublished analyses.

Note that co-occurrence with prey is a secondary stressor stemming from species invasions and environmental manipulation that is affected by several drivers and primary stressors. These include the spatial distribution of suitable delta smelt habitat (a function of X_2 , water quality, and submerged vegetation), water temperature, overbite clam grazing, entrainment of the food web components that support delta smelt (e.g., Jassby et al. 2002; DRERIP Food Webs model), and pesticide loading (DRERIP Contaminants Model), and possibly *Microcystis* blooms that poison copepods. The relative importance of these factors to delta smelt food availability is unknown.

9. *Depensatory Predation (Secondary stressor)*

Predation is a key component of mortality in our hypothesis about delta smelt population dynamics in the ancestral Delta and delta smelt are adapted to absorb high predation losses (Section 4.2). In undisturbed systems, predators do not typically drive prey to extinction. Thus, predation in the context of this conceptual model is predation that is no longer modulated by the factors that historically constrained it. Here we discuss depensatory predation, a secondary stressor that can stem from an altered environment. Specifically, depensatory predation means that the rate of predation increases as prey numbers decrease. This has been hypothesized to be a mechanism underlying exploited fish population crashes because heavy fishing reduces the size of fish schools to a point that the school no longer serves its protective function against natural predators (Roughgarden and Smith 1996). Similarly, depensatory predation stemming from small population size has been reported for terrestrial mammals (Sinclair et al. 1998).

The predation dynamics involving delta smelt are very poorly understood. The major predator of juvenile and adult delta smelt is probably striped bass because of its high spatial overlap with delta smelt and because it was the most frequent consumer of delta smelt several decades ago (Stevens 1963; 1966). Delta smelt were the most common prey of striped bass during spring of 1963 in the reach of the Sacramento River between Freeport and Rio Vista (~ 80% of stomach content volume in March and April; Stevens

1963). As stated above, Stevens (1963) hypothesized that delta smelt were so commonly eaten because they had abundant spawning aggregations in this reach of the river.

In a companion study of the Delta conducted during 1963-1964, delta smelt were a far less common prey overall and essentially absent from the stomachs of adult striped bass (Stevens 1966). However, delta smelt represented up to 4% of the age 1-2 striped bass diet during spring and up to 8% during summer. This is consistent with a recent study of striped bass diet composition that showed the similarly sized inland silverside was eaten by subadult rather than adult striped bass (Nobriga and Feyrer 2008). There are numerous other fishes that might eat delta smelt occasionally, but the relative importance and cumulative effects of different predators are unknown. A recent predator diet study did not find any delta smelt in piscivore stomachs, probably because they are so rare relative to many other Delta fishes (Nobriga and Feyrer 2007). Without accurate data on the current frequency of delta smelt losses to predators, modeled cumulative predation impacts ranging from insignificant to highly depensatory are equally plausible.

Mississippi silversides¹ are a small, annual fish native to eastern North America (Moyle 2002). They invaded the Delta in the 1970s and have flourished; they are the most numerous fish occurring in shoreline habitats of Suisun Marsh (Matern et al. 2002) and the Delta (Nobriga et al. 2005). They are highly tolerant of warm water, salinity variability and they are trophic generalists compared to delta smelt (Moyle 2002). Thus, they are among the more common fishes even in tidal marshes of the Napa River and San Pablo Bay (Visintainer et al. 2006; Cohen and Bollens 2008) seaward of habitats typically inhabited by delta smelt. One short-term study showed that when delta smelt and Mississippi silverside were held in captivity together, delta smelt growth was impaired relative to controls, but silverside growth was not (Bennett 2005). Mississippi silversides also were efficient predators of striped bass larvae in Delta waters that were experimentally enclosed with nets (Bennett and Moyle 1996).

It is unclear whether these laboratory and enclosure studies scale up to interactions that are relevant to delta smelt in the wild. As described above, delta smelt typically occupy offshore environments, whereas Mississippi silversides typically occupy shallow, nearshore environments. This may limit opportunities for interaction. Further, it has not been demonstrated that Mississippi silversides have the ability to reduce calanoid copepod densities more than the numerous other factors that affect delta smelt food availability (e.g., overbite clams, SWP and CVP diversions, nutrient and pesticide loading, etc.). If delta smelt spawn in shallow, nearshore sandy environments and Mississippi silverside are effective at finding delta smelt eggs, it is possible that egg predation by Mississippi silverside might be a mechanism for Allee effects, but like other predator-prey dynamics involving delta smelt, this is speculation.

10. Disease (Secondary stressor)

The dynamics of disease transmission are fairly well known for animals in general, but have not been studied as well in fish (Reno 1998). Disease effects on delta smelt population dynamics have not been studied. Fish disease incidence typically is driven by

¹ Formerly thought to be inland silverside

crowding, water pollution, and species invasions that introduce new pathogens to a system (Reno 1998; Prenter et al. 2004). There are no published studies of delta smelt disease, but juvenile delta smelt collected from Suisun Bay in summer 2005 have been preliminarily reported to show substantial incidence of viral infection, whereas adults collected later the same year did not (Baxter et al. 2008). Bennett et al. (2008) reported strong size-selective mortality of juvenile delta smelt during summer-early autumn 2005 that was associated with a thermally stressful environment and rapidly receding low-salinity zone. Thus, it is possible the viral infection reported in the summer of 2005 was a stressor and symptom of poor environmental quality.

Table 4. Life history versus stressor matrix for delta smelt: the listed stressors are components of degraded habitat. All of these mechanisms are influenced by one or more drivers ([Figure 11](#)) and sometimes by each other. See the sections of Chapter 5 referenced in the table for details. U = understanding, I = importance, P = predictability. The numbers under the UIP columns are standard DRERIP categories. Ranges denote plausible values and re-emphasize uncertainty regarding the importance of certain stressors.

Stressor	Ch. 5 reference	Adults			Eggs/embryos			Larvae			Juveniles		
		U	I	P	U	I	P	U	I	P	U	I	P
Water exports	5.2.1a	4	4	3	4	1	4	4	4	4	4	3-4	4
Delta Cross Channel	5.2.1b	1	1-3	4	4	1	4	3-4	1-2	4	3-4	1-2	4
South Delta Temporary Barriers	5.2.1c	4	1	4	4	1	4	3	3-4	4	3	3-4	4
SMSCG	5.2.1d	1	1-2	4	4	1	4	3	1	4	3	1-2	4
Mirant power plants	5.2.1e	3	1-2	1	3	1-2	1	3	1-2	1	3	1-4	1
Waterfowl/ag diversions	5.2.1f	4	1-2	4	4	1	4	3-4	1-2	2	3-4	1-2	2
Overbite clam	5.2.2	4	1	4	4	1	4	4	3	4	4	3	4
Pesticide toxicity	5.2.3a	2-3	1-3	1	3-4	1-4	1	2-3	1-3	1	2-3	1-3	1
Copper toxicity	5.2.3b	3	1-3	1	2-3	1-3	1	2-3	1-3	1	3	1-2	1
MeHg and Se toxicity	5.2.3c	3	1-2	3	1-2	1-2	2-3	3	1	3	3	1	3
Wastewater toxicity	5.2.3d	2-4	2-3	3-4	1	1-2	1	2	1-4	1	2-4	1-4	1
Increasing	5.2.4	4	4	4	1	1-3	4	4	1-4	4	4	4	4

water transparency													
Low dissolved oxygen	5.2.5	4	1	4	4	1	4	4	1	4	4	1-2	4
Submerged aquatic vegetation	5.2.6	2	2-4	4	1	1-4	4	4	1	4	2-4	2-3	4
Microcystis toxicity	5.2.7	4	1	4	4	1	4	4	1	4	1-3	1-4	4
Altered co-occurrence with prey	5.2.8	3	1	2	4	1	4	3	3-4	2	3	3-4	2
Depensatory predation or other Allee effects	5.2.9	1	1-4	1	1	1-4	1	1	1-4	1	1	1-4	1
Disease	5.2.10	1	1-3	1	1	1-3	1	1	1-3	1	1	1-3	1

VI. Future research

There has been a rapid increase in the scientific understanding of delta smelt biology in the last 10-15 years and additional work is furthering the scientific knowledge needed to assist with its conservation.

Key questions (based on [Figures 8-10](#) and [Table 4](#))

1. In the contemporary Bay-Delta, are summer bioenergetic conditions ever not stressful to delta smelt?

There is a pressing need to develop an accurate set of bioenergetics models for larvae, juveniles and maturing adults to support the life cycle models currently being developed under a CALFED Science Program research grant. This DRERIP conceptual model emphasizes the effects of exposure to warm water on reproductive output, health, fecundity, and survival. Only with models based on sound empirical data can the relative importance of “natural” environmental stressors be objectively compared to the key management issue, entrainment loss.

There is also a need to continue to monitor delta smelt health directly. The tools to do this include evaluations of growth rates, histopathology, and diet composition. There are also a variety of laboratory studies that could be used to test mechanistic hypotheses generated from field data. For instance, how do water temperature and prey density interact to affect growth and mortality? How does exposure to pesticides affect the result?

2. Does spatial variation in how the Delta warms during spring lead to high entrainment loss of early-spawned larvae?

At this writing, there is an apparent paradox among scientific findings for delta smelt regarding the effects of SWP/CVP entrainment. Kimmerer (2008) estimated entrainment and found it to be an episodic source of high mortality but statistically, largely washed out by apparent summertime mortality. However, Bennett (unpublished data) has found that since 1999, high proportions of delta smelt collected in the fall after all of the entrainment and summer mortality have occurred were born during the VAMP pulse flow. The VAMP pulse flow experiment occurs in April-May and represents the only time of year that San Joaquin River flows are consistently seaward. Monitoring conducted by the Department of Fish and Game consistently shows most spawning occurs in the north Delta (e.g. [Figure 6](#)) where risk of entrainment is very low (Kimmerer and Nobriga 2008). Does this VAMP-associated pattern arise because spawning happens first on the San Joaquin River due to warmer water temperatures ([Figure 10](#)) and/or because survival of larvae is much higher for fish spawned on the San Joaquin River when they can escape entrainment? Does this mean “bulk” assessments of entrainment miss important spatial differences in larval survival rates or is there just high temporal overlap between optimal hatching temperatures and the VAMP pulse flows?

3. Are delta smelt presently suffering from depensatory Allee effects? Can artificial propagation be used effectively to supplement numbers of wild fish? How many propagated fish would be necessary for successful supplementation?

The very low numbers of delta smelt that might lead to Allee effects also make the direct field study of any such effects very difficult. This is particularly true since the most likely Allee effects are demographic rather than the more readily assessable genetic drift problems that can occur in very small populations. It would be useful to repeat a study like that of Alo and Turner (2005) to monitor trends in effective population size. It is our opinion that depensatory predation on adults and/or eggs is one of the more plausible demographic Allee effects that might be occurring (see DeBlois and Leggett 1991 for an example from a marine member of delta smelt's family). It might be possible to examine stomach contents of Mississippi silverside and other plausible egg predators in the Sacramento Deep Water Ship Channel, a region of apparently high delta smelt reproduction, to try to quantify losses to egg predators. These data could be used to inform artificial propagation programs if decisions are made to supplement the wild population.

4. Do contaminants play significant roles in delta smelt population dynamics? Are contaminant effects separable from freshwater flow variation?

There is a long list of contaminants that might affect delta smelt; the few discussed in this model are only some of those known or suspected of being problems for aquatic life in the Bay-Delta system. We do not think maternally transferred contaminants currently pose major problems for delta smelt because the UC Davis Fish Culture program has successfully raised the progeny of wild fish with high success for about 10 years. Rather, we suggest that adult maturation and egg-larval grow-out experiments using water from different parts of the estuary might provide insights into whether there are local hot spots for acute toxicity or sublethal toxicity that subsequently affects egg viability and larval survival rates. We also suggest that careful comparisons between delta smelt and Mississippi silverside might be informative. As stated above, Mississippi silverside is an ecologically similar fish that is currently very successful in the Bay-Delta despite the plethora of toxic inputs. We offer a simple question that may pose a difficult scientific challenge – how do Mississippi silverside maintain large populations while exposed to most of the same contaminant mixtures as delta smelt?

Part of the answer may have to do with the different temperature tolerances of these fishes. If summer water temperatures are chronically stressful to delta smelt, an important aspect of habitat restoration will be determining how best to reduce that stress. There are three key aspects to mitigating thermal stress. First, research should focus on ways of reducing low-salinity zone water temperatures (if possible). The restoration of tidal marsh habitat might offer some cooling (Chris Enright, Department of Water Resources, pers. comm.), but it is highly uncertain whether enough land area can be restored to reduce offshore water temperatures. Secondly, there is a need to determine whether the food web supporting delta smelt can be enhanced. Overbite clam grazing, water diversions and contaminants will likely continue to constrain copepod standing

stocks. The establishment of zebra and/or quagga mussels will worsen the current situation. However, it might be possible to increase calanoid copepod and mysid shrimp production through improved water quality management. Research should continue into the roles that nutrients, pesticides, and water diversions play in constraining primary and secondary production both in the current ecosystem and in likely future ecosystem configurations (Lund et al. 2007; 2008).

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VII. Literature Cited

- Allee, WC. 1931. *Animal aggregations. A study in general sociology.* University of Chicago Press, Chicago.
- Alo, D, Turner, TF. 2005. Effects of habitat fragmentation on effective population size in the endangered Rio Grande silvery minnow. *Conservation Biology* 19:1138-1148.
- Baldwin, DH, Sandahl, JF, Labenia, JS, Scholz, NL. 2003. Sublethal effects of copper on coho salmon: impacts on non-overlapping receptor pathways in the peripheral olfactory nervous system. *Environmental Toxicology and Chemistry* 22:2266-2274.
- Baskerville-Bridges, B, Lindberg, JC, Doroshov, SI. 2004. The effect of light intensity, alga concentration, and prey density on the feeding behavior of delta smelt larvae. *American Fisheries Society Symposium* 39:219-228.
- Baxter, R, Breuer, R, Brown, L, Chotkowski, M, Feyrer, F, Gingras, M, Herbold, B, Mueller-Solger, A, Nobriga, M, Sommer, T, Souza, K. 2008. Pelagic organism decline progress report: 2007 synthesis of results. (available at http://www.science.calwater.ca.gov/pdf/workshops/POD/IEP_POD_2007_synthesis_report_031408.pdf)
- Beckon, WN, Maurer, TC. 2008. Species at risk from Selenium exposure in the San Francisco Estuary: Final Report to the U. S. Environmental Protection Agency. Interagency Agreement Number DW14922048-01-0. 84pp.
- Bennett, WA. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. *San Francisco Estuary and Watershed Science* 3:<http://repositories.cdlib.org/jmie/sfews/vol3/iss2/art1>.
- Bennett, WA, Hobbs, JA, Teh, S. 2008. Interplay of environmental forcing and growth-selective mortality in the poor year-class success of delta smelt in 2005. Final Report to the Interagency Ecological Program.
- Bennett, WA, Kimmerer, WJ, Burau, JR. 2002. Plasticity in vertical migration by native and exotic fishes in a dynamic low-salinity zone. *Limnology and Oceanography* 47:1496-1507.
- Bennett, WA, Moyle, PB. 1996. Where have all the fishes gone? Interactive factors producing fish declines. Pages 519-541 in Hollibaugh, JT, editor. *San Francisco Bay: the ecosystem.* Pacific Division of the American Association for the Advancement of Science. San Francisco, CA.
- Berec, L., E. Angulo and F. Courchamp. 2006. Multiple Allee effects and population management. *TRENDS in Ecology and Evolution* 22:185-191.
- Bergamaschi, BA, Kuivila, KM, Fram, MS. 2001. Pesticides associated with suspended sediments entering San Francisco Bay following the first major storm of water year 1996. *Estuaries* 24:368-380.
- Brown, LR, May, JT. 2006. Variation in spring nearshore resident fish species composition and life histories in the lower Sacramento-San Joaquin watershed and delta. *San Francisco Estuary and Watershed Science* 4:<http://repositories.cdlib.org/jmie/sfews/vol4/iss2/art1>.
- Brown, LR, Michniuk, D. 2007. Littoral fish assemblages of the alien-dominated Sacramento-San Joaquin Delta, California, 1980-1983 and 2001-2003. *Estuaries and Coasts* 30:186-200.
- Brown, LR, Moyle, PB. 2005. Native fishes of the Sacramento-San Joaquin drainage, California: a history of decline. *American Fisheries Society Symposium* 45:75-98.

- Courchamp, F, Clutton-Brock, T, Grenfell, B. 1999. Inverse density-dependence and the Allee effect. *Trends in Ecology and Evolution* 14:405-410.
- Davis, JA, Greenfield, BK, Ichikawa, G, Stephenson, M. 2008. Mercury in sport fish from the Sacramento-San Joaquin Delta region, California, USA. *Science of the Total Environment* 391:66-75.
- DeBlois, EM, Leggett, WC. 1991. Functional response and potential impact of invertebrate predators on benthic fish eggs: analysis of the *Calliopiopus laeviusculus*-capelin (*Mallotus villosus*) predator-prey system. *Marine Ecology Progress Series* 69:205-216.
- Dege, M, Brown, LR. 2004. Effect of outflow on spring and summertime distribution and abundance of larval and juvenile fishes in the upper San Francisco Estuary. *American Fisheries Society Symposium* 39:49-66.
- Dettinger, MD. 2005. From climate-change spaghetti to climate-change distributions for 21st Century California. *San Francisco Estuary and Watershed Science* 3:<http://repositories.cdlib.org/jmie/sfews/vol3/iss1/art4>.
- DFG (Department of Fish and Game) 1998. Environmental monitoring for chemical control of *Egeria densa* in the Sacramento-San Joaquin Delta. Report 3. State of California, The Resources Agency.
- Dugdale, RC, Wilkerson, FP, Hogue, VE, Marchi, A. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. *Estuarine, Coastal, and Shelf Science* 73:17-29.
- Enos, C, Sutherland, J, Nobriga, M. 2007. Results of a two-year fish entrainment study at Morrow Island Distribution System in Suisun Marsh. *Interagency Ecological Program Newsletter* 20(1):10-19. Available online at http://www.iep.ca.gov/report/newsletter/2007_newsletters/IEPNewsletterfinal3_winter2007.pdf
- Erkkila, LF, Moffett, JW, Cope, OB, Smith, BR, Nelson, RS. 1950. Sacramento-San Joaquin Delta fishery resources: effects of Tracy Pumping Plant and Delta cross channels. Special Scientific Report. Fisheries 56. US Fish and Wildlife Service.
- Feyrer, F, Herbold, B, Matern, SA, Moyle, PB. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. *Environmental Biology of Fishes* 67:277-288.
- Feyrer, F, Nobriga, ML, Sommer, TR. 2007. Multi-decadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 64:723-734.
- Feyrer, F, Nobriga, M, Sommer, T, Newman, K. In review. Modeling the effects of future freshwater flow on the abiotic habitat of an imperiled estuarine fish. Manuscript submitted to *Estuaries and Coasts*.
- Floyd, EY, Geist, JP, Werner, I. 2008. Acute, sublethal exposure to a pyrethroid insecticide alters behavior, growth, and predation risk in larvae of the fathead minnow (*Pimephales promelas*). *Environmental Toxicology and Chemistry* 27:1780-1787.
- Ger, KA, Teh, SJ, Goldman, CR. 2009. Microcystin L-R toxicity on dominant copepods *Eurytemora affinis* and *Pseudodiaptomus forbesi* of the upper San Francisco Estuary. *Science of the Total Environment* 407: 4852-4857.
- Gregory, RS, Levings, CD. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. *Transactions of the American Fisheries Society* 127:275-285.
- Grimaldo, LF, Sommer, T, Van Ark, N, Jones, G, Holland, E, Moyle, P, Smith, P, Herbold, B. Factors

- affecting fish entrainment into massive water diversions in a freshwater tidal estuary: can fish losses be managed? *North American Journal of Fisheries Management* 29:1253-1270.
- Hallock, RJ, Van Woert, W. 1959. A survey of anadromous fish losses in irrigation diversions from the Sacramento and San Joaquin rivers. *California Fish and Game* 45: 227-521.
- Herbold, B, Jassby, AD, Moyle, PB. 1992. Status and trends report on aquatic resources in the San Francisco Estuary. Report to the EPA San Francisco Estuary Project. 257 p.
- Herren, JR, Kawasaki, SS. 2001. Inventory of water diversions in four geographic areas in California's Central Valley. *California Department of Fish and Game Fish Bulletin* 179(vol.2):343-355.
- Hirose, T, Kawaguchi, K. 1998. Spawning ecology of Japanese surf smelt, *Hypomesus pretiosus japonicus* (Osmeridae), in Otsuchi Bay, northeastern Japan. *Environmental Biology of Fishes* 52:213-223.
- Hobbs, JA, Bennett, WA, Burton, J, Gras, M. 2007. Classification of larval and adult delta smelt to nursery areas by use of trace elemental fingerprinting. *Transactions of the American Fisheries Society* 136:518-527.
- Houde, ED. 1987. Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium* 2:17-29.
- Israel, JA, Fisch, K, Clarke, R, Turner, TF, Waples, R, Hedrick, P, Nobriga, M. In review. Artificial propagation in native fish conservation in the western US: an assessment of its role in the preservation of Central Valley Chinook salmon, delta smelt, and green sturgeon. Manuscript submitted to *San Francisco Estuary and Watershed Science*.
- Jassby, A. 2008. Phytoplankton in the upper San Francisco Estuary: recent biomass trends, their causes, and their trophic significance. *San Francisco Estuary and Watershed Science* 6:
<http://repositories.cdlib.org/jmie/sfews/vol6/iss1/art2>.
- Jassby, AD, Cloern, JE, Cole, BE. 2002. Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal ecosystem. *Limnology and Oceanography* 47:698-712.
- Jassby, AD, Kimmerer, WJ, Monismith, SG, Armor, C, Cloern, JE, Powell, TM, Schubel, JR, Vendlinski, TJ. 1995. Isohaline position as a habitat indicator for estuarine populations. *Ecological Applications* 5:272-289.
- Jassby, A. D., A. B. Mueller-Solger, and M. Vayssieres. 2005. Subregions of the Sacramento-San Joaquin Delta: identification and use. *Interagency Ecological Program Newsletter* 18(2):68-75. Available at http://iep.water.ca.gov/report/newsletter/2005_newsletters/IEPNews_spring2005final.pdf
- Jassby, AD, Van Nieuwenhuysse, EE. 2006. Low dissolved oxygen in an estuarine channel (San Joaquin River, California): mechanisms and models based on long-term time series. *San Francisco Estuary and Watershed Science* 3: <http://repositories.cdlib.org/jmie/sfews/vol3/iss2/art2>.
- Jobling, S, Nolan, M, Tyler, CR, Brighty, G, Sumpter, JP. 1998. Widespread sexual disruption in wild fish. *Environmental Science and Technology* 32:2498-2506.
- Kidd, KA, Blanchfield, PJ, Mills, KH, Palaco, VP, Evans, RE, Lazorchak, JM, Flick, RW. 2007. Collapse of a fish population after exposure to a synthetic estrogen. *Proceedings of the National Academy of Science* 104:8897-8901.
- Kimmerer, WJ. 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? *Marine Ecology Progress Series* 243:39-55.
- Kimmerer, WJ. 2004. Open-water processes of the San Francisco Estuary: from physical forcing to

biological responses. San Francisco Estuary and Watershed Science 2:
<http://repositories.cdlib.org/jmie/sfews/vol2/iss1/art1>.

Kimmerer, WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. Marine Ecology Progress Series 324: 207-218.

Kimmerer, WJ. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science 6:
<http://repositories.cdlib.org/jmie/sfews/vol6/iss2/art2>.

Kimmerer, W, Avent, SR, Bollens, SM, Feyrer, F, Grimaldo, LF, Moyle, PB, Nobriga, M, Visintainer, T. 2005. Variability in length-weight relationships used to estimate biomass of estuarine fish from survey data. Transactions of the American Fisheries Society 134:481-495.

Kimmerer, WJ, Burau, JR, Bennett, WA. 2002. Persistence of tidally-oriented vertical migration by zooplankton in a temperate estuary. Estuaries 25:359-371.

Kimmerer, WJ, Gartside, E, Orsi, JJ. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Marine Ecology Progress Series 113:81-93.

Kimmerer, W. J., E. S. Gross, and M. L. MacWilliams. 2009. Is the response of estuarine nekton to freshwater flow in the San Francisco Estuary explained by variation in habitat volume? Estuaries and Coasts 32:375-389.

Kimmerer, WJ, Nobriga, ML. 2008. Investigating particle transport and fate in the Sacramento-San Joaquin Delta using a particle tracking model. San Francisco Estuary and Watershed Science 6:
<http://repositories.cdlib.org/jmie/sfews/vol6/iss1/art4>.

Kuivila, KM, Moon, GE. 2004. Potential exposure of larval and juvenile delta smelt to dissolved pesticides in the Sacramento-San Joaquin Delta, California. American Fisheries Society Symposium 39:229-242.

Kumaraguru, AK, Beamish, FWH. 1981. Lethal toxicity of permethrin (NRDC-143) to rainbow trout, *Salmo gairdneri*, in relation to body weight and water temperature. Water Research 15:503-505.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455-1460.

Lehman, PW, Boyer, G, Hall, C, Waller, S, Gehrts, K. 2005. Distribution and toxicity of a new colonial *Microcystis aeruginosa* bloom in the San Francisco Bay Estuary, California. Hydrobiologia 541:87-99.

Lehman, PW, Boyer, G, Satchwell, M, Waller, S. 2008. The influence of environmental conditions on the seasonal variation of *Microcystis* cell density and microcystins concentration in San Francisco Estuary. Hydrobiologia 600:187-204.

Lott, J. 1998. Feeding habits of juvenile and adult delta smelt from the Sacramento-San Joaquin River Estuary. Interagency Ecological Program Newsletter 11(1):14-19 (available at <http://iep.water.ca.gov/report/newsletter/>)

Lund, J, Hanak, E, Fleenor, W, Bennett, W, Howitt, R, Mount, J, Moyle, P. 2008. Comparing futures for the Sacramento-San Joaquin Delta. Public Policy Institute of California. (www.ppic.org)

Lund, J, Hanak, E, Fleenor, W, Howitt, R, Mount, J, Moyle, P. 2007. Envisioning futures for the Sacramento-San Joaquin Delta. Public Policy Institute of California. (www.ppic.org)

Mager, RC, Doroshov, SI, Van Eenennaam, JP, Brown, RL. 2004. Early life stages of delta smelt. American Fisheries Society Symposium 39:169-180.

- Marine, KR, Cech, JJ, Jr. 2004. Effects of high water temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River Chinook salmon. *North American Journal of Fisheries Management* 24:198-210.
- Matern, SA, Moyle, PB, Pierce, LC. 2002. Native and alien fishes in a California estuarine marsh: twenty-one years of changing assemblages. *Transactions of the American Fisheries Society* 131:797-816.
- Meng, L, Matern, SA. 2001. Native and introduced larval fishes of Suisun Marsh, California: the effects of freshwater flow. *Transactions of the American Fisheries Society* 130:750-765.
- Monsen, NE, Cloern, JE, Burau, JR. 2007. Effects of flow diversions on water and habitat quality: examples from California's highly manipulated Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science* 5: <http://repositories.cdlib.org/jmie/sfews/vol5/iss3/art2>.
- Moyle, PB. 2002. *Inland fishes of California, revised and expanded*. University of California Press, Berkeley, CA.
- Moyle, PB, Herbold, B, Stevens, DE, Miller LW. 1992. Life history and status of delta smelt in the Sacramento-San Joaquin Estuary, California. *Transactions of the American Fisheries Society* 121:67-77.
- Moyle, PB, Israel, JA. 2005. Untested assumptions: effectiveness of screening diversions for conservation of fish populations. *Fisheries* 30(5):20-28.
- Nichols, FH, Cloern, JE, Luoma, SN, Peterson, DH. 1986. The modification of an estuary. *Science* 231:567-573.
- Nobriga, ML. 2002. Larval delta smelt diet composition and feeding incidence: environmental and ontogenetic influences. *California Fish and Game* 88:149-164.
- Nobriga, ML, Feyrer, F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science* 5: <http://repositories.cdlib.org/jmie/sfews/vol5/iss2/art4>.
- Nobriga, ML, Feyrer, F. 2008. Diet composition in San Francisco Estuary striped bass: does trophic adaptability have its limits? *Environmental Biology of Fishes* 83:495-503.
- Nobriga, ML, Feyrer, F, Baxter, RD, Chotkowski, M. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies and biomass. *Estuaries* 28:776-785.
- Nobriga, M, Hymanson, Z, Oltmann, R. 2000. Environmental factors influencing the distribution and salvage of young delta smelt: a comparison of factors occurring in 1996 and 1999. *Interagency Ecological Program Newsletter* 13(2):55-65. Available online at http://www.iep.ca.gov/report/newsletter/2000spring/IEPNewsletter_Spring2000.pdf
- Nobriga, ML, Matica, Z, Hymanson, ZP. 2004. Evaluating entrainment vulnerability to agricultural irrigation diversions: a comparison among open-water fishes. *American Fisheries Society Symposium* 39:281-295.
- Nobriga, ML, Sommer, TR, Feyrer, F, Fleming, K. 2008. Long-term trends in summertime habitat suitability for delta smelt, *Hypomesus transpacificus*. *San Francisco Estuary and Watershed Science* 6: <http://repositories.cdlib.org/jmie/sfews/vol6/iss1/art1>.
- Oros, D.R. and I. Werner. 2005. *Pyrethroid Insecticides: an analysis of use patterns, distributions, potential toxicity and fate in the Sacramento-San Joaquin Delta and Central Valley*. San Francisco Estuary Institute, Oakland, California.

- Passell, HD, Dahm, CN, Bedrick, EJ. 2007. Ammonia modeling for assessing potential toxicity to fish species in the Rio Grande, 1989-2002. *Ecological Applications* 17:2087-2099.
- Pickard, A, Baracco, A, Kano, R. 1982. Occurrence, abundance, and size of fish at the Roaring River Slough intake, Suisun Marsh, California, during the 1980-81 and the 1981-82 diversion seasons. Interagency Ecological Program Technical Report 3. California Department of Water Resources, Sacramento, CA.
- Prenter, J, MacNeil, C, Dick, JTA, Dunn, AM. 2004. Roles of parasites in animal invasions. *Trends in Ecology and Evolution* 19:385-390.
- Purchase, CF, Hasselman, DJ, Weir, LK. 2007. Relationship between fertilization success and the number of milt donors in rainbow smelt *Osmerus mordax* (Mitchell): implications for population growth rates. *Journal of Fish Biology* 70:934-946.
- Quist, MC, Hubert, WA, Rahel, FJ. 2004. Relations among habitat characteristics, exotic species, and turbid-river cyprinids in the Missouri River drainage of Wyoming. *Transactions of the American Fisheries Society* 133:727-742.
- Reno, PW. 1998. Factors involved in the dissemination of disease in fish populations. *Journal of Aquatic Animal Health* 10:160-171.
- Robson, BJ, Hamilton, DP. 2003. Summer flow event induces a cyanobacterial bloom in a seasonal western Australian estuary. *Marine and Freshwater Research* 54:139-151.
- Roughgarden, J, Smith, F. 1996. Why fisheries collapse and what to do about it. *Proceedings of the National Academy of Sciences* 93:5078-5083.
- Ruhl, CA, Schoellhamer, DH, Stumpf, RP, Lindsay, CL. 2001. Combined use of remote sensing and continuous monitoring to analyse the variability of suspended-sediment concentrations in San Francisco Bay, California. *Estuarine, Coastal, and Shelf Science* 53:801-812.
- Sinclair, ARE, Pech, RP, Dickman, CR, Hik, D, Mahon, P, Newsome, AE. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology* 12:564-575.
- Sommer, T, Armor, C, Baxter, R, Breuer, R, Brown, L, Chotkowski, M, Culberson, S, Feyrer, F, Gingras, M, Herbold, B, Kimmerer, W, Mueller-Solger, A, Nobriga, M, Souza, K. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries* 32(6):270-277.
- Stevens, DE. 1963. Food habits of striped bass, *Roccus saxatilis* (Walbaum), in the Sacramento-Rio Vista area of the Sacramento River. Master's Thesis. University of California, Davis.
- Stevens, DE. 1966. Food habits of striped bass, *Roccus saxatilis*, in the Sacramento-San Joaquin Delta. Pages 68-96 in Turner, JL, Kelley, DW (editors). 1966. *Ecological studies of the Sacramento-San Joaquin Delta, part II, fishes of the Delta*. California Department of Fish and Game Fish Bulletin 136.
- Stevens, DE, Miller, LW. 1983. Effects of river flow on abundance of young Chinook salmon, American shad, longfin smelt, and delta smelt in the Sacramento-San Joaquin river system. *North American Journal of Fisheries Management* 3:425-437.
- Stewart, AR, Luoma, SN, Schlekot, CE, Doblin, MA, Hieb, KA. 2004. Food web pathway determines how selenium affects aquatic ecosystems: a San Francisco Bay case study. *Environmental Science and Technology* 38:4519-4526.

- Swanson, C, Reid, T, Young, PS, Cech, JJ, Jr. 2000. Comparative environmental tolerances of threatened delta smelt (*Hypomesus transpacificus*) and introduced wakasagi (*H. nipponensis*) in an altered California estuary. *Oecologia* 123:384-390.
- Swanson, C, Young, PS, Cech, JJ, Jr. 1998. Swimming performance of delta smelt: maximum performance, and behavioral and kinematic limitations on swimming at submaximal velocities. *Journal of Experimental Biology* 201:333-345.
- Sweetnam, DA. 1999. Status of delta smelt in the Sacramento-San Joaquin Estuary. *California Fish and Game* 85:22-27.
- Takamura, N, Iwakuma, T, Yasuno, M. 1987. Uptake of ^{13}C and ^{15}N (ammonium, nitrate, and urea) by *Microcystis* in Lake Kasumigaura. *Journal of Plankton Research* 9:151-165.
- Thompson, JR, Kimmerer, WJ, Brown, LR, Newman, KB, Mac Nally, R, Bennett, WA, Feyrer, F, Fleishman, E. In press. Bayesian change-point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecological Applications*.
- Thornton, KW, Lessam, AS. 1978. A temperature algorithm for modifying biological rates. *Transactions of the American Fisheries Society* 107:284-287.
- Tilman, D, May, RM, Lehman, CL, Nowak, MA. 1994. Habitat destruction and the extinction debt. *Nature* 371:65-66.
- Unmack, PJ, Fagan, WF. 2004. Convergence of differentially invaded systems toward invader-dominance: time-lagged invasions as a predictor in desert fish communities. *Biological Invasions* 6:233-243.
- USFWS (United States Fish and Wildlife Service). 2008. Formal Endangered Species Act consultation on the proposed coordinated operations of the Central Valley Project (CVP) and State Water Project (SWP).
- USGS (United States Geological Survey) 1998. Water quality assessment of the Sacramento River basin, California – water quality of fixed sites, 1996-1998. Water resources investigations report 00-4247. U.S. Department of the Interior, USGS.
- Van Nieuwenhuysse, EE. 2007. Response of summer chlorophyll concentration to reduced total phosphorus concentration in the Rhine River (Netherlands) and the Sacramento-San Joaquin Delta (California, USA). *Canadian Journal of Fisheries and Aquatic Sciences* 64:1529-1542.
- Wang, JCS. 2007. Spawning, early life stages, and early life histories of the Osmerids found in the Sacramento-San Joaquin Delta of California. *Tracy Fish Facilities Studies California Volume 38*. U.S. Bureau of Reclamation, Mid-Pacific Region.
- Werner, I, Deanovic, L, Markiewicz, D, Stillway, M, Offer, N, Connon, R, Brander, S. 2008. Pelagic organism decline (POD): Acute and chronic invertebrate and fish toxicity testing in the Sacramento-San Joaquin Delta, 2006-2007. Final report to the Interagency Ecological Program, April 30, 2008.
- Wilkerson, FP, Dugdale, RC, Hogue, VE, Marchi, A. 2006. Phytoplankton blooms and nitrogen productivity in San Francisco Bay. *Estuaries and Coasts* 29:401-416.
- Winemiller, KO, Rose, KA. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2196-2218.
- Wright, SA, Schoellhamer, DH. 2004. Trends in the sediment yield of the Sacramento River, California, 1957-2001. *San Francisco Estuary and Watershed Science* 2:
<http://repositories.cdlib.org/jmie/sfew/svol2/iss2/art2>.

VIII. Figures

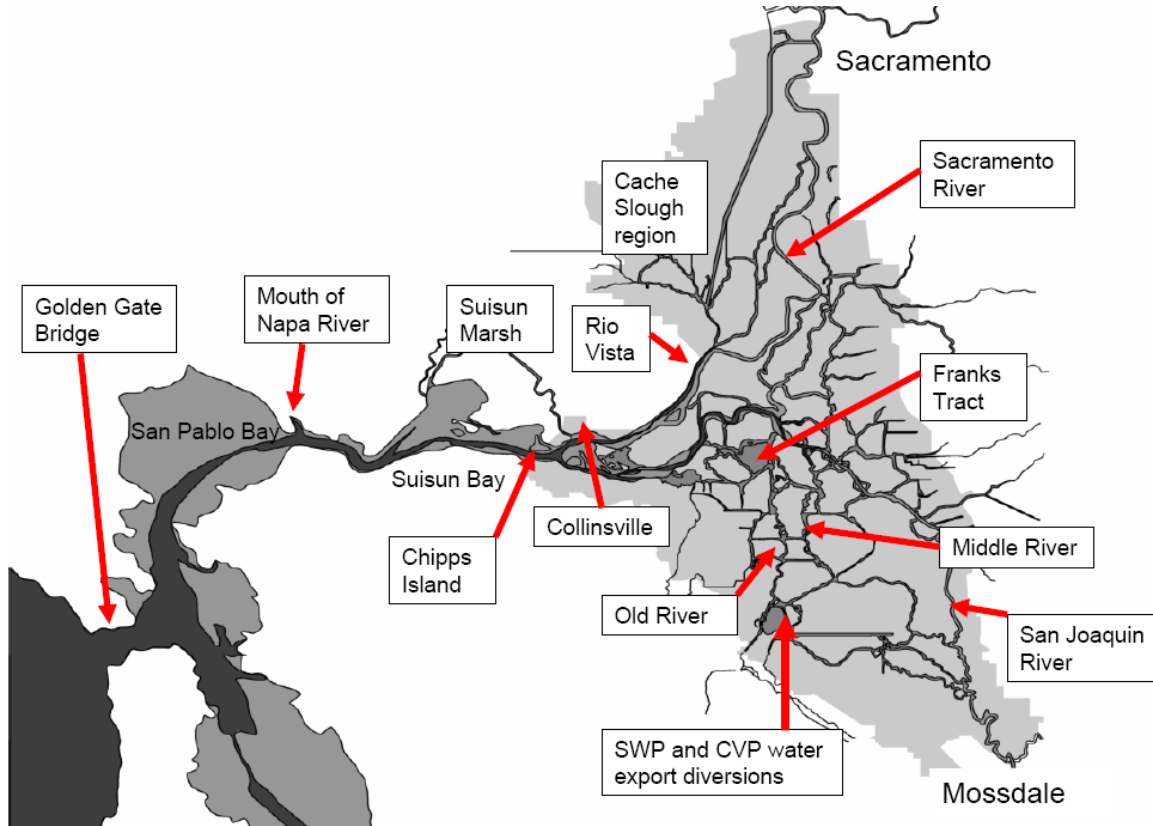


Figure 1. Map of the San Francisco Estuary showing locations mentioned in section 1.2 Regional definitions.

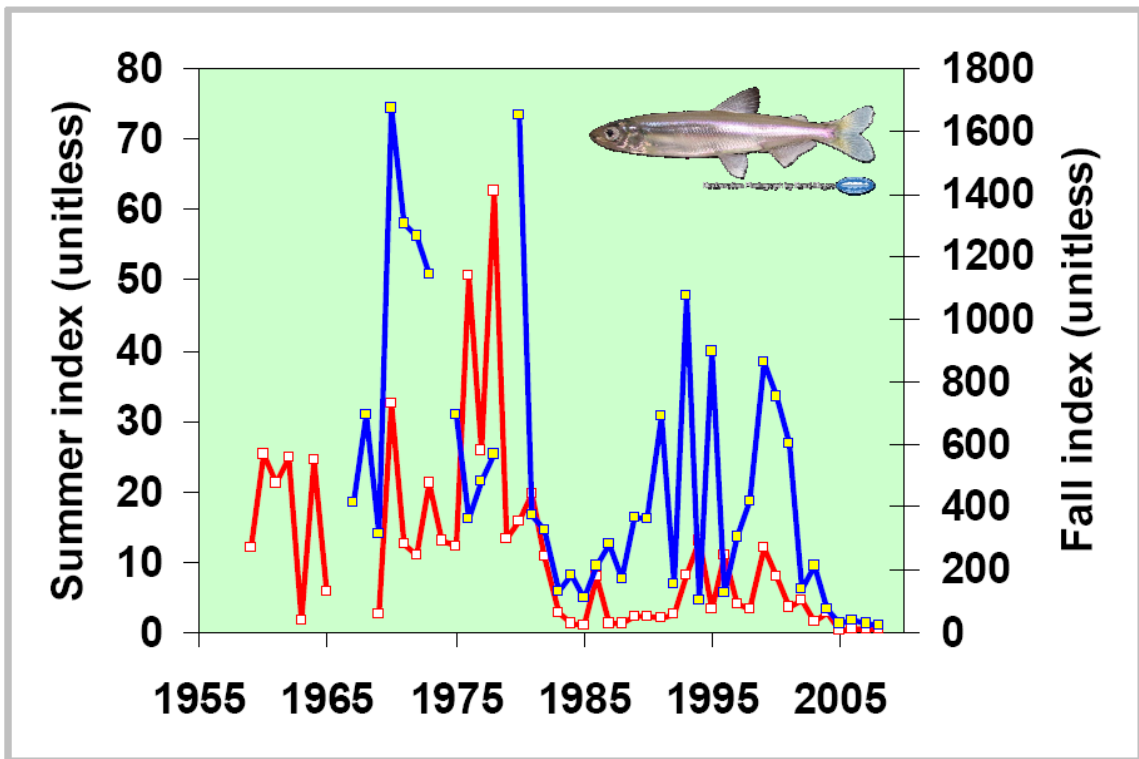


Figure 2. Time series of delta smelt relative abundance from the Department of Fish and Game summer townet survey (1959-2008) and fall midwater trawl survey (1967-2008).

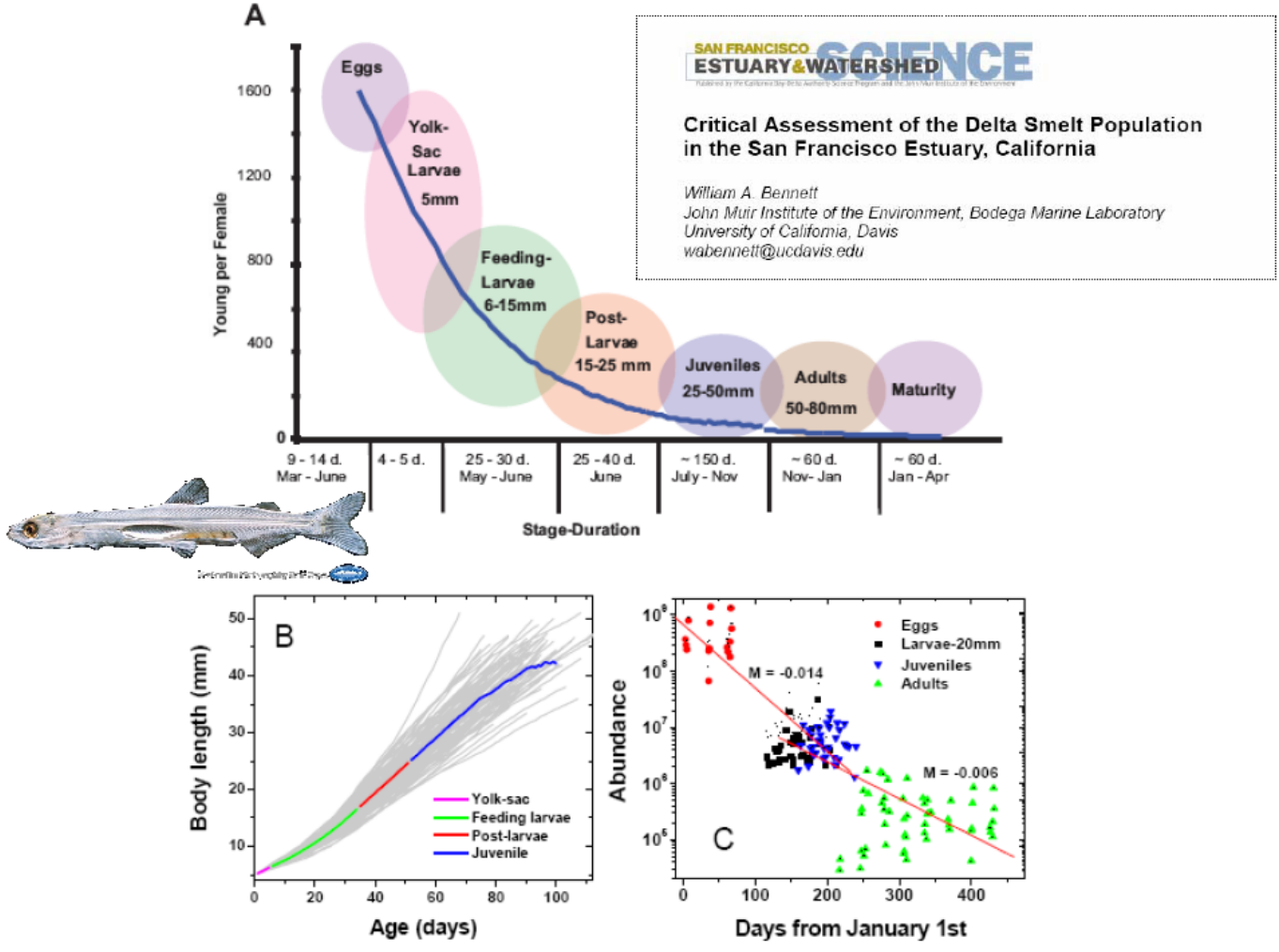


Figure 3. Conceptual model of delta smelt life history. A hypothetical pattern of mortality (dark blue line) for young produced by a female is shown with the approximate life stage durations (A). Also shown is a pattern of individual growth calculated from 144 otoliths during 1999 (B), and mortality as represented by the slope of regression lines (M) among different life stages (C). This figure and its caption were taken from Bennett (2005).

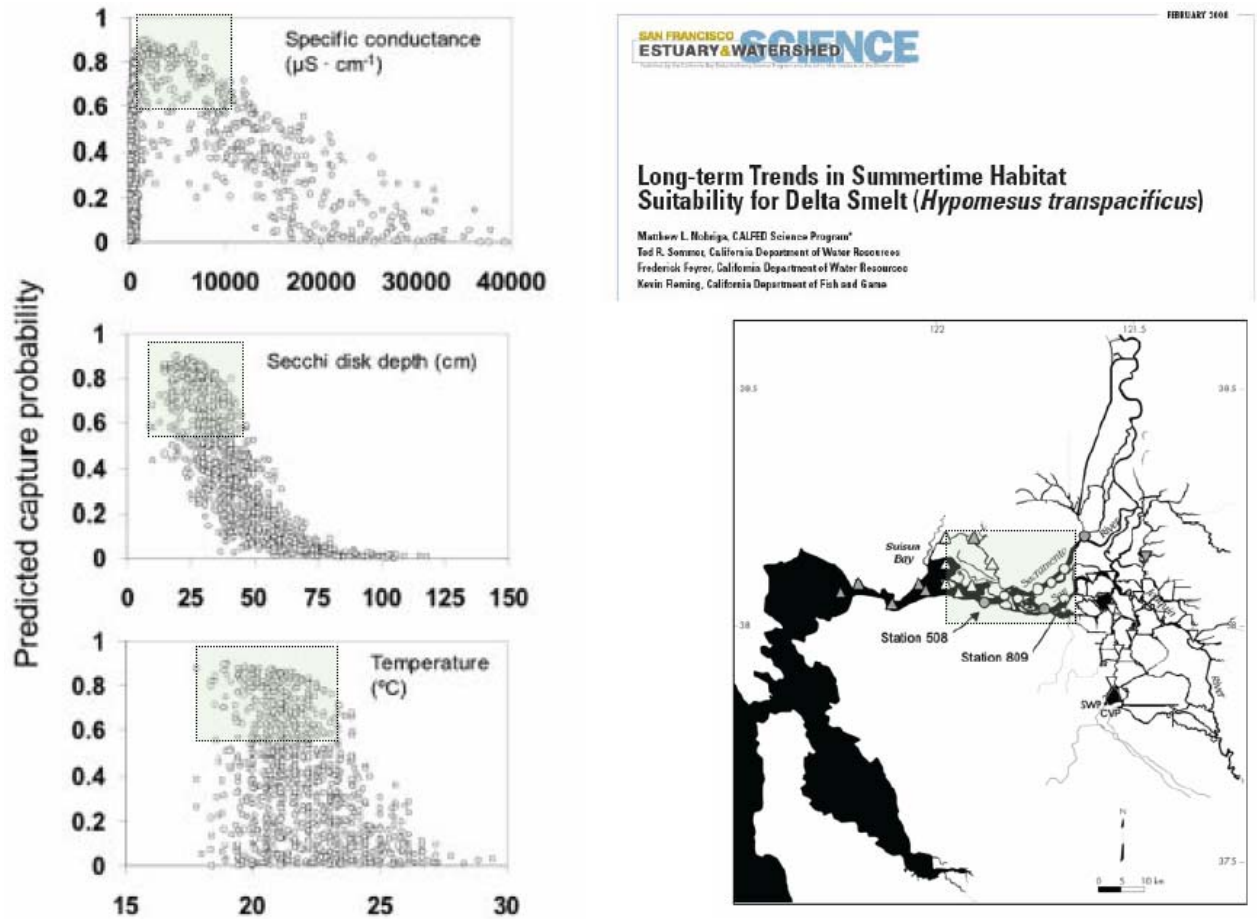


Figure 4. Predicted capture probabilities for juvenile delta smelt relative to water quality variables in the upper San Francisco Estuary. The capture probabilities were based on a binomial generalized additive model including all three water quality variables as explanatory variables; the scatter in each panel is due to the interactive influence of the other two variables. Plots taken from Nobriga et al. (2008). The shaded areas on the scatterplots show approximate ranges of optimal habitat conditions. The shaded area on the map shows the approximate spatial location of optimal delta smelt habitat during summer.

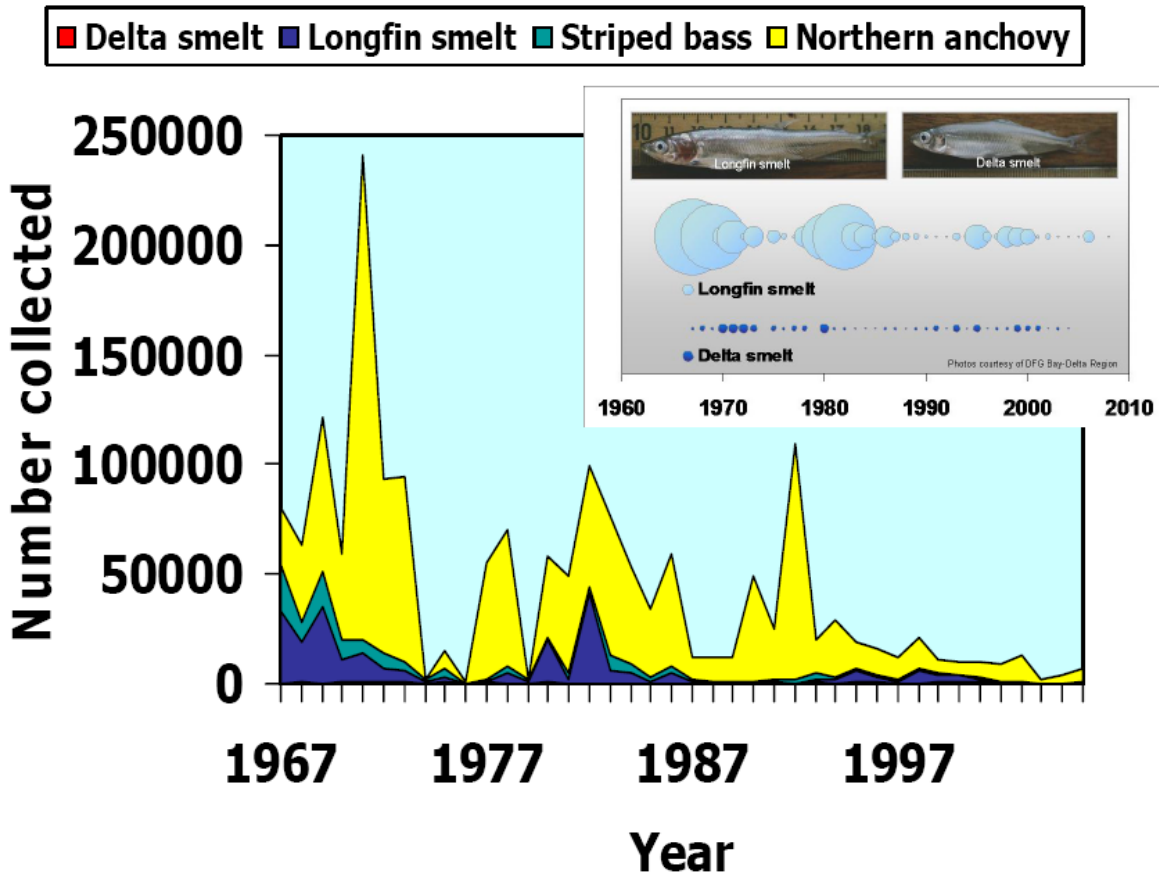


Figure 5. Two plots depicting the very low relative abundance of delta smelt among pelagic fishes inhabiting the San Francisco Estuary low-salinity zone. The larger plot shows the number of northern anchovy (*Engraulis mordax*), longfin smelt (*Spirinchus thaleichthys*), striped bass (*Morone saxatilis*), and delta smelt (*Hypomesus transpacificus*) collected in the Fall Midwater Trawl survey from 1967-2006. Note that delta smelt is not visible on this plot. The inset shows the same trend for longfin smelt and delta smelt only, but depicts the relative number collected into a relative surface area.



Figure 6. Bubble plots of staging adult delta smelt distributions from midwater trawl and otter trawl sampling in 1963-1964 (Turner and Kelley 1966) and the Spring Kodiak Trawl Survey in 2005, during above average outflow and 2008 during below-normal outflow. The bubbles are sized based on the catch per unit effort of delta smelt at each sampling site. Color-coding in the Kodiak data indicates the reproductive stage of the sampled fish (<http://www.delta.dfg.ca.gov/data/skt/DisplayMaps.asp>).

Transition Matrix: Delta Smelt

Figure 7

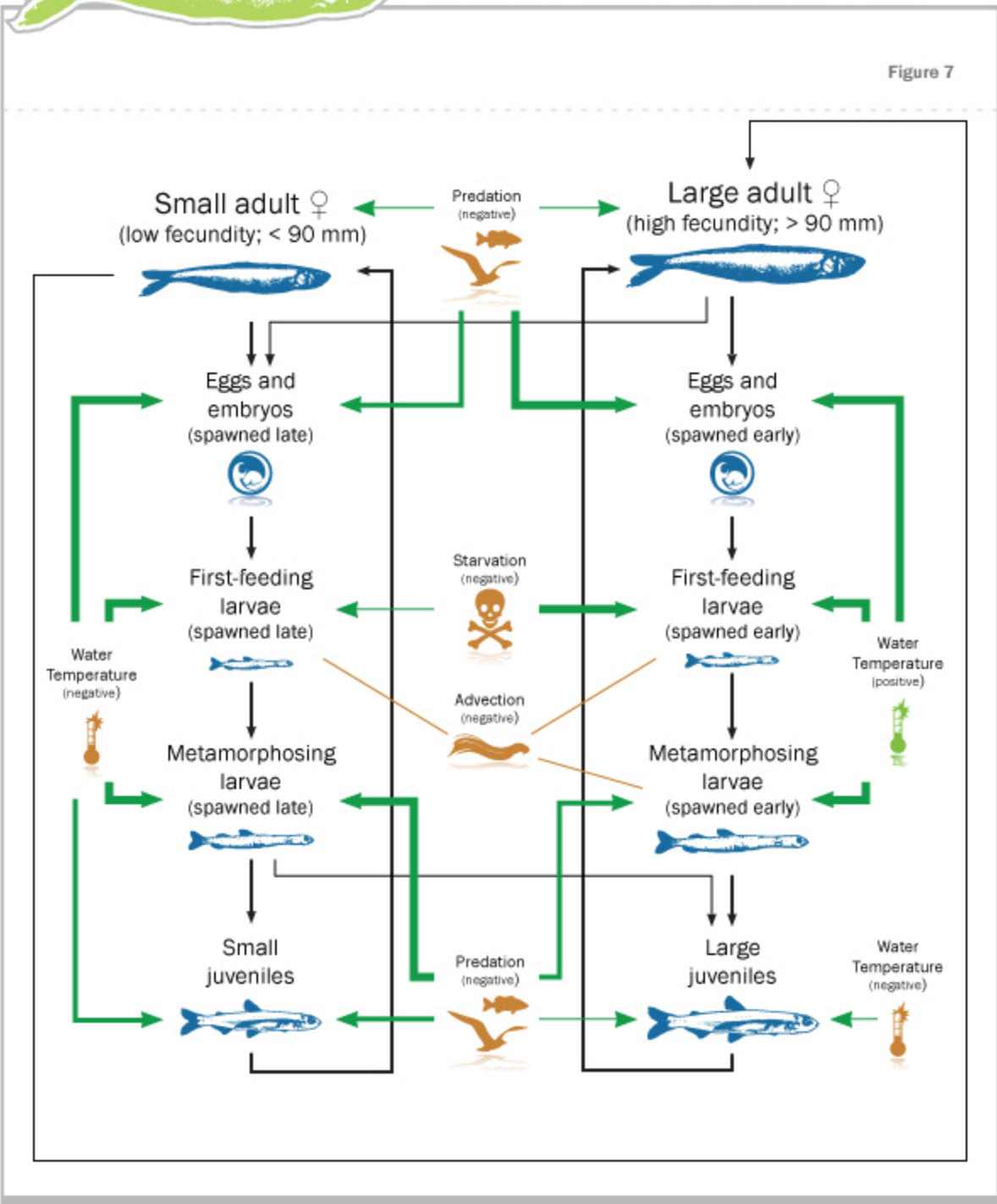


Figure 7. Life-history transition matrix for delta smelt showing hypothesized influences of major population drivers on the likelihood the fish survive from one life stage to the next.



Life History Ecology: Delta Smelt

Figure 8

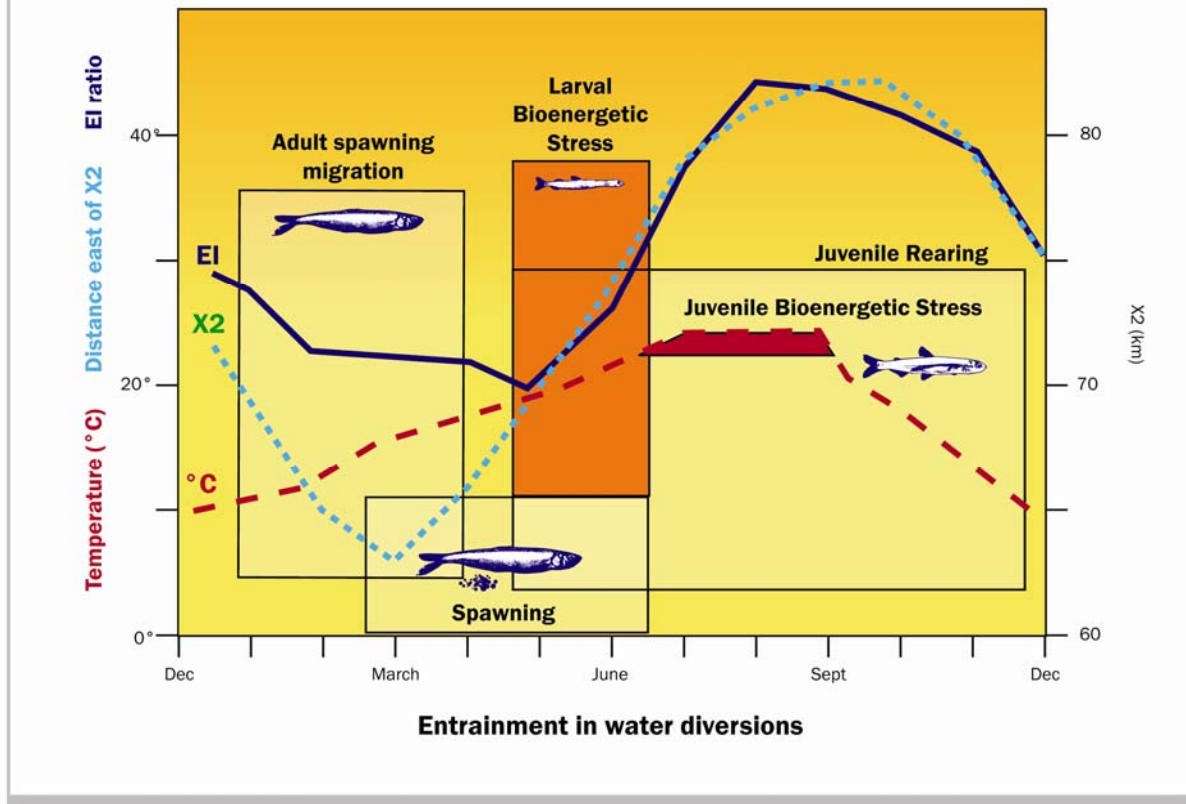


Figure 8. A conceptual depiction of the life cycle of delta smelt relative to selected influences: salinity distribution or Delta outflow (X2), the SWP/CVP water export to Delta inflow ratio (EI), and an idealized seasonal water temperature cycle.

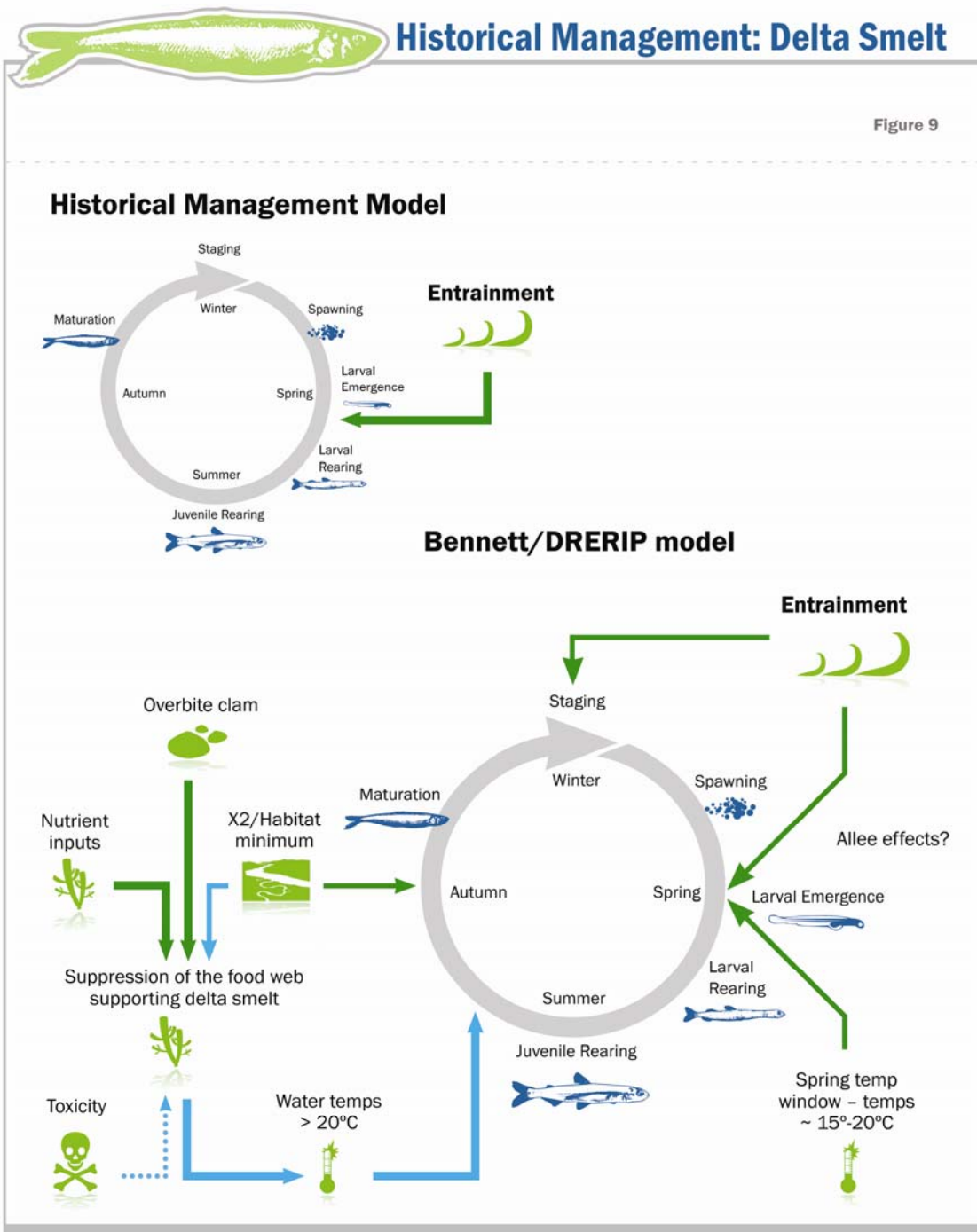


Figure 9. Conceptual diagrams contrasting the historical (pre-2000) model of delta smelt management with the simplest plausible model for the DRERIP. These diagrams depict the sequential nature of stressors on the delta smelt population and the greater current awareness of multiple stressor hypotheses proposed by Bennett and Moyle (1996) and Bennett (2005).

Spawning Temperature Window (15-20 C°)

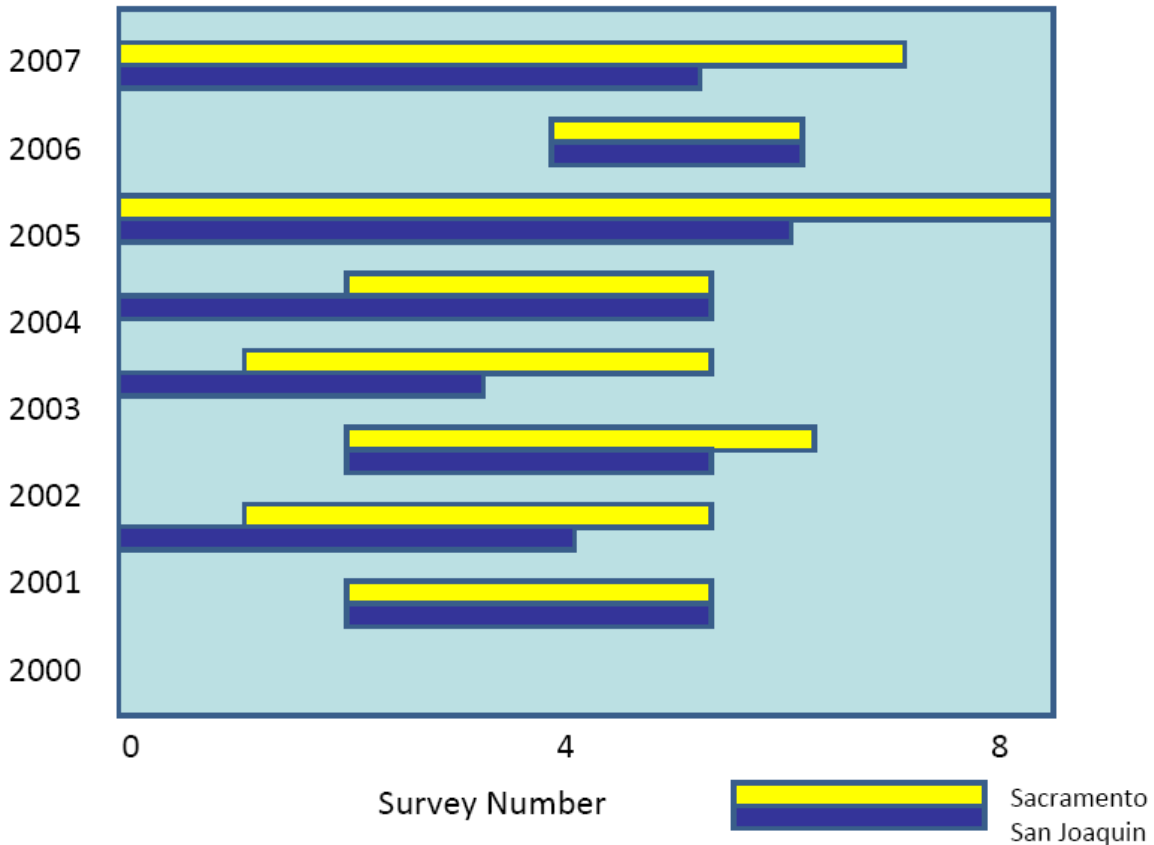


Figure 10. Temporal distributions of the delta smelt 15°-20°C spawning temperature window (Bennett 2005), 2000-2007. The data show the distributions for the tidal Sacramento River (20mm Survey stations numbered in the 700s) and south Delta (20 mm Survey stations numbered in the 900s) relative to the 20 mm survey number shown on the x-axis. Higher survey numbers generally reflect surveys conducted further into a calendar year. The data were compiled from discrete measurements of water temperature available at: <ftp://ftp.delta.dfg.ca.gov/Delta%20Smelt/>

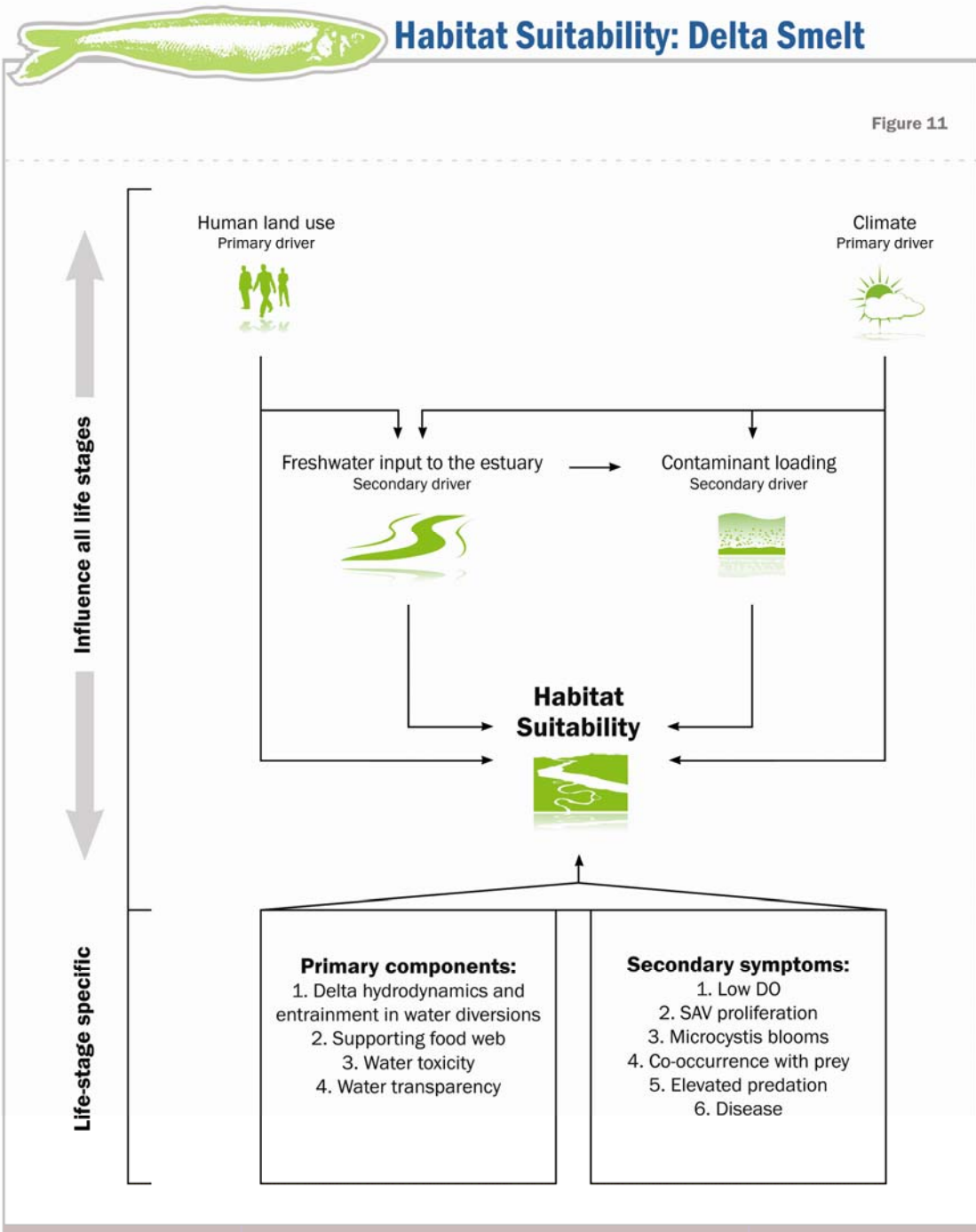


Figure 11. Conceptual hierarchical linkage among primary and secondary drivers influencing delta smelt population dynamics and the resultant primary components of habitat suitability and secondary population stressors that emanate from the interactions of these influences.

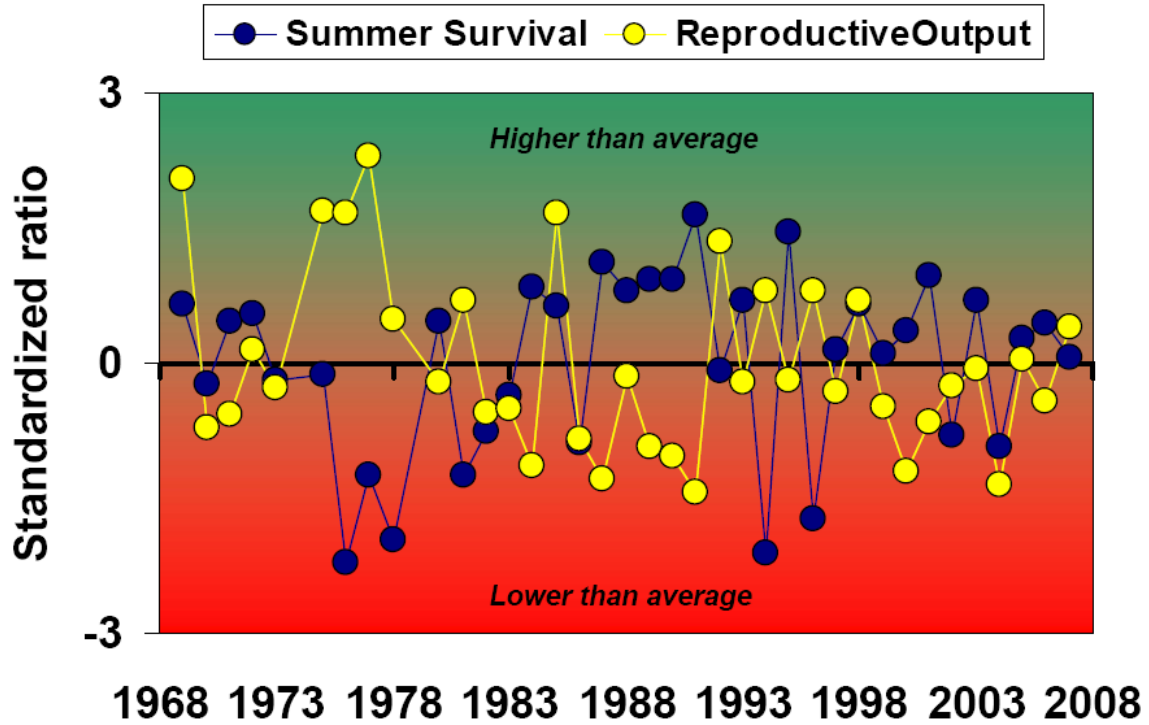


Figure 12. Time series of the \log_{10} -transformed and z-scored ratios of the Fall Midwater Trawl index for delta smelt to the prior Summer Townet Survey index (labelled “summer survival” sensu Kimmerer 2008) and the \log_{10} -transformed and z-scored ratios of the Summer Townet Survey index to the Fall Midwater Trawl index from the previous autumn (labelled “reproductive output”). The zero line depicts the long-term average of both index ratios.