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Delta Smelt: Life History and Decline of a Once-Abundant Species in the San Francisco Estuary

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HAIKU

Hey there, delta smelt
If you hang on for a while
You will fool us all.

ABSTRACT

This paper reviews what has been learned about Delta Smelt and its status since the publication of *The State of Bay-Delta Science, 2008* (Healey et al. 2008). The Delta Smelt is endemic to the upper San Francisco Estuary. Much of its historic habitat is no longer available and remaining habitat is increasingly unable to sustain the population. As a listed species living in the central node of California's water supply system, Delta Smelt has been the focus of a large research effort to understand causes of decline and identify ways to recover the species. Since 2008, a remarkable record of innovative research on Delta Smelt has been achieved, which is summarized here. Unfortunately, research has not prevented the smelt's continued decline, which is the result of multiple, interacting factors. A major driver of decline is change to the Delta ecosystem from water exports, resulting in reduced outflows and high levels of entrainment in the large pumps of the South Delta. Invasions of alien species, encouraged by environmental change, have also played a contributing role in the decline. Severe drought effects have pushed Delta Smelt to record low levels in 2014–2015. The rapid decline of the species and failure of recovery efforts demonstrate an inability to manage the Delta for the "co-equal goals" of maintaining a healthy ecosystem and providing a reliable water supply for Californians. Diverse and substantial management actions are needed to preserve Delta Smelt.

KEY WORDS

Hypomesus transpacificus, Sacramento-San Joaquin Delta, endangered species, extinction, co-equal goals, pelagic organism decline (POD)

INTRODUCTION

The Delta Smelt (*Hypomesus transpacificus*) is a small, translucent fish endemic to the upper San Francisco Estuary (estuary). Until the 1980s, it was an abundant fish in the upper estuary, moving with tides and river flows between the freshwater Delta and brackish Suisun Bay (Moyle 2002). The rapid decline of its population led to its listing as threatened under state and federal Endangered Species Acts in 1993 (Appendix A, Table A–1). Listing was controversial because the principal home of Delta Smelt is the center of California's water supply system. The need for information on Delta Smelt has resulted in over 300 peer-reviewed publications since it was proposed for listing in 1989 (Figure 1), as well as countless reports, technical memos, and blogs on its biology and management.

Knowledge about Delta Smelt has been synthesized by Moyle et al. (1992), Bennett and Moyle (1996), Moyle (2002), Bennett (2005), and the IEP Management, Analysis, and Synthesis Team (IEP MAST 2015). In *The State of Bay-Delta Science, 2008* (Healey et al. 2008), the Delta Smelt was treated mostly as part of the decline of pelagic fishes in the estuary, with the causes of Delta Smelt decline determined to be uncertain. Since that report, major advances in understanding Delta Smelt biology have occurred (Table 1). Here, we present a synthesis of recent studies, as the smelt dives towards extinction. We cover the following topics: (1) taxonomy and genetics; (2) historic and current distribution; (3) ecology; (4) population trends and dynamics; (5) conceptual models; and (6) causes of decline. We discuss why the present environment of the Delta no longer supports Delta Smelt and what conservation actions can be implemented. Survival of Delta Smelt

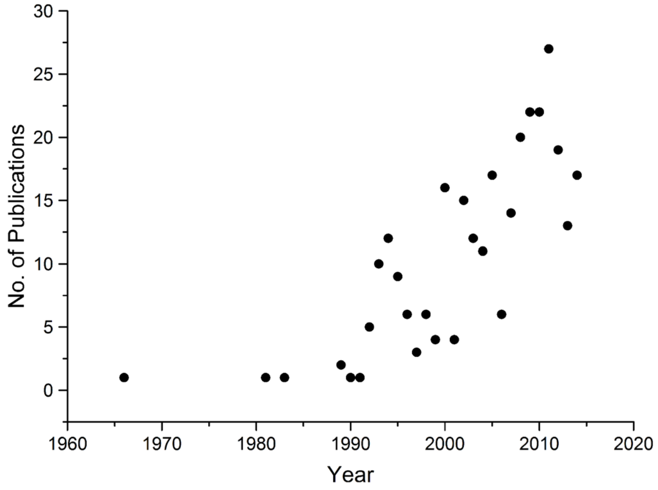

Figure 1 Number of peer-reviewed publications referring to Delta Smelt, by year. Data (from Google Scholar) include only publications with at least one citation.

Table 1 Key scientific findings on Delta Smelt (DS) since Healey et al. (2008). Details of these findings are presented in the chapter text. Findings are not listed in order of importance.

1.	There is a single population of DS, with recently reduced genetic diversity (Fisch et al. 2009, 2011)
2.	Spring Kodiak Trawl surveys show DS population approaching extinction, reflecting trends in other sampling surveys (unpublished data, CDFW 2015).
3.	Some DS remain year-round in fresh water, primarily in the north Delta (Merz et al. 2011; Sommer et al. 2011; Sommer and Mejia 2013). This was known previously but generally not recognized (e.g., Erkkila et al. 1951).
4.	DS are sensitive to warm temperatures, with thermal stress beginning at about 4–5°C below the critical thermal maxima of 24–28°C, depending on life history stage and acclimation temperatures (Komoroske et al. 2015).
5.	DS are strongly associated with turbid water in spring and summer, continuing into fall (Feyrer et al. 2007; Nobriga et al. 2008; Sommer and Mejia 2013). Increased turbidity in the Delta (around >10 NTU) is associated with entrainment of adult DS in the State Water Project and Central Valley Project pumps in the south Delta (Grimaldo et al. 2009).
6.	DS movements track turbidity and salinity gradients (Feyrer et al. 2007; Bennett and Burau 2015). Increased turbidity in fall and early winter triggers adult movement toward spawning areas (Grimaldo et al. 2009; Sommer et al. 2011).
7.	DS engage in "tidal surfing" behavior, moving laterally into shallow water to avoid peak ebb tide flows (Bennett and Burau 2015).
8.	DS gonads exhibit multiple stages of oocyte development, indicating that females can spawn more than once, increasing total fecundity (Lindberg et al. 2013).
9.	DS experience poor nutritional condition in Suisun Bay during summer months, and there was evidence of contaminant effects in freshwater (Hammock et al. 2015).
10.	DS survival from summer to fall is correlated with biomass of calanoid copepods in the low salinity zone (Kimmerer 2008b). As calanoids decline after mid-summer, DS revert to smaller, less nutritious prey items (Slater and Baxter 2014; Kratina and Winder 2015).
11.	Thomson et al. (2010) used Bayesian change point analysis to confirm the abrupt decline in delta smelt abundance in the early 1980s and in the early 2000s.
12.	The UC Davis Fish Conservation and Culture Laboratory now rears DS through their entire life cycle while maintaining genetic diversity and making large numbers of fish available for laboratory studies (Lindberg et al. 2013).

depends on new, flexible approaches to management (*Luoma et al. 2015*) as does survival of endangered species worldwide (Helfman 2007).

TAXONOMY AND GENETICS

The Delta Smelt is a distinctive estuarine-dependent species (McAllister 1963; Trenham et al. 1998), whose closest relative is the Surf Smelt (*H. pretiosus*), a marine species that occurs in San Francisco Bay (Stanley et al. 1995). Delta Smelt comprise one interbreeding population. Although genetic diversity of the population is fairly high, there are signs of bottlenecks associated with reduced population size (Fisch et al. 2011). The related Japanese osmerid, Wakasagi (*H. nipponensis*) has invaded the estuary from upstream reservoirs, but very limited hybridization with Delta Smelt has been detected (Trenham et al. 1998).

HISTORIC AND CURRENT DISTRIBUTION

During the first systematic surveys of fish in the upper estuary, Delta Smelt were widely distributed throughout the Delta, Suisun Bay and Marsh, and western San Pablo Bay (Erkkila et al. 1950; Ganssle 1966; Radtke 1966; Moyle 2002). Despite being tolerant of meso-haline salinities (see "Ecology," page 4), their distribution was largely confined to low salinity (<7 psu) tidal regions (Bennett 2005). The early surveys showed high abundance in Suisun Bay and Marsh, with the highest catches occurring in the Sacramento River channel near Sherman and Decker islands (Bennett 2005). Recent findings that Delta Smelt can reside in fresh water for their entire life cycle (Merz et al. 2011; Sommer et al. 2011; Sommer and Mejia 2013) indicate that their upstream limits are determined by tidal action to transport them to favorable habitats (cool, zooplankton-rich environments).

An analysis of data from seven widespread, long-term sampling programs and 23 regional and short-term (since 2000) sampling programs described the total distribution as extending from San Pablo Bay to the confluence of the Sacramento and Feather rivers in the north Delta and the fork of the Old and San Joaquin rivers in the south Delta, an area encompassing approximately 51,800 ha. Smelt of all stages were most abundant in the center of their range, from Suisun Marsh and Grizzly Bay up the Sacramento River to the Cache-Lindsey Slough Complex (Merz et al. 2011). Because the standard Delta fish surveys (Bennett 2005) sample mainly larger channels and embayments, the importance of peripheral areas as year-around habitat for smelt has been discovered only recently. These include the Napa River, the Cache–Lindsay Slough Complex, the Toe Drain, the Sacramento Deepwater Ship Channel and Liberty Island (Sommer and Mejia 2013). This discovery should probably be labeled as "rediscovery" because the first extensive survey of Delta fishes (Erkkila et al. 1951), caught smelt year-round during 2 years of sampling the fresh waters of the Delta. A similar pattern was shown in Radtke (1966).

The distribution of Delta Smelt changes on a seasonal basis with life stage (Figure 2) (Sommer et al. 2011). In winter, sub-adult and adult smelt move into fresh water for spawning and are sampled using the Fall Midwater Trawl (FMWT) and Spring Kodiak Trawl (SKT). In spring and summer, larval and juvenile smelt move into brackish water, primarily in Suisun Bay and Suisun Marsh (Dege and Brown 2004), and are sampled using the 20-mm Survey. Most Delta Smelt rear in low salinity habitat in summer and fall (Feyrer et al. 2007; Nobriga et al. 2008), allowing them to feed on abundant zooplankton; they are sampled by the Summer Townet Survey (TNS) and the University of California at Davis' (UC Davis) Suisun Marsh Survey. This seasonal pattern of distribution is used as evidence that Delta Smelt are a migratory "semi-anadromous" species, following the original conceptual model of Moyle et al. (1992). Recent distributional studies, however, indicate that movement patterns of smelt are highly variable, depending on outflow, exports, channel configurations, and other factors.

As Delta Smelt abundance has declined and habitat conditions have changed, their distribution has become more restricted, excluding most of the central and south Delta (Merz et al. 2011). In both old and recent surveys, most smelt have been caught in the arc of habitat from the Cache–Lindsay Slough Complex in the north Delta, down the Sacramento River, to Montezuma Slough in Suisun Marsh. This arc of tidal habitat is connected by flows from the Sacramento River. An increasingly higher

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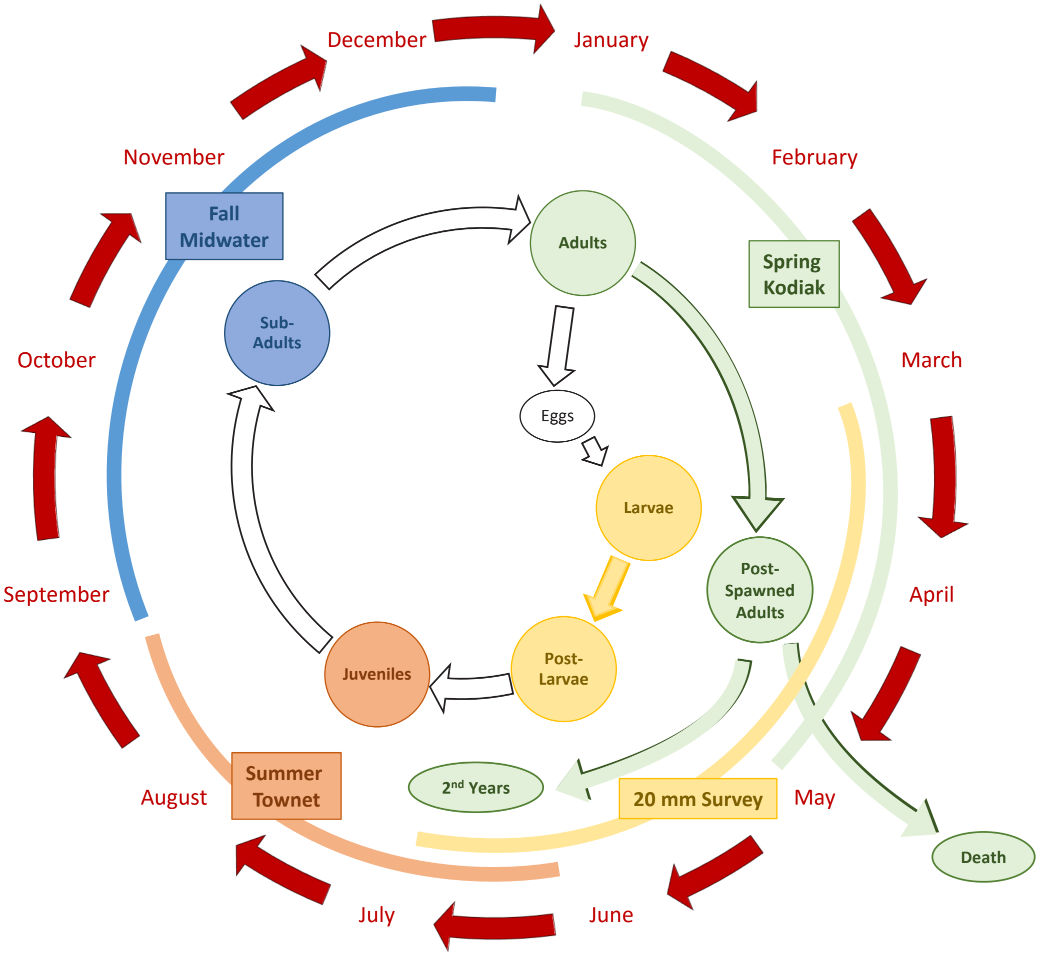

Figure 2 Delta Smelt distribution and abundance, in relationship to four key surveys, calendar year, and the Delta Smelt life cycle. Larvae and post-larvae are sampled in the 20-mm Survey (shown in yellow); juveniles by the Summer Townet Survey (shown in orange); sub-adults by the Fall Midwater Survey (blue); and adult spawners and post-spawners by the Spring Kodiak Trawl (green). A small number of smelt survive a second year, allowing them another opportunity to spawn the following winter.

percentage of smelt caught in various surveys are found in freshwater areas, year around, such as the Sacramento Deepwater Ship Channel and the Toe Drain of the Yolo Bypass (Merz et al. 2011; Sommer et al. 2011; Sommer and Mejia 2013).

Currently, Delta Smelt rarely occur in the central and south Delta, especially during summer/fall because the water is too warm or too clear to sustain them. However, hydraulic conditions created by water operations can cause net flows to pull larvae and juveniles towards the south Delta, although survival is likely low (Kimmerer and Nobriga 2008; Grimaldo et al. 2009). Restrictions on pumping have limited occurrence of these events since 2009 (USFWS 2008; SLDMWA et al. vs. Salazar et al. 2009).

ECOLOGY

Temperature

Delta Smelt are commonly found at temperatures of 10 to 22 °C. Wild-caught Delta Smelt show a critical thermal maximum of 25 °C for juvenile fish acclimated to 17 °C (Swanson and Cech 2000). Cultured smelt acclimated to 16 °C have a critical thermal maximum of about 28 °C, but thermal tolerance decreases from late-larval to post-spawning fish (Komoroske et al. 2014, 2015). Molecular assays suggest that thermal stress begins at about 20 to 21 °C depending on life history stage. Delta Smelt are unable to compensate for thermal stress, meaning short-term exposure to stressful conditions can lead to chronic stress (Komoroske et al. 2015).

These results are consistent with reduced smelt catch at higher temperatures. The majority of Delta Smelt juveniles (TNS) and pre-adults (FMWT) are caught at temperatures of <22 °C (Nobriga et al. 2008). This is consistent with the absence of Delta Smelt from the San Joaquin River and the south-central Delta during summer. Presumably, Delta Smelt of different life stages avoid areas (or die) where water temperatures are near thermal maxima, and are therefore less likely to be captured in surveys.

Salinity

Delta Smelt is a euryhaline species mostly inhabiting salinities from 0 to 7 psu, but can tolerate up to 19 psu (Swanson and Cech 2000; Moyle 2002) and even sea water for short periods of time (Komoroske et al. 2014). Data from the TNS and FMWT indicate that over 70% of juvenile and 60% of pre-adult Delta Smelt are caught at salinities less than 2 psu, with over 90% occurring at less than 7 psu (Bennett 2005). Recent studies indicate that there is a small part of the population that stays in fresh water for its entire life cycle. The fact that Delta Smelt can be reared in captivity in fresh water through their entire life cycle supports these findings. However, most smelt spend part of their life cycle near or slightly upstream of 2 psu in the entrapment or low-salinity zone (LSZ). Both the TNS (Nobriga et al. 2008) and FMWT (Feyrer et al. 2007) found peak occurrences of Delta Smelt in areas with low specific conductance, with somewhat lower occurrences in fully fresh water. This finding is consistent with the observation that most juveniles and sub-adults rear in the low-salinity region of the estuary, as they presumably did historically (Feyrer et al. 2007; Nobriga et al. 2008; Hasenbein et al. 2013; Komoroske et al. 2014).

Turbidity

Juvenile and sub-adult smelt are strongly associated with turbid water in spring and summer (Nobriga et al. 2008; Sommer and Mejia 2013), continuing into fall (Feyrer et al. 2007). The translucent body color and small size of Delta Smelt may make them less visible to predators in moderately turbid water. Turbidity reduces Largemouth Bass predation on Delta Smelt in mesocosm experiments (Ferrari et al. 2014).

Delta turbidity above 10 NTU coincides with increased entrainment of adult Delta Smelt (Grimaldo et al. 2009). This turbidity increases results from the flush of suspended material in rivers, after major storms. The "first flush" of the rainy season is likely a trigger for adult Delta Smelt to move toward spawning areas, including areas within the influence of the south Delta pumping plants (Sommer et al. 2011; Bennett and Burau 2015).

Feeding Behavior

Delta Smelt are visual zooplankton feeders, using suspended particles (i.e., turbidity) as a background to increase visual acuity in the near-field during daylight (Hobbs et al. 2006; Slater and Baxter 2014). As with all visual feeders, visual range and prey density determine feeding success. Optical attributes of the water column are affected by turbidity from organic particles, such as algae and detritus, and from inorganic particles, such as sand and silt (Utne–Palm 2002; Hecht and Van der Lingen 2012). Feeding of larval Delta Smelt is increased at high algae concentrations and light levels (Baskerville-Bridges et al. 2003). The addition of algae or other suspended particles is standard practice for successfully rearing Delta Smelt larvae in culture facilities (Mager et al. 2003; Baskerville–Bridges et al. 2005; Lindberg et al. 2013). Presumably, the suspended particles provide a background of stationary particles that helps the larvae detect moving prey. Hasenbein et al. (2016) observed highest feeding rates of late-larval Delta Smelt at beween 25 and 80 NTU. Feeding success of juvenile and adult Delta Smelt is reduced by high turbidity (250 NTU) when light levels are very low (Hasenbein et al. 2013), supporting observations that smelt feed largely in the daytime (Hobbs et al. 2006). However, such high turbidities are rarely observed in the wild.

Swimming Behavior

Laboratory smelt have maximum sustained swimming velocities of about 28 cm s^{-1}. (Swanson et al. 1998). A discontinuous "stroke-and-glide" behavior is used at water velocities of less than 10 cm s^{-1}, while sustained swimming occurs above

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15 cm s^{-1}. However, many fish will not swim above water velocities of 10-15 cm sec^{-1}. Stroke and glide swimming may be advantageous for a diel-feeding planktivore because it minimizes continuous movement that might attract predators.

Despite this swimming performance, Delta Smelt can travel large distances by using tidal currents (Bennett and Burau 2015). Lateral turbidity gradients change with tides and around first flush events, and these gradients coincide with lateral Delta Smelt movements toward the mid-channel during flood tides and toward the shoreline during ebb tides. Delta Smelt are caught more frequently throughout the water column during flood tides. On ebb tides they are observed only in the lower half of the water column and along the sides of the channel. By behaviorally selecting positions on the edge or center of the channel and near the surface or bottom of the water column, Delta Smelt can use tidal currents to move upstream or downstream, or avoid such currents to maintain position (Bennett et al. 2002; Feyrer et al. 2013; Bennett and Burau 2015).

Food and Feeding

Delta Smelt feed mainly on small crustacean zooplankton, particularly calanoid copepods (Moyle et al. 1992; Lott 1998; Slater and Baxter 2014). This is true across decades of study. For example a study from 1972–1974 showed that the dominant food item was the calanoid copepod *Eurytemora affinis*, with cladocerans and mysid shrimp (*Neomysis mercedis*) being important at times (Moyle et al. 1992). By the late 1980s, *E. affinis* was largely replaced in smelt diets, except in early spring, by the similar-sized introduced calanoid *Pseudodiaptomus forbesi*. Smelt also eat other calanoids, including the larger *Acartiella sinensis* and the more evasive *Sinocalanus doerri*, but they are less commonly found in diets. In fresh water, a higher proportion of cladocerans and native cyclopoid copepods appear in diet studies (Nobriga 2002; Hobbs et al. 2006; Slater and Baxter 2014). In general, most copepod prey of Delta Smelt are of similar nutritive value (Kratina and Winder 2015). Larger smelt are capable of supplementing their diet with larger crustaceans such as mysids and amphipods, as well as with larval fishes (Moyle et al. 1992; Lott 1998; Feyrer et al. 2003). First food tends to be copepod nauplii or copepodites. The tiny invasive cyclopoid *Limnoithona tetraspina* is poorly represented in diets; this is presumably a function of capture evasion and low nutritional value (Bouley and Kimmerer 2006; Kratina and Winder 2015).

Predators and Competitors

Historically, Delta Smelt were likely occasional prey for aquatic predators such as Thicktail Chub (*Gila crassicauda*), Sacramento Perch (*Archoplites interruptus*), Sacramento Pikeminnow (*Ptychocheilus grandis*), Chinook Salmon and Steelhead smolts, Sturgeon, and perhaps avian predators as well (Grossman, this volume). After the Gold Rush, native predatory fish were largely replaced by a suite of non-native species, most conspicuously Striped Bass (*Morone saxatilis*), a pelagic piscivore (Stevens 1966; Thomas 1967; Moyle 2002; Grossman, this volume).

Predation rates on smelt were likely linked to their presumed abundance, given that their behavior and translucent color makes them difficult to target as a prey species. Currently, Delta Smelt are rarely seen in diets of fish predators. This is probably because low encounter rates make it difficult for active, mobile predators to detect it, as an uncommon, nearly invisible prey (Grossman et al. 2013; Grossman, this volume). The alien fish that may be the most significant predator on Delta Smelt is Mississippi Silverside (*Menidia audens*). Silversides feed diurnally along shallow water edge habitat and could be potentially important predators on smelt eggs and larvae (Bennett and Moyle 1996; Bennett 2005). Delta Smelt DNA has been isolated in silverside guts (Baerwald et al. 2012), suggesting that silversides do prey on smelt. However, no quantitative evidence exists for the overall effect of predation or competition by silversides.

The potential for alien piscivores to affect Delta Smelt abundance is suggested by (1) by inverse correlations of predatory fish (including Striped Bass, Largemouth Bass [*Micropterus salmoides*] and Mississippi Silverside) with Delta Smelt (Bennett and Moyle 1996; Brown and Michniuk 2007), and (2) by bioenergetics models of Striped Bass that show they can potentially be significant predators on smelt (Loboschefsky et al. 2012). However, empirical evidence and statistical modeling have shown scant evidence for a cause-and-effect relationship between smelt and predator abundances (Mac Nally et al. 2009; Thomson et al. 2010; Maunder and Deriso 2011; Miller et al. 2012; O'Rear 2012; Nobriga et al. 2013), a pattern that follows much of the general literature on predation (e.g., Doherty and Richie 2016).

Historic competitors may have been other planktivorous fishes, especially Northern Anchovy (*Engraulis mordax*) and Longfin Smelt in Suisun Bay, and juveniles of other native fishes in the Delta. Potential alien competitors include American Shad (*Alosa sapidissima*), Threadfin Shad (*Dorosoma petenense*), Golden Shiner (*Notemigonus chrysoleucas*), juvenile centrarchids, and juvenile Striped Bass and Mississippi Silverside (an intraguild predator).

Competition may occur if zooplankton resources are limited during critical points of the smelt life cycle. Today, the most effective, if indirect, competitors are overbite (*Potamocorbula amurensis*) and Asian clams (*Corbicula fluminea*) (Kimmerer et al. 1994; Kimmerer 2006), which depress zooplankton abundance by grazing down phytoplankton and zooplankton nauplii (Durand 2015). Although Delta Smelt remained abundant in the Delta and Suisun Bay through the 1970s, long after most introduced fish predators and competitors had established populations (Grossman, this volume), smelt began rapidly declining after the invasions of overbite clam and Mississippi Silverside in the 1980s. At the same time, presumed predators and competitors, such as other planktivorous fishes and Striped Bass, began parallel long-term decreases in abundance.

REPRODUCTION

Delta Smelt have a protracted spawning season, given their life span, from late January through June. Larvae are seen from late February through early May (Moyle et al. 1992; Bennett 2005). They are thought to spawn on shallow sandy beaches, although spawning has not been observed in the wild. In laboratory culture, Delta Smelt spawn on the bottom and sides of tanks, indicating they need substrate for deposition of their adhesive eggs (Lindberg et al. 2013). The number of eggs per female is exponential to length for cultured fish, although the relationship is less clear in wild fish (Lindberg et al. 2013). The number of eggs per female for small fish (60 to 80 mm) ranges from 1,000 to 2,500. Larger females (80 to 120 mm) can have 2,500 to 12,000 eggs (Bennett 2005; Lindberg et al. 2013). Mature eggs have been found in females as small as 56-mm fork length (FL) in the wild (Kurobe et al. 2016).

Spawning behavior of captive Delta Smelt has been observed and studied using parentage genetic techniques in outdoor mesocosms. Females can spawn repeatedly with multiple males (LaCava et al. 2015) up to four times in a season, with resting periods of 40 to 50 days (M. Nagel, pers. comm., 2016, with J. Hobbs, unreferenced, see "Notes"). The capacity of females to produce multiple clutches of eggs in the wild when environmental conditions are favorable for reproduction could be important for maintaining population resilience during periods of low adult abundance (Kurobe et al. 2016).

POPULATION TRENDS AND DYNAMICS

Abundance indices for Delta Smelt are calculated from the catch-per-unit-effort of key agency surveys, shown in Figure 3 (IEP MAST 2015). Indices of abundance, rather than abundance estimates or absolute numbers, are used for two principal reasons. First, their distribution is patchy and mobile, and smelt may at times occupy regions that are difficult to sample. This is true even in areas of peak abundance, where likelihood of capture increases. Second, capture efficiencies of the various types of sampling gear are poorly known and difficult to compare among surveys. With the exception of the SKT surveys, none of the sampling programs were specifically designed to capture Delta Smelt and they all have biases related to how and where they sample. But together they survey a wide variety of habitats and regions of the estuary, at all times of year, providing a reasonable picture of smelt distribution and abundance (IEP MAST 2015).

Because actual smelt population size cannot be known with certainty, the indices are a convenient way to track population trends and their response to environmental conditions. Delta Smelt is mostly an annual species, resulting in highly variable year to year abundance (Bennett 2005). Small changes in vital rates such as growth, survival and fecundity

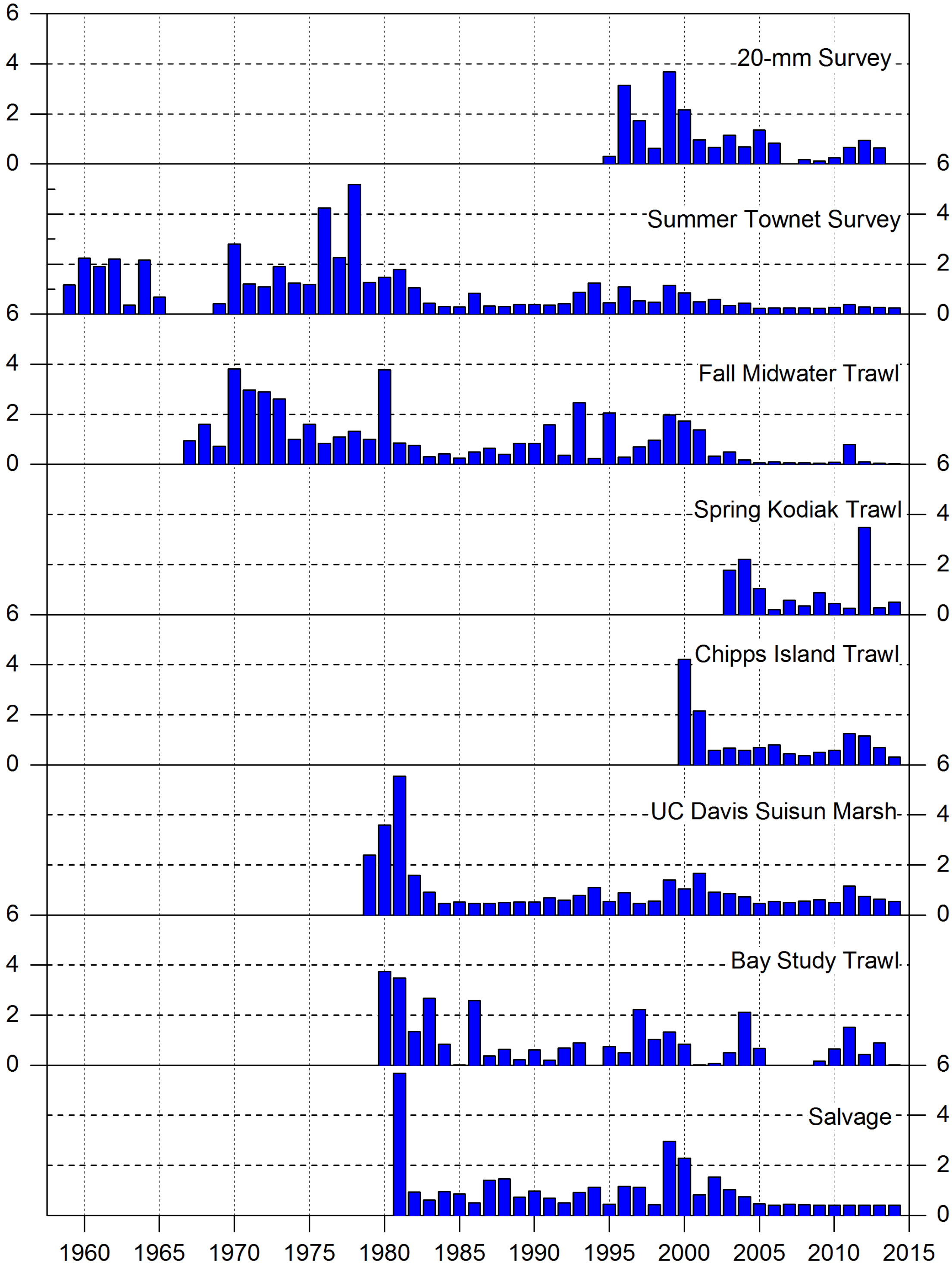

Figure 3 Abundance indices for life stages of Delta Smelt including larvae and juveniles (20-mm Survey), juveniles (Summer Townet Survey), sub-adults (Fall Midwater Trawl), and adults (Spring Kodiak Trawl). The initiation of each individual survey is indicated by the first bar; missing bars indicating years for which an index was not calculated. Indices for each survey were standardized by subtracting each yearly index from the global mean for each survey and dividing by the standard deviation. (Sources: Interagency Ecological Program unpublished data, CDFW and CDWR).

can have large effects on adult abundance (Bennett 2005), although long-term trends are apparent. Delta Smelt experienced a major decline in the early 1980s (Manly and Chotkowski 2006; Thomson et al. 2010), followed by a substantial but brief increase in 1998–1999 (Manly and Chotkowski 2006). This, in turn, was followed by an abrupt decline in the early 2000s, part of the so-called pelagic organism decline (POD) (Manly and Chotkowski 2006; Sommer et al. 2007; Thomson et al. 2010).

The population dynamics of Delta Smelt have been examined by calculating ratios of various indices to estimate survival or population growth within or between cohorts (Maunder and Deriso 2011; Mac Nally et al. 2010; Miller et al. 2012). The role of density dependence has been an area of emphasis for these population dynamic studies. An apparent decrease in the carrying capacity of the estuary in the 1980s resulted in an increase in density-dependent mortality from the juvenile stage in late summer through the adult stage in fall (i.e., between the TNS and FMWT indices) (Sweetnam and Stevens 1993; Bennett 2005; Maunder and Deriso 2011). This is supported by chronically low zooplankton prey density in summer (Miller et al. 2012). However, apparent density-independent survival from late larvae to juveniles (i.e., between the 20-mm Survey and TNS indices, Figure 3), suggests that carrying capacity is not a limitation during spring (Maunder and Deriso 2011). High summer temperatures are associated with reduced juvenile abundance and density-independent mortality from larval to juvenile stages (Mac Nally et al. 2009; Maunder and Deriso 2011).

Yearly recruitment based upon adult population abundance (stock size), has been described as density "vague" because, while there is some evidence of reduced survival with higher density, survival is highly variable from year to year (Maunder and Deriso 2011; Mac Nally et al. 2010; Miller et al. 2012). In general, the relationship between sub-adult (spawner) abundance indices and juvenile abundance in the following year is poor (i.e., between the FMWT and TNS indices, Figure 2), as is the relationship between subadult indices from one year to the next. This suggests that inter-generational abundance is driven more by environmental conditions, rather than by density-dependent factors.

As the Delta Smelt population approaches zero, density dependence becomes increasingly less likely. However, shrinking habitat volume, or declining food abundance in fall, might facilitate periods of density-dependent mortality, particularly between the juvenile to adult stage. The most useful explanatory variables for Delta Smelt stock–recruit relationships appear to be factors associated with juvenile survival, e.g., summer–fall food availability, summer temperatures, and egg production (Rose et al. 2013a, 2013b).

CONCEPTUAL MODELS

Conceptual models that link ecosystem functions with proposed management actions are valuable tools to highlight key uncertainties in fisheries management (Thom 2000; Ogden et al. 2005). In the Sacramento–San Joaquin Delta, conceptual models have been used extensively to synthesize knowledge of species–habitat relationships (Baxter et al. 2010; DiGennaro et al. 2012), developing predictions for adaptive management actions (USBR 2012) and evaluating outcomes of drought (L. Conrad, pers. comm. to L. R. Brown, 2016, unreferenced, see "Notes"). Many such efforts have been conducted for Delta Smelt since its listing in 1993, which was accompanied by the first smelt conceptual model (Moyle et al. 1992). Since then, a series of conceptual models followed (Bennett 2005; Nobriga and Herbold 2009; Baxter et al. 2010).

A new ecosystem-based conceptual model framework for linking environmental drivers to stage-specific Delta Smelt responses is based on a literature review of Delta Smelt biology and ecology (IEP MAST 2015). The model format is process-driven rather than descriptive, so it uses a box and arrow diagram. The model is structured around four quadrants that represent each life stage (life cycle module) and embedded within a series of hierarchical tiers. The tiers represent direct and indirect effects from landscape-level attributes, environmental drivers, and habitat attributes which drive vital rate responses (i.e., growth and survival) through the life cycle. For each life stage module, a more traditional box-and-arrow diagram links various habitat attributions to the transition of the smelt through the life stage. The diagrammatic representation is complex and comprehensive, and allows identification of disparate linkages between environmental variables and vital rates of smelt. The framework is also flexible enough to adapt to most management scenarios and is being used as a management tool to assess the effects of the recent drought on Delta Smelt and to guide monitoring plans for tidal wetland restoration (IEP TWMPWT 2016).

Here, we present two diagrams that synthesize our understanding of Delta Smelt biology and ecology based on information in this report (Figures 4 and 5). Our synthesis is presented as a hypothesis, grounded in our combined expertise (collectively more than 100 years of accumulated experience in the system).

Figure 4 describes physical controls on foraging effectiveness during the growth phase of Delta Smelt (March to December), as a different example of conceptual models that can capture various aspects of smelt behavior and life history. The vertical arrow on the left of the Figure represents a hydrodynamic gradient of mixed to stratified conditions or from low to high residence time. The horizontal arrow shows a depth gradient from deep to shallow. Delta Smelt move opportunistically across the environmental gradients to optimize their physiological needs, represented by the triangle, as a series of trade-offs. Smelt perform best in turbid conditions, but turbidity is likely to be greatest in highly turbulent areas, either from wind or high-velocity currents, where smelt, with limited swimming ability, have a hard time sustaining themselves (Bever et al. 2016). Foraging success can improve in some shallow regions of the estuary, where less turbulent conditions and higher residence time allow zooplankton to aggregate. This became particularly true after the 1986 invasion of the overbite clam, which led to greatly decreased zooplankton abundance. However, the ability of Delta Smelt to find turbid, food-dense regions is mediated by thermal tolerance, especially in summer/fall. Thermal refuges may exist away from abundant food resources (e.g., in deep water). We hypothesize that smelt must actively negotiate conditions to maximize their needs (i.e., turbidity, food abundance, and temperature) and are potentially most viable if they can find conditions where these needs converge.

Figure 5 shows a life cycle diagram for Delta Smelt, using a format similar to that in Figure 2. Key stressors referenced in the text, both direct and indirect, are shown at vulnerable stages of the life cycle. Chronic low-level stressors are omitted.

In December adults begin upstream movement, timed to the first pulse of outflow that is sufficient to increase turbidity (Bennett and Burau 2015). Spawning habitat has been reduced in part because of the effect of restricted inflow and increased export, which have reduced turbidity and promoted the colonization of alien species, in particular dense stands of Brazilian waterweed, *Egeria densa* (Durand 2015). This submersed aquatic vegetation (SAV) has created highly unfavorable habitat by occupying likely spawning areas, and by slowing the water further, making it clearer and warmer. This makes it even less suitable for Delta Smelt and more suitable for alien fishes such as Largemouth Bass and sunfishes.

Delta Smelt have generally been abundant in the north Delta, even before their decline, which is where most current reproduction is thought to occur. While the habitat is less degraded than in the south Delta, predation on eggs and larvae by Mississippi Silversides may lead to high mortality. Most post-larval fish move out of the north Delta in spring, at which point they may be vulnerable to entrainment in the south Delta pumps and, hence, high mortality. These conditions have been reduced when springtime pumping restrictions are put in place during periods of vulnerability.

Apparently, most juvenile smelt once reared in Suisun Bay and Marsh, where historically, they fed upon abundant plankton resources. Since the 1980s, phytoplankton declines resulting from poor water-quality conditions (possibly high levels of ammonium) and intensive grazing by overbite clam, have led to food limitation in much of Suisun Bay, especially in late summer and fall. Foraging success is further limited by decreases in outflow that constrain the LSZ to a deeper and more spatially constricted region, rather than the shallow habitats of Little Honker Bay and Suisun Marsh. Food limitation likely reduces fall juvenile growth, limits survivorship to adulthood, and limits reproductive output.

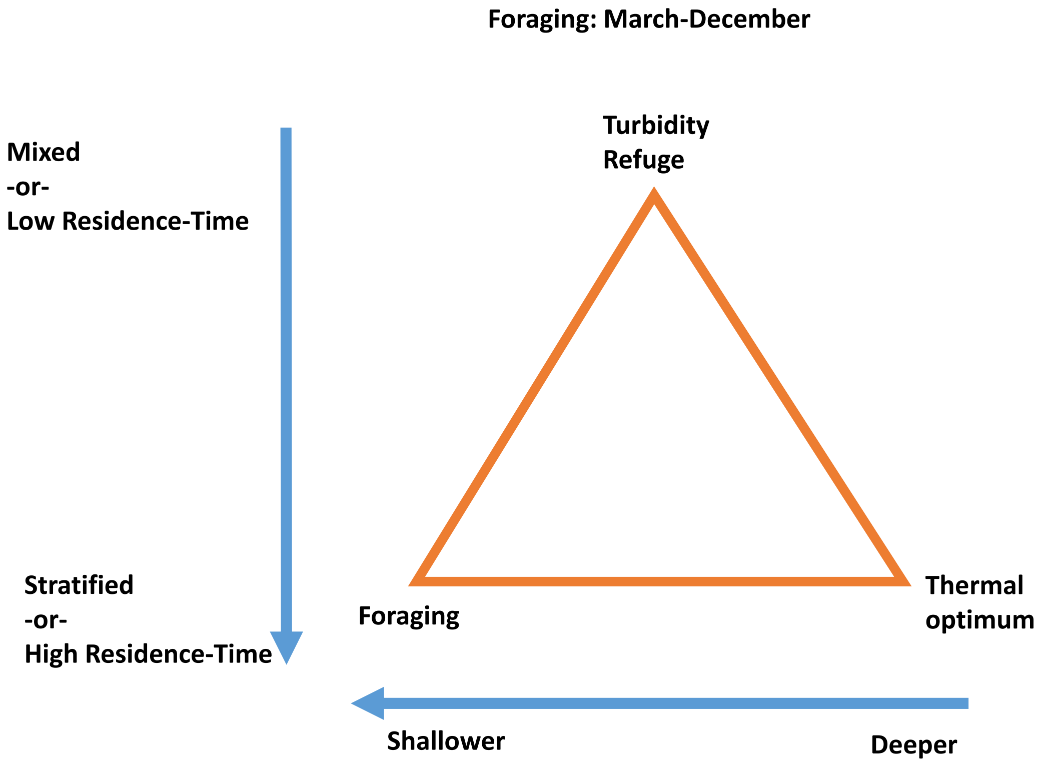

Figure 4 Physical controls on growth phase of delta smelt life cycle. The points of the triangle represent smelt physiological requirements, such as cool temperatures, high turbidity for refuge and feeding, and dense zooplankton concentrations for foraging. The axes represent gradients of geophysical conditions upon which these conditions may occur. The horizontal axis shows a depth gradient. Water temperature in large, deep distributary channels tends to be cooler and more favorable to smelt than the shallower regions of terminal channels and shoals of embayments. However, foraging opportunities may increase in shallow water areas because of high productivity and reduced clam abundance, which can lead to high plankton densities. The vertical axis represents both vertical and horizontal mixing of the water column from hydrodynamic, geomorphic and Aeolian processes. In well-mixed or low residence-time regions of the estuary, dynamics increase the amount of sediment in the water column, increasing turbidity, which offers refuge for smelt. In contrast, under stratified conditions or in regions with high residence time, foraging opportunities may increase because of the concentration of zooplankton biomass. Optimal conditions rarely coincide in the Delta, forcing smelt to satisfy their physiological requirements by making continuous adjustments that represent tradeoffs. For example, less than optimal turbidity or temperature conditions in shallow, less turbulent water may be offset by higher concentrations of food. Likewise, at cool temperatures in deep water, less food is needed to maintain the fish.

CAUSES OF DECLINE

> “Uncontrolled drivers of change (population growth, changing climate, land subsidence, seismicity) means that the Delta of the future will be very different from the Delta of today.”
>
> —Healey at al. 2008

The ultimate cause of decline in Delta Smelt is competition with people for water and habitat. The explosive growth of the California economy since the Gold Rush resulted in rapid and extensive habitat alteration, invasions of new predators and competitors, and changes in hydrology. Changes continue at an accelerated pace, tracking both population and economic growth (Hanak et al. 2011; Hanak and Lund 2011). In this section we briefly review proximate drivers of decline: entrainment, altered hydrology, food, predation, contaminants, habitat change, drought, and climate change. We finish by integrating the science into a synthetic understanding of Delta Smelt biology.

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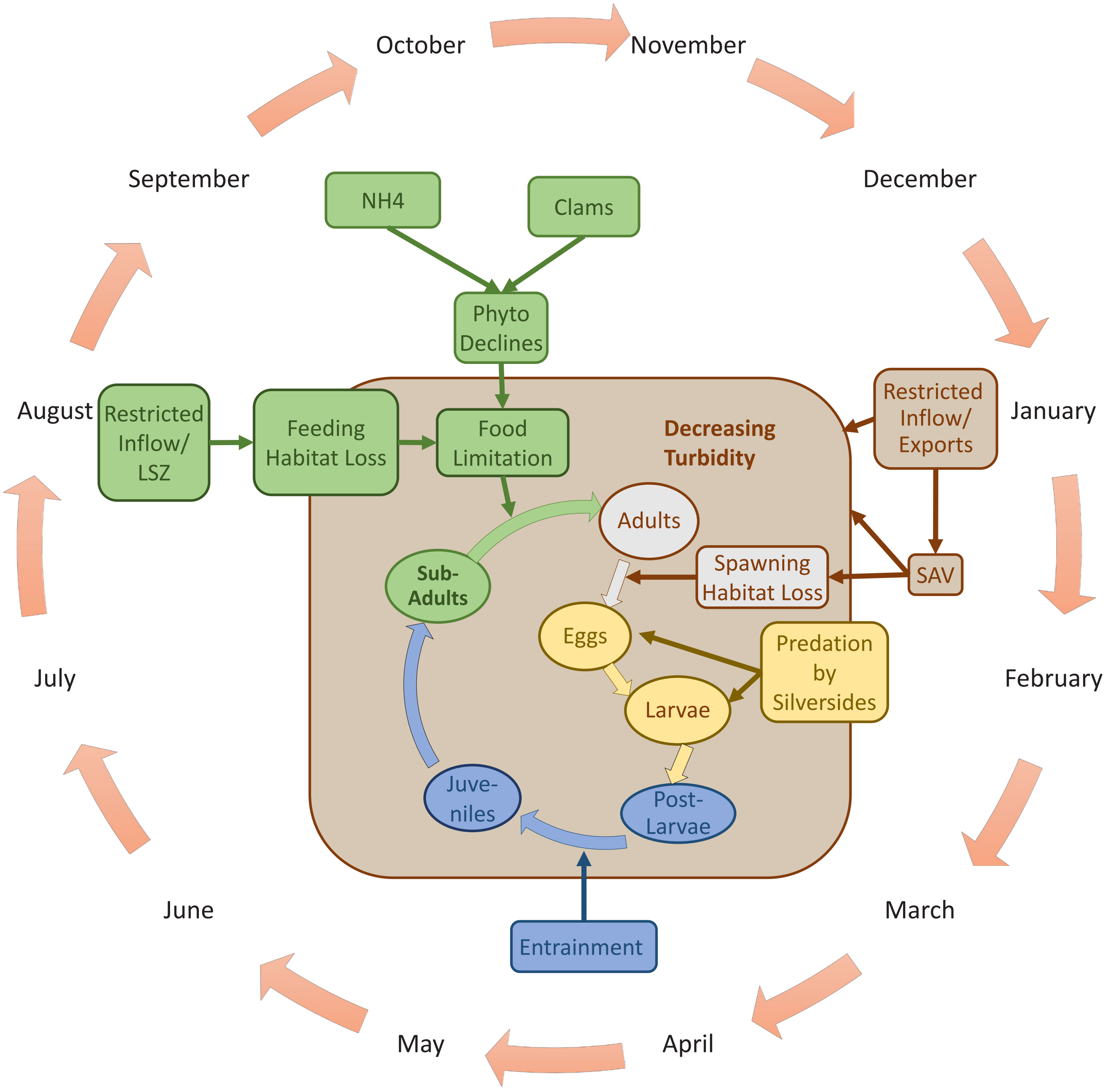

Figure 5 Simplified conceptual model of key hypothesized factors that limit Delta Smelt recovery. Note that direct factors of food limitation, predation, and spawning habitat loss are linked to underlying causes. Orange arrows represent the calendar year; yellow shapes represent predation by Mississippi Silversides on eggs and larvae; blue shapes represent entrainment of post-larvae and juveniles at the south Delta water export facilities; green shapes represent factors that affect food limitation on sub-adults; brown/grey shapes represent factors that affect turbidity (brown) and spawning habitat (grey). Low turbidity (brown box, middle) increases stress and interacts with other factors to decrease smelt success. For a more detailed model, see IEP MAST (2015).

Entrainment

The Delta has thousands of water diversions, but most entrainment of Delta Smelt is by the giant pumps of the Central Valley Project (CVP) and State Water Project (SWP) located in the south Delta. High exports of freshwater and low inflows to the Delta can create reverse flows and asymmetrically strong flood tides, which carry smelt, especially larvae, toward the pumps (Monsen et al. 2007; Grimaldo et al. 2009). Few Delta Smelt are entrained by small diversions found throughout the Delta (Nobriga and Herbold 2009). The pump intakes are generally small and close to shore, and most diversions take place at times and places when Delta Smelt, especially larval smelt, are not likely to be present.

The intakes to the south Delta pumping plants have louvers that divert fish to a capture facility where they are collected and trucked for release at downstream locations, a process known as salvage. A sub-sample of these fish is counted, but estimates do not include larvae and juvenile fish less than 20 mm total length (TL). For Delta Smelt, these counts provide a rough estimate of >20-mm-long fish killed by the operation because most smelt do not survive being salvaged (Miranda et al. 2010a, 2010b; Aasen 2013; Afentoulis et al. 2013; Morinaka 2013). Because of high pre-screen mortality (especially in Clifton Court Forebay, at the SWP) and a lack of estimates for fish <20 mm long, only a small percentage of all smelt entrained are counted (Castillo et al. 2012), and mortality estimates for handling and transport are biased low. Moreover, most smelt moved into the central and south Delta do not make it to the pumps; they likely die because of poor water quality or other factors. The population-level effect of removing spawning adults is likely high. Salvage mortality tends to be highest at times when the Old–Middle River flow is most negative (i.e., flows are reversed) and turbidity is high (USFWS 2008). Salvage also tends to be highest at times when exports are high relative to outflow, so a greater proportion of the water is moving towards the pumps; this changes the pattern of water movement through the central and south Delta (Kimmerer 2008).

Delta Smelt are most vulnerable to entrainment by the CVP and SWP pumps during upstream adult spawning movements and as larvae move downstream from fresh to brackish water (Sweetnam 1999; Sommer et al. 2011). In the early 1980s, when smelt were still abundant, high salvage occurred at all export levels, dominated by adults between December and March–April, and by larvae and juveniles from April through July (Kimmerer 2008; Grimaldo et al. 2009). Since the 1990s, May-June juvenile salvage has declined and July–August late juvenile and sub-adult salvage has nearly disappeared, because Delta Smelt no longer reside over summer in the central–south Delta.

During years of high exports, up to 25% of larval–juvenile smelt and up to 50% of the adult population may be entrained at the CVP and SWP, annually (Kimmerer 2008). Salvage increased greatly in winter of 2002, coincident with the first year–class of the POD (Figure 6). Modeling efforts suggest that these periodic entrainment losses may have adversely affected the Delta Smelt population (Kimmerer 2011; Maunder and Deriso 2011; Miller et al. 2012; Rose et al. 2013a, 2013b). In particular, the high entrainment of Delta Smelt in the winter of 1982, followed by high rates of pumping in the following spring, when larvae were most abundant, is associated with the beginning of the major smelt decline over the next 3 decades. Whether or not this is cause-and-effect needs further study. The drastic reduction in the population during the 1980s made it more difficult for it to recover from other events such as overbite clam and silverside invasions. Given the annual life cycle, any episodic salvage event may undermine population resilience by keeping numbers low, even when environmental conditions are good.

Food and Feeding

Food resources for Delta Smelt, particularly calanoid copepods and mysid shrimp, have decreased since the 1980s, corresponding to declines in phytoplankton abundance (Brown et al., submitted). POD species abundances are related to prey abundance, and decreases in prey have reduced the carrying capacity of the system to support fish (Sommer et al. 2007; Kimmerer 2012). Modeling exercises support the hypothesis that food limitation affects Delta Smelt population trends (Miller et al. 2012; Rose et al. 2013b).

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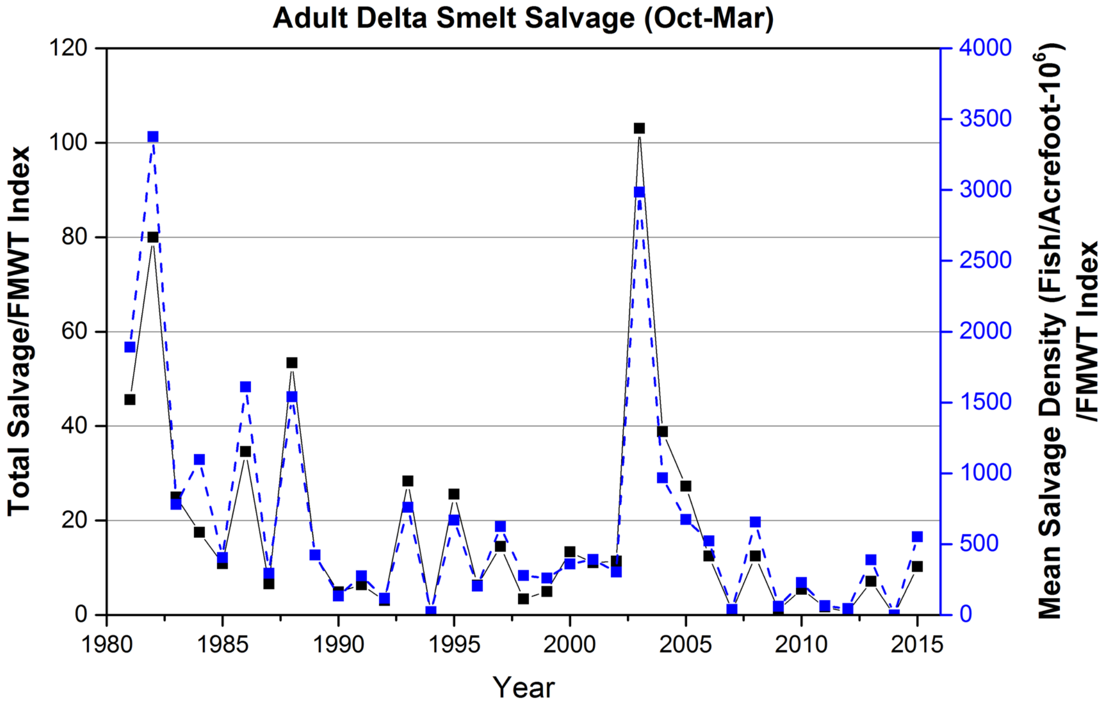

Figure 6 Total reported October–March salvage for adult Delta Smelt and the corresponding mean salvage density based on the total monthly salvage and water volume exported by the CVP and SWP. Note that the salvage is standardized to the Fall Midwater Trawl Index (IEP MAST 2015).

Studies of smelt gut fullness, growth, condition, and histology provide additional evidence for food limitation, particularly in spring and fall (Feyrer et al. 2003; Bennett 2005; Bennett et al. 2008; Baxter et al. 2008; Hammock et al. 2015). A mismatch between smelt and their prey in spring may decrease juvenile recruitment (Bennett 2005). Both Lott (1998) and Slater and Baxter (2014) found that >30% of Delta Smelt larvae <14 mm FL had empty guts in April. The frequency of empty guts increased during late spring-early summer during metamorphosis of larvae to juveniles (fish ca. 20 to 24 mm FL). Low calanoid abundance in late summer may affect survival to fall abundance (Kimmerer 2008; Mac Nally et al. 2009; Thomson et al. 2010; Miller et al. 2012). Smelt diets in Suisun Bay revert to smaller prey items after mid-summer and into fall, including less nutritious nauplii (Kratina and Winder 2015) and the smaller *Limnoithona tetraspina* (Slater and Baxter 2014). Warm water temperatures during summer exacerbate stress from low food availability and may explain reduced survival from summer to fall in some years (Bennett 2005; Bennett et al. 2008). Hammock et al. (2015) found that Delta Smelt captured from Suisun Marsh, the north Delta, and the Sacramento Deep Water Ship Channel showed more stomach fullness and better condition and growth indices than did fish captured in Suisun Bay and the confluence. Food limitation effects on Delta Smelt growth and survival varied considerably with season, year, and location (Hammock et al. 2015)

Predation

Delta Smelt have adaptations that make them surprisingly unavailable as prey for other fishes, except as larvae. Both native and alien potential Delta Smelt predators are generalists that focus on abundant prey, rather than on species as rare as Delta Smelt today (Grossman et al. 2013, Grossman, this volume). There is no evidence that these predators had a major effect on Delta Smelt populations in the past (see earlier discussion). Presently, Mississippi silverside is probably the most important predator of Delta Smelt larvae because of their ability to prey on eggs and larvae and their high abundance in shallow areas where Delta Smelt spawn (Bennett and Moyle 1996; Bennett 2005; Baerwald et al. 2012).

In the south Delta, warm temperatures, high water clarity, low flows, and expansion of invasive aquatic vegetation have created a novel ecosystem that largely excludes Delta Smelt and favors alien fishes. The alien fishes feed on a variety of alien and native prey, including invertebrates such as crayfish and amphipods. Largemouth Bass will consume Delta Smelt in mesocosms (Ferrari et al. 2014), but are unlikely to be a major predator in the wild because of limited habitat overlap between the two species.

Contaminants

Delta Smelt are exposed to a variety of contaminants throughout their life cycle but the nature and degree of the effects of contaminants on Delta Smelt health are not well documented (Johnson et al. 2010; Brooks et al. 2012). If contaminants significantly affect smelt, the effects are likely chronic rather than acute (Werner et al. 2010) but overall effects on wild populations are not known. Because of their short life cycle, smelt are more likely to suffer contaminant effects from direct exposure than from cumulative effects (biomagnification). Contaminants are most likely to affect smelt in combination with other stressors, such as starvation. The categories of contaminants that may affect Delta Smelt are pesticides, ammonia and ammonium, heavy metals, polycyclic aromatic hydrocarbons (PAHs) and polychlorinated biphenyls (PCBs), contaminants of emerging concern, and mixtures of any of the above (Fong et al., submitted). An increasingly wide array of contaminants are present in the water in which smelt live and in the prey they eat. New, highly toxic compounds (e.g., pyrethroids) have appeared coincident with the decline of Delta Smelt. Their contribution to the decline, if any, is most likely through indirect effects.

Pesticides. Pesticide concentrations in surface waters of the Delta are typically highest during winter and spring in runoff from rainfall. Thus pesticides are most likely to affect freshwater life stages of smelt. Peak densities of larval and juvenile Delta Smelt can coincide with elevated concentrations of dissolved pesticides (Kuivila and Moon 2004). Pesticides can affect Delta Smelt in diverse ways, by altering swimming behavior, gene expression, immune response, detoxification, and growth and development (Connon et al. 2009; Jeffries et al. 2015).

Ammonia and Ammonium. Delta Smelt spawning and larval nursery areas in the northern Delta may be at risk from exposure to ammonia and ammonium, mainly from discharge by the Sacramento Regional Wastewater Treatment Plant into the lower Sacramento River (Connon et al. 2011). However, concentrations of ammonia used in laboratory studies to assess risk were higher than concentrations measured in the wild.

Heavy Metals. Heavy metals and other elements of concern in the Delta include copper, mercury, and selenium. Sublethal effects of these elements on fishes include reduced fertility and growth, impaired neurological and endocrine functions, and skeletal deformities that affect swimming performance (Boening 2000; Chapman et al. 2010). These elements are often associated with sediment and may affect adult and larval life stages of smelt, because sediment is transported with significant rain events, especially the "first flush."

PAHs and PCBs. PAHs and PCBs from urban and industrial sources are found in excess of established water quality objectives in the Delta (Thompson et al. 2000; Oros et al. 2007), and are known to cause endocrine disruption in fish (Nicolas 1999; Brar et al. 2010).

Contaminants of Emerging Concern. Contaminants of emerging concern, such as pharmaceuticals, hormones, personal care products, and industrial chemicals are widespread in the aquatic environment, biologically active, and are largely unregulated (Kolpin et al. 2002; Pal et al. 2010). They are known to cause sublethal effects in fish including endocrine disruption, changes in gene transcription and protein expression, and morphological and behavioral changes (Brander et al. 2013).

Contaminant Mixtures. Interactions among contaminants can have both synergistic and antagonistic effects on fish physiology (e.g., Jordan et al. 2011). There is increasing evidence that compounds in mixtures show adverse effects at concentrations at which no effects are observed for single toxicants (e.g., Silva et al. 2002; Walter et al. 2002; Baas et al. 2009).

Habitat Change

Delta Smelt are pelagic fish that primarily inhabit the Delta and Suisun Bay. Here, we discuss some of the more important factors that influence their pelagic habitat: hydrology, salinity and outflow, turbidity, harmful algae blooms, drought, and climate change.

Hydrology. Since the construction of Oroville Dam in the 1960s, upstream diversions of water and exports from the Delta have increased in most years, while inflow (and consequently outflow) has decreased (Lund et al. 2007). These dramatic changes in hydrology and related factors have made much of the south and central Delta unsuitable as habitat for smelt and have interacted with other factors to create unfavorable conditions for smelt survival (Moyle and Bennett 2008). Changes in the timing and magnitude of seasonal Delta outflows have changed the size and location of places where smelt can find adequate food resources, especially in the fall. Changes to hydrology have likely promoted alien invasions including the spread of Brazilian waterweed, Mississippi Silverside and Largemouth Bass. These combined changes have caused Delta Smelt largely to disappear from the central and southern Delta, signifying major habitat loss (Feyrer et al. 2007; Nobriga et al. 2008). Most adult Delta Smelt now either move into the Sacramento River and Cache Slough region for spawning and rearing or stay year around in fresh water.

Salinity. While Delta Smelt have a fairly broad salinity tolerance; they were historically most abundant in the low salinity zone (LSZ) of the estuary, the position of which is determined by outflow (Moyle et al. 1992; Kimmerer et al. 2013; Sommer and Mejia 2013). Moderate hydrological conditions in late winter and spring place the LSZ in the Grizzly Bay region of Suisun Bay (Jassby et al. 1995). These conditions were beneficial to the Delta Smelt population at least partly because of high food abundance. At present, there is little evidence of the benefit of summer and fall occupancy in the LSZ (IEP MAST 2015). The relationship of smelt life stage abundance indices to spring (February to June) X2 (location of the 2-ppt isohaline) shifted downward after each sharp "step" decline in overall abundance. However, the slope of the relationship before and during the POD has not changed significantly (IEP MAST 2015), suggesting that years that carry the LSZ in western Suisun Bay through spring (e.g., 2011) have a positive effect on Delta Smelt abundance. In addition to moving the LSZ to a favorable location for smelt, increased outflow influences habitat quality through its effect on food supply, dilution of contaminants, and turbidity.

Turbidity. Long-term declines in turbidity may be a key reason that juvenile Delta Smelt now rarely occur in the south Delta during summer (Nobriga et al. 2008). Turbidity is usually lower in the central and south Delta than in the Suisun Bay and north Delta regions (Nobriga et al. 2008; Durand 2014). This may result, in part, from changes in flow patterns, river inputs ,and sediment trapping by SAV (Hestir 2010). Occurrence of adult Delta Smelt at the SWP salvage facilities is linked with high Delta turbidity associated with winter "first flush" events. Relatively high turbidity (mean of 27 NTU in 2009 and 2010) in the Cache Slough region (from tidal asymmetry, a limited tidal excursion, and wind-wave re-suspension) may help to make this region a year-round refuge for Delta Smelt (Morgan–King and Schoellhamer 2013). Overall, turbidity is recognized increasingly as an important influence on smelt distribution and, perhaps, abundance. The increasing clarity of Delta water in recent years may, therefore, have played a role in its decline, or at least limited the amount of suitable habitat.

Microcystins. Periodic blooms of toxic blue-green cyanobacteria, *Microcystis aeruginosa*, most commonly occur in August and September. They are an emerging concern for Delta Smelt (Lehman et al. 2005, 2013) because *M. aeruginosa* can produce toxic microcystins. Blooms typically begin on the San Joaquin River side of the Delta, away from the core summer distribution of Delta Smelt. However, some overlap is apparent during and after blooms and as cells and toxins are dispersed downstream after blooms (Baxter et al. 2010). *M. aeruginosa* distribution has expanded north during the drought (Morris 2013). Studies by Lehman et al. (2010) found microcystins in the tissues and food of pelagic fishes, including Striped

Bass and Threadfin Shad, suggesting that Delta Smelt could be exposed to microcystins, depending on the degree of co-occurrence of Delta Smelt with blooms. Microcystins are toxic to other fish of the region (Acuña et al. 2011, 2012). Laboratory studies have shown that *M. aeruginosa* also can have a negative effect on calanoid copepods, an important food source for Delta Smelt, although it is unclear how laboratory results translate to field conditions (Ger et al. 2009, 2010). Factors that are thought to cause more intensive *M. aeruginosa* blooms include warmer temperatures, longer water residence times, high nitrogen levels, and clear water (Lehman et al. 2005, 2013; Baxter et al. 2010; Morris 2013). These conditions, which are generally unsuitable for Delta Smelt, occur in the estuary during dry years (Lehman et al. 2013). The intensity and duration of *M. aeruginosa* blooms are expected to increase over the long-term, along with any negative effect on Delta Smelt, from the increased frequency of drought conditions associated with climate change (Lehman et al. 2013). In short, *M. aeruginosa* blooms have not been implicated in Delta Smelt decline but they may be influential in the future as an added stressor during generally unfavorable conditions.

Water Temperature. Unfavorable temperatures are increasingly characteristic of much of the Delta in summer, and are associated with the absence of Delta Smelt from the central and south Delta during summer. Delta Smelt do occur in freshwater habitats of the north Delta during summer months. This region is typically cooler than the central and south Delta as a result of cooler flows from the Sacramento River. Years with warm water conditions result in increased energetic demand and, given persistent food limitation, small increases in temperatures could have large effects on Delta Smelt. For example, several modeling and empirical studies have suggested the summer to fall transition period may be critical for Delta Smelt survival (Maunder and Deriso 2011; Mac Nally et al. 2010; Miller et al. 2012; Rose et al. 2013a, 2013b). This coincides with the warmest time of the year in both freshwater and low-salinity habitats. Because Delta Smelt are sensitive to warm temperatures (Komoroske et al. 2014), they may experience chronic stress during summer months. Climate change projections suggest that all regions of the Delta that currently maintain summer water temperatures suitable for smelt will be unsuitable in 50 or so years, depending on the models used (Brown et al. 2013).

Drought. Drought is a factor that influences smelt distribution and abundance because of its effects on water quality and smelt habitat. While long-term drought is part of the evolutionary history of smelt, modern droughts exacerbate human-caused changes to the estuary, creating conditions that are much worse than would have occurred historically. Under current conditions, not only does the water become warmer and clearer in response to drought, but there is likely less dilution of contaminants and increased likelihood of harmful algae blooms. The suppression of Delta Smelt populations in 2007–2009 and since 2012 is presumably at least partly an artifact of drought. The drought of the 1980s enabled the rapid invasion of the overbite clam, expansion of Mississippi Silverside populations, and the spread of Brazilian waterweed, which reduced the ability of much of the Delta to support Delta Smelt.

Climate Change. The effects of anthropogenic climate change on the Delta are covered in Dettinger et al. (submitted). Extreme weather patterns in recent decades indicate that climate change is already affecting the Delta ecosystem, making the water warmer and reducing outflows. Arguably, climate change is an additional stressor to smelt, one that is making it increasingly difficult for the species to recover. Changes in precipitation, air temperature, proportions of rain and snow, and runoff patterns are increasing. It is highly likely that water temperature will increase, and salinity intrusion will occur in the Delta (Cloern et al. 2011; Wagner et al. 2011). Brown et al. (2013) evaluated the effects of projected changes in water temperature, salinity field, and turbidity on Delta Smelt and determined that habitat suitability (see Feyrer et al. 2011) and the position of the LSZ during fall converged on values observed only during recent severe droughts (Brown et al. 2013). These more or less permanent changes are expected by mid-century. Higher water temperatures are expected to render much of the historic Delta Smelt habitat, from the confluence of the Sacramento and San Joaquin rivers and upstream, uninhabitable by smelt during summer and early fall. Such high temperatures will restrict distribution of smelt (Brown et al. 2013, 2016), likely interfering with maturation of fish and population fecundity (Brown et al. 2016), and inhibiting their recovery. Human responses to these events, such as changes in water project operations and new water infrastructure, are difficult to predict, but are not likely to favor Delta Smelt.

Overview: Causes of Decline

There is no "smoking gun" or single cause of the Delta Smelt decline. Instead, multiple factors have created habitat that is significantly less able to support smelt in large numbers (Figure 5). Moreover, the annual life cycle, relatively low fecundity, and current low abundance of this species increases probability of extinction due to stochastic effects in any given year. For example, droughts such as the one that began in 2012, worsen estuarine conditions for smelt, favor alien species, and generally create conditions that are likely to squeeze Delta Smelt between effects of natural stressors and anthropogenic stressors. Such droughts are likely to become longer and more severe as climate changes (Ingram and Malmud–Roam 2013). The lack of a single cause is not surprising considering that Delta Smelt is an annual species that lives in a highly dynamic and highly altered estuarine environment. The decrease of just one of its vital rates over a short period of time can cause a significant change in abundance.

Nevertheless, the outlook is not entirely bleak. The slight increase in Delta Smelt populations in 2011, a cool year with high outflows in spring and fall (Brown et al. 2013) suggests that outflows strongly interact with other factors, and can dilute toxicants, reduce temperatures, reduce entrainment, improve food supplies, and delay reproduction of potential predators and competitors. Higher outflows essentially allow more favorable habitat conditions for smelt to return to at least the north and west Delta. In addition, the capture of a few smelt in Montezuma Slough in Suisun Marsh every year suggests that some smelt move up and down the estuary even in dry years (W. Bennett, pers. comm. with P. Moyle, 2015, unreferenced, see "Notes"). There is also evidence that some smelt spend their entire life in the fresh waters of the north Delta, including the Sacramento Deepwater Ship Channel.

DISCUSSION: THE FUTURE OF DELTA SMELT

The Delta Smelt is well adapted for an estuary that no longer exists. Although we can only speculate on conditions for Delta Smelt in the historic estuary, it seems likely that Delta Smelt could always find abundant food and places to spawn and rear, whether in flood or drought, allowing it to remain abundant. The bulk of the population moved between the Delta and Suisun Bay, although presumably part of the population never left the fresh waters of the Delta, no matter what the conditions were like elsewhere. The Delta was originally a great wetland complex, absorbing freshwater outflows in winter and spring, and slowly releasing the water and the food it contained throughout the summer (Whipple et al. 2012). Delta Smelt were able to capitalize on rich food resources in a variety of habitats provided by the sloughs, backwaters, and channels of the entire historic Delta during winter and spring. As river inflows decreased and water temperatures warmed, larval and juvenile smelt could move, or be carried by the tides and rivers, into Suisun Bay and Marsh. There, the mixing of fresh and salt water created a concentration of planktonic organisms, ideal for plankton-feeding fishes, including Delta Smelt, Longfin Smelt, and Northern Anchovy. Similar conditions were probably present in the many isolated ponds present in the marshlands of the Delta and Suisun Marsh that may have sustained resident populations of smelt. No matter how wet, or how dry, a year might be, these conditions would have existed somewhere in the estuary, including the south and central Delta. In extreme wet years, most juvenile smelt might be advected to San Pablo Bay, while in dry years they might be retained in the Delta. Considering the dramatic changes to the estuary in recent decades, it is remarkable that Delta Smelt remained abundant through the 1970s; even though the estuary had changed markedly, the smelt still found the conditions they needed to thrive.

As discussed previously, human populations and water demand finally caught up with the smelt in the 1980s and its populations have spiraled rapidly downward as a consequence. The proximate causes of decline are interactions of multiple factors that have altered their habitat, making it increasingly unsuitable. None of these factors by themselves have caused the severe decline Delta Smelt has experienced in recent years, but together they are devastating, transforming the Delta into a novel ecosystem (*sensu* Hobbs et al. 2009; Moyle et al. 2010; Morse et al. 2014) dominated by alien species, highly altered in structure, and generally inhospitable to Delta Smelt (Figure 7). This is the Delta described by *Luoma et al. (2015)* as a "wicked problem" with no single solution to its many conflicts and contradictions, requiring radically different management to have positive outcomes, such as prevention of Delta Smelt extinction.

Can the downward trend of the Delta Smelt be reversed? Does the Delta Smelt have a future in the estuary? We see three major alternative pathways: (1) complete extinction, (2) a conservation-reliant species with small populations, and (3) an uncommon species in an intensely managed arc of habitat in the north Delta and Suisun Marsh.

Extinction

The Delta Smelt appears to be on the pathway to extinction in the wild. All trends have been downward especially since 2002 (Figure 3). Delta Smelt have been almost undetectable in surveys since 2012. The discovery of freshwater resident smelt and continued persistence of small aggregations in Suisun Marsh provides some hope, but the population is likely so small that stochastic factors, such as continued drought, the loss of key spawning or rearing sites, or an increase in local abundance of competitors or predators (e.g., Mississippi Silverside) could cause extinction in the near future. The captive population at the UC Davis Fish Culture and Conservation Laboratory (Box 1) can prevent actual extinction for a while, but the loss of wild fish to interbreed with cultured fish to maintain genetic diversity will eventually result in domesticated smelt, best suited for survival inside the hatchery rather than outside of it. Reintroductions will have to be done within a few years of loss of wild fish, into an environment with better capacity to sustain them. One promising experimental approach would be to replicate culture techniques used in Japan for a similar smelt, Wakasagi (Mizuno 2012). Mats containing fertilized eggs that were spawned by

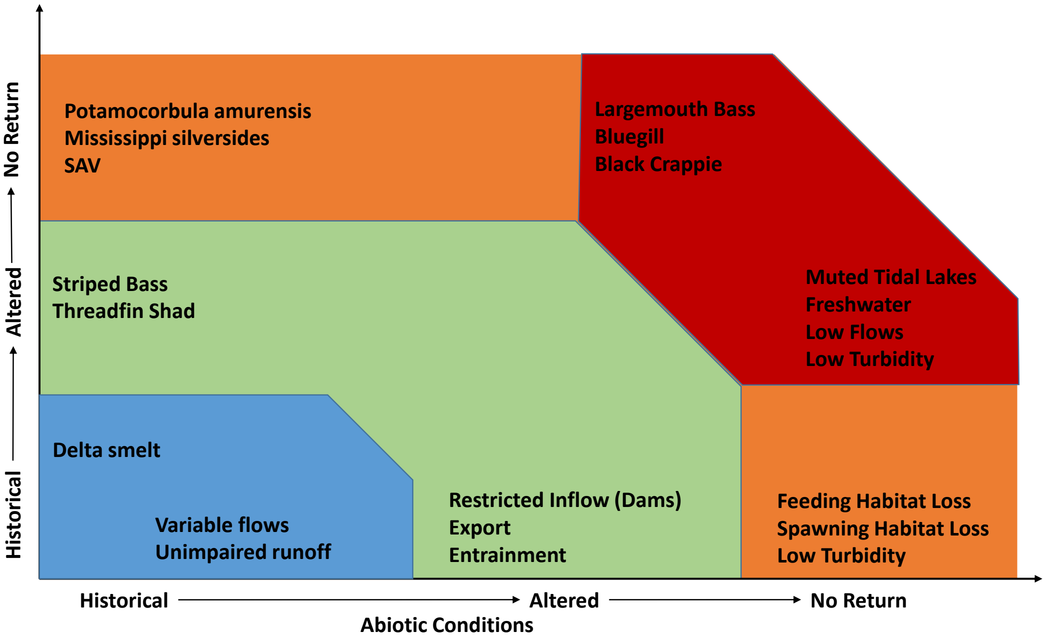

Figure 7 The progression of the San Francisco Estuary to a novel ecosystem. Abiotic factors on the bottom axis, in concert with biotic factors on the vertical axis, have led to a system that supports a diverse array of introduced fishes, but has limited capacity to be restored to a condition that will support Delta Smelt (*sensu* Hobbs et al. 2009). The blue polygon represents historical conditions; the green polygon represents conditions that retain some feasibility of restoration to historic ecosystem structure or function; the orange polygons represent conditions that make restoration difficult or impossible; the red polygon represents conditions that dominate the novel ecosystem that typifies much of the Delta.

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cultured fish (Box 1) could be placed in protected enclosures in food-rich environments, such as the flooded Yolo Bypass, or ponds such as those on Twitchell Island in the Delta. The eggs would hatch and larvae would live in the enclosures, before being released for a natural return to the Delta. This would be contingent, of course, on favorable conditions being present in the Delta.

Conservation-Reliant Species

> "A species is conservation reliant when the threats that it faces cannot be eliminated, but only managed."
>
> —Goble et al. (2012), p. 869)

This definition seems to fit the Delta Smelt well in its present circumstances. If it does avoid extinction, then it will only persist as a wild fish if its population is intensely monitored and managed. The focus may have to be on creating a more stationary freshwater sub-population, perhaps in a flooded island or in a reservoir outside the estuary. Alternatively, refuge areas could be created within Delta polders (islands) and perhaps the Napa River in which habitat quality is maintained, and potential competitors and predators controlled. The wild population would be critical for maintaining the genetic diversity of the captive population and the captive population may have to be used to help maintain the wild population during droughts. If increasingly unfavorable temperatures for smelt occur, predicted as a result of climate change, then special refuges may have to be created that can take advantage of cooler water in the Sacramento River or from water that is piped in from some other source.

North Delta Arc Species

Without massive investments in management, the south and central Delta are highly unlikely to continue to contain suitable habitat for Delta Smelt in most years. Realistically, habitat for a migratory population of Delta Smelt will have to be in the aquatic arc from Yolo Bypass, through the Cache–Lindsay Slough complex and the lower Sacramento River and into Suisun Bay and Marsh, a drastic reduction in its native range. Assuming temperatures stay cool enough, management programs will be necessary to maintain habitat quality including (1) invasive species control, (2) managing contaminants to keep concentrations low, (3) providing adequate flow down the Sacramento River at crucial times of year to promote environmental variability and transport of larvae, (4) providing high-quality habitat for spawning, (5) promoting production of the right food organisms in the right places for rearing, (6) keeping smelt out of the Central and South Delta and (7) thermal regime management. Such efforts, of course, could also provide major benefits to declining anadromous fishes such as Longfin Smelt, Chinook Salmon, and Green Sturgeon. In this scenario, the

BOX 1

Culture for Conservation

As it became clear that the Delta Smelt was in severe decline, the UC Davis Fish Conservation and Culture Laboratory (FCCL) was established in 1996 at the State Water Project pumping plant in Byron, California. The purpose of the facility initially was to rear smelt in captivity for use in various experimental studies, because of their increasing unavailability in the wild. By 2004, the laboratory had the capacity to rear Delta Smelt through their entire life cycle. The program was remarkably successful in breeding a very delicate annual fish about which little was known in terms of culture (Lindberg et al. 2013). As a result, researchers had a ready supply of experimental fish. In 2008, the focus of the FCCL also became to establish a "refuge population" as a hedge against extinction in the wild. The breeding program was then set up to have strong genetic basis with reproductive success tracked for individuals and families. After starting with 2-year-old fish from the initial culture operation, wild fish were brought in every year to spawn with fish already in captivity, to enhance genetic diversity. The program has easily met its goals of having an annual spawning population of 500 fish, derived from a pool of 6,000 adults. An additional backup population was established at the Livingston Stone Hatchery below Shasta Dam. Ongoing studies are showing the difficulty of preventing domestication of cultured Delta Smelt, especially when wild adults are in short supply. For example, LaCava et al. (2015) showed a small but significant loss of genetic diversity after one generation of experimental breeding of Steelhead Trout.

number of smelt each year is likely to be directly proportional to the effort put into providing high-quality habitat for it.

CONCLUSIONS: LESSONS LEARNED FROM DELTA SMELT

The continued decline of Delta Smelt demonstrates a general failure to manage the Delta for the "co-equal goals" of maintaining the Delta as a healthy ecosystem while providing a reliable water supply for Californians. When the goals were first stated, the smelt and other native fishes were already in serious decline, so the ecosystem goal started on the path to co-equality from a position of great inferiority to the water supply goal. Efforts to manage Delta Smelt independently of its ecosystem, especially by reducing exports on an emergency basis when smelt approached the pumps in the South Delta, have reduced salvage but have not recovered the population. This is equivalent to treating the symptoms without acknowledging the disease. The condition of the smelt population is an indicator of the failure to manage the Delta as a valuable ecosystem that provides more than just fresh water for human use.

An opportunity for more ecosystem-based management of the Delta was presented in *Recovery Plan for the Sacramento-San Joaquin Delta Native Fishes* (USFWS 1995), the original recovery plan for Delta Smelt. The idea of the plan was to manage the Delta simultaneously for eight native fishes chosen because (1) they were known to be in decline, (2) they were important or historically important in the Delta ecosystem, (3) they depended on the Delta for a significant part of their life history, (4) the combined species required a wide range of conditions, so could collectively work for de facto ecosystem management, and (5) they were sufficiently well studied for managers to "make reasonable judgments as to measures that could reverse downward trends (USFWS 1995, p. 1)." At the time of the plan, the Delta Smelt was the only listed species; but even the section of the Recovery Plan devoted to just Delta Smelt had an ecosystem focus because it defined recovery by continued occurrence throughout the Delta as well as by total abundance. Ultimately, the plan was never adopted, because actions to protect Delta Smelt trumped actions for all other species under the Endangered Species Act. Since then, four of the seven remaining species have been listed as threatened or endangered.

Failure to implement a viable recovery plan has been instrumental in the decline of Delta Smelt and their virtual absence from the south and central Delta. Much of the Delta ecosystem has undergone irreversible changes, from estuarine conditions that favored native fishes to conditions that largely favor alien warm water fishes, invertebrates, and aquatic macrophytes (Moyle and Bennett 2008). The Delta is now a novel ecosystem, physically and chemically altered and dominated by alien species, to the point that going back to a past condition is no longer an option (Figure 7). Creating conditions that will allow native fishes such as Delta Smelt to exist in this novel ecosystem is a major challenge; it requires restoring at least some features of the historic environment, especially related to flows, and engaging in active management of other features (Moyle et al. 2010). As *Luoma et al. (2015)* state for the Delta in general, saving the Delta Smelt will require "finally and honestly embracing the equal value of water supply and ecological health (p. 5)."

The basic lesson from the collapse of Delta Smelt is that to save species, ecosystem-based actions have to be taken quickly to halt irreversible change, or at least to guide inevitable change in a more favorable direction. The longer the delay, the harder the decisions, and the less likely they are to produce positive results. For the Delta Smelt, the time to make key decisions for its survival in the Delta may have already passed.

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NOTES

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Conrad L. 2016. Louise Conrad, California Department of Water Resources. In-person meetings, e-mails, and manuscript drafts from the Interagency Ecological Program Management, Analysis and Synthesis Team's analysis of drought effects.

Nagel M. 2016. Meredith Nagel, University of California, Davis. In-person conversation and e-mail with J. Hobbs about Delta Smelt clutch rearing and development in studies performed at the UC Davis Fish Culture and Conservation Laboratory.