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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 chapter reviews what has been learned about delta smelt and its status since the 2008 *State of Bay-Delta Science* report. The delta smelt has been in decline since the 1970s, and conditions associated with severe drought pushed its populations to record low levels in 2014-15. The delta smelt is endemic to the upper San Francisco Estuary, especially the Delta. However, much of its historic habitat is no longer available and the remaining habitat is increasingly unfavorable. Its population is now small enough that stochastic events could drive it to extinction, despite being listed under state and federal endangered species acts. As a listed species living in the central node of California's water supply system, it has been the mission 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, making it the most studied fish in the estuary. Unfortunately, research has not prevented its continued decline. The rapid decline and inability to recover the species 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

KEY WORDS
Hypomesus transpacificus, Sacramento-San Joaquin Delta, endangered species, extinction, coequal goals, POD.

INTRODUCTION
The delta smelt (*Hypomesus transpacificus*) is a small, translucent fish that smells like cucumbers; it is endemic to the upper San Francisco Estuary (SFE). Until the 1980s, it was one of the most 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

in its population led to it being listed as threatened under state and federal endangered species acts in 1993 (Appendix Table A). This action was immediately 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 meant that it has been intensively studied. As a result, it is now perhaps the best studied fish in the estuary, with over 300 peer-reviewed publications (Figure 1) countless reports, technical memos, and blogs on its biology and management.

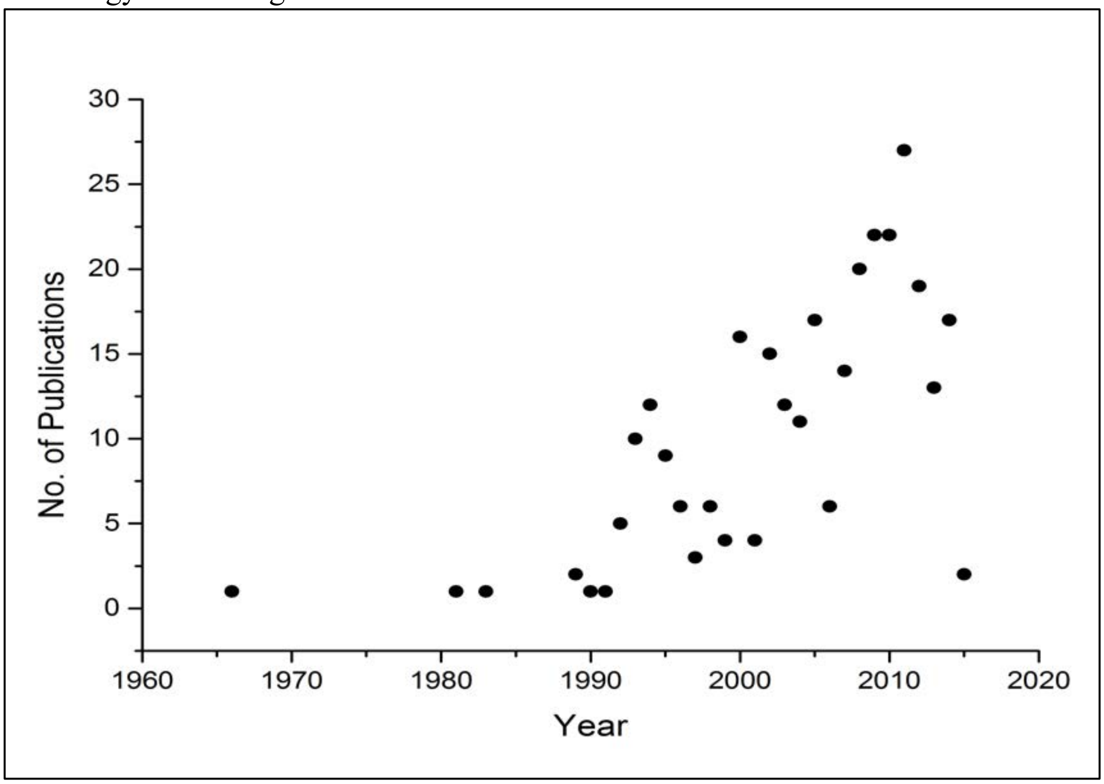

Figure 1. Number of peer-reviewed publications referring to Delta smelt, by year. Data (from Google scholar) include only publications with at least one citation.

Knowledge about delta smelt has been synthesized by Moyle et al. (1992), Bennett and Moyle (1996), Moyle (2002), Bennett (2005), and, most recently, the IEP Management, Analysis, and Synthesis Team (2015). In the 2008 report, *The State of Bay-Delta Science* (Healey et al. 2008), the delta smelt was treated mostly as part of the broad decline of pelagic fishes in the estuary, with the causes of decline determined to be uncertain. In this chapter, we present a new synthesis of recent studies, as the smelt dives towards extinction. Since the 2008 report, major advances in our understanding of delta smelt biology have occurred (Table 1). These advances are further described throughout this chapter. We cover the following topics: (a) taxonomy and genetics; (b) historic and current distribution; (c) ecology; (d) population trends and dynamics; (e) conceptual models; f) causes of decline. We conclude with a discussion of why the present environment of the Delta no longer fits the needs of delta smelt and what conservation actions can be implemented. Survival of delta smelt into the future will depend on developing new, flexible approaches to management (Luoma et al. 2015).

Table 1. Key scientific findings on delta smelt (DS) since Healey et al (2008). Details of these findings are presented in the chapter text.

There is a single population of DS, with recently reduced genetic diversity (Fisch et al. 2009, 2011).
Spring Kodiak Trawl surveys show DS population approaching extinction, reflecting trends in other sampling surveys (unpublished data, CDFW, 2014).
Some DS remain year-round in fresh water (Merz et al. 2011, Sommer et al. 2011, Sommer and Mejia 2013).
DS are sensitive to warm temperatures, with thermal stress occurring 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).
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 (around 12 NTU) is associated with entrainment of delta smelt in the pumps of the south Delta (Grimaldo et al. 2009).
DS movements track turbidity and salinity gradients (Feyrer et al. 2007, Bennett and Burau 2015). Increased turbidity in fall triggers adult movement toward spawning areas (Bennett and Burau 2015).
DS gonads exhibit multiple stages of oocyte development, indicating females can spawn more than once, greatly increasing total fecundity (Lindberg et al. 2013). Factors reducing fecundity include time in spent in fresh water, low lipid (triglyceride) storage, *Mycobacterium* infections, and exposure to contaminants (Teh 2013, Hammock et al. 2015).
DS survival from summer to fall is correlated with biomass of calanoid copepods in the low salinity zone (Kimmerer 2008b), reflecting that smelt diets revert to smaller, less nutritious prey items after mid-summer(Slater and Baxter 2014, Kratina and Winder 2015).
Thomson et al. (2010) used Bayesian change point analysis to show an abrupt decline in delta smelt abundance in the early 1980s and in the early 2000s (i.e., pelagic organism decline, POD). There is little evidence of density dependent population regulation between years, although there is within years.
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).

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 which occurs in San Francisco Bay (Stanley et al. 1995). Delta smelt comprise one large interbreeding population in the SFE. Although genetic diversity of the population is fairly high, there are signs of bottlenecks associated with reduced population size (Fisch et al. 2011). While the related Japanese osmerid wakasagi (*Hypomesus nipponensis*) has invaded the SFE from upstream reservoirs, 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 SFE, delta smelt were widely distributed throughout the Delta, Suisun Bay and Marsh, and western San Pablo Bay (Erkkila and others 1950, Ganssle 1966, Radtke 1966, Moyle 2002). Despite being tolerant of meso-haline salinities (see ecology), 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).

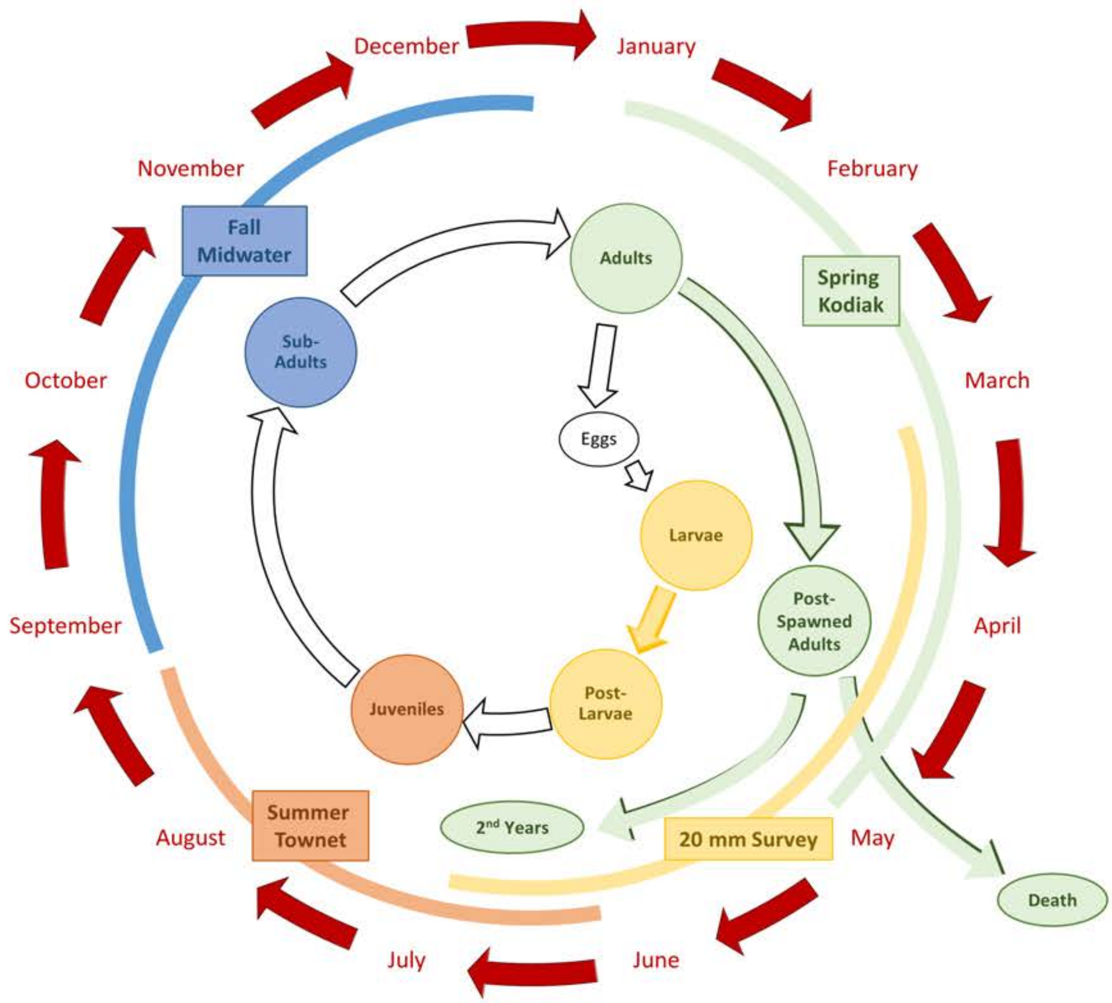

Figure 2. Key surveys obtaining data on delta smelt distribution and abundance, in relationship to calendar year and delta smelt life cycle.

An analysis of the data from six widespread, long-term sampling programs and 23 regional and short-term 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 disjunction of Old and San Joaquin rivers in the south Delta, an area encompassing only 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 seven standard delta fish surveys (Figure 4, Bennett 2005) sample mainly in the larger channels and open bay waters, only recently has the importance of peripheral areas for smelt been discovered such as the Napa River, the Cache-Lindsay Slough Complex, the Sacramento Deepwater Ship Channel and Liberty Island (Sommer and Mejia 2013).

The distribution of delta smelt usually changes on a seasonal basis with life stage (Figure 2) (Sommer et al. 2011). In winter, adult smelt move into fresh water for spawning and are sampled using the Fall Midwater Trawl (FMT) and Spring Kodiak Trawl (SKT). In spring and summer, young smelt move into brackish water, primarily in Suisun Bay and Suisun Marsh (Dege and Brown 2004), and are sampled using the 20 mm Survey (TMS). Delta smelt usually rear in low salinity habitat in summer and fall (Feyrer et al. 2007, Nobriga et al. 2008), allowing them to feed on abundant zooplankton in Suisun Bay and Marsh; they are sampled by the Summer Townet Survey (STS). However, each year some of the population remains in fresh water, likely as a bet-hedging strategy (Merz et al. 2011, Sommer et al. 2011, Sommer and Mejia 2013).

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 recent surveys, most smelt have been caught in in the Sacramento Deep Water Ship Channel and the Cache-Lindsey Slough Complex in the north Delta, and Montezuma Slough in Suisun Marsh. This arc of tidal habitat is connected by flows from the Sacramento River.

Smelt rarely occur in the central and south Delta, unless unfavorable hydraulic conditions occur due to water operations, causing net flows to pull larvae in that direction or creating conditions, such as increased turbidity, that stimulate adults to move there (Kimmerer and Nobriga 2008, Grimaldo et al. 2009). Current restrictions on pumping have limited occurrence of these events since 2009 (USFWS (United States Fish and Wildlife Service 2008, *San Luis & Delta-Mendota Water Authority et al v. Salazar et al* 2009).

ECOLOGY

Temperature

Delta smelt are commonly found at temperatures of 10-22°C. Wild caught delta smelt show a critical thermal maximum of 25.3°C for juvenile fish acclimated to 17°C (Swanson and Cech 2000). Hatchery smelt acclimated to 16°C have a critical thermal maximum of about 28°C but thermal tolerance differs among life stages with tolerance decreasing from late-larval to post-spawning fish (Komoroske et al. 2014, 2015). Molecular assays suggest that thermal stress can begin at about 20-21°C depending on life history stage, and 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 (Summer Townet Survey, STN) and pre-adults (Fall Midwater Trawl Survey, FMWT) are caught at water temperatures of <22°C (Nobriga et al. 2008, Komoroske et al. 2014). This is consistent with absence of delta smelt from the San Joaquin River and south/central Delta during summer. Presumably, delta smelt in the wild will avoid areas where water temperatures are near their thermal maximum and would be 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). Data from the TNS and MWT 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 that delta smelt can be reared in captivity in fresh water through their entire life cycle suggests that this is always an option for the species. However, most of the population is migratory and the distribution of this part of the population is usually centered near or slightly upstream of 2 psu in the entrapment or low salinity zone. Results from both the STN (Nobriga et al. 2008) and FMWT (Feyrer et al. 2007) found peak occurrences of delta smelt at low specific conductance, but with somewhat lower occurrence in fully fresh water, consistent with the bulk of the juvenile and sub-adult populations rearing in the low salinity region of the estuary (Feyrer et al. 2007, Nobriga et al. 2008, Hasenbein et al. 2013, Komoroske et al. 2014).

Turbidity

Juvenile and pre-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). Successful first feeding of young delta smelt relies upon sufficient turbidity (Baskerville-Bridges et al. 2004). Increased turbidity (around 12 ntu), coincides with increased entrainment of adult delta smelt (Grimaldo et al. 2009). An increase in turbidity resulting from the "first flush" of suspended material from inflowing rivers in late fall or winter, following the first major storm of the rainy season, is a likely a trigger for adult delta smelt to move toward spawning areas including areas within the influence of the south Delta pumping plants (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 for all visual feeders, visual range and prey density determine feeding success. Optical habitat attributes are affected by turbidity from suspended 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). Their large eyes, short snout, and well-developed protrusible jaws are used for suction feeding. Limited body-caudal fin propulsion apparently make delta smelt effective at quick, short movements that facilitate capture of zooplankton. They also can rely on low-velocity, discontinuous swimming to remain in areas where pelagic food sources are concentrated, while minimizing energy expenditure (Swanson and Cech 1998).

Delta smelt larval first feeding success is increased at high algae concentrations and light levels (Baskerville-Bridges et al. 2004). 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. The addition of algae or some other form of suspended particle 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.

Swimming Behavior

Delta smelt are considered poor swimmers based on laboratory studies of swimming performance (Swanson et al. 1998). Laboratory smelt had maximum sustained swimming velocities of about 28 cm/sec. A discontinuous "stroke and glide" behavior is used at water velocities of less than 10 cm/sec, while sustained swimming occurs above 15 cm/sec. However, many fish will not swim above water velocities of 10-15 cm/sec.

Despite this "poor" swimming performance delta smelt are capable of moving 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 were caught more frequently throughout the water column during flood tides. On ebb tides they were 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). Cross-channel gradients in water turbidity may act as a cue for this behavior (Feyrer et al. 2013, Bennett and Burau 2015).

The translucent body color and small size of delta may fit well with their apparent preference for water with moderate turbidity by making them less visible to predators. Turbidity has been demonstrated to reduce largemouth bass predation on delta smelt in mesocosm experiments (Ferrari et al. 2014). Stroke and glide swimming may be advantageous for a diel feeding planktivore because it minimizes continuous movement that might attract predators. The lack of schooling behavior in delta smelt, which requires synchronized swimming, may also reduce attractiveness to predators. Rather than forming schools, delta smelt appear to aggregate in spawning and feeding areas by responding to tidal cues.

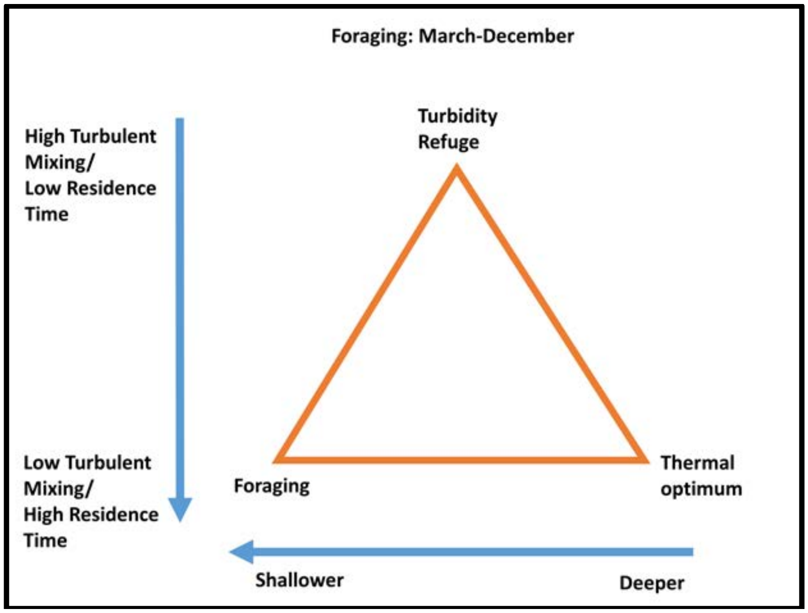

Figure 3. Physical controls on growth phase of delta smelt life cycle. The points of the triangle represent environmental optima for smelt requirements, such as cool temperatures, high turbidity for refuge and feeding, and zooplankton concentrations for foraging. These optima tend to occur along the two axes. The horizontal axis shows a gradient of habitat depths. The vertical axis shows water column mixing from high mixing to high water residence time. These conditions rarely coincide in the Delta, forcing smelt to optimize 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 would be necessary to maintain the fish.

Food and feeding

Delta smelt feed opportunistically on small crustacean zooplankton, but they feed preferentially on calanoid copepods (Moyle et al. 1992, Lott 1998, Slater and Baxter 2014). This is true across decades of study. For example a study from 1972-74 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 use 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 larval fishes (Moyle et al. 1992, Lott 1998, Feyrer et al. 2003, Slater and Baxter 2014). First food tends to be copepod nauplii or copepodites. The tiny invasive cyclopoid

Limnoithona tetraspina is poorly represented in diets; this may be a function of their low catchability and low nutritional value.

Predators and competitors

Historically, delta smelt were probably important prey for aquatic predators such as thicktail chub, Sacramento perch, Sacramento pikeminnow, salmon and steelhead smolts, and sturgeon. In addition, they presumably were prey for a diverse array of avian predators including herons, cormorants, grebes, terns, and pelicans. Following the Gold Rush, native predatory fish were largely replaced by a suite of non-native species, most conspicuously striped bass, a pelagic piscivore (Stevens 1966, Thomas 1967, Moyle 2002, Grossman, this volume), and Mississippi silverside (*Menidia audens*), a larval predator (Meinz and Mecum 1977, Moyle 2002).

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 have the most significant predation effect on delta smelt is the small, alien foraging fish, Mississippi silverside. 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 where the two species' spatial distributions overlap. However, no quantitative evidence exists for the overall effect of predation/competition by silversides.

The potential for alien piscivores to affect delta smelt abundance is suggested by inverse correlations of predatory fish (including striped bass, largemouth bass and Mississippi silversides) with delta smelt (Bennett and Moyle 1996, Brown and Michniuk 2007), and bioenergetics models of striped bass show they have the potential to be significant predators on fish such as 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, O'Rear 2012, Miller et al. 2012, Nobriga et al. 2013), although data on 1-3 year old striped bass, the age classes most likely to prey upon smelt, remains limited.

Historic competitors may have been other planktivorous fishes, especially northern anchovy and longfin smelt in Suisun Bay and Sacramento hitch and juveniles of other native fishes in the Delta. Competition may have occurred if zooplankton resources were limited during critical points of the smelt life cycle. The current wide array of potential non-native competitors include American shad, threadfin shad, golden shiner, juvenile centrarchids, and juvenile striped bass and Mississippi silverside (an intraguild predator). 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 (Durand 2015). It is worth noting that 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). The delta smelt decline does coincide, however, with invasion of overbite clam and increases in Mississippi silverside.

REPRODUCTION

Delta smelt have a protracted spawning season, ranging from January through June, and larvae are often seen from late February through early May (Moyle et al. 1992, Bennett 2005; Merz et al. 2011). They are thought to spawn on shallow sandy beaches, likely in the north Delta, although spawning has not been observed in the wild. Delta smelt fecundity is generally low. The number of eggs per female exhibits an exponential relationship with length for cultured fish, although the relationship is less clear in wild fish (Lindberg et al. 2013). The number of eggs per female for 60-80 mm fish, ranges from 1,000 to 2,500. Larger females (80-120 mm) can have 2,500-12,000 eggs; thus large body size can significantly increase individual fecundity (Bennett 2005, Lindberg et al. 2013). Mature eggs have been found in females as small as 56 mm fork length (FL) in the wild. Delta smelt have gonads that exhibit multiple stages of oocyte development, indicating females spawn more than once (Tomo et al., in press).

Spawning behavior of captive delta smelt has been studied using parentage genetic techniques in outdoor mesocosms. Females can spawn repeatedly with multiple males (LaCava et al. 2015) up to 4 occasions in a season, with resting periods of 40-50 days (Nagel et al. 2015). Repeat spawning in the wild could be important for maintaining population resiliency during periods of low adult abundance when environmental conditions are favorable for reproduction.

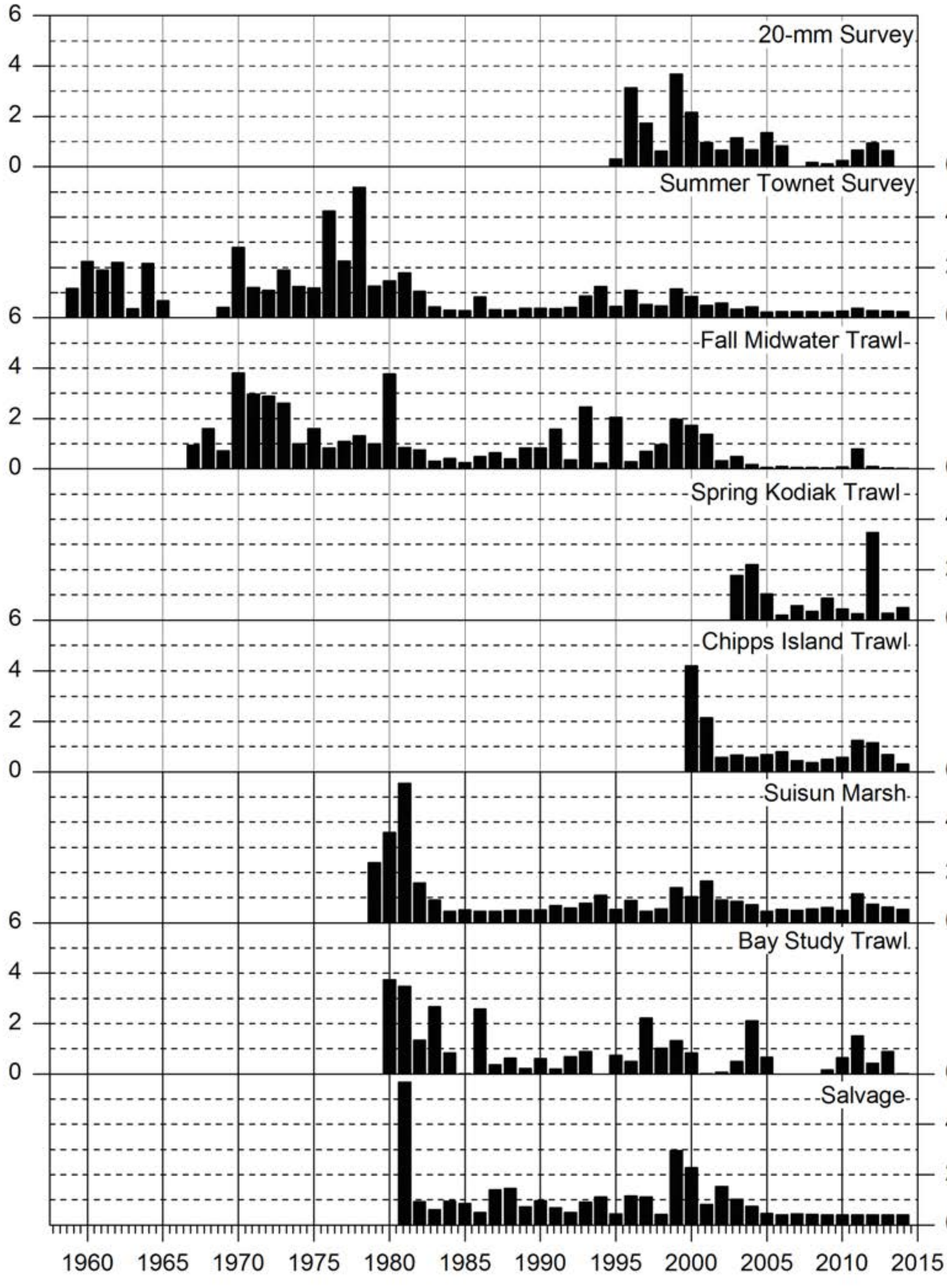

Figure 4. Delta Smelt abundance index for life stages of delta smelt including the larvae-juveniles (20 mm Survey), juveniles (Summer Townet Survey), sub-adults (Fall Midwater Trawl), and adults (Spring Kodiak Trawl). The initiation of each individual survey is indicated by the first bar with missing bars indicating years for which an index could not be calculated. Indices for each survey were standardized (by subtracting each yearly index from the global mean for each survey and dividing the standard deviation)

for easy comparison. (Source: Interagency Ecological Program unpublished data, CDFW and DWR)

POPULATION TRENDS AND DYNAMICS

Population estimates for delta smelt are based upon indices that are calculated from the catch per unit effort of the key agency surveys shown in Figure 2 (redrawn from IEP Management, Analysis, and Synthesis Team 2015). Indices, rather than absolute numbers, are used for two principal reasons. First, like most fish populations, the distribution of smelt is patchy and mobile, and may at times occupy regions that are difficult or impossible to sample. This is true even in areas of peak abundance, where the likelihood of capture increases. Second, the efficiencies of capture of the various types of sampling gear are poorly known and hard to compare among surveys. Because actual population size cannot be known with certainty, the indices are a convenient way to model population trends and dynamics in response to environmental conditions.
Both the indices and the catch per unit effort for delta smelt, in all life stages, in all surveys, have declined since 2000 (Figure 4). This trend parallels that of other pelagic fishes of the SFE, including juvenile striped bass, longfin smelt and threadfin shad (Sommer et al. 2007).

Because the delta smelt is a mostly annual species, population dynamics can be quite variable (Bennett 2005). Small changes in vital rates such as growth, survival and fecundity can have very large effects on the abundance of the species from year to year. This variability makes interpreting and predicting trends difficult. However, delta smelt appear to have 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 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).

An apparent decrease in delta smelt habitat carrying capacity in the 1980s (Bennett 2005, Baxter et al. 2015) has resulted in density-dependent survival during late summer and fall, between the juvenile and sub-adult life stages (i.e., between the STN survey and FMWT survey indices, see Figure 2) (Sweetnam and Stevens 1993, Bennett 2005, Maunder and Deriso 2011). Zooplankton prey density in summer is an important explanatory variable for survey-to-survey survival, providing further evidence of a late summer decrease in carrying capacity (Miller et al. 2012). A lack of density-dependence from late larvae to juveniles (i.e., between the 20mm survey and STN survey indices, Figure 2), suggests that during spring carrying capacity is not a limitation (Maunder and Deriso 2011), presumably because of calanoid copepod abundance throughout the Delta and Suisun Bay. However, low toxicity, high turbidity, low temperatures are all non-density dependent factors associated with spring months and they would tend to buffer the density dependent signal.

Stock-recruitment models, which aim to explain yearly recruitment based upon the adult population size, generally fail to be predict recruitment for delta smelt (Maunder and

Deriso 2011, MacNally et al. 2010, Thomson et al. 2010; Miller et al 2012). For example, the relationship between sub-adult abundance indices and juvenile abundance in the following year (i.e., between the FMWT survey and STNS survey indices, Figure 2) is poor, suggesting inter-generational abundance is largely driven by environmental conditions, rather than density-dependent factors. This observation becomes increasingly likely as the delta smelt population approaches zero. The most powerful explanatory variables for delta smelt populations dynamics appear to be summer food availability, summer temperatures and late-summer fall juvenile growth (Rose et al. 2013a, 2013b).

CONCEPTUAL MODELS

Developing conceptual models linking ecosystem functions with proposed management actions has become a valuable tool for highlighting key uncertainties in natural systems and environmental management (Thom 2000, Ogden et al. 2005). In the Sacramento-San Joaquin Delta, conceptual models have been used extensively to synthesize our current state of knowledge for species-habitat relationships (Baxter et al. 2010, DiGennaro et al. 2012), developing predictions for adaptive management actions (Bureau of Reclamation 2012) and evaluating outcomes of the recent drought (L.Conrad, DWR, personal communication to LRB). Many such modeling efforts have been conducted for delta smelt since its listing in 1992, which was accompanied by the first smelt conceptual model (Moyle et al. 1992). A series of conceptual models followed (Bennett 2005, Nobriga and Herbold 2009, Baxter et al. 2010).

A major literature review of delta smelt included a new conceptual model framework for linking environmental drivers to stage-specific delta smelt responses (IEP Management, Analysis, and Synthesis Team 2015). The model format is process-driven rather than descriptive (box and arrow diagram), is centered around four quadrants representing each life stage (life cycle module), and embedded within a series of hierarchical tiers representing direct and indirect effects from landscape level attributes, environmental drivers, 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, but the framework is flexible enough to adapt to most management scenarios. This framework is actively being used as a management tool to assess the effects of the recent drought on delta smelt as well as to guide monitoring plans for tidal wetland restoration (A. Low, DFW, personal communication to LRB).

Here, we present two diagrams that synthesize delta smelt biology and ecology based upon the known literature (Figures 3, 5). The synthesis is presented as a hypothesis, grounded in many years of research and our combined expertise (collectively greater than 100 years of accumulated experience in the system).

Figure 3 describes physical controls on foraging effectiveness as an example of one of many conceptual models that can be developed for various aspects of smelt behavior and life history. The triangle represents tension between desirable and undesirable habitat attributes that smelt must negotiate during this period. The vertical arrow on the left of the figure describes a hydrodynamic gradient from high mixing/low residence time to low mixing/high residence time. The horizontal arrow shows a depth gradient from deep to shallow. Delta smelt move among these gradients in a triad of optima. Smelt perform best in turbid conditions, which are typically found in highly active hydraulic conditions associated with shallow water, but foraging success might improve in less turbulent conditions where zooplankton can aggregate at higher densities. This is 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 might be most available in deep water, away from abundant food resources. Thus smelt must actively negotiate these conditions, and are potentially more viable if they can find conditions where all three of these resources are found in one place.

Figure 5 shows a life cycle diagram for delta smelt, using a format similar to that in Figure 2. Key stressors, both direct and indirect are shown at vulnerable stages of the life cycle. In December adults begin their upstream migration (timed to the first pulse of outflow that is sufficient to increase turbidity). Spawning habitat has been reduced because of landscape modifications dating back 150 years, and more recently from the spread of dense stands of submersed aquatic vegetation (SAV, especially *Egeria densa*) which has created highly unfavorable habitat in the south Delta in particular. The increase in SAV is due in part because of low flow conditions that result from water management decisions, which have created a lake-like environment, rather than the historically energetic, brackish environment that once characterized the south Delta.

Delta smelt have had better success in the north Delta, which is where most of the current reproduction is thought to occur. While the habitat is less degraded than in the south Delta, predation on eggs and larvae by Mississippi silverside 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 high mortality. However, these conditions have been limited since pumping restrictions have been put in place during periods of vulnerability.

Most larval smelt appear to rear in Suisun Bay and Marsh, where they historically fed upon abundant plankton resources. However, since the 1980s phytoplankton declines (resulting from poor water quality conditions and aggressive grazing by the overbite clam) have led to food limitation in much of Suisun Bay, especially in late summer and fall. Foraging success may be further limited by decreases in outflow that constrain the low salinity zone to a deeper and more spatially constricted region, rather than the shallow habitats of Little Honker Bay and Suisun Marsh. Food limitation likely leads to slow fall juvenile growth and limited survivorship to adulthood and reproductive output.

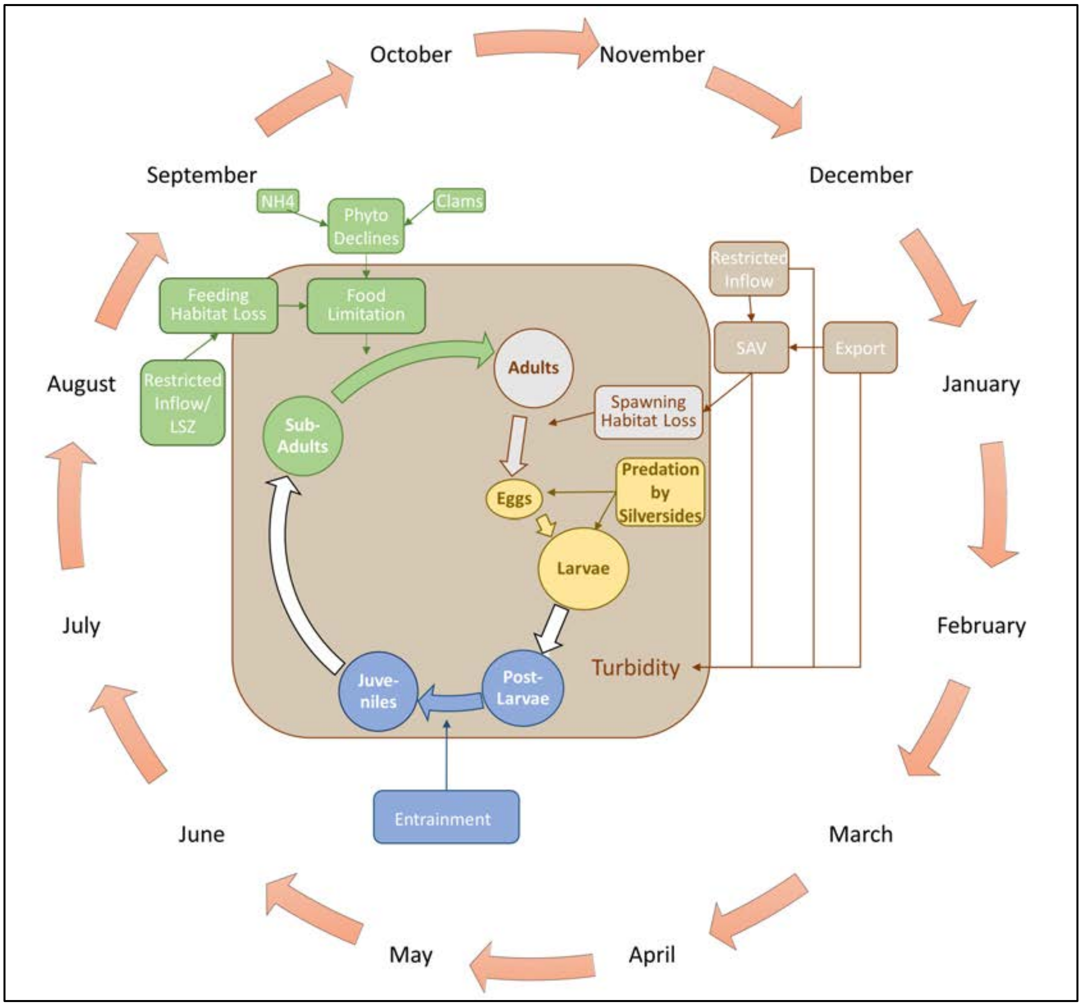

Figure 5. Conceptual model of main factors limiting delta smelt recovery. Note direct factors of food limitation, predation, and spawning habitat loss are linked to underlying causes. Low turbidity increases stress and interacts with other factors to decrease smelt success.

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 terrestrial and aquatic habitat alteration, invasions of new predators and competitors, and changes in hydrology. Changes are continuing at an accelerated pace, tracking both population and economic growth (Hanak et al. 2011, Hanak and Lund 2011). In this section we deal with the proximate causes of decline, because ultimate causes are beyond the scope of this chapter and likely science. We briefly review factors often considered as proximate drivers of decline: entrainment, altered hydrology, food, predation, contaminants, habitat change, drought, and climate change. We finish by integrating the known science into a synthetic understanding of delta smelt biology.

Entrainment

Entrainment (Figure 5) is the transport of fish by water from preferred habitat to a harmful one, often removing the animal from the water body. The Delta has literally thousands of water diversions, but the primary locations of delta smelt entrainment are the giant pumps of the Central Valley Project (CVP) and State Water Project (SWP) located in the South Delta. High exports and low inflows can create reverse flows and asymmetrically strong flood tides, which carry smelt, especially larvae, toward the pumps (Monsen et al. 2007, Kimmerer and Nobriga 2008, Grimaldo et al. 2009). Entrainment in the pumps of zooplankton may also reduce availability of smelt food in the south Delta (Jassby et al. 2002). 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 these pumping plants have screens (actually louvers) that divert fish to a collection 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 under 20 mm TL. For delta smelt, these counts provide a rough estimate of >20 mm long fish that are 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 pre-screen mortality (*e.g.* in Clifton Court Forebay) 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 are biased low. Moreover, we do not have a solid understanding of the fate of smelt entrained into the Central and South delta that do not make it to the pumps or the population-level effect of removal of spawning adults. Salvage tends to be highest at times when Old-Middle River flow is most negative (flows are reversed) and turbidity is high (USFWS (United States Fish and Wildlife Service 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, changing the pattern of water movement through the central and south Delta (Kimmerer 2008b).

Delta smelt are most vulnerable to entrainment by the CVP and SWP during upstream adult spawning migrations, or as larvae moving from fresh to brackish water (Sweetnam 1999, Sommer et al. 2011). In the 1980s, 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 2008b, 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 in the Central-South Delta over summer.

During years of high exports, 0-25% of larval-juvenile smelt and 0-50 % of the adult population may be entrained at the CVP and SWP annually (Kimmerer 2008b). Salvage increased greatly in winter of 2002, coincidentally the first year-class of the Pelagic Organism Decline for delta smelt (Fig 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). Given the annual life cycle, an episodic salvage event may undermine population resiliency by reducing population abundance, even when environmental conditions are good (e.g. the wet year of 2006).

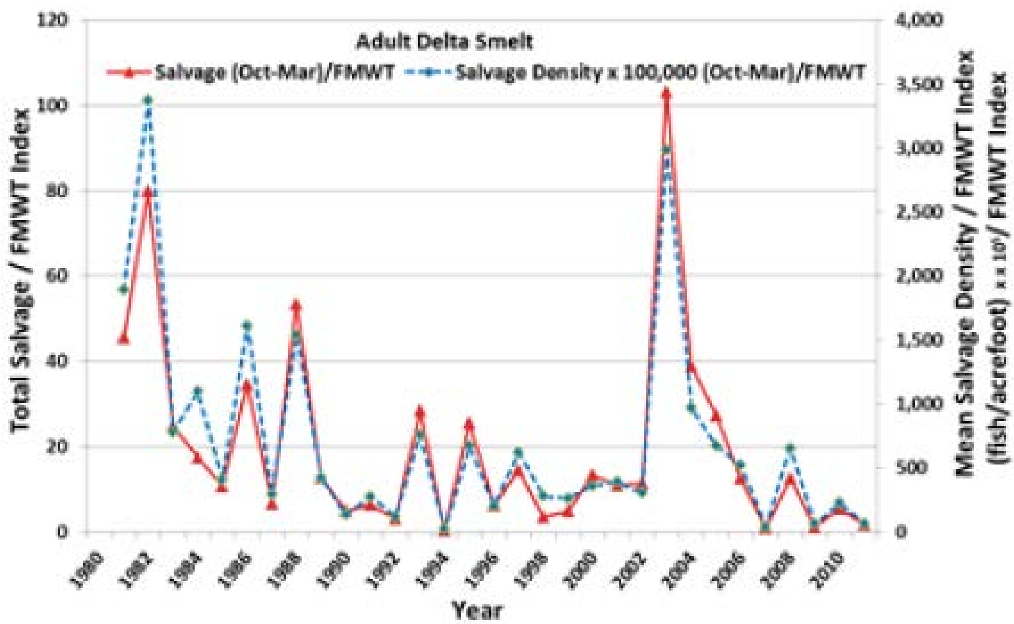

Figure 6: Total reported October-March salvage for adult Delta Smelt and the corresponding mean salvage density based on the total monthly salvage and water volume exported by CVP and SWP. Note that the salvage is standardized to the fall midwater trawl index.

Food and Feeding

Food resources for Delta smelt, particularly calanoid copepods and mysid shrimp, have decreased since the 1980s (Chapter 8) corresponding to declines in phytoplankton abundance. POD species abundances are related to prey abundance, and decreases in prey have reduced carrying capacity of the system to support fish (Sommer et al. 2007, Kimmerer 2008a). Modeling exercises support the hypothesis that food limitation affects delta smelt population trends (Miller et al. 2012; Rose et al 2013b).

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, IEP 2005, Bennett 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 completely empty guts in April. The frequency of empty guts increased during late spring-early summer during metamorphosis of late stage larvae to juveniles (fish ca. 20-24 mm FL). Low calanoid abundance in late summer may affect survival to fall abundance (Kimmerer 2008b, 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 the variability in survival from summer to fall (Bennett 2005, Bennett et al. 2008).

In general, delta smelt are probably food-limited at critical points in spring and fall in Suisun Bay, the Confluence and the south Delta. This likely contributes to lower growth rates, lower survivorship and decreased fecundity for survivors. However, food abundance may be heterogeneous across the region. Calanoid copepod densities can be higher in parts of Suisun Marsh and the north Delta, and cladocerans can be abundant in the north Delta. 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 those fish captured in Suisun Bay and the confluence (Hammock et al. 2015). Food limitation on delta smelt growth and survival may vary considerably with season, year, and location, contributing to their decline directly through starvation, or indirectly through poor body condition, which results in decreased growth, reduced fecundity, and increased vulnerability to other additional stressors.

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 the delta smelt today (Grossman et al. 2013, Grossman, this volume). There is no evidence that these predators had a major impact 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).

However, densities of potential smelt predators are increasing because of conditions that are increasingly favorable for alien species, particularly largemouth bass and other sunfish, across the Delta. 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; however, the frequency and magnitude of the effects of contaminants on delta smelt health and reproduction are not well understood (Johnson et al. 2010, Brooks et al. 2012). The effects on delta smelt of pesticides, ammonia/ammonium, heavy metals, PAHs and PCBs, contaminants of emerging concern and their mixtures are likely chronic rather than acute (Werner et al. 2010, 2010). In general, however, the extent to which contaminants affect delta smelt populations in the wild is not known.

Pesticides. Pesticide concentrations in surface waters of the Delta are typically highest during winter and spring in runoff from rainfall. Thus they 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 affecting 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 to exposure to ammonia/um, mainly due to discharge by the Sacramento Regional Wastewater Treatment Plant (SRWTP) into the lower Sacramento River (Connon et al. 2011). However, concentrations of ammonia used in these studies were higher than concentrations experienced by delta smelt in the wild.

Heavy Metals. Heavy metals and other elements of concern in the Delta include copper, mercury, and selenium. Sublethal effects on fishes of these elements 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."

Polycyclic Aromatic Hydrocarbons (PAHs) and Polychlorinated Biphenyls (PCBs). PCBs and PAHs 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 (CECs) 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).

Delta smelt are exposed to a myriad of toxic substances throughout their life cycle, but contaminants are most likely to have an impact on smelt health in combination with other stressors, such as starvation. While they may have considerable potential to influence smelt survival and reproduction, their effects on the population remain uncertain.

Habitat change

Delta smelt are pelagic fishes that primarily inhabit the open waters and river channels of the Delta and Suisun Bay. Here we discuss some of the more important factors influencing their pelagic habitat, from the perspective of smelt: 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 in this section 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). Patterns of Delta outflow have changed 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 (*Egeria densa)*, Asian clam (*Corbicula fluminea)*, overbite clam, Mississippi silverside and largemouth bass. The combined changes have altered the Delta ecosystem to a point that it is no longer hospitable for delta smelt. 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 do not move at all, staying year around in fresh water.

Salinity. While delta smelt have a fairly broad salinity tolerance (see physiology section), they are usually most common 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). Historically, these conditions were beneficial to delta smelt populations. At present there is little evidence of this benefit (IEP Management, Analysis, and Synthesis Team 2015) probably because the underlying processes have been disrupted by other habitat changes, such as reduced availability of food. The relationships between smelt life stages and spring (February to June) X2 (location of the 2 ppt isohaline) clearly underwent downward shifts after each step decline, associated with overall abundance change, but the slope of the relationship before and during the POD has not changed significantly (IEP-MAST 2015). Occasional years that maintain the LSZ in Suisun Bay through spring and fall (e.g. as in 2011) have had a positive effect on delta smelt abundance. However, the increases in abundance are temporary because the smelt is an annual fish. In addition to moving the LSZ to a favorable location for smelt, 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 central and south Delta compared to the Suisun and North Delta regions (Nobriga et al. 2008, Durand 2014). This may in part be due to changes in flow patterns, river inputs and sediment trapping by submerged aquatic vegetation (Hestir 2010). Occurrence of adult delta smelt at the SWP salvage facilities in the south Delta is linked with high turbidity associated with winter "first flush" events. Relatively high turbidity levels in the Cache Slough region may help to make it a year-round refuge for delta smelt. Overall, turbidity is increasingly recognized 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 occurring in August and September, are an emerging concern for delta smelt (Lehman et al. 2005, 2013). *M. aeruginosa* produces 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, occasionally as far down as San Francisco Bay (Baxter et al. 2010, J. Cloern, pers. comm.). *M. aeruginosa* distribution has expanded north during the drought (Morris 2013). Studies by Lehman et al. (2010) suggest that delta smelt likely are exposed to microcystin, which is known to be 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 the 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, lower flows, 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 during dry years in the SFE (Lehman et al. 2013). Intensity and duration of *M. aeruginosa* blooms are expected to increase over the long-term, along with any negative impact on delta smelt, due to 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.

Water temperature. Unfavorable temperatures are increasingly characteristic of much of the Delta in summer and are associated with delta smelt no longer living in 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 due to 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 modelling and empirical studies have suggested the summer to fall transition period may be critical for delta smelt survival. This coincides with the warmest time of the year in both freshwater and low-salinity habitats. Physiological studies have shown than delta smelt are sensitive to warm temperatures and may experience chronic stress during summer months. Climate change projections suggest much of the Delta 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. Long-term drought was nothing unusual in the evolutionary history of smelt but modern droughts exacerbate human-caused changes to the SFE, creating conditions that are much worse than would have occurred historically. 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, among other things. 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 ability of much of the Delta to support delta smelt.

Climate change

The effects of climate change on the Delta are covered in other chapters. The effects of changes in precipitation, air temperature, proportions of rain and snow, runoff patterns, and human responses to these factors in the form of changes in water project operations and new water infrastructure on the physical and biological habitat of Delta smelt are difficult to predict. However, it seems likely that water temperature will increase and salinity intrusion will occur (Cloern et al. 2011, Wagner et al. 2011). Brown et al. (2013) evaluated projected changes in terms of delta smelt environmental tolerances and determined that habitat suitability (see Feyrer et al. 2011) and the position of the low salinity zone during fall converged on values only observed during the worst droughts between 1969 and 2000 (their baseline period). These changes were expected by mid-century. Projected higher water temperatures were expected to render much of the historic delta smelt habitat from the confluence of the Sacramento and San Joaquin Rivers and upstream uninhabitable for large portions of the summer and early fall. Such high temperatures will restrict distribution of smelt and inhibit their recovery.

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. Moreover, the annual life cycle, relatively low fecundity, and current low abundance of this species increases the probability of extinction due to stochastic effects in any given year, particularly recently when persistent drought is worsening estuarine conditions. The fact that there is not a single cause is not surprising considering delta smelt is an annual species that lives in a highly dynamic and highly altered Mediterranean estuarine environment. The multiple drivers of delta smelt abundance only need decrease one of its vital rates over a short period of time to cause a significant change in abundance.

However; 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 have strong interactions with other factors, such as diluting toxicants, reducing temperatures, reducing entrainment, improving food supplies, and delaying 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.). 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. In the historic estuary, delta smelt could always find abundant food and places to spawn and rear, whether in flood or drought, allowing it to remain abundant. Its life revolved around moving between the Delta and Suisun Bay, although presumably a small 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 sponge of a 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). The smelt must have found the sloughs and channels of the entire historic Delta ideal for spawning and rich in food during winter and spring. As river inflows decreased and water temperatures warmed, the 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 nutrient rich soup of organisms, ideal for plankton feeding fishes of all sizes, including delta smelt, longfin smelt, and northern anchovy. 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, the juvenile smelt might find themselves in San Pablo Bay while in dry years they might never leave the Delta. Considering how much the SFE has changed 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 the decline are the 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 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 delta smelt extinction.

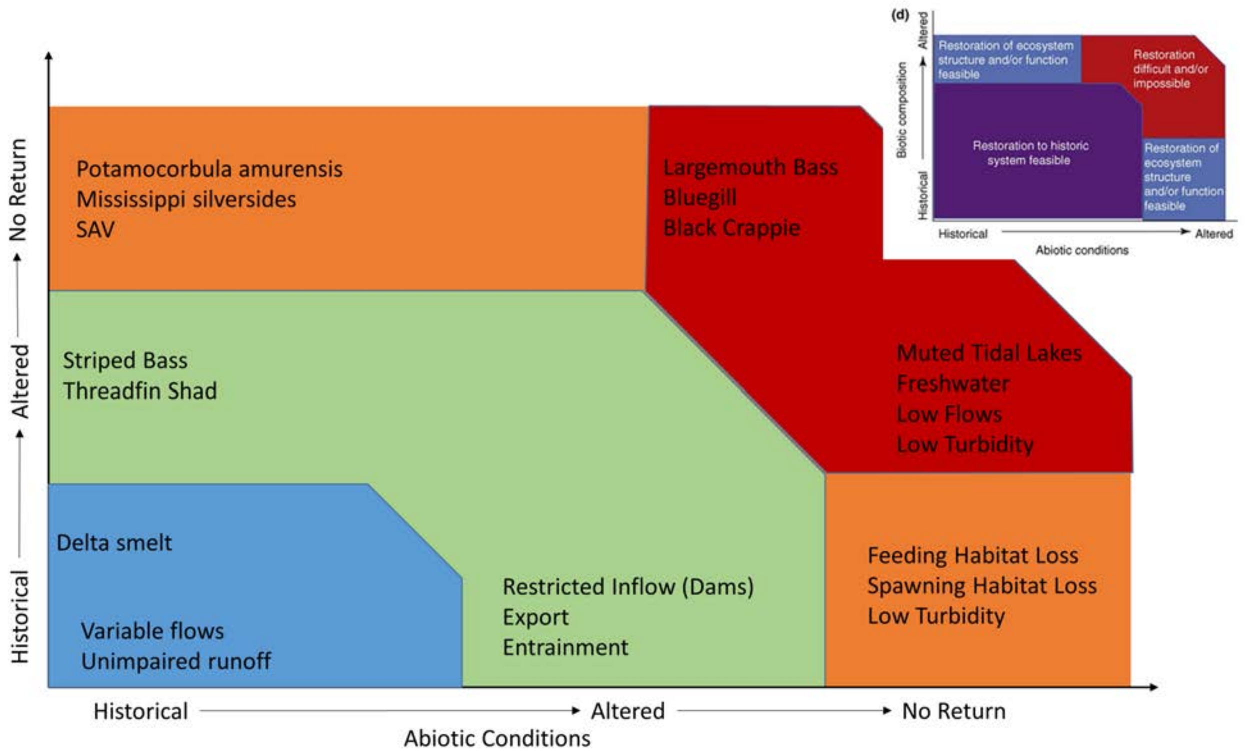

Figure 7. The progression of the SFE to a novel ecosystem. Abiotic factors on the bottom axis, in concert with biotic factors on the vertical axis, have led to a system that supports a diverse array of introduced fishes, but has limited capacity to be restored to a condition that will support Delta smelt (after Hobbs et al. 2009).

So, can this downward trend be reversed? Does the delta smelt have a future in the SFE? We see three major alternative pathways: (a) extinction, (b) a conservation-reliant species with small populations, and (c) an uncommon species in an intensely managed arc of habitat in the north Delta and Suisun Marsh.

Extinction.

Extinction in the wild is the pathway the smelt appears to be on today. All trends have been downward especially since 2002 (Figure 4). 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 a key spawning or rearing sites, or an increase in local abundance of competitor or predator (*e.g.*, Mississippi silverside) could cause extinction in the near future. The captive population at the UC Davis Fish Culture and Conservation Facility (Box 2) can prevent actual extinction for a while, but the loss of wild fish that can interbreed with cultured fish to maintain genetic diversity will eventually result in domesticated smelt, best suited for survival inside the hatchery rather than outside it. Reintroduction experiments would have to be done within a few years of loss of wild fish, into an environment that is better than the one from which wild smelt were extirpated.

Box 2. 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 carry 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 two 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. Thus, (LaCava et al. 2015) showed a small but significant loss of genetic diversity after one generation of experimental breeding. **End of Box.**

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 SFE. Alternatively, refuge areas could be created within Delta sloughs 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 piped in from some other source.

North Delta arc species.

It is highly unlikely that the south and central Delta will ever again 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 (a) invasive species control, (b) managing contaminants to keep concentrations low, (c) providing adequate flow down the Sacramento River at crucial times of year to promote environmental variability and transport of larvae, (d) providing high quality habitat for spawning, (e) promoting production of the right food organisms in the right places for rearing, and (f) keeping smelt out of the Central and South Delta. Such efforts, of course, could also provide major benefits to other declining fishes such as longfin smelt, Chinook salmon, and green sturgeon. In this scenario, the 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 started the path to co-equality from a position of 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, and an indicator of the short sighted and apathetic management of the Delta as a valuable ecosystem providing more than just freshwater as goods and services.

An opportunity for more ecosystem-based management of the Delta was present in the original recovery plan for delta smelt, which was written as the *Recovery Plan for the Sacramento-San Joaquin Delta Native Fishes* (USFWS 1995). 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 had adequate information on them to "make reasonable judgments as to measures that could reverse downward trends (p 1)." At the time of the plan, the delta smelt was the only listed species of the eight chosen, so the plan was never adopted because actions to protect delta smelt had to trump actions for all other species under the ESA. Unfortunately, four of the seven remaining species were eventually listed as threatened or endangered. 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 on total abundance.

Failure to develop and 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 subsequently 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 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, 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 it 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 for making key decisions for its survival may already have passed.

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Appendix Table A. Key years in the history of delta smelt.

1862	Gill (1862) describes surf smelt *Hypomesus pretiosus* from California, establishing the genus.
1925	Carl Hubbs (1925) describes 'pond smelt', *H. olidus,* as a freshwater species present in the "...upper or brackish portions of San Francisco Bay (p.55)."
1950	USFWS records 'pond smelt' as one of most abundant fishes in SFE in 1947-48 (Erkkila et al. 1950).
1961	Hamada (1961) recognizes delta smelt as distinct species of *Hypomesus* separate from *H. olidus* but does not formally describe it.
1963	McAllister (1963) formally describes delta smelt in revision of *Hypomesus.*
1966	Extensive survey of Delta fishes shows smelt to be abundant and widely distributed. Delta smelt not mentioned in *Inland Fisheries Management* published by CDFG, the standard reference for managers.
1967	Fall Midwater Trawl sampling program of DFG established for striped bass; becomes the best long-term record of smelt abundance.
1970	Kljukanov confirms that delta smelt is a distinct species based on skeletal features.
1976	Described as one of most abundant in fish in Delta (Moyle 1976)
1980	Last year of high delta smelt abundance
1989	Considered Fish Species of Special Concern by CDFW (Moyle et al. 1989). Petition to list as threatened species is rejected by California Fish and Game Commission.
1990	Petition to list delta smelt as threatened species filed with USFWS
1992	First major paper on delta smelt life history published (Moyle et al. 1992)
1993	Delta smelt listed as threated species under both state and federal ESAs.
1994	USFWS declares entire Delta and Suisun Bay as critical habitat for delta smelt
1995	Delta smelt shown to be most closely related to the surf smelt, a common marine species (Stanley et al. 1995)
1996	Delta Native Fishes Recovery Plan issued by USFWS
2002	Kodiak Trawl sampling program established for sampling delta smelt. Smelt abundance indices very low from this year forward.
2004	Delta smelt reported from Native American archaeological site (Gobalet et al. 2004).
2007	UC Davis Fish Conservation and Culture Laboratory for delta smelt established
2009	Delta smelt status changed to Endangered by California Fish and Game Commission.
2010	Change of federal status of delta smelt to Endangered is found to be "warranted but precluded" by other higher priority listing actions.
2011	Delta smelt numbers briefly spike in response to wet, cool conditions.
2014-15	Delta smelt reach record low numbers under conditions of severe drought.