INTERAGENCY ECOLOGICAL PROGRAM, MANAGEMENT, ANALYSIS, AND SYNTHESIS TEAM

An updated conceptual model of Delta Smelt biology: our evolving understanding of an estuarine fish

Technical Report 90
January, 2015

Interagency Ecological Program
for the
San Francisco Bay/Delta Estuary

A Cooperative Program of:

California Department of Water Resources
California Department of Fish and Wildlife
U.S. Bureau of Reclamation
U.S. Army Corps of Engineers
State Water Resource Control Board
U.S. Fish and Wildlife Service
U.S. Geological Survey
U.S. Environmental Protection Agency
National Marine Fisheries Service

Fall Midwater Trawl survey crew deploying net, circa 2005. Photo from CDFW.

Cover photo by Steven Culberson, USFWS

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Abbreviations

CCF	Clifton Court Forebay
CVP	Central Valley Project
Delta	Sacramento-San Joaquin River Delta
DRERIP	Delta Regional Ecosystem Restoration Implementation Program
DSC	Delta Stewardship Council
EMP	Environmental Monitoring Program
FLaSH	Fall Low Salinity Habitat
FMWT	Fall Midwater Trawl Survey
IEP	Interagency Ecological Program
LSZ	low salinity zone
MAST	Management, Analysis, and Synthesis Team
NRC	National Research Council
OMR	Old and Middle River
POD	Pelagic organism decline
SFE	San Francisco Estuary
SKT	Spring Kodiak Trawl Survey

SFPF	Skinner Fish Protection Facility
SRWTP	Sacramento Regional Water Treatment Plant
SSC	suspended sediment concentration
SWP	State Water Project
TFCF	Tracy Fish Collection Facility
TNS	Summer Tow Net Survey

An updated conceptual model of Delta Smelt biology: our evolving understanding of an estuarine fish

By Management, Analysis, and Synthesis Team

Executive Summary

The main purpose of this report is to provide an up-to-date assessment and conceptual model of factors affecting Delta Smelt (*Hypomesus transpacificus*) throughout its primarily annual life cycle and to demonstrate how this conceptual model can be used for scientific and management purposes. The Delta Smelt is a small estuarine fish that only occurs in the San Francisco Estuary. Once abundant, it is now rare and has been protected under the federal and California Endangered Species Acts since 1993. The Delta Smelt listing was related to a step decline in the early 1980s; however, population abundance decreased even further with the onset of the "pelagic organism decline" (POD) around 2002. A substantial, albeit short-lived, increase in abundance of all life stages in 2011 showed that the Delta Smelt population can still rebound when conditions are favorable for spawning, growth, and survival. In this report, we update previous conceptual models for Delta Smelt to reflect new data and information since the release of the last synthesis report about the POD by the Interagency Ecological Program for the San Francisco Estuary (IEP) in 2010. Specific objectives include:

1. Provide decision makers with a practical tool for evaluating difficult trade-offs associated with management and policy decisions.
2. Provide scientists with a framework from which they can formulate and evaluate hypotheses using qualitative or quantitative models.
3. Provide the general public with a new way of learning about Delta Smelt and their habitat.

Our updated conceptual model describes the habitat conditions and ecosystem drivers affecting each Delta Smelt life stage, across seasons and how the seasonal effects contribute to the annual success of the species. The conceptual model consists of two nested and linked levels of increasing specificity. The *general life cycle conceptual model* for four Delta Smelt life stages (adults, eggs and larvae, juveniles, and subadults) includes stationary ecosystem components and dynamic environmental drivers, habitat attributes, and Delta Smelt responses. The more detailed *life stage transition conceptual models* for each of the four Delta Smelt life stages describe relationships between environmental drivers, key habitat attributes, and the responses of Delta Smelt to habitat attributes as they transition from one life stage to the next.

Our analyses and conceptual model show that good larval recruitment is essential for setting the stage for a strong year class; however, increased growth and survival through subsequent life stages are also needed to achieve and sustain higher population abundance. We used our conceptual model to generate 16 hypotheses about the factors that may have contributed to the 2011 increase in Delta Smelt relative abundance. We then evaluated these hypotheses by comparing habitat conditions and Delta Smelt responses in the wet year 2011 to those in the

prior wet year 2006 and in the drier years 2005 and 2010. Larval recruitment was similarly high in both wet years and lower in the drier antecedent years, but juvenile and adult abundance increased only in 2011. In 2005 and 2006, the population was limited by very poor survival from the larval to the juvenile life stage. We found that in 2011, Delta Smelt may have benefitted from a combination of favorable habitat conditions throughout the year, including:

1. Adults and larvae benefitted from prolonged cool spring water temperatures, high 2011 winter and spring outflows which reduced entrainment risk and possibly improved other habitat conditions, and possibly enhanced food availability in late spring.

2. Juveniles benefitted from cool water temperatures in late spring and early summer as well as from improved food availability and low levels of harmful *Microcystis*.

3. Subadults also benefitted from improved food availability and from favorable habitat conditions in the large, low salinity zone (salinity 1-6) located more toward Suisun Bay in 2005-2006 and 2010.

Our comparisons of other habitat attributes either produced inconclusive results or were limited by a lack of suitable data or other necessary information. This was especially true for predation risk and toxicity, and other contaminant effects. Clearly more monitoring and studies are needed on these two topics, but we also found many other data and information gaps. Overall, we did not entirely reject any of our hypotheses. Together with the large amount of published information used to construct our conceptual model, this gives us some confidence that the majority of the elements and linkages of our conceptual model are relevant and (qualitatively) correct. However, the mechanisms they describe are likely variable in the degree to which they drive population outcomes, depending on the conditions in any given year and prior Delta Smelt abundance levels. In addition, the scientific merit of some linkages for which data are sparse (e.g., predation and contaminants effects) is impossible to evaluate without additional information.

Importantly, while this report identifies many data and information gaps that must be filled before some hypotheses can be objectively evaluated, the report includes a very large amount of pertinent data and information that is currently available. The San Francisco Estuary is clearly an intensely monitored and studied ecosystem and Delta Smelt may well be one of the most thoroughly studied endangered fish species in the world. The most critical data for this report came from four long-term Interagency Ecological Program fish monitoring surveys. These surveys provide sound, high-quality data about the annual distribution and relative abundance of Delta Smelt for time periods ranging from one to more than five decades. These four surveys, other monitoring surveys, and numerous research studies provide data about many habitat attributes and ecosystem drivers.

The report ends with key conclusions, a discussion of our hypothesis testing approach, and recommendations for future work and adaptive management applications. The final report Chapter contains many concrete examples of studies, modeling approaches, and management applications that are directly derived from the conceptual model. These examples are not meant to be exhaustive lists. Rather, they are primarily intended to illustrate science and management applications of our conceptual model.

We strongly recommend that analysis, synthesis and modeling efforts, such as this report, be a high priority for the management and science organizations that oversee monitoring and research in the estuary. Without these types of integrative efforts, ongoing and proposed adaptive management processes must conduct such efforts in an *ad hoc* manner, often driven by unrealistic schedules that are unlikely to be fulfilled. Such adaptive management processes in the estuary include the ongoing adaptive management of fall outflow for Delta Smelt, the new "Collaborative Science and Adaptive Management Program," the California Delta Stewardship Council's Delta Plan, and the multi-agency Bay Delta Conservation Plan. On a more basic level, such synthesis efforts identify data gaps that serve to focus research and management efforts on scientifically relevant topics rather than the "crisis of the day."

The 2011 increase in the Delta Smelt abundance index demonstrated that the species still has the ability to rebound to higher abundance levels. Delta Smelt has often been called an indicator – or canary in the coalmine – for overall ecosystem conditions in the estuary. The 2011 increase suggests that the system has not yet irreversibly shifted into an altered state that will no longer support native species. Given the profound habitat alterations in the San Francisco Estuary, continued study of the environmental drivers and habitat attributes and the subsequent responses of the Delta Smelt population seem critical to the wise management of the species. Some possible topics for future synthesis groups include:

1. Reviews and updates to existing conceptual and mathematical models.
2. Further development of mathematical models of Delta Smelt population abundance drawn specifically from the conceptual models described in this report; applications and extensions of recently published models to help make management decisions and guide new modeling efforts; additional modeling efforts and future research projects to improve resolution and understanding of the particular factors identified as critical to reproduction, recruitment, survival, and growth.
3. Review and refinement of new models such as the emerging comprehensive state-space population model (K. Newman, U.S. Fish and Wildlife Service, personal communication); development of additional models or modules of models specifically aimed at estimating effects of inadequately monitored or difficult to measure and evaluate habitat attributes such as predation risk and toxicity; development of new "nested" and/or "linked" mathematical modeling approaches that can accommodate multiple drivers and their interactive effects across temporal and spatial scales.
4. Interdisciplinary collaboration among scientists, managers, and stakeholders to develop and model management scenarios and strategies based on principles of integrative ecosystem and landscape-based management rather than relatively crude distinctions among categorical "water year types."

Continued growth of California's human population, climate change, new species invasions, and other changes will increase management challenges. Science and management have to go hand in hand to constantly identify, implement, evaluate, and refine the best management options for this ever-changing system. We hope that the conceptual model and information in this report will be useful for achieving these goals.

Chapter 1: Introduction

The San Francisco Estuary

Estuarine ecosystems are among the most complex ecosystems on earth (Wilson 1998). They are constantly changing ecosystems that respond to dynamic "drivers" of change (Healey et al. 2008, Baxter et al. 2010). Natural drivers include the geological and geographic setting, climatic and oceanic variability, dynamic hydrological and nutrient regimes, weather and disturbance regimes, biogeochemical processes, species assemblages, and many other biotic and abiotic features. Estuaries also respond to a broad range of human activities. Some of these "human drivers" have negative impacts on ecosystems. These negative human drivers are often called "stressors." Human stressors on estuarine ecosystems include water and land use, pollutant discharges, species introductions, and fishing (Townend 2004, Lotze et al. 2006, Cloern and Jassby 2012). The interplay of natural and human drivers and their effects on the San Francisco Estuary and in particular on the Delta Smelt (*Hypomesus transpacificus*), an endemic fish species, is the subject of this report.

The San Francisco Estuary (SFE; Fig. 1) is comprised of an upstream region consisting of channels and islands associated with the confluence of the Sacramento and San Joaquin Rivers known as the "Delta" and a series of downstream bays and marshes that are separated from the Pacific Ocean by the "Golden Gate," the sea passage between the San Francisco and Marin peninsulas. Because of California's Mediterranean climate, the SFE experiences large interannual and seasonal flow variations, which are modulated by tides and human management of the rivers within the Delta watershed (Moyle et al. 2010). These hydrological variations lead to a dynamic estuarine salinity gradient. In the winter and spring fresh water often extends into San Pablo Bay, while in the summer and fall brackish water can intrude into the western Delta. These seasonal differences are exacerbated by pronounced interannual differences in precipitation in the watershed. Extremely dry years with little precipitation and very wet years with widespread flooding do not occur in predictable patterns (Dettinger 2011).

The SFE has undergone dramatic morphological, hydrological, chemical, and biological alterations since the onset of the California Gold Rush in the middle of the 19th century (Nichols et al. 1986, Arthur et al. 1996, Baxter et al. 2010, Brooks et al. 2012, NRC 2012, Whipple et al. 2012, Cloern and Jassby 2012). These alterations include five human activities that have changed ecological functions and habitats in many riverine and estuarine systems with increasingly dense human populations: diking, draining, dredging, diverting, and discharging. Specifically, diking and draining have reduced the vast wetlands that once covered and surrounded the SFE to small remnants. There has been an 80-fold decrease in the ratio of wetland to open water area in the Delta, from a historical ratio of 14:1 to a current ratio of 1:6 (Whipple et al. 2012, Herbold et al. 2014). Diking and dredging have led to a substantial reconfiguration of the bays, sloughs, and channels, while large-scale water diversions, and discharge of contaminants have altered water quantity and quality. Small water diversions occur throughout the freshwater portion of the estuary, but the largest water diversions are at the pumping facilities of the federal Central Valley Project (CVP) and the State Water Project (SWP) that export water from the southwestern Delta to agricultural and urban areas to the south (Fig. 2). In addition, a wide variety of non-native plants and animals have been introduced and have become established in the SFE (Cohen and Carlton 1998, Light et al. 2005, Winder et al. 2011).

Figure 1. Map of the San Francisco estuary. The inset shows various values of X2, the distance in kilometers from the Golden Gate to the near bottom salinity 2 isohaline.

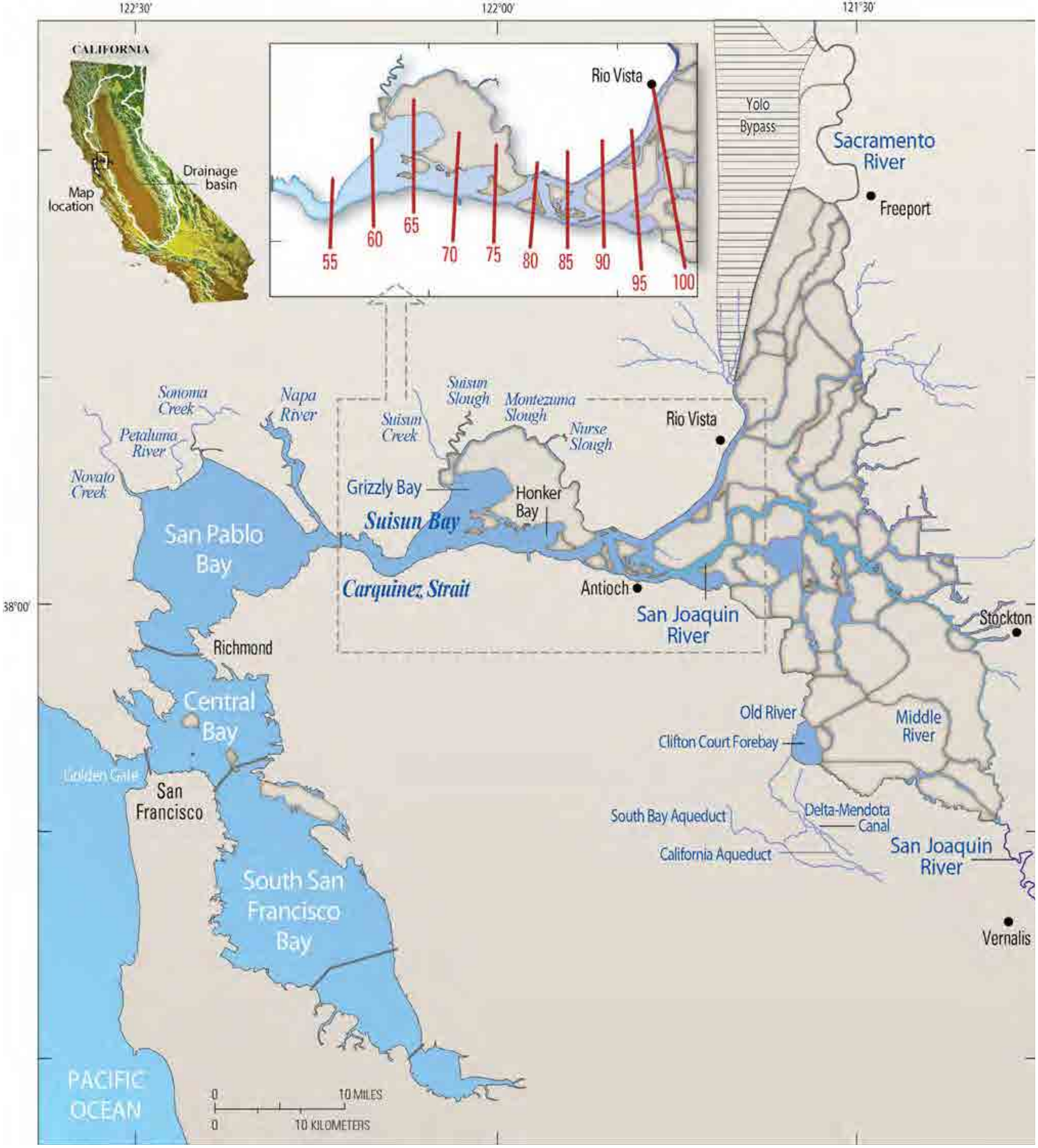
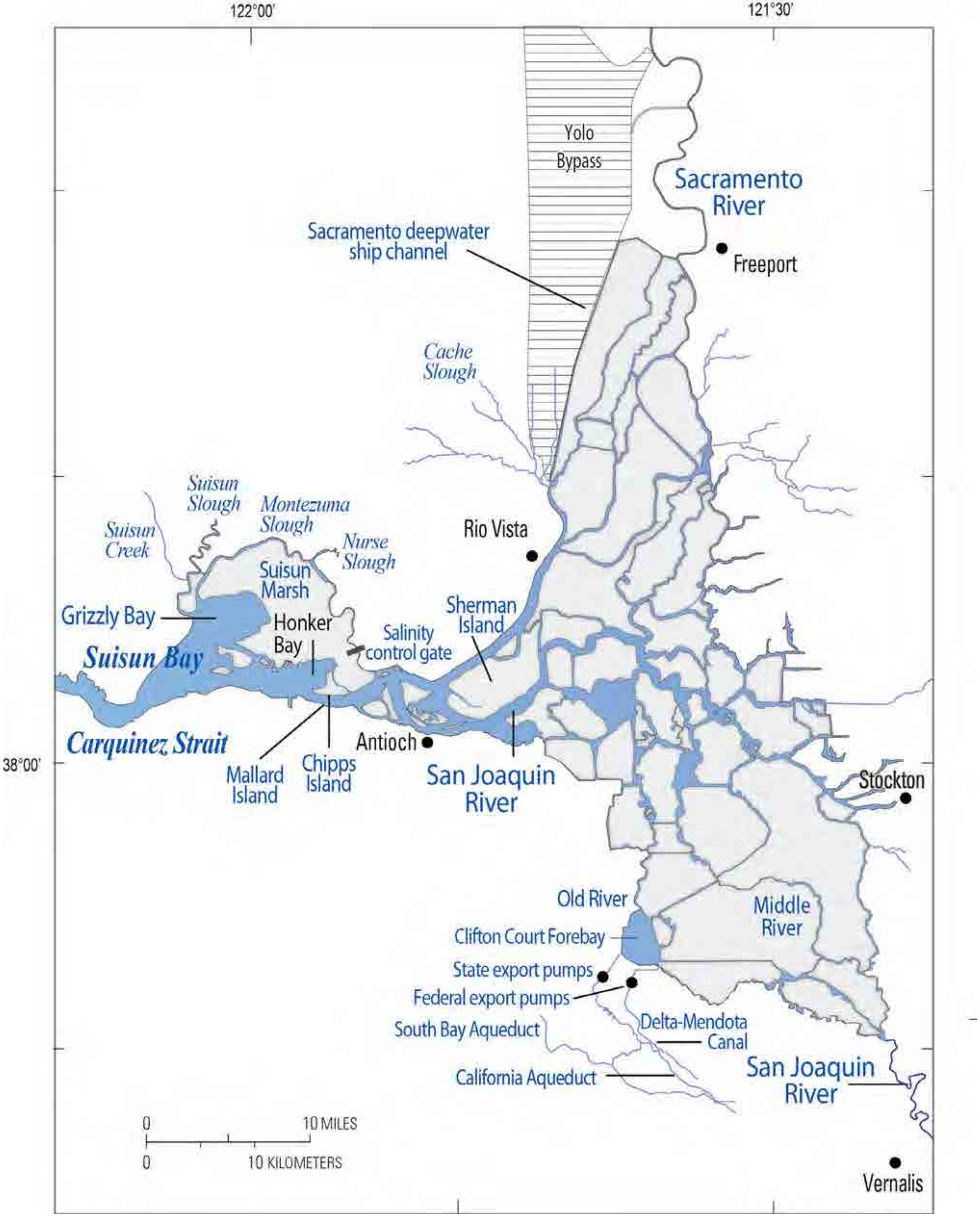


Figure 2. **Map of the upper San Francisco estuary. The upper estuary includes the Suisun Bay region and the Sacramento-San Joaquin Delta, which are west and east of Chipps Island respectively. The area from approximately Chipps Island to the west end of Sherman Island is referred to as the "confluence."**



Many of the more recent ecological changes in the SFE have been documented by long-term monitoring surveys. Most of these surveys are conducted under the auspices of the Interagency Ecological Program (IEP), an interagency science consortium with three State and six federal member agencies (http://www.water.ca.gov/iep/). Together with monitoring conducted by others, these monitoring surveys provide one of the longest and most comprehensive environmental and biological data records in a U.S. coastal ecosystem. With each additional year of monitoring, this data record serves as an increasingly valuable tool for observing gradual changes or abrupt shifts in ecological conditions and for identifying their underlying causes (Cloern and Jassby 2012).

The modern SFE continues to be a dynamic and complex ecosystem that supports many important ecosystem services (Millennium Ecosystem Assessment 2005), including the provision of fresh water, agricultural crops, commercial and recreational fisheries, and other recreational opportunities. However, it no longer provides adequate habitat for many of its native species as evidenced by severe declines in several of its native fish populations (e.g., Bennett and Moyle 1996, Brown and Moyle 2005, Sommer et al. 2007).

Pelagic fish declines

Among the native fishes of the upper SFE (Fig. 2), the endemic Delta Smelt is of high management concern because of a decline of its annual abundance indices (see Chapter 3 for details of fish surveys and indices), particularly longer term indices for juveniles and subadults, to persistent low levels (Fig. 3). This decline led to its listing under the federal Endangered Species Act in 1993. The Delta Smelt is a slender-bodied pelagic fish with a maximum size of about 120 mm standard length (length from snout to end of vertebral column) and a maximum age of two years. It is the most estuary-dependent of the native fish species in the SFE (Moyle et al. 1992, Bennett 2005). The continued existence of the species is dependent upon its ability to successfully grow, develop, and survive in the SFE.

Delta Smelt is not the only fish species currently in decline in the Delta. Abundance indices of Longfin Smelt (*Spirinchus thaleichthys*), age-0 Striped Bass (*Morone saxatilis*), and Threadfin Shad (*Dorosoma petenense*) declined simultaneously with those of Delta Smelt in about 2002. This simultaneous decline has become known as the pelagic organism decline (POD) (Sommer et al. 2007, Baxter et al. 2008, 2010) (Fig. 4). Given the very different life histories of these four pelagic species, it is unlikely that a single environmental variable could account for the POD declines. In general, researchers have suggested that the POD declines were likely multi-causal (Sommer et al. 2007, Baxter et al. 2008, 2010, Mac Nally et al. 2010, Cloern and Jassby 2012, NRC 2012). Several researchers have suggested that the SFE has undergone an ecological regime shift (Moyle and Bennett 2008, Baxter et al. 2010, Glibert et al. 2011, Cloern and Jassby 2012). In the present system, an invasive aquatic macrophyte (*Egeria densa*) dominates the littoral zone of many areas of the Delta and provides favorable habitat for many invasive fishes (e.g., Largemouth Bass *Micropterus salmoides*; Brown and Michniuk 2007); invasive clams (*Potamocorbula amurensis* and *Corbicula fluminea*) consume a large portion of the available pelagic phytoplankton (Alpine and Cloern 1992, Lopez et al. 2006, Lucas et al. 2002, Lucas and Thompson 2012); agricultural, industrial, and urban discharges transport large quantities of nutrients and a plethora of contaminants into many regions of the estuary; and current management of water for agricultural, industrial and urban purposes is focused on optimizing the reliability of water exports by the CVP and SWP.

Figure 3. Delta Smelt abundance index for life stages of Delta Smelt including the larvae-juveniles (20 mm Survey), juveniles (Summer Townet Survey), subadults (Fall Midwater Trawl), and adults (Spring Kodiak Trawl). The initiation of each individual survey is indicated by the initial bar with subsequent missing bars indicating when an index could not be calculated. See Chapter 3 for details of sampling programs, including geographic coverage, and Appendix B for details of calculationg abundance indices.

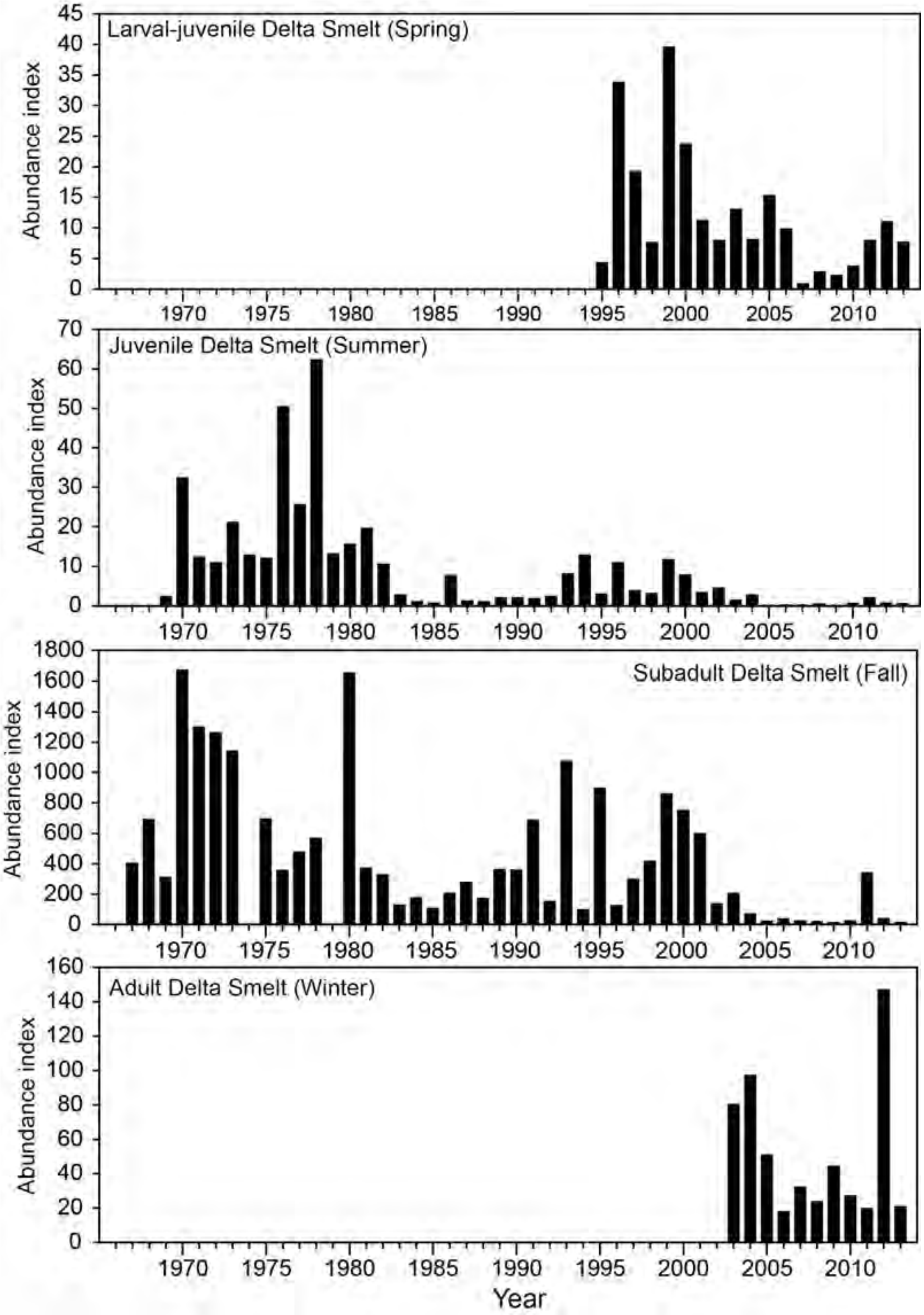
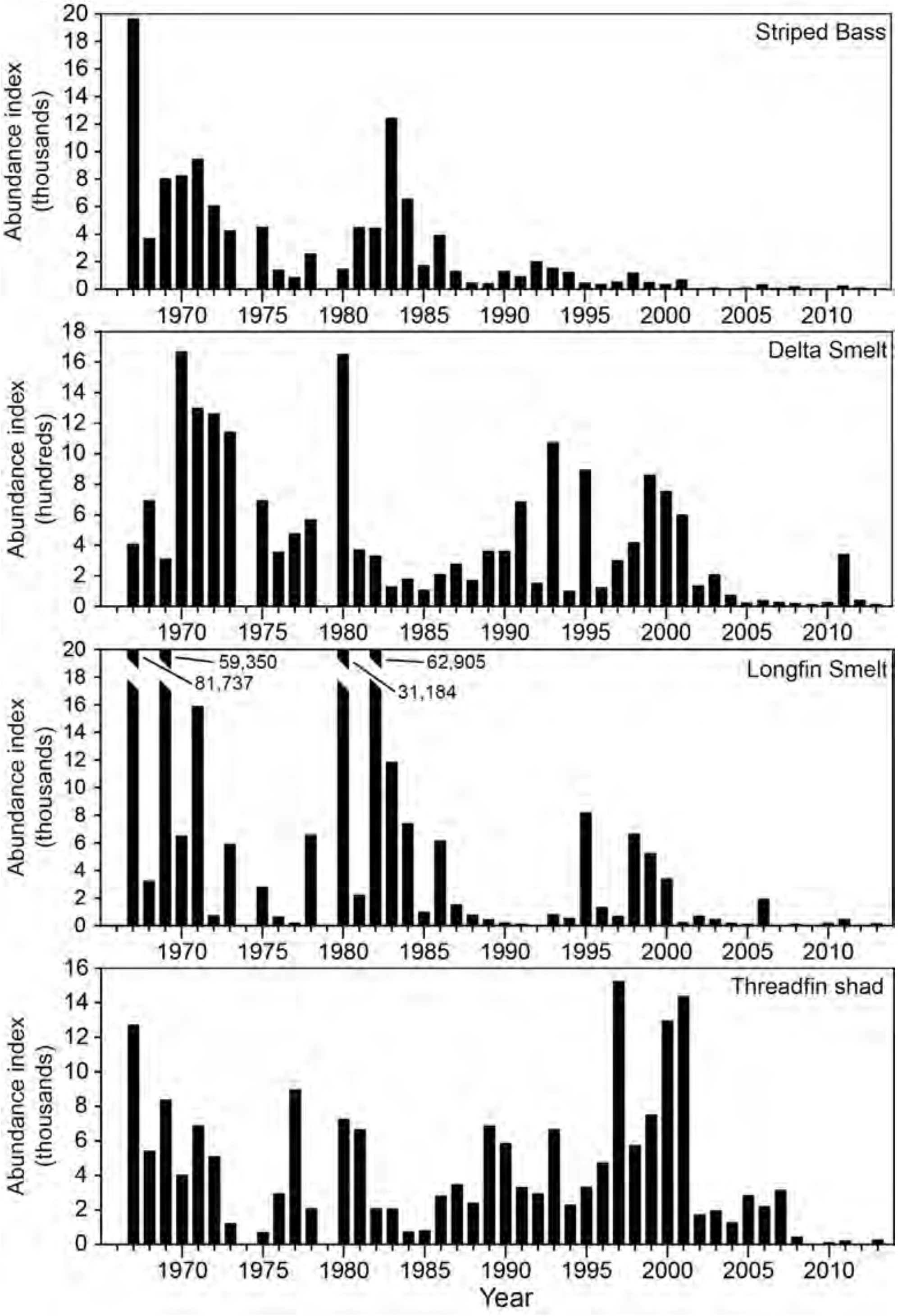


Figure 4. Abundance indices from Fall Midwater Trawl for Delta Smelt, Longfin Smelt, age-0 Striped Bass, and Threadfin Shad. Missing bars indicate when an index could not be calculated. See Chapter 3 for details of sampling programs, including geographic coverage, and Appendix B for details of calculationg abundance indices.



Changes in Delta Smelt distribution and abundance

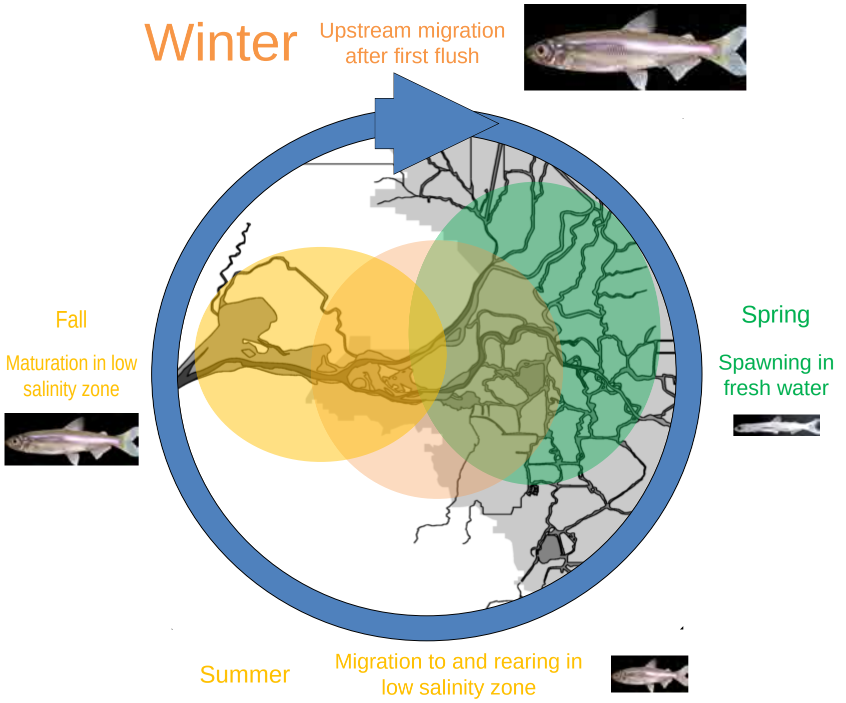
Long-term monitoring surveys conducted by the IEP have documented substantial changes in the distribution and abundance of Delta Smelt in its small native geographic range which extends from the upstream boundaries of tidal influence in the northern, eastern and southern Delta region of the estuary to Suisun and San Pablo Bays in the north-western region of the estuary. The geographic range of Delta Smelt also includes some of the larger tidal sloughs and tributaries adjacent to Suisun and San Pablo Bays, including some Suisun Marsh sloughs and the lower Napa River (Bennett 2005, Hobbs et al. 2007, Sommer et al. 2011, Merz et al. 2011, Sommer and Mejia 2013, Murphy and Hamilton 2013). Delta Smelt are generally considered a pelagic species. While they are commonly found in shallow shoal areas such as Honker and Grizzly Bays in the Suisun Bay region of the estuary and larger marsh sloughs such as Suisun and Montezuma Sloughs in Suisun Marsh and the lower reaches of Cache and Lindsey Sloughs in the northern Delta, they are less commonly encountered in near-shore areas and only rarely in smaller marsh sloughs (Bennett 2005, Merz et al. 2011, Sommer and Mejia 2013).

The Delta Smelt has been characterized as a “semi-anadromous” fish species that spawns in fresh water and rears in fresh to brackish water (Fig. 5; Dege and Brown 2004, Bennett 2005, Sommer et al. 2011, Merz et al. 2011). While Delta Smelt have been documented throughout their geographic range during most months of the year (Sommer et al. 2011, Merz et al. 2011, Murphy and Hamilton 2013), their distribution varies seasonally in response to dynamic abiotic and biotic habitat attributes such as salinity, temperature, turbidity, and presumably food supplies (Bennett et al. 2005, Sommer et al. 2013, Brown et al. 2014). In years with high freshwater discharge in winter and spring, spawning and rearing of larval and early post-larval fish can temporarily extend seaward into San Pablo Bay, while in years with less discharge it usually occurs in the Delta, Suisun Bay and Suisun Marsh. Juveniles and adults are distributed across a broader salinity range (0 to about 18) than larval and post-larval fishes which tend to be most abundant in the low salinity zone (salinity 1-6). Dege and Brown (2004) and Sommer et al. (2011) found that the center of the Delta Smelt distribution is associated with salinities of about 2 during most months and moves with the estuarine salinity gradient as the salinity gradient responds to flow.

Historically, Delta Smelt were commonly observed throughout the fresh and low salinity portions of their geographic range (Erkkila et al. 1950, Radke 1966). Over the last two decades, their geographic distribution has become more constricted during the summer and fall. At present, Delta Smelt are less commonly found in the southern and eastern Delta during the winter and spring and are largely absent from this region in the summer and fall (Nobriga et al. 2008, Sommer et al. 2011). While Delta Smelt continue to be found in the northern Delta year-round and individual catches in this region are sometimes large, particularly during winter and spring, the majority of the population is usually observed in the region near to and west of the Sacramento-San Joaquin River confluence, especially in the summer and fall (Sweetnam 1999, Feyrer et al. 2007, Nobriga et al. 2008, Merz et al. 2011, Sommer et al. 2011, Sommer and Mejia 2013).

In addition to documenting changes in distribution, long-term IEP surveys also reveal that the annual abundance indices of Delta Smelt have greatly declined since the first long-term pelagic fish monitoring survey began in summer 1959 (Fig. 3). Both a gradual, long-term decline and step changes, most recently around 2002, have been described using a variety of qualitative and statistical approaches for subadult Delta Smelt caught in the fall (e.g., Bennett and Moyle 1996, Bennett 2005, Manly and Chotkowski 2006, Thomson et al. 2010). These declines have not been smooth or entirely unidirectional and also include a great deal of interannual variability (Fig. 3).

Figure 5. Simplified life cycle of Delta Smelt (modified from Bennett 2005). Colors correspond to different seasons with the low salinity zone changing position with season.



Since the beginning of the POD in 2002, the Delta Smelt abundance indices have often been at record low levels, leading to concerns about declines in effective population size (Fisch et al. 2011) and a loss of population-level resilience, meaning the ability of the population to recover to higher population abundances when conditions are suitable. For example, population sizes might become too small to produce enough eggs or larvae to outpace predation on eggs and larvae.

Delta Smelt had previously rebounded from low population abundances, most recently in the wet years of the late 1990s (Fig. 3). The lack of increase in Delta Smelt in the wet year of 2006 combined with new evidence for genetic bottlenecks and a significant decline in effective population size from 2003 to 2007 (Fisch et al. 2011) were thus a source of great concern. However, during 2011, the next wet year after 2006, the species did increase in abundance (Fig. 3). Unfortunately, the increase in Delta Smelt abundance was short-lived and did not carry over into the following year-class in 2012, a drier year. Nevertheless, the temporary increase gave some cause for renewed optimism about the resilience of the species and its potential recovery. In addition, the contrasts between habitat conditions and Delta Smelt responses in 2006 and 2011 provided an opportunity to gain new insights into the Delta Smelt habitat requirements that might help better manage this species and its habitat.

Protecting Delta Smelt

Delta Smelt are currently protected under both California and federal endangered species legislation. The protection and recovery of Delta Smelt and its estuarine habitat in the SFE will likely require the human population of California to reduce its dependence on some of the natural resources provided by the SFE. This will become even more challenging in the future because of climate change and the continued growth of California's human population. California's population has increased by approximately 38 million people compared to the population when California became a state in 1850 and has increased by about 22.5 million compared to 1959 when Delta Smelt monitoring started 55 years ago (U.S. Census Bureau data). More than three quarters of today's 38 million Californians live south of the SFE, and the majority of these Californians and millions of acres of farmland rely on fresh water diverted from the Delta for all or part of their water supply. The conflicts and trade-offs between species protection measures and actions to provide water and other natural resources to California's growing human population have resulted in repeated attempts to reconcile these seemingly irreconcilable objectives through regulatory requirements, new institutional arrangements, and management plans.

Among the regulatory requirements are the State water right decisions issued by the California State Water Resources Control Board, which grant SWP and CVP water rights permits, but also include requirements to protect fish. State regulations also include increasingly more stringent waste discharge permits. For example, the new permit recently issued to the Sacramento Regional County Wastewater Treatment Plant includes new requirements for major treatment upgrades to better protect downstream water uses and the health of the estuary. Federal regulations include water quality requirements under the Clean Water Act and Biological Opinions (BiOps) issued under the federal Endangered Species Act. Two BiOps assess the effects of the coordinated operations of the SWP and CVP on Delta Smelt, Green Sturgeon, and salmonid fish populations, and their designated critical habitat. These BiOps include "reasonable and prudent alternatives" to lessen negative impacts of SWP and CVP operations and avoid jeopardy to the species, while at the same time trying to avoid major reductions in water exports from the Delta.

Recent institutional reconciliation attempts include the multiagency, State and federal CALFED Bay-Delta Program and Authority (CALFED) and the California Delta Stewardship Council (DSC), a new State agency. From 1994 to 2010, CALFED attempted to reconcile water allocation and ecosystem restoration efforts in the estuary in a way that would allow them to "get better together" (Doremus 2009). After the demise of CALFED, the State of California created the DSC to address what the legislature termed the "co-equal goals" of providing a more reliable water supply for California and protecting, restoring, and enhancing the Delta ecosystem (CA Water Code §85054, http://deltacouncil.ca.gov/).

Among the many management plans aimed at reconciling species protection and human water and land use objectives are plans by the DSC, SWRCB, and new groupings of multiple agencies and stakeholders. The DSC recently completed and is now starting to implement its comprehensive "Delta Plan" (http://deltacouncil.ca.gov/delta-plan-0) to achieve the co-equal goals, while the SWRCB is on track to complete a major update to its "Bay-Delta Plan" which may result in changes to water right permits (http://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/). Three California State agencies recently completed a new California Water Action Plan that includes actions to help achieve the co-equal goals (http://resources.ca.gov/california_water_action_plan/). A multi-agency planning effort that includes State and federal agencies as well as local Public Water Agencies (water contractors) is working to complete the "Bay-Delta Conservation Plan" (BDCP, http://baydeltaconservationplan.com). The BDCP is a proposed Habitat Conservation Plan under the federal Endangered Species Act and a Natural Community Conservation Plan under the California Natural Community Conservation Planning Act. It proposes to implement habitat restoration measures, stressor reduction activities, improved water project operations criteria, and new water conveyance infrastructure. If approved by the regulatory agencies, this plan would provide long-term permits for the various projects and water operations to proceed over a 50-year time frame.

Management actions, regulatory requirements, and institutional arrangements in the SFE have undergone substantial and complex changes over the last 150 years. Hanak et al. (2011) describe a progression from an early disorganized “laissez-faire” era of California and SFE water management followed by increasingly organized and large-scale management schemes, from local water use to state-wide water projects, which led to a current “era of conflict” and the hope for a new “era of reconciliation.” A complete review of these changes is outside the scope of this report and the reader is referred to Hanak et al. (2011) and other existing reports on this topic. It is important to note, however, that increasingly, these changes have been “adaptations” based on the results of monitoring, studies, and other scientific activities in the SFE. Many of these scientific activities have been conducted under the auspices of the IEP (Herrgesell 2013). It can be argued that some of the activities preceding and ultimately leading to the creation of the IEP in 1970 ushered in an era of increasingly intense and formalized “adaptive management” before the term itself was coined.

Adaptive management is a formal approach to natural resource management that closely connects science with management to devise, track, and improve management outcomes. This connection started to become an important aspect of fisheries management in the 1950s (e.g., Beverton and Holt 1957), although the term itself was not coined until 1978 when Holling (1978) and Walters and Hilborn (1978) provided a conceptual framework for adaptive resources management. This framework was later refined to distinguish between “passive” and “active” adaptive management. According to Williams (2011), “active adaptive management actively pursues the reduction of uncertainty through management interventions, whereas passive adaptive management focuses on resource objectives, with learning a useful but unintended byproduct of decision making […]. In practice this means that a key difference between passive and active adaptive management is the degree to which the objectives that guide decision making emphasize the reduction of uncertainty.” In active adaptive management, management actions are designed as “experimental treatments” with clear hypotheses about outcomes that are tested through rigorous data collection and analyses. This accelerates learning, but can come at the expense of achieving resource objectives because potentially less effective management actions may be included in the experimental design. Moreover, the more intense science efforts needed for active adaptive management can be costly over the short term (Williams 2011). This may explain why passive adaptive management, while not always referred to by this name or implemented in the formal and rigorous way now advocated by the DSC’s Delta Plan (DSC 2013), has been and continues to be common in the SFE, but active adaptive management – viewed by some as the only “real” adaptive management – is still rare.

Of all current management actions and requirements affecting Delta Smelt, the actions required in the 2005 and 2008 BiOps issued by the U.S. Fish and Wildlife Service (FWS) are most directly aimed at the protection of Delta Smelt. The 2008 BiOp takes a life cycle approach to protecting Delta Smelt and includes an explicit requirement for adaptive management of fall outflow. After initial steps to design a passive adaptive management program, the U.S. Bureau of Reclamation (Reclamation) decided to take a more active approach aimed at more rapidly reducing uncertainties about the underlying mechanisms and effects of fall outflow management on Delta Smelt (Reclamation 2011, 2012, Brown et al. 2014). The study component of the fall outflow adaptive management plan, also known as the “fall low salinity habitat” (FLaSH) studies, was developed with the help of a new conceptual model (FLaSH conceptual model, Brown et al. 2014) and has been implemented by the IEP starting in 2011. The FLaSH studies provided an opportunity to intensely study the increase in the Delta Smelt abundance index observed in 2011. At this initial stage of the adaptive management program and the FLaSH studies, the 2011 data were compared to data gathered in the previous wet year, 2006, during which fall outflow was lower. The intitial data analysis effort also considered antecedent conditions in 2010 and 2005, resulting in a simple comparative approach focusing on four years (Brown et al. 2014).

Report Purpose and Organization

It is clear that the recovery of Delta Smelt and other listed and unlisted native species will be a key requirement of any plan to manage the resources of the SFE. Understanding the factors driving Delta Smelt population dynamics is a major goal of resource management agencies. The main purpose of this report is to provide an up to date assessment of factors affecting Delta Smelt throughout its primarily annual life cycle. Specific goals are to provide decision makers with scientific information for evaluating difficult trade-offs associated with management and policy decisions, provide scientists with a resource for formulating and testing hypotheses and mathematical models, and provide the general public with a new way for learning about Delta Smelt and their habitat.

We address these goals through a synthesis of scientific information about Delta Smelt with an emphasis on new information since the release of the last POD synthesis report in 2010 (Baxter et al. 2010). As in previous reports, conceptual models play a key role in this report. Conceptual models are useful tools for organizing and synthesizing information, designing research and modeling studies, and for evaluating potential outcomes of management actions. Here, we revisit previously developed conceptual models for Delta Smelt, and synthesize new information about factors affecting Delta Smelt and Delta Smelt responses to those factors. This comprehensive body of information is then used to construct and populate a Delta Smelt conceptual model, within a new framework.

Numerous conceptual models have been developed to describe the relationships and linkages among environmental drivers of ecosystem change, ecosystem and habitat attributes, and Delta Smelt responses. In Chapter 2 of this report, we provide a brief introduction to conceptual models and review some of the conceptual models developed for the SFE and for Delta Smelt. In Chapter 3, we introduce a new conceptual model framework for Delta Smelt and describe our approach to updating the previously developed Delta Smelt conceptual models. We also describe the data sources and analytical approaches used in this report. In Chapter 4, we review and synthesize recent information about drivers and habitat attributes affecting Delta Smelt and Delta Smelt responses to habitat attributes. In Chapter 5, we present an updated conceptual model for Delta Smelt that include key drivers, habitat attributes, interactions between them, and Delta Smelt responses discussed in Chapter 4. In Chapter 6, we review and synthesize recent information about Delta Smelt population dynamics, life history, and population trends. In Chapter 7, we use the updated conceptual model to formulate hypotheses about Delta Smelt responses and changing habitat conditions and test them using a simple comparative approach similar to the FLaSH approach (Brown et al. 2014), but for all life stages of Delta Smelt. The purpose of Chapter 7 is to put the new conceptual model along with the comparative approach to an immediate test that is of high relevance to the management of Delta Smelt. Chapter 8 presents key results and conclusions from the preceding Chapters. In Chapter 9, we discuss next steps for future conceptual, qualitative, and quantitative modeling as well as the science and management implications of the information contained in this report.

Chapter 2: Conceptual Models

Overview

We learn and think about the world we live in through mental models of how the world looks and how it works. Our mental models guide all our conscious decisions and actions. They are never static; we constantly update them with new information gained by observing the world around us and by assessing the outcomes of our decisions and actions. In our minds, we compare the new information against our existing mental models. Observations that agree with our mental models strengthen them, observations that don't agree with our mental models force us to modify, adjust, and update them.

Conceptual models are formalized versions of mental models that are communicated to others verbally and graphically. Ecologists and environmental managers use them to communicate hypotheses about "how ecosystems work" and to explore how human actions and other drivers change ecosystems. They usually use a combination of narrative text and graphical illustrations about ecosystem components and the relationships among them. More informal narrative conceptual models verbally describe cause-effect relationships, while more formal conceptual models may express them through scientific hypotheses or mathematical equations.

Conceptual model illustrations often take the form of pictures, plots, schematic images or diagrams, matrices, or tables (Fischenich 2008). For example, the IEP Estuarine Ecology Team used elaborate matrices to illustrate and assess the likely mechanisms underlying the statistically determined relationships between SFE fishes and "X2," an indicator of estuarine salinity dynamics (Estuarine Ecology Team 1997), while Reclamation (2011, 2012) used a table format to illustrate how fall outflow interacts with other features of Delta Smelt habitat and affects Delta Smelt. Schoellhamer et al. (2012) used a series of conceptual X-Y plots to illustrate a conceptual model of sediment supply reduction and downstream propagation in the SFE. Glibert (2012) and Glibert et al. (2011) used schematic images to conceptualize changes in nutrients, flows, biogeochemical processes, and the food web of the SFE. Many schematic conceptual model diagrams use boxes to depict ecosystem components and arrows to illustrate the relationships, flows, and interactions among them. The conceptual models developed by the IEP for its POD investigations (see below) include examples of schematic conceptual model depictions with few boxes and arrows, while some of the conceptual models developed for the "Delta Regional Ecosystem Restoration Implementation Plan" (DiGennaro et al. 2012, see below) and the "effects hierarchy" of factors affecting Delta Smelt abundance developed by Miller et al. (2012) provide examples of more complex schematics with a large number of boxes and arrows.

Conceptual models have become essential tools for summarizing, synthesizing, and communicating scientific understanding of ecosystem structure and functioning. They are also key to successful planning and implementation of ecological research and mathematical modeling as well as to adaptive management, restoration and recovery of ecosystems, and environmental science education (e.g., Thom 2000, Ogden et al. 2005, Fortuin et al. 2011). Conceptual models are also essential tools for identifying management and science priorities and for the selection of key ecological attributes to be used to evaluate the performance of management actions (i.e., performance measures) and assess the present relative to a desired state of an ecosystem (i.e., indicators) (Washington State Academy of Sciences 2012).

Conceptual models have clear limitations. For example, even the most complex conceptual models are highly simplified descriptions of a small part of an ecosystem – they can never tell the "whole" story. Just like our every-day mental models, they are also never final. To remain relevant, ecological conceptual models must evolve and change with the evolution of our knowledge about ecosystems. Furthermore, conceptual models identify key ecosystem components and relationships, but they do not quantify them and unless they are coupled with mathematical models, conceptual models cannot be used to make quantitative predictions.

Conceptual models can be used to make qualitative predictions about changes in ecosystem components and their relationships. These qualitative predictions can serve as testable hypotheses that help design scientific analyses and studies. The creation or revision of the conceptual models themselves usually forces the formulation of hypotheses and their testing with available data and information, as will be demonstrated in the later Chapters of this report. Qualitative predictions and testable hypotheses are also at the heart of active adaptive management. They are needed to design experimental adaptive management actions and the studies and monitoring needed to assess the outcomes from such actions. The fall outflow adaptive management plan (Reclamation 2011, 2012) provides an example of how a conceptual model was used to make qualitative predictions and design a comprehensive set of studies, the FLaSH studies. Finally, the formulation of conceptual models is usually the essential first step for constructing quantitative models. Mathematical models are sets of mathematical expressions that quantify the components and relationships in the conceptual models and can be used to make quantitative predictions about the state of ecosystem components and linkages under specific circumstances (Jackson et al. 2000). The (few) quantitative predictions in the fall outflow adaptive management plan (Reclamation 2011, 2012) are based on such mathematical models.

Ecological conceptual models generally link ecological "drivers" with ecological effects or "outcomes." Drivers are physical, chemical, or biological factors of human or natural origin (for example, nutrients from natural soils and applied fertilizers). Outcomes can be physical, chemical or biological responses to the drivers (for example, phytoplankton growth and biomass), but can also be social and economic impacts on human components of the ecosystem (for example, harmful algal blooms that affect recreational use or costs of water treatment for drinking water supply). Drivers and outcomes are the components of the system under consideration. They are linked by mechanistic cause-effect relationships. Conceptual models can also be nested within each other, for example, to accommodate different temporal or spatial scales, or conceptual models can be coupled so that the outcome of one conceptual model becomes a driver in the next one. Drivers are often categorized in various ways, including their causal proximity to specific outcomes, whether they are natural or anthropogenic, and whether they can be altered by human management strategies and actions. Graphically, drivers are often arranged in hierarchical tiers that reflect these categories.

For example, Gentile et al (2001) describe a basic three-tiered approach that links environmental outcomes (tier 1) to proximal anthropogenic drivers termed "stressors" (tier 2) and the natural and anthropogenic drivers that act on these stressors (tier 3). Davis et al. (2010) show how different ecological regimes in Australian lakes (outcomes, tier 1) arise from the interplay of stressors (tier 2) and hydrological changes (tier 3) acting on the original ecological regime (tier 4). Carr et al. (2007) review a widely used five-tiered "Driver–Pressure–State–Impact–Response" (DPSIR) framework that focuses on identifying human-caused environmental problems and solutions. In this framework, the ultimate drivers (D) are social processes that result in specific human activities that manifest as proximal "pressures" (P) that change the "state" (S), or condition, of the environment. This can have "impacts" (I) on human well-being that are recognized as problems. Some impacts are so severe that they require a human response (R), usually in the form of institutional solutions aimed at reducing high-priority impacts. The Puget Sound Partnership Science Panel (2012) recently used the DPSIR framework to develop a conceptual model that links management strategies (i.e., responses; e.g., reduce pollution) to anthropogenic drivers (e.g., human population growth) and pressures (e.g., pollution) that affect the state of ecosystem components (e.g., habitats and species) and impact the provisioning of ecosystem services (e.g., fishing). This model helped identify scientific knowledge gaps and decision-critical issues and questions that needed to be answered in response to management priorities.

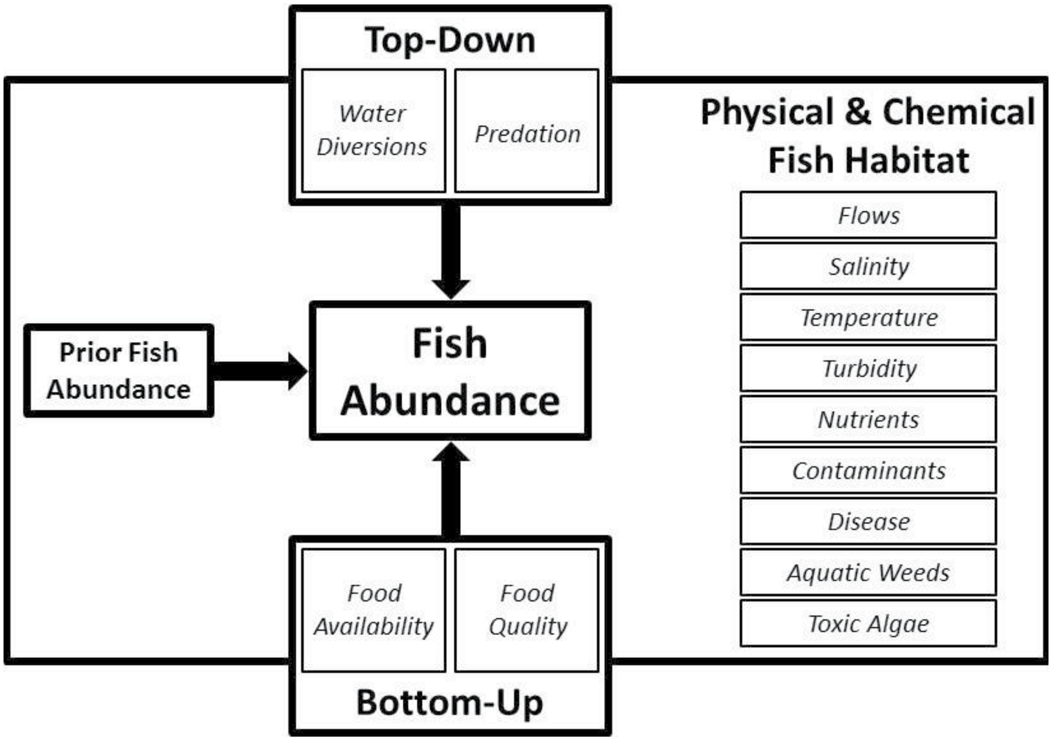
Recent Conceptual Models for the San Francisco Estuary

Over the last decade, two integrated sets of conceptual models have been developed for portions of the SFE. The first conceptual model set was developed by the Ecosystem Restoration Program (http://www.dfg.ca.gov/ERP/) to evaluate restoration actions in the Delta under the "Delta Regional Ecosystem Restoration Implementation Plan" (DRERIP; DiGennaro et al. 2012). DRERIP conceptual models were developed for ecological processes, habitats, specific species, and stressors. The DRERIP conceptual models were built around environmental drivers, their expected effects termed "outcomes," and cause-and-effect relationships between the two shown as one-way arrows termed "linkages." In the graphical depiction of the DRERIP conceptual models, different arrow widths, colors, and styles denote the importance, degree of understanding, and predictability, respectively, of the driver-linkage-outcome relationships, while symbols next to the arrows denote the direction and nature of the effect (positive, negative, or non-linear) (DiGennaro 2012, Opperman 2012). The DRERIP species conceptual models include "transition matrix" diagrams depicting how environmental drivers affect the probability of one life stage successfully transitioning to the next.

The second set of conceptual models was developed by the IEP as a comprehensive conceptual framework intended to guide investigations of the POD and to synthesize and communicate results (Sommer et al. 2007, Baxter et al. 2010). This framework includes a "basic" POD conceptual model about key drivers of change affecting pelagic fish and their habitat (Fig. 6), more narrowly focused "species-specific" conceptual models about drivers affecting the different life stages of each of the four POD fish species (e.g., Fig. 7), and a broader "ecological regime shift" conceptual model that placed the POD decline in a longer-term historical context (not shown; see Baxter et al. 2010). The basic POD conceptual model placed the four fish species in the center of interacting drivers affecting the quantity and quality of their habitat (Fig. 6), while the species-specific models identified key seasonal drivers in red, with proximal causes and effects in yellow (Fig. 7).

The National Research Council Committee on Sustainable Water and Environmental Management in the California Bay-Delta (NRC Committee) (NRC 2012) called the POD conceptual model framework "an important example of supporting science. This framework identifies and links, in the context of both ecosystem structure and functioning, the key stressors that help to explain the decline of pelagic organisms." The NRC Committee further noted that the "drivers of change" identified in the POD conceptual models "are quantifiable" and "suitable for model evaluation" and that the:

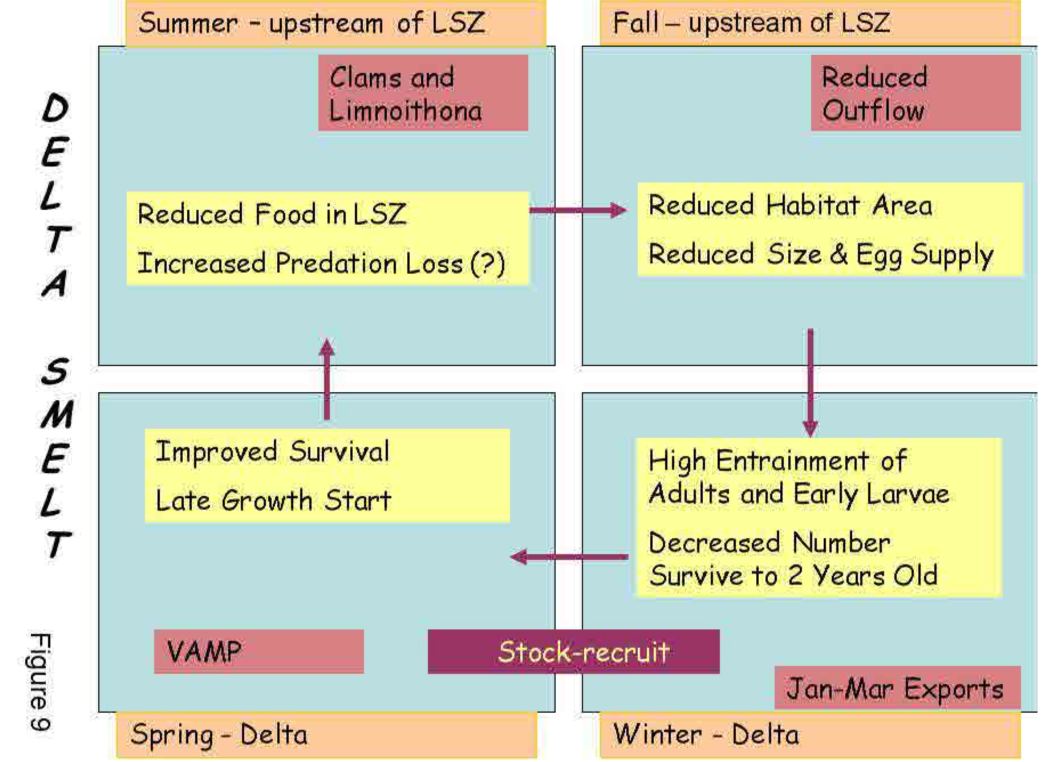
Figure 6. **The basic conceptual model for the pelagic organism decline (Baxter et al. 2010).**



> “types of stressors identified are integrative, reflecting co-occurring physical, chemical, and biotic changes. They also apply to multiple structural (food web structure, biodiversity) and functional (food transfer changes, biogeochemical cycling) changes taking place in the Delta. The framework and associated detail are both comprehensive and useful in terms of linking these drivers to changes taking place at multiple levels of the food web. This type of conceptual approach will also be useful for examining other drivers and impacts of ecological change, including observed changes in fish community structure and production; specifically, how these changes are affected and influenced by changes in physico-chemical factors (e.g., salinity, temperature, turbidity, nutrients/contaminants) and at lower trophic levels (phytoplankton, invertebrate grazers, and prey)” (NRC 2012, p. 34-35).

Since the release of the 2012 NRC report, the POD conceptual model framework has been used as the basis for additional conceptual models developed to aid planning and quantifying the ecological effects of active adaptive management of Delta outflow to improve fall low salinity habitat for Delta Smelt and to guide the associated fall low salinity habitat (FLaSH) studies (Reclamation 2011, 2012). A more complete summary of the POD and FLaSH conceptual models along with additional information about related conceptual and quantitative models in the SFE can be found in the initial FLaSH report (Brown et al. 2014, see also http://deltacouncil.ca.gov/science-program/fall-low-salinity-habitat-flash-studies-and-adaptive-management-plan-review-0).

Figure 7. **Species-specific conceptual model for Delta Smelt. This is one of four species-specific conceptual models developed as part of the conceptual framework for the pelagic organism decline (Baxter et al. 2010). The low salinity zone (LSZ) is defined as salinity 1-6. The Vernalis Adaptive Management Plan (VAMP) included reductions in spring exports with possible effects on Delta Smelt.**



One important new feature of the conceptual model developed for the fall outflow adaptive management plan and the FLaSH studies was the explicit consideration of interacting dynamic and relatively more stationary (geographically and temporally fixed) habitat components that was based on a conceptual model of environment-habitat-production linkages in tidal river estuaries developed by Peterson (2003). In the FLaSH conceptual model, the interactions among dynamic and stationary habitat components determine the characteristics of Delta Smelt habitat in the fall and lead to varying Delta Smelt outcomes. In essence, the dynamic flow and salinity regimes of the SFE move water, particles, and organisms across the estuary's stationary topography, which has distinct physical features that modulate the dynamic habitat components. Together, these stationary and dynamic habitat components are hypothesized to control the survival, health, growth, fecundity, and, ultimately, the reproductive success of estuarine pelagic species, such as Delta Smelt. The interplay between stationary and dynamic habitat components also helps explain the distribution and movement of Delta Smelt across its range which cannot be understood – or managed – based on geography alone.

Numerous other conceptual and quantitative models have been developed for the SFE. Kimmerer (2004) summarized many of the earlier conceptual models. More recent conceptual model examples include those by Glibert (2012) and Glibert et al. (2011) as well as the five-tiered effects hierarchy by Miller et al. (2012). Recent examples of mathematical models of habitat use and population dynamics of Delta Smelt include models based on statistical approaches (e.g., Manly and Chotkowski 2006, Feyrer et al. 2007, Nobriga et al. 2008, Feyrer et al. 2010, Thomson et al. 2010, Mac Nally et al. 2010, Miller et al. 2012). There is also a rapidly developing body of life cycle models for Delta Smelt and other SFE fish species that use statistical and numerical simulation approaches (e.g. Blumberg et al., 2010, Maunder and Deriso 2011, Massoudieh et al. 2011, Rose et al. 2011, Rose et al. 2013a,b).

Chapter 3: Approach

This report is the result of a team effort by the IEP Management, Analysis, and Synthesis Team (MAST, often referred to as "we" in this report). Appendix A briefly describes the MAST and the report development process and schedule which included a public and independent expert peer review step that led to major revisions to the draft report.

General Approach

Our general approach in this report was to develop a new conceptual model framework for Delta Smelt and to use this framework to synthesize new scientific information and update and integrate existing conceptual models including the "basic" and "species-specific" POD conceptual models, the DRERIP "transition matrix" models, the tabular FLaSH conceptual model and the hierarchical conceptual model in Miller et al. (2012) described in Chapter 2.

The development of the new conceptual model framework was guided by the conceptual model literature (see Chapter 2) and by recommendations from the independent "FLaSH Panel" of national experts convened by the Delta Science Program. The FLaSH Panel recommended to:

> "develop a schematic version of the [FLaSH] conceptual model that matches the revised, written version of the conceptual model in the draft 2012 FLaSH study report. The conceptual model in written and schematic form should continue to emphasize processes and their interactions over simple correlations, should ensure Delta Smelt vital rates remain central to thinking, and should be designed for routine use by scientists as an organizational tool and for testing hypotheses associated with the AMP [adaptive management plan]; it should be as complex as necessary to achieve these purposes. The conceptual model should also be able to encompass processes and interactions that extend before and after Fall Outflow Action periods, including areas both upstream and downstream of the LSZ" (FLaSH Panel 2012, page ii).

The conceptual modeling approach in this report is intended to provide a basis, not a substitute for the development or use of mathematical models. While mathematical models are outside of the scope of this report, we briefly discuss the promise and challenges of mathematical models for Delta Smelt, summarize some of the highlights of existing mathematical modeling efforts for Delta Smelt, and offer a brief description of two additional proposed mathematical modeling efforts — one qualitative and the other quantitative — we think are natural outgrowths of the information in this report (see Chapter 8). Development of a variety of flexible working tools to facilitate discussion of elements of the conceptual model is one intended outcome of the MAST effort. Even simple quantitative and qualitative models based on our revised conceptual model will serve to further organize thinking and characterize weaknesses in current data collection and analysis efforts.

In this Chapter, we introduce the new conceptual model framework for Delta Smelt. This framework consists of a series of nested and tiered conceptual models: a general life cycle conceptual model and more detailed life stage transition conceptual models. It was developed following recommendations by the FLaSH Panel (FLaSH Panel 2012) and extensive reviews of a draft version of this report (see http://www.water.ca.gov/iep/pod/mast.cfm and Appendix A). In Chapter 4 we review and synthesize existing information about drivers, habitat attributes, and Delta Smelt responses with a focus on new information since 2010. We use the drivers in the basic POD conceptual model as the basis for this synthesis. This information is then used to populate the nested conceptual models in the new conceptual model framework with key drivers and their linkages to Delta Smelt responses. The fully populated nested conceptual models are presented in Chapter 5. Chapter 6 focuses on Delta Smelt life history and population dynamics and trends. Chapters 4 and 6 include some new analyses of long-term monitoring data, but are largely based on a review and synthesis of the existing published literature. In Chapter 7, we compare data pertaining to ecosystem drivers (drivers), habitat attributes (drivers or outcomes) and Delta Smelt responses (outcomes) in four recent years with moderate to wet hydrology: the two most recent wet years (2006 and 2011) and the two drier years immediately before them (2005 and 2010). The intent is to assess the utility of the conceptual model for formulating and testing hypotheses that expand the comparative FLaSH approach (Brown et al. 2014) that focused on the fall to a more comprehensive year-round investigation of why Delta Smelt abundance increased in the wet year of 2011, but failed to respond to wet conditions in 2006. In each of the sections in Chapter 7 covering a specific life stage, the hypotheses inherent in the conceptual model are stated and the reasoning for including each hypothesis is explained. Although we attempted to develop independent hypotheses, this was not always possible because many drivers were related and important habitat attributes were influenced by multiple drivers and their interactions, as shown in the conceptual model diagrams and explored in Chapter 4.

Key insights from Chapters 4–7 are summarized in Chapter 8. In Chapter 8, we also discuss limitations of the analytical approaches in this report. In Chapter 9, we describe additional data and analyses needed to test hypotheses that could not be conclusively tested with the available data and our simple comparative analysis approach. We also present some ongoing or possible next steps for future years, including some recommendations for future synthesis and mathematical lifecycle modeling efforts aimed at Delta Smelt and other species and for future adaptive management, including the fall outflow adaptive management and FLaSH studies effort.

Framework for the Delta Smelt Conceptual Model

The updated Delta Smelt conceptual model framework in this report integrates and modifies features of the “basic” and “species specific” POD conceptual models (Baxter et al 2010), the FLaSH conceptual model (Brown et al. 2014), the DRERIP “transition matrix” conceptual models (DiGennaro et al. 2012), and the hierarchical conceptual model in Miller et al. (2012). It consists of two nested and linked conceptual models of increasing specificity:

1. A *general life cycle conceptual model* for the four Delta Smelt life stages (adults, eggs and larvae, juveniles, and subadults) that includes stationary landscape attributes and dynamic environmental drivers, habitat attributes, and Delta Smelt responses; and

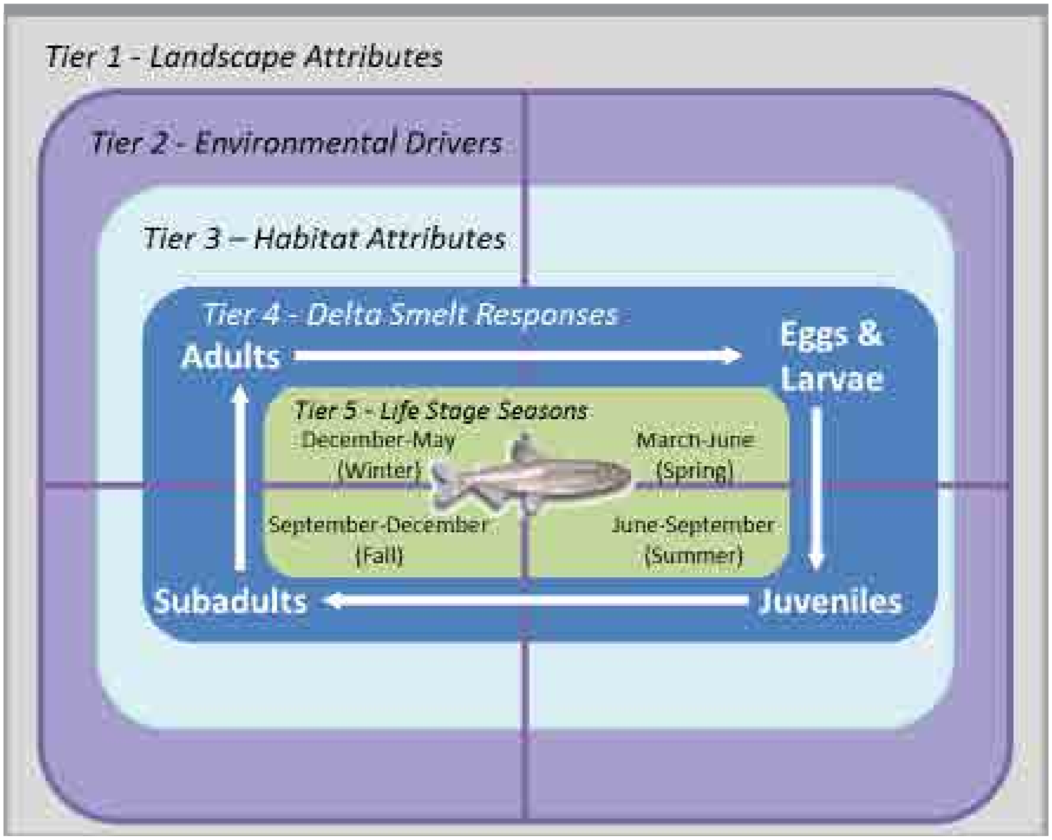
2. More detailed *life stage transition conceptual models* for each of the four Delta Smelt life stages that describe relationships between environmental drivers, key habitat attributes, and the population-level probability of successfully transitioning from one life stage to the next. This probability is dependent on the effects of environmental drivers and habitat attributes on the growth, survival, reproduction, and movements of Delta Smelt but data are currently inadequate to provide causal links for most of these processes individually.

General Life Cycle Conceptual Model

The updated general life cycle conceptual model for Delta Smelt (Fig. 8) follows the FLaSH Panels (2012) recommendation to "ensure Delta Smelt vital rates remain central to thinking" and is structurally similar to the basic POD conceptual model (Fig. 6). The general life cycle conceptual model is divided vertically and horizontally into four sections representing four Delta Smelt life stages from eggs and larvae to adults occurring in four "life stage seasons" indicated in the center of the diagram (Fig. 8; tier 5 box, green shading). This is similar to the four seasonal compartments of the species-specific conceptual model diagram in Baxter et al. (2010). Importantly, these life stage seasons are not exactly the same as calendar-based seasons. Instead, they have somewhat variable duration and overlapping months. This is because life stage transitions from eggs to adults are gradual and different life stages of Delta Smelt often overlap for a period of one to three months. Delta Smelt responses (Fig. 8; tier 4 box with dark blue shading) to important habitat attributes throughout their usually annual life cycle are placed within a box representing habitat attributes important to their growth and survival, which conveys the idea that biotic and abiotic habitat elements drive Delta Smelt responses (Peterson 2003; Fig. 8; tier 3 box with light blue shading). For each life stage season, there are a set of natural and anthropogenic environmental drivers associated with the estuarine environment (Fig. 8; tier 2 box with purple shading) that generate the habitat attributes important to Delta Smelt growth and survival. Surrounding the environmental drivers box is a fourth, outer box that represents the stationary (geographically and temporally fixed) landscape attributes of the estuarine ecosystem associated with its physical geometry and the orientation and connections of its component waterbodies (Fig. 8; tier 1 box with grey shading). In contrast to this outer box, the components and processes described in the inner boxes of this conceptual model are dynamic in space and time. Note that the fixed landscape attributes are considered fixed in the context of Delta Smelt population biology in any particular year rather than across longer time scales. The different spatial and temporal scales for each tier of the conceptual model are shown in Figure 9.

The tiered components of the general life cycle conceptual model for Delta Smelt can vary over a wide range of spatial and temporal scales (Fig. 9). Landscape attributes of the San Francisco Estuary (tier 1) encompass local to estuarine-wide features and change slowly over decades or longer periods. Environmental drivers (tier 2) that affect Delta Smelt habitat attributes vary and manifest over the broadest range of spatial and temporal scales, from local variations over tidal or daily cycles to long-term changes at the watershed or even larger geographic scales. Similar to environmental drivers, habitat attributes of Delta Smelt (tier 3) can be highly dynamic at small spatial and temporal scales or change gradually over many years, but they don't extend beyond the geographic range of the species, which in the case of Delta Smelt is the SFE. Delta Smelt responses (tier 4) vary in response to changing habitat attributes within subregions of the estuary. In this small fish species with its maximum age of two years and extremely small geographic range, population-level responses can range from rapid (e.g., in response to toxic spills) to more

Figure 8. **A new conceptual model for Delta Smelt showing Delta Smelt responses (dark blue box) to habitat attributes (light blue box), which are influenced by environmental drivers (purple box) in four "life stage seasons" (green box). Environmental drivers are influenced by landscape attributes (grey box).**



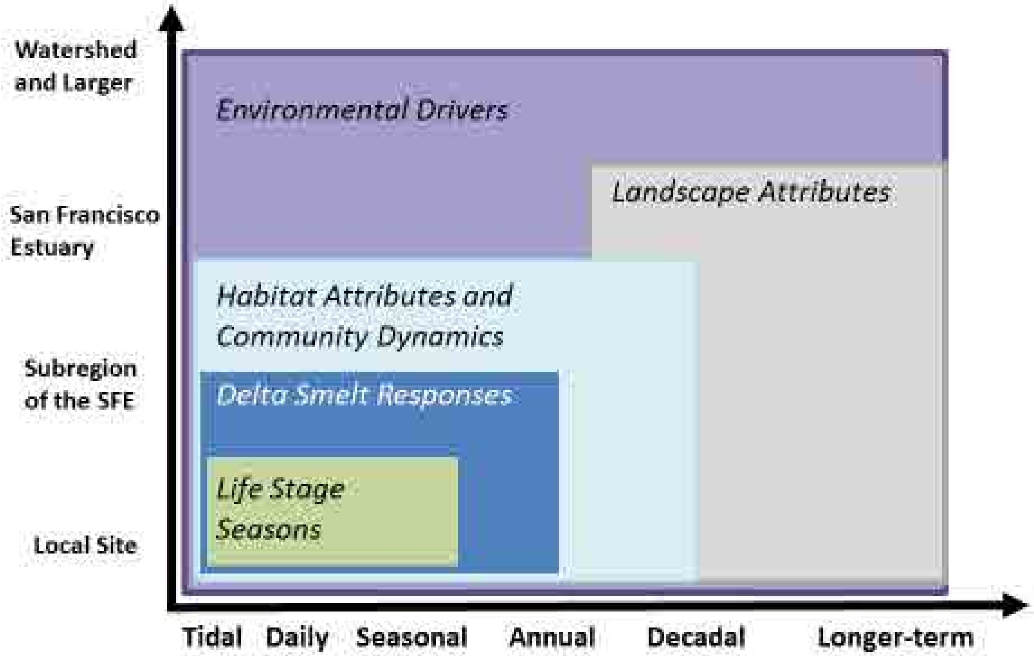
slowly over the course of one or more years. Life stage seasons (tier 5) occur over the course of a year in seasonally occupied areas of the estuary.

Similar to the POD and DRERIP conceptual models, the updated Delta Smelt life cycle conceptual model includes only those landscape attributes and environmental drivers with plausible mechanistic linkages to outcomes, which in this case are changes in habitat attributes and resulting Delta Smelt responses in the four life stage seasons. These mechanistic linkages are depicted as arrows in a series of four new conceptual models for each life stage season (Fig. 10). These life stage season conceptual models are nested components of the general life cycle conceptual model as shown in Fig. 8. They will be described in detail in Chapter 5.

Data Sources

Our examination of environmental drivers in Chapter 4, Delta Smelt life history and population dynamics and trends in Chapter 6, and the evaluation of hypotheses about Delta Smelt responses to changing habitat attributes in Chapter 7 rely largely on results of previously published data and analyses, but in several cases we update these analyses with more recent data. We also include some additional analyses (described below). All these analyses depend largely on environmental monitoring data collected by IEP agencies during routine, long-term monitoring surveys

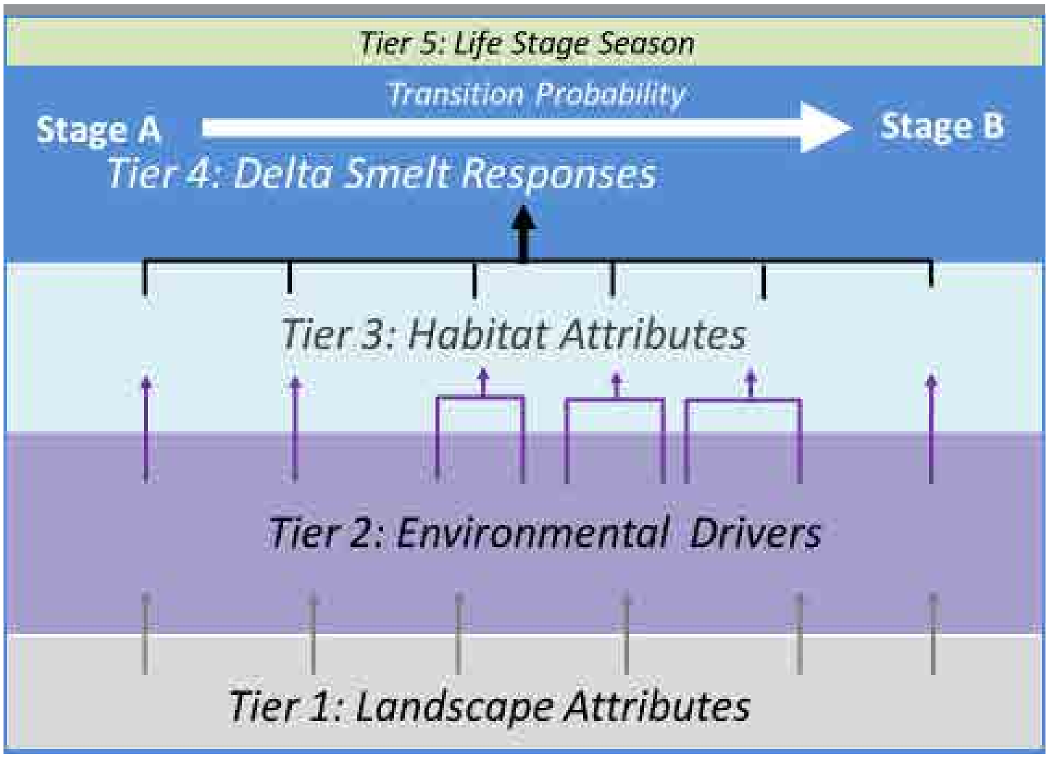
Figure 9. **Spatial and temporal scales of the component tiers in the general life cycle conceptual model framework for Delta Smelt.**



(http://www.water.ca.gov/iep/products/data.cfm). These surveys provide the long-term records and geographic coverage necessary and the data collected by these surveys are publicly available. Available data includes data on fish, invertebrates, phytoplankton, water quality variables, and flow. Use of these particular data sources does not reflect any preference for those data. Results from other ongoing research efforts were included as appropriate.

For the purposes of this report, we consider each stage, larvae through adults, of the Delta Smelt life cycle in the context of the monitoring programs that provide data on the Delta Smelt population. Delta Smelt eggs are not monitored and have in fact never been found in the wild. Monitoring surveys in the late winter and spring include the spring Kodiak trawl (SKT, Fig. 11), which samples maturing, spawning and post-spawning adults. The SKT is conducted monthly from January through May. Spring also includes the 20 mm survey (20 mm, Fig. 12), which samples larval and post-larval Delta Smelt and is conducted every two weeks from mid-March through mid-July. Summer includes the summer townet survey (TNS, Fig. 13); which samples juvenile fish and currently runs every two weeks from June through August. The Fall Midwater Trawl (FMWT, Fig. 14) survey samples subadult Delta Smelt monthly from September through mid-December. Each of these surveys samples fishes broadly within the upper SFE and generally covers the geographic habitat range used by Delta Smelt (Merz et al. 2011). Exceptions to complete coverage occur in some high outflow years when Delta Smelt can temporarily inhabit San Pablo Bay in association with decreased salinities caused by increased Delta outflows (Moyle 2002) and in other years when some adult fish move upstream of the geographic range of these surveys (probably to spawn) in the Yolo Bypass and Sacramento River (e.g., Feyrer et al. 2006, Merz et al. 2011). Also, FMWT and TNS sampling in the Cache Slough complex was instituted over several years starting in the 1990s for FMWT and 2000s for TNS. The current sampling locations have been in place since 2011. These exceptions to complete spatial coverage are believed to reflect small fractions of the population. Additional geographic coverage along

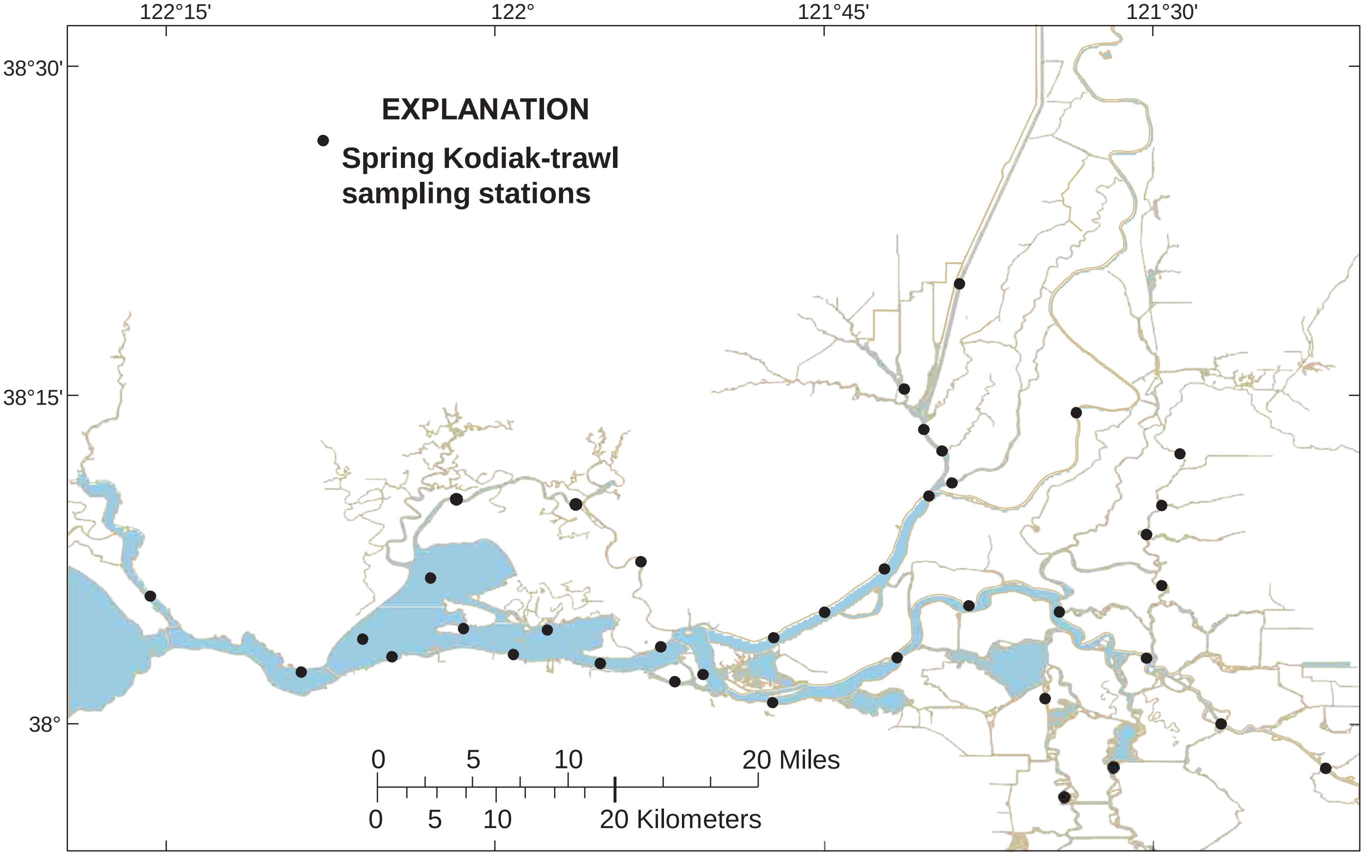
Figure 10. **Framework for the Delta Smelt life stage season conceptual models.**



or outside of the margins of the other four monitoring surveys is provided by other IEP fish monitoring surveys such as the San Francisco Bay Study, trawling and seining conducted by the Delta Juvenile Fish Monitoring Program in the Sacramento River and the north Delta, as well as the fish salvage monitoring at the fish protection facilities associated with the SWP and CVP export pumps in the south Delta. All Delta Smelt life stages (larvae-adult) are also commonly collected from nearshore habitats and in shallow open water where trawls cannot be used effectively (e.g., Aasen 1999, Nobriga et al. 2005, Brown and May 2006); however, there are no data indicating these are preferred habitats, that these fish represent different populations (see Fisch et al. 2011), or that their abundance varies differently than data from the aforementioned trawl surveys would suggest.

Annual abundance indices for Delta Smelt life stages are calculated from the catch data provided by each of the four surveys (See Appendix B for details). Together, they provide a comprehensive account of long-term changes in the relative abundance of Delta Smelt (Fig. 3). The long series of abundance index records for the summer and fall have provided the basis for many data analyses and modeling studies (e.g., Jassby et al. 1995, Kimmerer 2002a,b, Bennett 2005, Manly and Chotkowski 2006, Thomson et al. 2010, MacNally et al. 2010, Maunder and Deriso 2011, Miller et al. 2012) and for regulatory actions (USFWS 2008). They have also been used to estimate absolute population abundance (Newman 2008). The Delta Smelt and other SFE fish abundance indices are generally considered useful indicators of the status and trends of the Delta Smelt population as well as of the status of other resident fishes in the SFE in general and serve as performance metrics for the success of management actions. All monitoring surveys have strengths and weaknesses, and the long-term fish monitoring programs in the SFE are no exception (Honey et al. 2004). In the case of Delta Smelt, strengths include reasonably good coverage of the geographic extent of Delta Smelt habitat and coverage of all life stages except

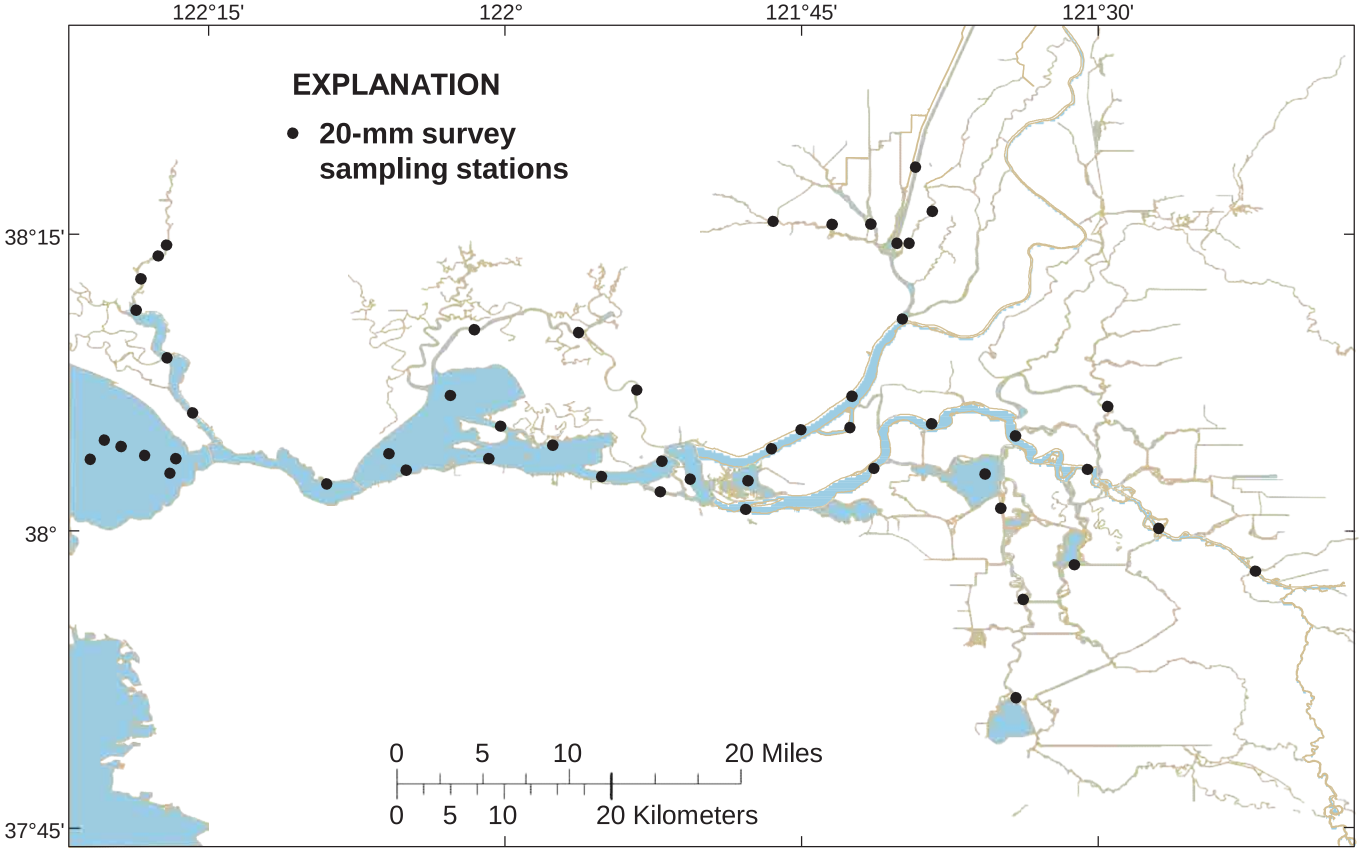
Figure 11. **Map of Spring-Kodiak Trawl Survey sampling stations.**



eggs (Gaines et al. 2006). They also include exceptionally long and consistent data records going back to 1959 in the case of the TNS, the oldest of the four surveys described here. There is a large amount of ancillary data (covariates), including data collected during the fish surveys, additional fish data from other monitoring surveys (Honey et al. 2004) as well as invertebrate, phytoplankton, water quality and hydrological data. Possible weaknesses include no measure of precision of abundance indices and imprecise estimates due to a high frequency of zero catches of Delta Smelt. These problems combine with survey design issues such as differences in Delta Smelt catchability with different nets and trawl regimes under changing environmental conditions, behavioral changes in distribution (Newman 2008) and the current low abundance of the species. For example, several studies have shown that Delta Smelt can exhibit lateral and vertical movements associated with tide and time of day (Bennett et al. 2002, Feyrer et al. 2013, Bennett and Burau 2014) but the overall frequency or effects of such local movements on abundance indices are unclear. Studies to further evaluate and address these issues are currently underway.

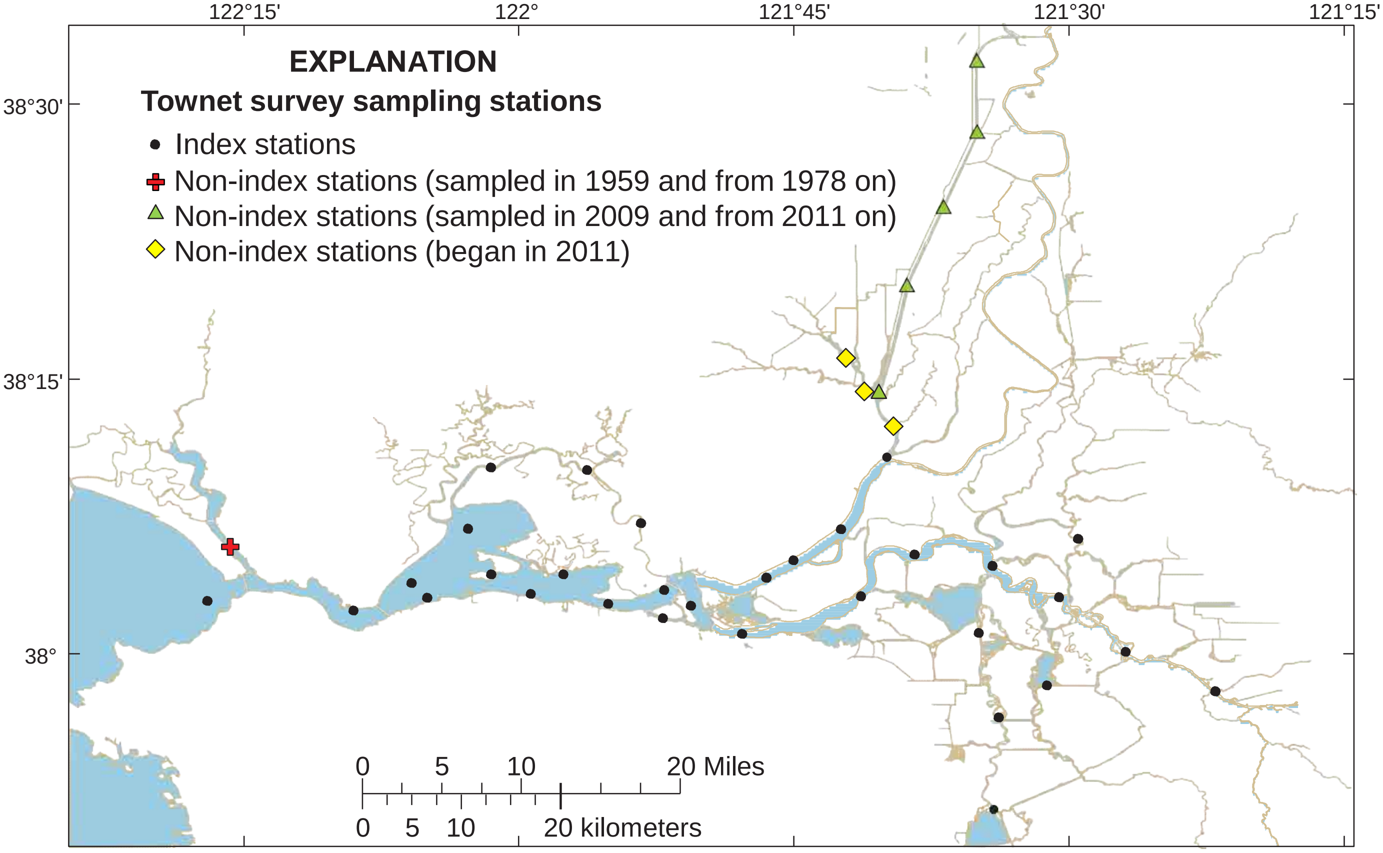
Two of the four fish monitoring surveys described here specifically target Delta Smelt; the other two do not. The SKT was designed and implemented specifically to improve detection of maturing adult Delta Smelt moving upstream in the winter and spring, particularly into the central and south Delta (Souza 2002). The 20 mm survey was designed and implemented specifically to capture late-stage larval Delta Smelt of about 20 mm in length; the SKT and 20 mm survey data help managers assess the risk of entrainment of these life stages by south Delta

Figure 12. Map of 20 mm Survey sampling stations.



export pumps (Dege and Brown 2004). The TNS was designed to target small juvenile Striped Bass of about 17-50 mm fork length (the distance from the snout to the indentation of the tail fin) (Stevens 1977, Turner and Chadwick 1972); however, Delta Smelt tend to be of appropriate size for capture by the TNS net during the survey period. This occurs because Delta Smelt (see below) and Striped Bass spawning overlaps in time and growth of both are linked to water temperature, such that peak larval abundance occurs in April or May in most years. The TNS traditionally started and ended based on mean length of Striped Bass; however, young Delta Smelt attain sizes vulnerable to the TNS net during the same time period Striped Bass are vulnerable (Miller 2000). The survey ends when young Striped Bass surpassed 38 mm fork length (Miller 2000). Thus, regardless of the particular number of sampling surveys in a year or the index calculation method, Delta Smelt juveniles are generally vulnerable to the TNS whenever it samples. Similarly, the FMWT survey was designed to capture young-of-the-year Striped Bass, but in the 60-140 mm fork length size range (Stevens 1977). Although the survey and gear is generally effective for small pelagic fishes, the cod-end mesh (1.3 mm stretch mesh) on the net is large enough to allow some smaller sub-adult Delta Smelt to escape during the first couple survey months (see Newman 2008 for an approach to correct this effect). Even though the gear is not completely effective at retaining all sub-adult Delta Smelt, FMWT provides a reasonable relative measure of sub-adult abundance through time (Kimmerer and Nobriga 2005), albeit with low precison at the current low catch levels and given additional variation related to changes in growth, and thus changes in retention in the net from year to year. With the aforementioned caveats, we believe these surveys provide useful and valid relative abundance measures to examine the various life stage transition

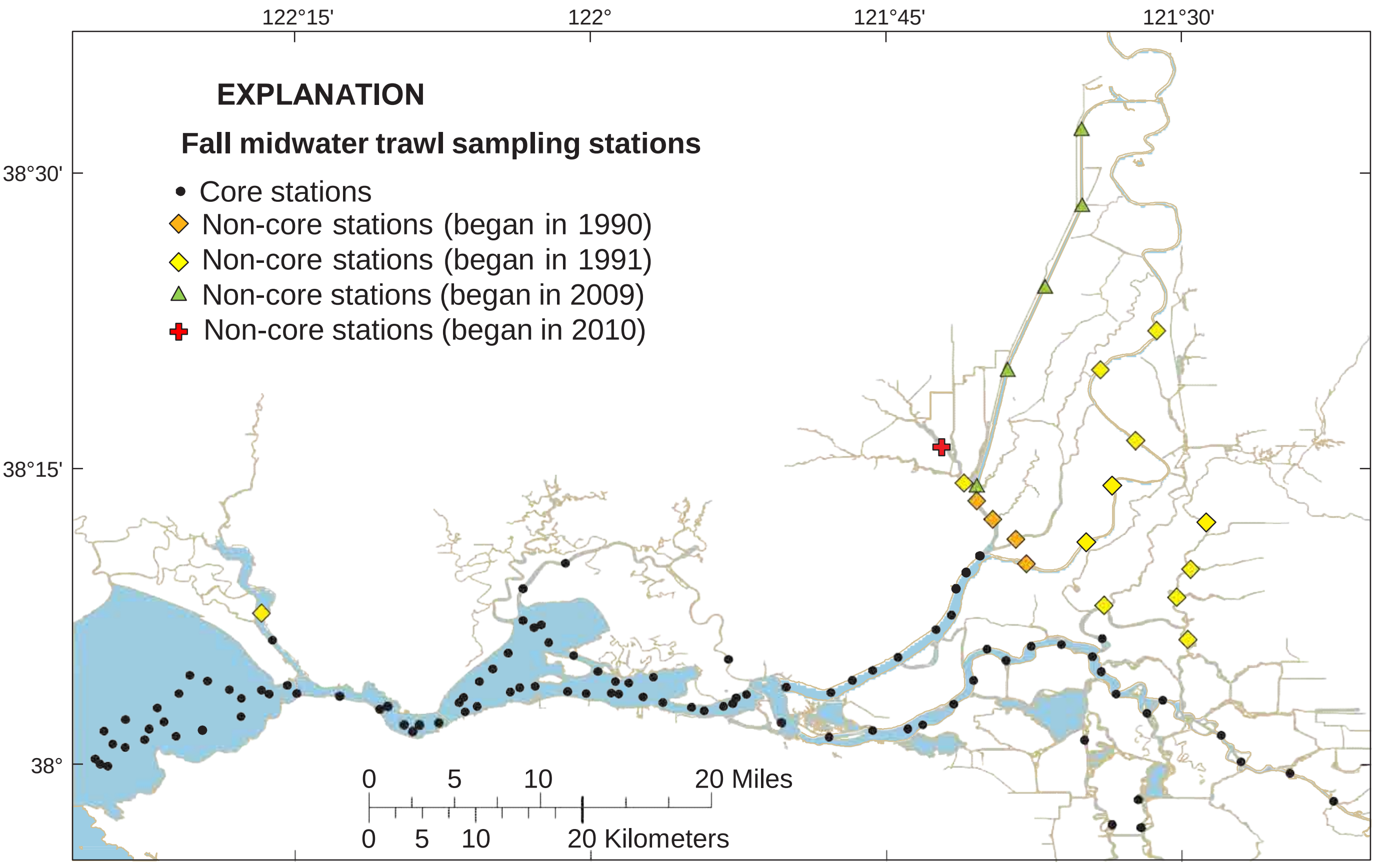
Figure 13. **Map of Summer Townet Survey sampling stations.**



relationships described in this report as well as in many of the previously published studies cited in this report.

In addition to the annual abundance indices for Delta Smelt provided by the monitoring surveys described above, we also present annual indices of recruitment and survival. In this report, a survival index is simply the ratio of an abundance index for a particular life stage divided by the abundance index for a preceding life stage of the same Delta Smelt cohort. A recruitment index is the ratio of an abundance index for a particular life stage divided by an abundance index for a life stage of the preceding Delta Smelt year-class. These types of indices have been used in previous analyses (e.g. Miller et al. 2012), but it is important to note that they may compound the observation errors inherent in the annual abundance indices in complicated ways. This is likely more problematic for survival and recruitment indices that use the TNS and FMWT abundance indices because these surveys were not specifically designed to target Delta Smelt. It may be less problematic for the recruitment index calculated by dividing the 20 mm abundance index for larval and post-larval Delta Smelt by the preceding SKT abundance index for adult Delta Smelt because both surveys specifically target Delta Smelt. We use this recruitment index in some additional analyses included in this report. All other survival and recruitment indices are only used as a rough approximation and illustration of differences in recruitment and survival rates among different annual cohorts and life stages; they are not used for additional analyses.

Figure 14. Map of Fall Midwater Trawl Survey sampling stations.



Data Analysis

As noted previously, we review long-term trends in this report using published results, but in some cases include some additional analyses of long-term monitoring data (Chapters 4 and 7). These analyses are kept deliberately simple, for example, simple graphical explorations of time series, examinations of simple statistics such as medians and arithmetic means, and investigation of univariate relationships using simple correlation and least squares regression analyses. Such analyses are readily reproducible with the publicly available data described above. The purpose of presenting the results of these new analyses is to update previously published information with the most recent data. In many cases, the data presented in this report are summarized using boxplots. The center horizontal line in each box represents the median of the data. The upper and lower ends of the box represent the upper and lower quartiles of the data. These are also known as “hinges.” The “whiskers” are the lines extending above and below the box. The whiskers show the range of values falling within 1.5 times the inter-quartile distance from the nearest hinge. Values outside this range are shown as individual symbols. Asterisks denote values within 1.5 to 3.0 times the inter-quartile distance and circles denote values greater than 3.0 times the inter-quartile distance. Other types of plots are explicitly identified in the figure caption.

Some graphs and analyses refer specifically to the POD period. Analyses suggest the POD period started as early as 2002 or as late as 2004 (Thomson et al. 2010). We somewhat arbitrarily selected 2003-present as the POD period for this report. This period is not being recommended as the baseline for management agencies to use when considering recovery of Delta Smelt. The time period simply reflects the consistently low level of Delta Smelt abundance in recent years and a useful baseline for identifying years with improved Delta Smelt abundance indices, which would indicate improved environmental conditions for Delta Smelt. Similarly, we also consider the 1982-2001 period between the two major step declines in Delta Smelt abundance identified by Thomson et al. (2010) separately in some graphs and analyses. Finally, some graphs and analyses refer to calendar years while others refer to water years. In California, a water year starts on October 1 and ends on September 30 of the next calendar year. California water year classifications are based on calculations of annual unimpaired runoff, which represents the natural water production of a river basin, unaltered by upstream diversions, storage, and export of water to or import of water from other basins.

In Chapter 7, we explore a series of hypothesized driver-outcome linkages using a comparative approach. The purpose is to demonstrate the utility of our conceptual model framework for generating hypotheses about the factors that may have contributed to the 2011 increase in Delta Smelt abundance. Specifically, we compare Delta Smelt responses to habitat conditions in four recent years with moderate to wet hydrology: the two most recent wet years (2006 and 2011) and the two drier years immediately before them (2005 and 2010). This comparative approach and data sources (described in Chapter 4) are deliberately similar to the comparative approach used in the FLaSH investigation (Brown et al. 2014). This approach allows us to place the results of the FLaSH investigation in a year-round, life cycle context and to more comprehensively evaluate factors that may have been responsible for the strong Delta Smelt abundance and survival response in 2011, including any possible relevant antecedent conditions from 2010. We attempt to draw comparisons with a similar set of data collected during 2005 and 2006. Our working assumption is that different Delta Smelt abundances in 2006 and 2011 should be attributable to differing environmental conditions, in some cases attributable to management actions, and subsequent ecological processes affecting the Delta Smelt population.

In Chapter 9 we briefly describe three examples of additional mathematical modeling approaches that can be used to further explore some of the linkages and interactions in our conceptual models and complement previously published and other ongoing mathematical modeling efforts for Delta Smelt. Importantly, results from the three modeling examples in Chapter 9 are included for illustrative purposes only; peer-reviewed publications of these analyses need to be completed before they can be used to draw firm conclusions.

Chapter 4: Environmental Drivers and Habitat Attributes

The general approach of this Chapter is to focus on how environmental drivers and interactions among them create habitat attributes of importance to Delta Smelt. Specifically, we review and synthesize existing information about drivers and habitat attributes and Delta Smelt responses to habitat attributes with a focus on new information since Baxter et al. (2010). We use the drivers and habitat attributes depicted in the basic POD conceptual model (Fig. 6) as the basis for this synthesis. We consider habitat attributes important when there are published studies suggesting ecological responses by Delta Smelt. Each section focuses on a habitat attribute that can be the outcome of one or more environmental drivers. Physical habitat attributes are presented first, followed by biological habitat attributes. The order of presentation does not imply any kind of ranking of relative importance. For simplicity, we consider all habitat attributes discussed here as equally important because, as noted in Chapter 2, habitat arises from the combination of *all* physical and biological attributes affecting a species. We fully acknowledge that as Delta Smelt research proceeds and the system continues to change, additional habitat attributes my need to be added to the conceptual model, while others may be deemphasized or even deleted.

Each section starts with the general importance of a specific habitat attribute for estuarine biota followed by a brief discussion of its linkages with environmental drivers and its dynamics in space and time. Each habitat attribute is then placed in the context of Delta Smelt biology.

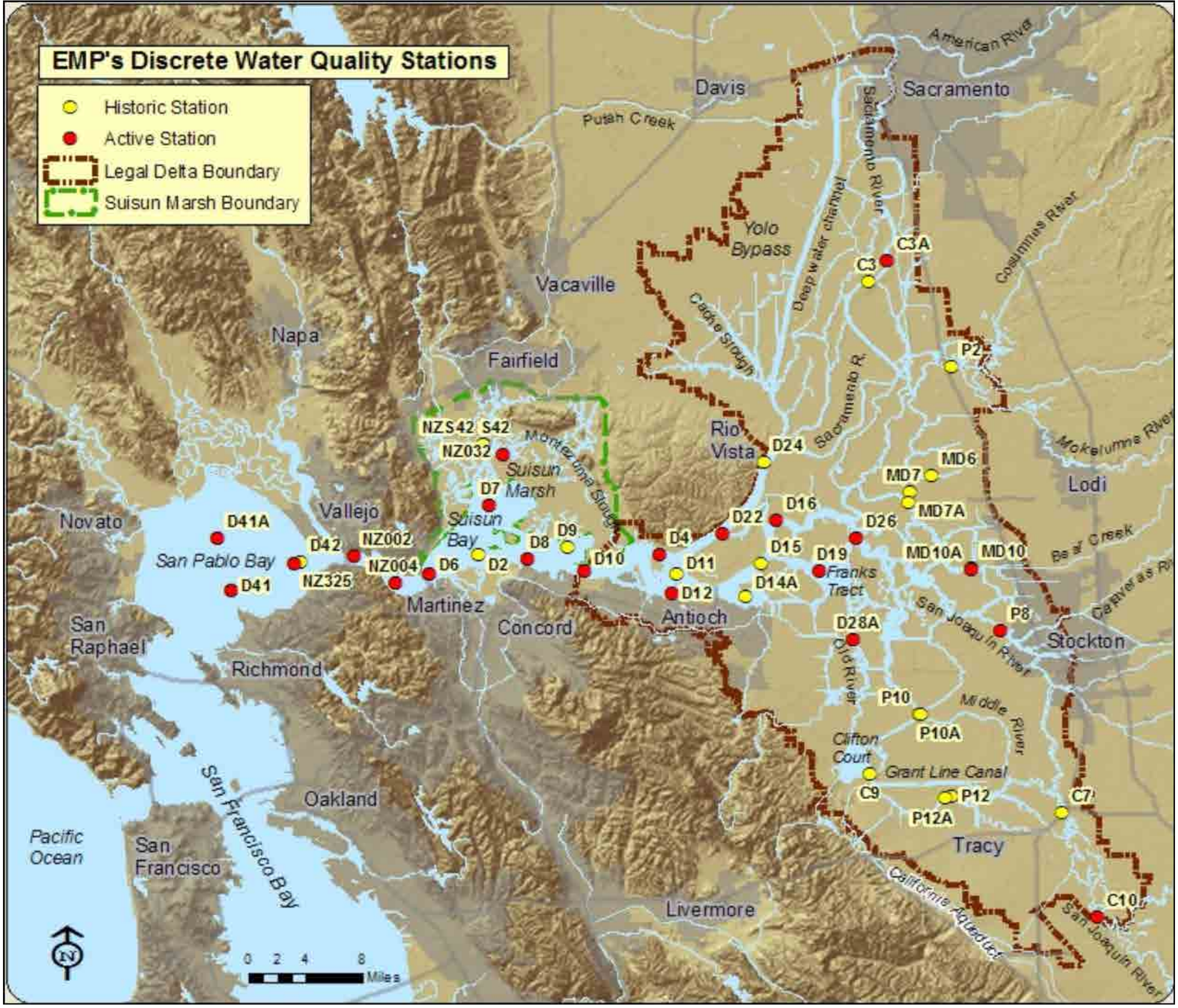
Water Temperature

Water temperature is fundamental to aquatic ecosystem health and function. It directly influences biological, physical, and chemical properties such as metabolic rates and life histories of aquatic organisms, dissolved oxygen levels, primary productivity, and cycling of nutrients and other chemicals (Vannote and Sweeney 1980, Poole and Berman 2001, Null et al. 2013). Water temperature is an important variable for ectothermic (“cold-blooded”) animals, including all fishes and invertebrates in the SFE. In the most extreme case, when water temperature exceeds the thermal tolerance of an organism, it will die. Temperatures within the thermal tolerance of an organism control the rate and efficiency of many physiological processes, including activity, digestion, growth, reproductive development, and reproductive output. We return to these processes after giving an overview of water temperature variability and its drivers in the Delta.

Long term temperature records from selected sites in the SFE show substantial seasonal and daily fluctuations in water temperature (Kimmerer 2004). While daily variations are evident and likely important to organisms, seasonal variations are much greater (Wagner et al. 2011). Median water surface temperatures across all stations monitored by the IEP Environmental Monitoring Program (EMP) (Fig. 15) from 1975-2012 range from 9 °C in January (minimum: 6 °C) to 22 °C in July (maximum: 28 °C). There are also clear regional variations in water temperature (Fig. 16). In July and August, the hottest summer months, water temperatures are usually highest at monitoring stations in the south Delta (average 23-26 °C, maximum 28 °C), lower at stations in the northern and western Delta (average 21-23 °C, maximum 25 °C) and lowest at stations in Suisun and San Pablo Bays (average 19-21 °C, maximum 24 °C). In January, the coldest winter month, average water temperatures are uniformly below 10 °C in the entire Delta, but above 10 °C in San Pablo Bay.

There is currently little evidence for increasing water temperatures in the Delta, although with climate change such increases are expected over the course of the century (Cloern et al. 2011, Wagner et al. 2011, Brown et al. 2013). In Spring (March-June) water temperature at IEP EMP water quality monitoring stations in the Delta increased during 1996–2005 by about 0.2 °C per year, but a similar trend was not apparent for the longer-term data record from 1975-2005 or for stations in Suisun Bay (Jassby 2008). These findings are similar to the results of Nobriga et al. (2008) who found no long-term (1970-2004) trends in temperature data collected during summer fish monitoring surveys in the Delta. Nobriga et al. (2008) also noted that the long-term (1970-2004) mean July water temperature at TNS fish monitoring stations in the southern region of the Delta is 24 °C, with current mid-summer temperatures often exceeding 25 °C. This agrees with average monthly EMP data from 1975-2012 which shows July and August water temperatures at

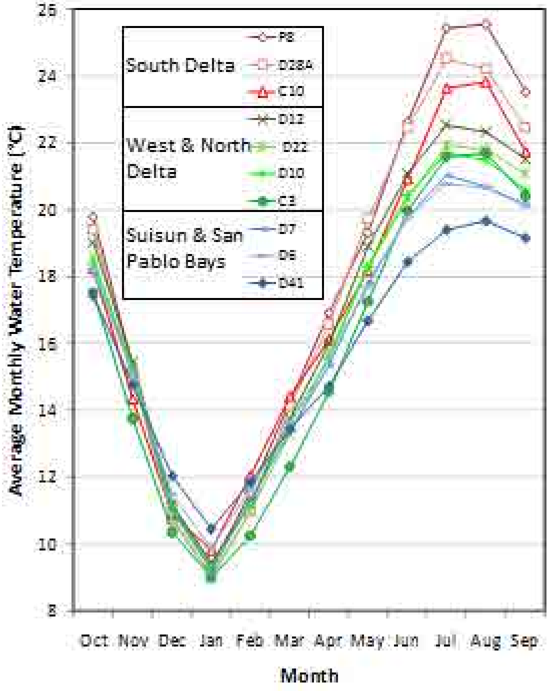
Figure 15. **Map of active and historic IEP Environmental Monitoring Program (EMP) sampling stations.**



a monitoring station located in Old River (station D28A) and in the San Joaquin River near the Port of Stockton (station P8) of more than 24 °C and 25 °C, respectively (Fig. 16).

In tidal systems, water temperature at a particular location is determined by the interaction between atmospheric forcing (e.g., air temperature and wind), tidal dispersion and riverine flows across the estuarine landscape (Monismith et al. 2009). In particular, estuarine water temperature is driven by heat exchange at the air–water interface and mediated by tidal and riverine flow dynamics and estuarine geomorphology (Enright et al. 2013). Wagner et al. (2011) found that regional weather patterns including air temperature and insolation (sunlight), are the primary drivers of water temperature variations in the SFE. Water flow and interaction with the stationary topography of the system also affects water temperature in the SFE, especially over shorter time scales and at smaller spatial scales. For example, Enright et al. (2013) showed that interaction

Figure 16. Average monthly water temperature for stations monitored by the Environmental Monitoring Program from 1975-2012.



of tides with tidal marsh topography can have a mediating effect on water temperature in tidal sloughs and on thermal variability at smaller spatial scales. Wagner et al. (2011) showed that high winter and spring flows can temporarily lower water temperatures. Greenberg et al. (2012) found that the present riparian vegetation on Delta levees lowers insolation by about 9% compared to a hypothetical situation without vegetation and suggested that riparian vegetation thus contributes to locally cooler water temperatures. This suggests that at least to some degree, water temperature can be managed locally and for short periods. Over larger scales, however, these types of locally mediated effects are overwhelmed by the effects of air temperature and insolation.

Air temperature and insolation in the SFE are correlated with each other (Wagner 2012) and vary strongly with proximity to the Pacific Ocean because of the contrasting climate regimes prevailing in inland central California and the central California coast. While inland central California has a large annual air temperature range with hot, dry, sunny summers and cool, wet, and often foggy winters, the central California coast has a smaller annual air temperature range with cooler and often foggy summers and milder winters (Conomos et al. 1985). The SFE has a transitional climate with greater spatial and temporal variability in air temperature than either the coastal or the inland regions (Whipple et al. 2012). This is due to the interplay of the dynamic air masses from these regions across the stationary estuarine topography. In the summer, this interplay often results in strong afternoon winds from the ocean locally known as the “Delta breeze.” These onshore winds usually advance into the western and central Delta and, depending on the depth of the marine layer, often also into its marginal areas. In the Delta, these southwest to northeast winds can persist throughout the night and into the next morning and produce a marked decline in daily temperature. In the morning, this low is often followed by rapid warming once the winds subside and the high temperature inland air masses return to dominance (National Weather Service 2003). In the winter, ocean winds are weak and, during calm periods, cold air flows from the mountains into the estuary. This results in the formation of dense, overnight, near-surface fog locally known as “tule fog.” These calm and foggy periods are interrupted by winter storms. Many of these storms arrive from the south and southeast as “atmospheric rivers” that can often produce gale force winds and heavy rains lasting several days (Conomos et al. 1985, Dettinger and Ingram 2013).

The large variability in air temperature in the Delta is reflected by the larger annual variability in water temperature measured from 1998-2002 at continuous monitoring stations in the interior Delta compared to stations further upstream or downstream (Wagner et al. 2011). This high variability is also apparent in monthly water temperature data collected by the IEP Environmental

Monitoring Program since 1975 (Fig. 11). From 1975 to 2012, annual fluctuations in average monthly water temperature were greatest at stations in the south Delta (14-16 °C), smaller at stations in the northern and western Delta (12-13 °C), and lowest at stations in Suisun and San Pablo Bays (9-12 °C). Jassby (2008) reported that maximum daily air temperature could explain almost half the variability in maximum daily water temperature at the continuous monitoring station at Antioch during the summer months. The relationship between air and water temperature was also strong in all other months except January.

Wagner et al. (2011) and Wagner (2012) developed simple regression models for predicting water temperature at fixed temperature monitoring stations in the SFE using only air temperature and insolation on the day of interest and the water temperature from the previous day. Water temperature from the previous day accounts for both previous air temperature and the sources of water to the site, including advective flow from rivers or dispersive flow from more downstream reaches of the SFE. Each model had a different set of coefficients because of the differing influences of incoming river water or tidal exchange with San Francisco Bay. For stations with greater than 1 year of calibration data, model R^2 for daily average temperature exceeded 0.93, indicating that water temperature was highly predictable within the limits of the calibration data sets. High winter and spring flows were responsible for the largest divergences of the model outputs from measured temperatures.

The simple statistical models for water temperature developed by Wagner et al. (2011) and Wagner (2012) should be used with caution because they only predict temperature at the site of the recording instrument and do not explicitly account for mechanistic heat exchange. The analyses therefore do not incorporate the possible effect of site-specific features such as shading by riparian vegetation (Greenberg et al. 2012). Similarly, there are lateral and vertical variations in temperature on daily time scales (Wagner 2012) that could be important to organisms. For example, such variation might include substantial heterogeneity and formation of thermal refugia, which may be important to Delta Smelt.

In contrast to statistical modeling, which produces site-specific results, water temperature across regions is commonly modeled with computation-intensive deterministic simulation models. Such models use energy budgets to predict water temperature. Simple stochastic models are also possible. Like most statistical models, these stochastic models generally rely on the relationship between air and water temperature (Caissie 2006, Null et al. 2013). We are not aware that these types of models have been developed for the San Francisco Estuary.

Upper temperature limits for juvenile Delta Smelt survival are based on laboratory studies and corroborated by field data. Interpretation of the laboratory results is somewhat complicated as temperature tolerances can be affected by various factors including acclimation temperature, salinity, turbidity, and feeding status. Based on the critical thermal maximum, CT_{max}, juvenile Delta Smelt acclimated to 17 °C could not tolerate temperatures higher than 25.4 °C (Swanson et al. 2000). However, for juvenile Delta Smelt acclimated to 11.9, 15.7 and 19.7 °C, consistently higher CT_{max} were estimated (27.1, 28.2 and 28.9 °C, respectively; Komoroske et al. 2014), which corresponded closely to the maximum water temperatures recorded in the TNS and FMWT surveys. Swanson et al. (2000) used wild-caught fish, while Komoroske et al. (2014) used hatchery-reared fish, which may have contributed to the differences in results. Based on the TNS (Nobriga et al. 2008) and the 20 mm Survey (Sommer and Mejia 2013), most juvenile Delta Smelt were predicted to occur in field samples when water temperature was below 25 °C. In a multivariate autoregressive modeling analysis with 16 independent variables, MacNally et al. (2010) found that high summer (June – September) water temperature had a negative effect on Delta Smelt subadult abundance in the fall. Water temperature was also one of several factors affecting Delta Smelt life stage dynamics in the state-space model of Maunder and Deriso (2011) and in an individual-based Delta Smelt life-cycle model (Rose et al. 2013a,b).

In addition to lethal effects, water temperature also has direct effects on the bioenergetics (interaction of metabolism and prey density) of Delta Smelt (Bennett et al. 2008) and it may affect their tolerance to other habitat attributes, such as toxicity (Brooks et al. 2012) and predation risk. Responses of different life stages of Delta Smelt to various temperature, salinity, and turbidity conditions are currently being further assessed as part of a larger UC Davis laboratory study about the "fundamental niche" of Delta Smelt (Komoroske et al. 2014, R. Connon et al., U.C. Davis, unpublished data).

The topic of bioenergetics is an important consideration in much of the remainder of this report, so we address it in more detail here. In general, the total metabolic rate of a fish will increase with temperature to an optimum temperature at which, given unlimited food, there is the maximum ability to grow and develop reproductive products (eggs or sperm) in addition to maintaining the basal metabolic rate required for survival, which also increases with temperature (Houde 1989, Hartman and Brandt 1995). As temperature increases beyond the optimum, metabolic rate continues to increase but physiological processes become less and less efficient and more energy is required just to meet the basal metabolic rate of the organism. Eventually, the metabolic rate begins to decline as temperatures approach the physiological limits of the organism and the basal metabolic rate can no longer be maintained.

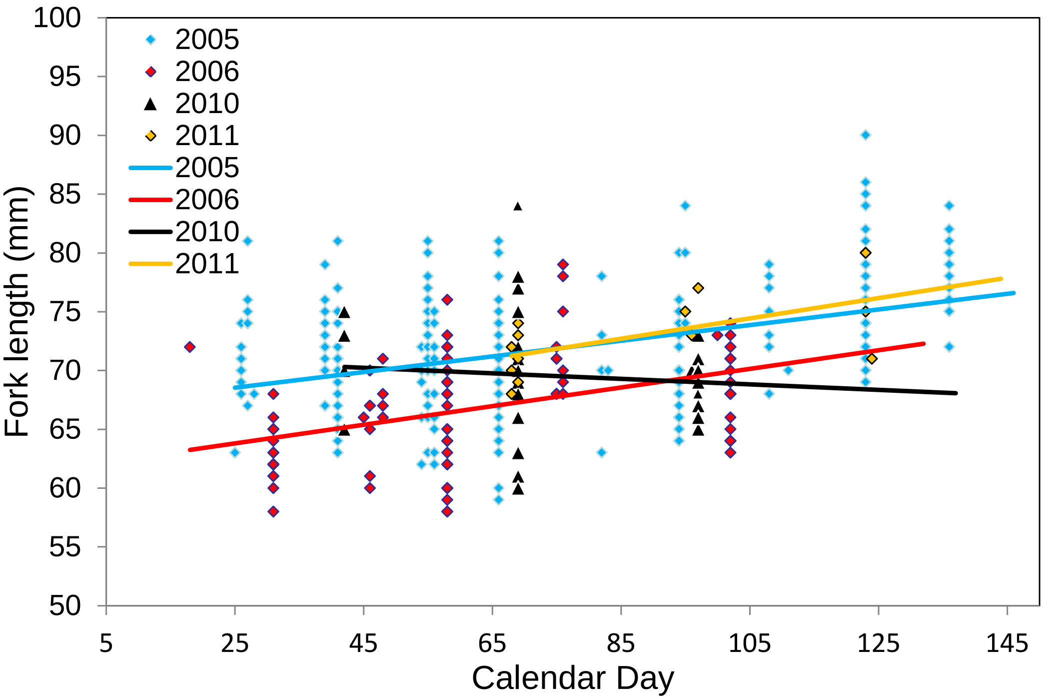
At temperatures beyond the optimum, the ability to grow and mature becomes increasingly impaired. Long-term exposure to such stressful temperatures can eventually be lethal. In addition, resistance to disease and contaminants can also be affected (Brooks et al. 2012). The responses to contaminants can vary depending on the type of contaminant. For example, low temperatures can decrease the toxicity of organophosphate insecticides, but increase the toxicity of pyrethroid and organochlorine insecticides (Harwood et al. 2009), a characteristic that has been used in toxicity identification and evaluation (Weston and Lydy 2010). The previous discussion assumes unlimited food, which is unlikely to be the case for Delta Smelt or any organism in nature. Even at the optimum temperature, growth and reproductive development will depend on the quantity and quality (energy and nutrient content) of the food consumed. If the fish is unable to ingest enough food to meet its nutrient and energetic requirements, including the energy expended to capture and digest prey, it will starve, after first depleting any available energy stores (fat or muscle). Given an array of food items, fish will generally choose larger prey items. This is because the energy required to detect, chase, and capture multiple smaller prey that are equivalent in nutritional value to a single large prey item will, in many cases, exceed the energy required to capture the single prey item. Note that these same ideas apply to predatory fish that might consume Delta Smelt.

Water temperature is also thought to affect the number of eggs produced by female Delta Smelt. Egg production (i.e., fecundity) of the population is influenced not only by individual female size and number (Bennett 2005, DFW unpublished), but also by the duration of a temperature "spawning window" (Bennett 2005, Mac Nally et al. 2010), variously defined as: 15-20 °C by Bennett (2005); 7-15 °C by Wang (1986); and 12-15 °C by Baskerville-Bridges et al. (2004b). Bennett (2005) further stated that during cool springs this spawning window persists longer, allowing more cohorts to recruit. Given a sufficiently long spawning window, individual females may also repeat-spawn during the spawning season. This has been documented in culture (see Bennett 2005; J. Lindberg, U.C. Davis, personal communication 2013) and appears to occur in the wild as well (L. Damon, CDFW, written communication 2012). Lindberg (U.C. Davis, personal communication 2013) observed that most females in culture spawned twice, some spawned three times and a very small number spawned four times. Each spawning was separated by a 4-5 week refractory period during February through June when water temperatures remained within the spawning window. Though laboratory conditions may not necessarily be representative of conditions in the wild, ripe females ready to release their second complete batch of eggs and developing a third batch have been detected in the wild during March and April (i.e., mid-season) suggesting that three spawns are possible (L. Damon, CDFW, written communication 2012). Thus, a longer spawning window would allow more females to repeat spawn adding both additional cohorts hatching under different conditions, and multiplying the fecundity of each repeat spawner (i.e., increasing the total fecundity of the individual), and thus, the total fecundity of the population. Moreover, in culture, individual females continued to grow through the spawning season and become more fecund with each batch of eggs (J. Lindberg, U.C. Davis, personal communication 2013). In the wild, the size of mature females generally increases month to month through the spawning season (Fig. 17), suggesting a potential increase in fecundity with each batch, but this has yet to be confirmed for wild fish. However, in culture, fish hatched later in the spawning season (mid-May to mid-June) grew up to be smaller-sized adults that started spawning later and had progeny with lower survival than the progeny of fish hatched earlier in the season (Lindberg et al. 2013). These observations are consistent with the reproductive patterns suggested for the wild Delta Smelt population (Bennett 2011). Overall, the effect of a prolonged spawning season on Delta Smelt population size and dynamics would seem to be positive; however, there is some uncertainty.

In the culture experiments reported by Bennett (2005), temperature strongly influenced hatching success of eggs. Specifically, Bennett (2005) reported that optimal hatching success and larval survival were estimated to occur at 15–17 °C based on studies conducted at 10, 15, and 20 °C. The data indicated that as incubation and early rearing temperatures increased, size at hatching and size at first feeding linearly decreased, possibly because basal metabolism of the developing embryo used more energy leaving less for growth. Fish that hatch relatively late in the season may experience high temperatures at a small size, which may reduce larval survival by several possible mechanisms. First, small size would limit the size of food items that the larvae could ingest because of smaller mouth size (see Nobriga 2002). Temperature may also affect food type and availability as discussed below. Second, small larvae are likely vulnerable to a larger range of predators for a longer period compared to larger larvae (e.g., “stage duration hypothesis;” Anderson 1988). Third, these fish could be potentially more vulnerable to transport toward the CVP and SWP export facilities, when Old and Middle River (OMR) flow restrictions are lifted. Restrictions are lifted when the 3-day mean water temperatures in Clifton Court Forebay (CCF) reach 25 °C or by the end of June.

As explained above, higher water temperatures increase energetic requirements and thus the food requirements of fish. To meet the increased need for food, it is possible that Delta Smelt spend more time foraging during the day. Since greater foraging time during the day increases visibility to predators, and those predators would also increase their foraging rates at higher temperatures, the encounter rate of predator and prey would likely increase at higher water temperatures. The net effect could be an increase in Delta Smelt predation risk (e.g., Walters and Juanes 1993). High temperatures can also decrease antipredator behavior, as described for Sacramento River Chinook Salmon (*Oncorhynchus tshawytscha*) (Marine and Cech 2004). In other words, the fish may make a behavioral choice to feed, grow, and become less vulnerable to predators as rapidly as possible, even though the short-term predation risk might increase. Water temperatures in the upper SFE are usually highest from June to September and decline rapidly between October and December

Figure 17. **Individual female fork lengths by calendar day for mature female Delta Smelt collected in the Spring Kodiak Trawl Survey, January through May, 2005, 2006, 2010 and 2011. These data include both monthly distribution survey fish and directed survey fish. The directed survey (which targeted smelt spawning areas) was discontinued after January 2010.**



(Fig. 16). The reported optimal culture temperatures for Delta Smelt larvae and late-larvae are 16.4 ± 0.25 °C (Komoroske et al 2014). Moreover, the chronic lethal thermal maximum for Delta Smelt varies by life stage (Komoroske et al. 2014). Juvenile and subadult Delta Smelt are observed in the field most commonly at temperature near or below 20 °C (Bennett et al. 2008, Nobriga et al. 2008), a temperature which is often exceeded beginning in May or June and continuing through September and more rarely in October (see Chapter 7). Thus, we suggest that the same tradeoffs between feeding and predation risk may persist through the warmer months and into early fall, but become less likely as the season progresses into late fall and winter. Note, however, that predation risk is also influenced by a complex suite of other factors such as turbidity, life stage, and proximity to predator habitat, so the level of risk to Delta Smelt can't be determined.

Another possible indirect effect of higher water temperatures is that they may promote harmful agal blooms (HAB) (Lehman et al. 2005), which may degrade Delta Smelt habitat quality in the summer and early fall (Baxter et al. 2010). In the Delta, Lehman et al. (2013) found that blooms of the harmful cyanobacteria (blue-green algae) *Microcystis aeruginosa* required a water temperature of at least 19 °C for initiation. Other drivers of HABs and the possible effects of HABs are discussed more fully in a separate section of this Chapter. The combination of large seasonal and regional water temperature variability in the SFE and substantial direct and indirect effects of water temperature for all life stages of Delta Smelt means that this variable should be considered one of the most important habitat attributes for Delta Smelt. Differences in water temperature between regions or time periods may have important effects on the Delta Smelt population (Rose et al. 2013b).

Salinity and the Size and Location of the Low Salinity Zone

A dynamic salinity gradient from fresh water to salt water is one of the most characteristic features of an estuary (Kimmerer 2004). It originates from the mixing of fresh inland water with salty ocean water through tidal dispersion and gravitational circulation (Monismith et al. 2002). Many estuarine-dependent organisms occur in distinct salinity ranges (e.g., Kimmerer 2002a) and the extent and location of water with suitable salinities is thus an important habitat attribute for estuarine organisms. Over the time period of available monitoring data, there is no clear long-term trend in salinity levels and distributions in the estuary. Significant increases and decreases linked to changing flow patterns have been detected for various stations and months (e.g., Jassby et al. 1995, Enright and Culberson 2009, Shellenbarger and Schoellhamer 2011, Cloern and Jassby 2012).

The brackish (oligohaline) “low salinity zone” (LSZ) is an important region for retention of organisms and particles and for nutrient cycling. In the SFE, the LSZ provides important habitat for numerous organisms including Delta Smelt (Turner and Chadwick 1972, Kimmerer 2004, Bennett 2005). In this report we define the LSZ as salinity 1-6; however, other salinity ranges have been used by others, such 0.5-6 (Kimmerer et al. 2013) or 0.5-5 (Jassby 2008).

In the SFE, the position of the LSZ is commonly expressed in terms of X2, which is the distance from the Golden Gate in km along the axis of the estuary to the salinity 2 isohaline measured near the bottom of the water column (Jassby et al. 1995). X2 represents the approximate center of the LSZ (Kimmerer et al. 2013).

X2 is an index of the physical response of the estuary to freshwater outflow from the Delta; it decreases with increasing outflow because increasing freshwater outflow prevents seawater from moving landward. The X2 index was developed two decades ago as an easily-measured, policy-relevant “habitat indicator.” Its ecological significance for multiple species and processes was established through statistical analyses of biological responses to seasonally or annually averaged X2 values (Jassby et al. 1995) and has since been reaffirmed in additional studies (e.g., Kimmerer et al. 2002a,b, 2009, 2013, Thomson et al. 2010, Mac Nally et al. 2010). There is, however, still much uncertainty regarding the causal mechanisms for the observed biological responses of biota to X2. As with all statistically derived functional relationships, biological responses to X2 do not necessarily reflect direct causal relationships and it is generally recognized that some of the causal mechanisms may not be directly linked to the size and location of the LSZ.

Most of the scientific and management attention has focused on the LSZ and X2 from late winter to early summer (hereafter “spring X2”) depending on the species of interest, but in recent years the LSZ and X2 during the fall months (“fall X2”) has also received considerable scientific and policy attention. Annual abundance indices of several estuarine fish and invertebrate species have a negative relationship with spring X2, meaning that abundance indices increase when X2 and the LSZ are more westward and Delta outflow is higher in the late winter and spring months (Jassby et al. 1995, Kimmerer 2002a, Kimmerer et al. 2009). Delta Smelt summer abundance indices have a significant relationship with prior fall X2 and fall abundance (USFWS 2008, Mount et al.

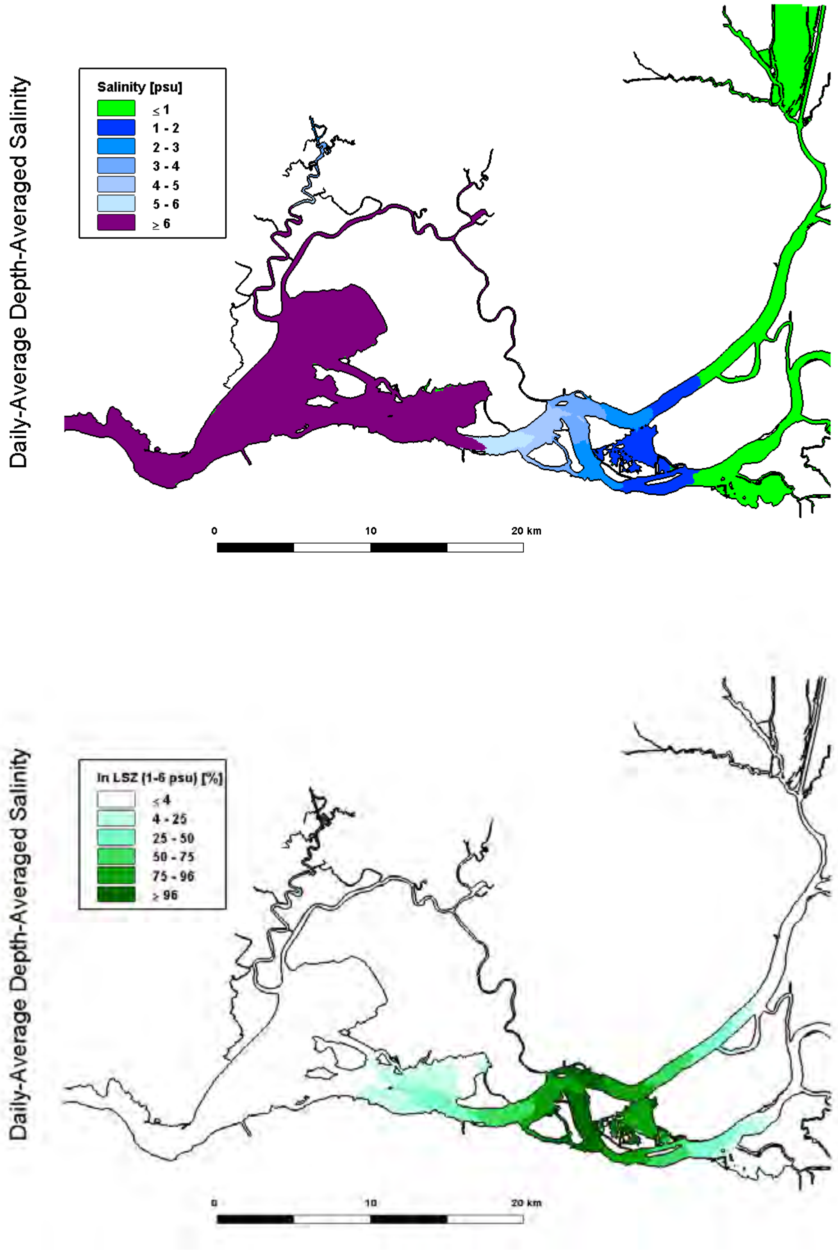
2013). Changes in spring and fall X2 have also been linked to long-term fish declines in the SFE (Thomson et al. 2010, Mac Nally et al. 2010).

The size and location of the LSZ are considered key factors determining the quanity and quality of low salinity rearing habitat available to Delta Smelt and other estuarine species. LSZ size and location are determined by the interaction of dynamic tidal and river flows with the stationary topography of the region (Reclamation 2011, 2012, Kimmerer et al. 2013). In a recent study, Kimmerer et al. (2013) used the three-dimensional hydrodynamic "UnTRIM" model which has an unstructured grid (Casulli and Zanolli 2002, 2005) to produce detailed maps of the distribution of salinity in the SFE under different outflow conditions. These maps (figure 2 in Kimmerer et al. 2013 and Fig. 18 and 19 in this report) show that under low outflow conditions typical of summer and fall months (outflow = 140 $m^3 s^{-1}$, X2 = 85 km), the LSZ is in the western Delta confluence region, including the Sacramento and San Joaquin Rivers upstream of Chipps Island (Fig. 18), while under high outflow conditions typical of wet winter months (outflow = 1,440 $m^3 s^{-1}$, X2 = 51 km), the LSZ is much further west in San Pablo Bay. At intermediate outflows (intermediate X2 = 74 km).), it is located east of Carquinez Strait and covers Suisun Bay and parts of Suisun Marsh (Fig. 19).

Kimmerer et al. (2013) also examined the relationships between X2 and the area, average depth, and volume of the LSZ. They found that these relationships were bimodal, with the largest volumes and areas and shallowest depths at X2 values below 50 km when the LSZ is located in the large San Pablo Bay, and secondary peaks at X2 values between 60 and 75 km when the LSZ overlays the smaller Suisun Bay (Fig. 20). Area and volume were smallest and depth greatest when the LSZ was constricted in Carquinez Strait (X2~50-60 km) and in the confluence region of the Sacramento and San Joaquin Rivers (X2~80-85 km).

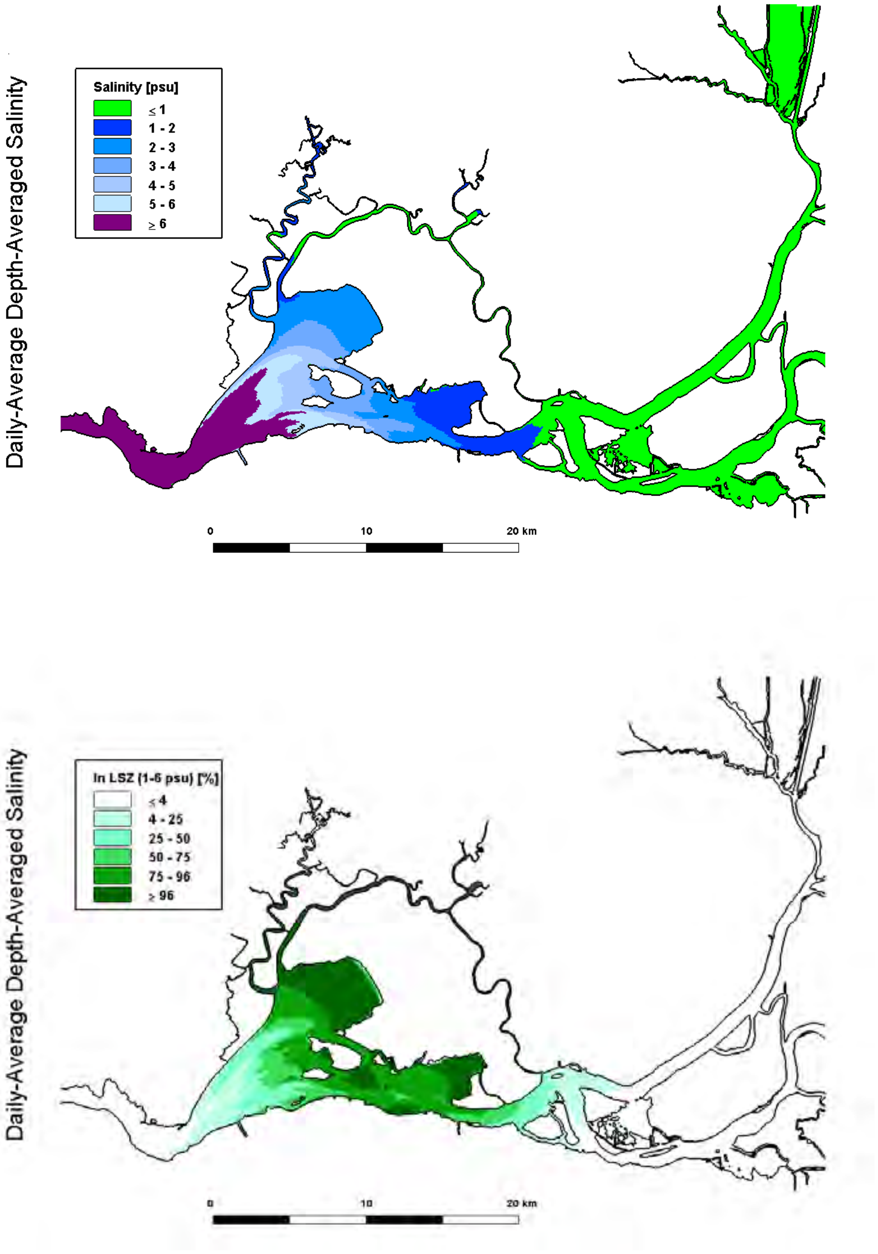
Paleosalinity investigations going back several thousand years indicate that the Delta has historically been largely fresh, while the Suisun region has alternated between brackish (oligohaline) and fresh (Ingram and Malamud-Roam 2013, Drexler et al. 2014). The LSZ and X2 likely moved according to predictable annual and interannual rhythms. Interannually, X2 was most variable in the higher-flow winter and spring months and least variable in the low-flow fall months. Seasonally X2 moved from the west in winter and spring to the east in summer and fall. CDWR (CDWR 2007) computes monthly "unimpaired" outflows which remove the effects of dam operations and water diversions. Annual X2 dynamics based on these unimpaired flows may give a sense of these historical fluctuations (Fig. 21). It is important to note, however, that unimpaired flows are not the same as historical "natural" flows because they do not take into account upstream water losses (e.g., consumption and evaporation) or physical water body alterations such as channelization, groundwater depletion, draining of wetlands, and disconnection of floodplains. The historical wetlands, floodplains, and groundwater basins would have naturally retained and released water (Whipple et al. 2012) and likely affected flows and the LSZ in different ways than today's man-made reservoirs. Work is currently underway at UC Davis, the San Francisco Estuary Institute, and elsewhere to explore these issues, but results have not yet been published (W. Fleenor, U.C. Davis, personal communication). At this time, considerable uncertainty remains regarding the natural ranges in the timing and volume of the historical seasonal and interannual freshwater flows and how they caused the LSZ to spread out and contract across the estuary's historical landscape. There is, however, little doubt that interannual variations in precipitation and hence river flows caused a high degree of interannual variability in the size and location of the low-salinity zone (Dettinger 2011).

Figure 18. **Salinity distribution at low outflow. The upper panel shows the area of the low-salinity zone (4,262 hectares) at X2 = 85 km, when positioned mostly between Antioch and Pittsburg. Connections to Suisun Bay and Suisun Marsh are minimal. The lower panel shows the percentage of day that the low-salinity zone occupies different areas.**



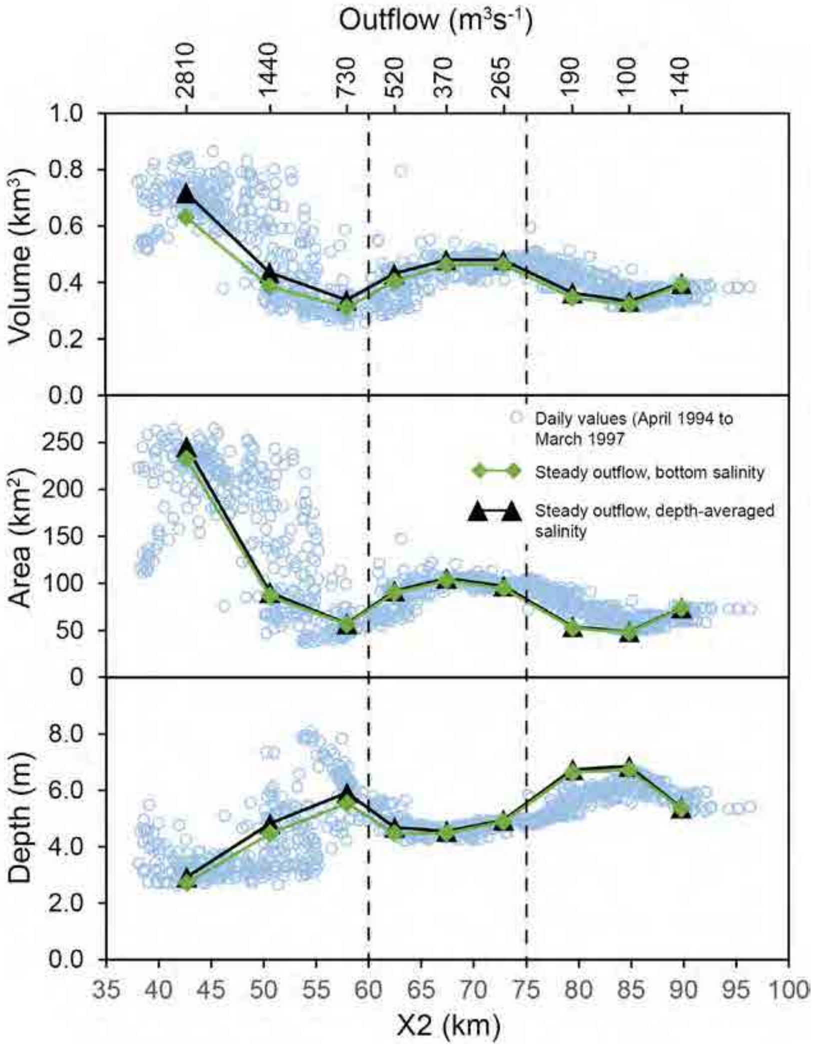
There is also no doubt that human water use and landscape alterations have changed flows into and out of the Delta and, consequently, salinity dynamics in the SFE, though changing precipitation patterns also play a role (Enright and Culberson 2009). Before the construction of today's major reservoirs, upstream water diversions coupled with the isolation of floodplains and wetlands, which had naturally stored runoff, from river channels by levees exacerbated salinity intrusions into the Delta in dry years. This was especially evident during the severe drought from

Figure 19. **Salinity distribution at intermediate outflow. The upper panel shows the area of the low-salinity zone (9,140 hectares) at X2 = 74 km (at Chipps Island). The lower panel shows the percentage of day that the low-salinity zone occupies different areas.**



1929 to 1934 when salinities of 2 were observed at Paintersville Bridge which is located on the Sacramento River at a distance of about 136 km from the Golden Gate (Mathew 1931). Operation of the large CVP and SWP reservoirs that were constructed after this drought has prevented such severe salinity intrusions since then and X2 has remained west of Rio Vista located on the Sacramento River 100 km upstream of the Golden Gate. Beginning with the salinity requirements in SWRCB water right decision D-1275 of 1967, salinity and the position of the LSZ have also

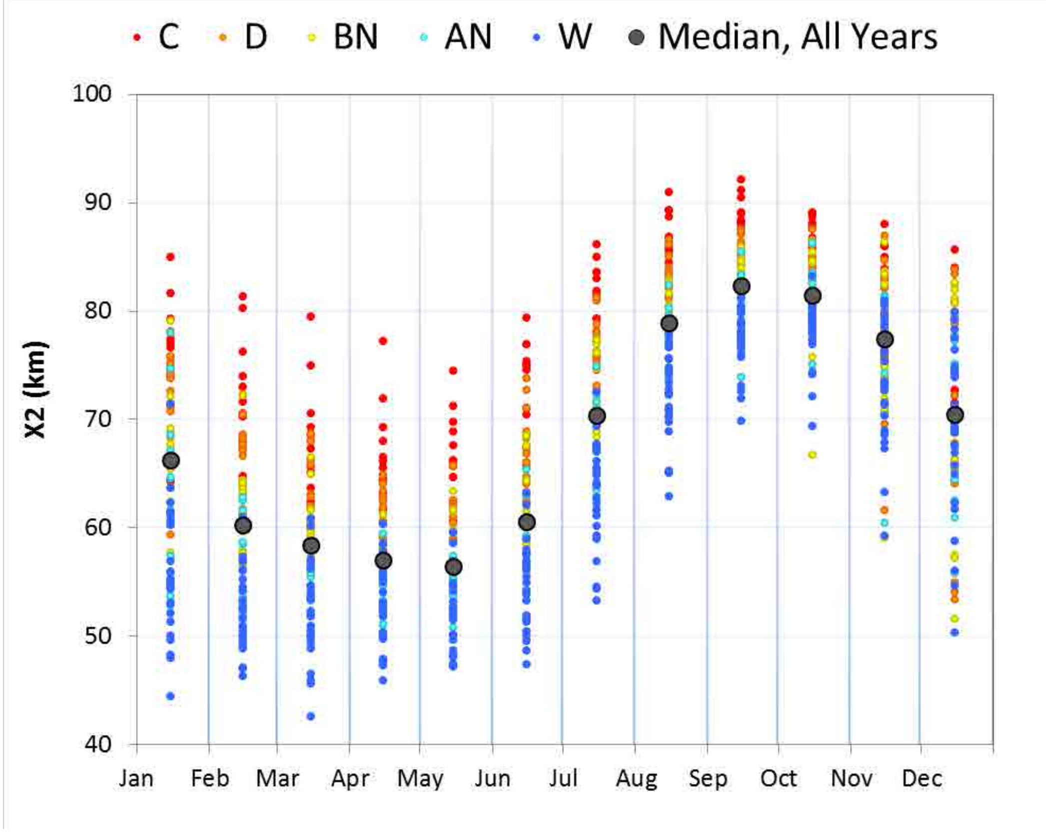
Figure 20. Modeled volume, area, and depth of the low salinity zone (salinity 0.5 to 6 at various values of X2 for 9 steady state values of outlow using bottom salinity (green diamonds) and depth-averaged salinity (black diamonds and for daily values based on variable values from April 1994 through March 1997 (blue circles) (modified from Kimmerer et al. 2013). The top axis gives the Delta outflow corresponding to the 9 steady state scenarios.



been increasingly regulated to protect "beneficial uses," including habitat and fish protections (see Chapter 1).

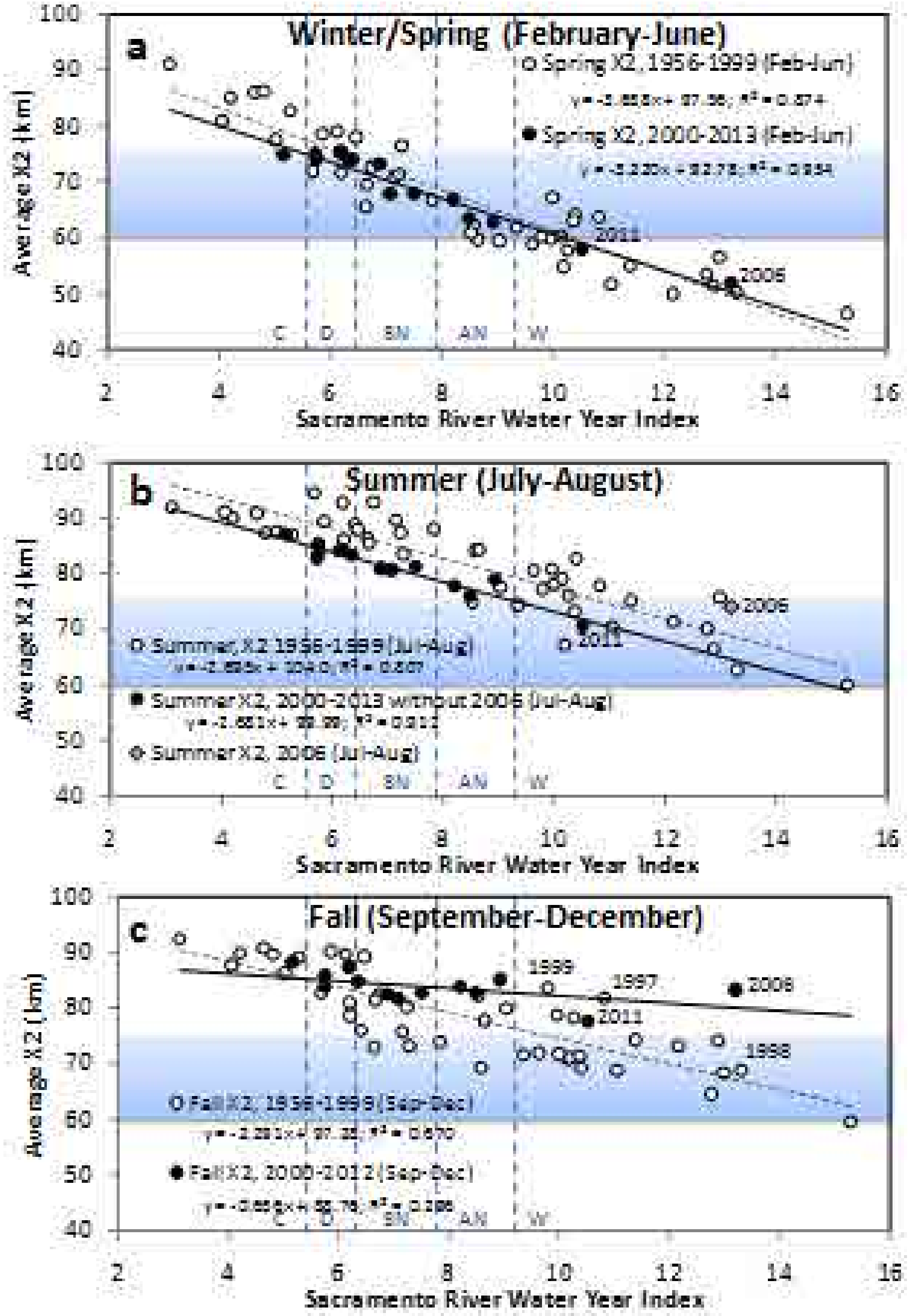
CVP and SWP water exports from the Delta began in the early 1950s with the completion of the CVP C.W. Bill Jones Pumping Plant (formerly known as the Tracy Pumping Plant) in 1951 and then increased with the completion of SWP's Harvey O. Banks Pumping Plant in 1968. Long-term variability in the trend of Delta outflow has been reduced seasonally for the period 1921-2006, in part due to water project operations (Enright and Culberson 2009), but also due to overriding climate changes. Analyzing data from 1956–2010, Cloern and Jassby (2012) found significant increases in water exports from the Delta in all months of the year except May, but in the first half of the year, these increases in exports did not significantly affect Delta outflow. We

Figure 21. Plot of monthly X2 (km) values calculated from mean monthly unimpaired Delta outflows from 1921-2003. X2 values are categorized by water year type for the Sacramento Valley. Also shown are the median X2 values from 1921-2003 across all water year types (grey circles) C, red dots: critically dry; D, orange dots: dry; BN, yellow dots: below normal; AN, light blue dots: above normal; W, dark blue dots: wet. Water year type data from http://cdec.water.ca.gov/cgi-progs/iodir/WSIHIST. Unimpaired flow data from DWR 2007 (available at http://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/bay_delta_plan/water_quality_control_planning/docs/sjrf_spprtinfo/dwr_2007a.pdf). X2 equation from Jassby et al. 2005.



show this by plotting the relationship between the Sacramento River Water Year Index, a measure of runoff, and average spring X2 (February-June) for two periods before (1956 to 1999) and after (2000-2013) the current flow and salinity requirements in SWRCB water right decision D-1641 became mandatory. The relationship appeared to remain essentially unchanged when the two time periods were compared (Fig. 22a). Cloern and Jassby (2012) further found that inflow to the Delta significantly increased in July and August, but these increases in inflow did not translate into significant increases in Delta outflow due to concurrent increases in exports during these months. Nevertheless, plots of recent data show that July and August outflows increased and the relationship between the Sacramento River Water Year Index and summer-time X2 (July-August) shifted downward in the years since the SWRCB water right decision 1641 went into effect in 2000 relative to previous years (Fig. 22b). The wet year 2006 did not fit this pattern because it had high summer X2 in spite of a high water year index. This means that with the exception of 2006, the LSZ has generally been located somewhat more westward in July and August since 2000 than from 1956 to 1999 under similar runoff conditions.

Figure 22. Plots of monthly X2 as a function of the Sacramento River Water Year Index (a measure of runoff) for the years 1956 to 1999 and 2000 to 2013 for: a, winter/spring; b, summer; and c, fall. The regression equation for each set of points is also shown. The index is calculated as: 0.4 * Current April to July Runoff Forecast (in millions of acre feet, maf) + 0.3 * Current October to March Runoff in (maf) + 0.3 * Previous Water Year's Index (if the Previous Water Year's Index exceeds 10.0, then 10.0 is used) (see http://cdec.water.ca.gov/cgi-progs/iodir/WSIHIST for futher detail).



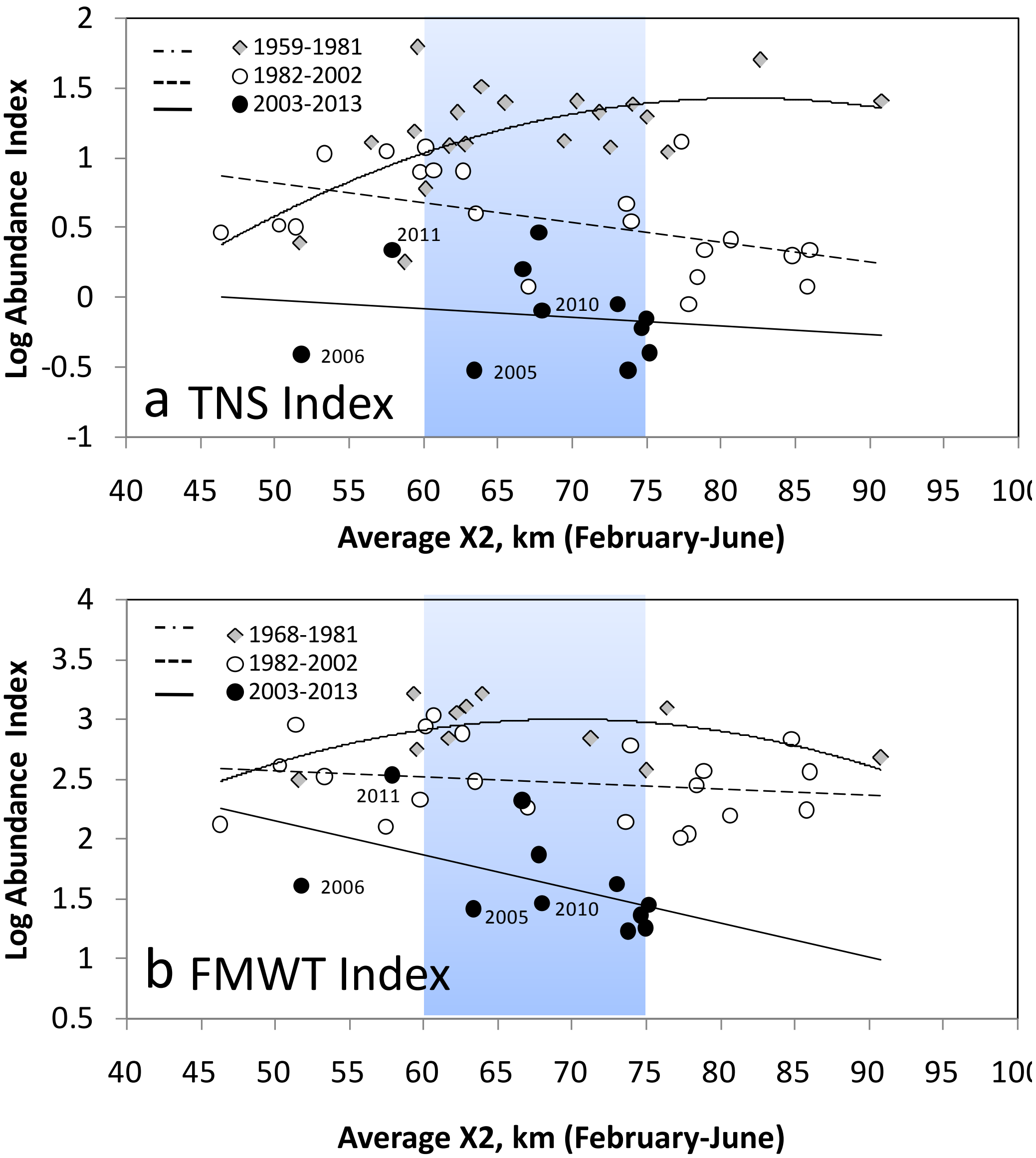
Cloern and Jassby (2012) also showed that significantly increasing exports combined with declining inflows led to significant declines in Delta outflow in each month from September to December. In plots of recent data, this led to a shallower slope of the relationship between the Sacramento River Water Year Index and fall X2 (September-December) and a more eastward LSZ location in the fall months of wetter years (below normal, above normal, and wet water year types) during 2000-2012 compared to 1956-1999, with the exception of two wet years at the end of the time series, 1997 and 1999, which fall on the 2000-2012 line (Fig. 16c, see also Feyrer et al. 2007, 2010). The areas with light blue shading in the three plots shown in Figure 16 show the range of X2 that places the LSZ over Suisun Bay and are associated with a high LSZ volume, area, and shallow LSZ depths (Kimmerer et al. 2013, Fig. 14). Fall X2 commonly fell into this range from 1956-1999 (in 18 of 44 years; Fig. 22c), but never after 2000. In 2011, the most recent wet year, fall X2 was lower than in the preceding wet years of 2006, 1997, and 1999, but still elevated relative to the majority of previous wet years. Overall, the changes in flows in the summer and fall months described by Cloern and Jassby (2012) have resulted in more muted seasonal and interannual variations in X2 and in the size and location of the LSZ in more recent years and possibly also relative to historical variability (Fig. 21).

Delta Smelt are found in the estuary at salinities up to 18 (Bennett 2005), but are most common in the in the LSZ (< 6) (Moyle et al. 1992, Sommer and Mejia 2013, Kimmerer et al. 2013). Sommer et al. (2011a) described Delta Smelt as a “diadromous species that is a seasonal reproductive migrant.” In the winter, adult Delta Smelt move upstream into fresh water for spawning. In the spring and summer, young Delta Smelt are transported or swim downstream into the LSZ (Dege and Brown 2004). Delta Smelt usually rear in low salinity habitat in the summer (Nobriga et al. 2008) and fall (Feyrer et al. 2007), although some Delta Smelt remain year-round in fresh water (Sommer et al. 2011a, Merz et al. 2011, Sommer and Mejia 2013).

The recruitment success of Longfin Smelt and age-0 Striped Bass increases linearly with more westward positions of the LSZ during spring (Jassby et al. 1995, Kimmerer 2002a). In contrast, the relationships of annual Delta Smelt indices with spring X2 are more complex because they have not been consistent over the period of record (Fig. 23). Jassby et al. (1995) found that from 1968-1991, the highest fall abundance indices for Delta Smelt coincided with intermediate values of average April-July X2 when the LSZ was positioned in Suisun Bay. Low fall abundances were, however, also observed at these intermediate X2 values. The analyses by Jassby et al. (1995) were later updated and augmented with an analysis of the relationship between Delta Smelt summer abundance and spring X2 (Kimmerer 2002a, Kimmerer et al. 2009).

We updated the analyses by Jassby et al. (1995) with more recent data and data from additional monitoring surveys to examine the hypothesis that during periods of relatively stable abundance (i.e. without step changes, Thomson et al. 2010), the abundance of different Delta Smelt life stages is related to spring outflow and the position of the LSZ as expressed by spring X2. To obtain spring X2, we first calculated mean monthly X2 values calculated from daily X2 values. We then averaged the mean monthly X2 values for February to June. This is different from the April-July period used by Jassby et al. (1995) for their Delta Smelt analyses, but similar to the spring X2 averaging period used by Kimmerer (2002a). Note that different averaging methods for calculating seasonal X2 values account for the small quantitative differences between results presented here and those of previously published analyses that used the same data, but this does not affect the overall patterns. We partitioned the data into the periods before, between, and after the 1981 and 2002 step declines in Delta Smelt abundance identified by Thomson et al. (2010). The 1981-1982 partition, but not the 2002-2003 partition, has been previously applied by Kimmerer (2002a) and Kimmerer et al. (2009).

Figure 23. Plots of the log transformed a) Delta Smelt Summer Townet Survey abundance index and b) Delta Smelt Fall Midwater Trawl Survey abundance index, in relation to monthly averaged daily X2 position from February to June. Lines are either simple linear least squares regression (lines) or quadratic regression (curves).



Kimmerer (2002a) and Kimmerer et al. (2009) found that the relationship between spring X2 and Delta Smelt juvenile abundance indices was positive before the step decline in Delta Smelt abundance that started in 1981 (Thomson et al. 2010), suggesting that historically, Delta Smelt population recruitment may have benefitted from lower outflows and a more upstream LSZ in the late winter and spring. In our analysis, we found that the relationship was perhaps more unimodal than linear (Table 1, Fig. 23a) because a model that included a quadratic spring X2 term explained more of the variation in the data than a linear model that did not, although the statistical significance of the linear model was slightly higher than that of the quadratic model because of the loss of a degree of freedom due to the additional quadratic term included in the quadratic model. Similar to Kimmerer (2002a) and Kimmerer et al. (2009), we found that in the period after the 1981 step change and also in the period after the 2002 step change, the relationship of log-transformed summer abundance with spring X2 shifted downward and became more clearly negative than unimodal (Fig. 23a). The relationship remained statistically significant at the $P < 0.05$ level in the period after the 1981 step decline, but is no longer statistically significant after 2001. Similarly, the relationship is also not significant across the entire 52-year time series (Table 1).

Kimmerer et al. (2009) found a non-significant and essentially flat relationship between spring X2 and the entire log-transformed sub-adult abundance time series for Delta Smelt; this remains the case when data from the five most recent years is included in the analysis (Table 1). Similar to Jassby et al. (1995), we found a weakly unimodal relationship between spring X2 and log-transformed Delta Smelt subadult abundance indices before the first step change, but this relationship was not statistically significant at the $P < 0.05$ level (Table 1, Fig. 23b). Similar to juvenile abundance, the relationship of log-transformed subadult abundance with spring X2 shifted downward in the periods after each of the two step changes and became more negative than unimodal (Fig. 23b), but again these relationships were not statistically significant at the $P < 0.05$ level (Table 1).

Taken together, these findings are generally consistent with previous conclusions that moderate hydrological conditions in the late winter and spring and a large LSZ located in the Suisun region can be beneficial to Delta Smelt population abundance (Jassby et al. 1995). Historically, this may have been the case for several life stages. At present, however, juvenile and subadult Delta Smelt seem to barely respond to spring X2. As Jassby et al. (1995) point out, this does not mean that there is no longer an effect of spring X2 on juveniles and subadults; the spring X2 effect may just be masked or weakened by changes in other habitat attributes. The relationships between these life stages and spring X2 clearly underwent downward shifts after each step decline. These persistent downward shifts indicate that occasional years with beneficial spring X2 conditions continue to have a positive effect on Delta Smelt, but they are by themselves not enough to overcome the depressed abundance levels and recover the population.

The downward shifts and changes in shape of the spring X2-Delta Smelt abundance index relationships (Fig. 23) also illustrate the difficulties of determining and understanding functional responses of biota to dynamic physical habitat attributes in changing ecosystems; the species of interest, other habitat attributes, and their interactions may all change as much or more than the habitat attribute under consideration. Further, these changes may not always be gradual, but can take the form of sudden step changes that may be associated with system-wide regime shifts (Davis et al. 2010, Baxter et al. 2010, Cloern and Jassby 2012). Moreover, prior conditions and prior abundance may also influence outcomes. In Chapter 9 of this report we give a relatively simple example of additional multivariate analyses aimed at exploring the effects of hydrology and prior abundance on the abundance and recruitment of Delta Smelt larvae. More sophisticated multivariate life cycle modeling that greatly exceeds the scope of this report is needed to account for these simultaneous changes and interactive effects on all life stages.

Changes in the size, location, and dynamics of the LSZ likely also interact in complex ways with other changes, such as changes in sediment and nutrient loadings and resulting turbidity and nutrient dynamics and their effects on Delta Smelt and the food web. For example, LSZ position affects recruitment of the invasive clam *Potamocorbula amurensis*, which may in turn affect phytoplankton and zooplankton biomass, size, and production (Thompson 2005, Winder and Jassby 2011), and has likely affected fish-X2 relationships (Kimmerer et al. 2002a).

Table 1. Summary of relationships between log-transformed annual abundance indices for four Delta Smelt life stages (response variable) and spring X2 (February-June, see text): Survey: see description of monitoring surveys in Chapter 3; Regression: least squares linear or quadratic regression: n, number of observations (years); P, statistical significance level for the model; R^2, coefficient of determination; adjusted R^2, R^2 adjusted for the number of predictor terms in the regression model. Bold font indicates statistically significant relationships.

Life Stage	Season	Survey	Period	Regression	n	P	R^2	Adjusted R^2
Juvenile	Summer	TNS	1959-2013	Linear	52	0.614	0.005	
Juvenile	Summer	TNS	1959-1981	Linear	20	0.033	0.230	0.187
Juvenile	Summer	TNS	1959-1981	Quadratic	20	0.052	0.295	0.212
Juvenile	Summer	TNS	1982-2002	Linear	21	0.023	0.243	0.203
Juvenile	Summer	TNS	2002-2013	Linear	11	0.689	0.019	
Subadult	Fall	FMWT	1968-2013	Linear	43	0.290	0.027	0.003
Subadult	Fall	FMWT	1968-1981	Linear	11	0.699	0.017	
Subadult	Fall	FMWT	1968-1981	Quadratic	11	0.295	0.263	0.079
Subadult	Fall	FMWT	1982-2002	Linear	21	0.394	0.038	
Subadult	Fall	FMWT	2002-2013	Linear	11	0.107	0.263	0.181

Ongoing studies coordinated by the IEP as part of the POD and FLaSH studies focus on the processes that link physics, chemistry, and biology in the LSZ and its habitat value for Delta Smelt and other native and non-native species. Similar to Monismith et al. (2002), preliminary results indicate that the strength of physical mixing (lateral dispersion) in the LSZ changes with the volume of freshwater outflow, underscoring the importance of variable hydrodynamics on not just the location of the LSZ, but how ecological services (nutrient mixing, organism dispersal) are influenced by variable estuarine outflow (Monismith, U.C. Berkeley, personal communication).

Turbidity

In this report, turbidity is considered an environmental driver that interacts with other environmental drivers, resulting in habitat attributes that directly affect Delta Smelt responses, rather than a stand-alone habitat attribute. Clearly, studies have shown that distribution of Delta Smelt is correlated with turbidity (e.g., Feyrer et al. 2007, Nobriga et al. 2008, Grimaldo et al. 2009, Sommer and Mejia 2013). In the conceptual model we chose to incorporate turbidity as a modifier of several important linkages between environmental drivers and habitat attributes that are important to Delta Smelt, primarily food visibility for small larvae and predation risk for all life stages. If we had incorporated turbidity as a habitat attribute and, for example, predation risk was discussed separately from turbidity, there would have been a great deal of overlapping text between the two sections because turbidity interacts with the presence of predators to determine predation risk. Our approach is not ideal but should reduce redundant text and contribute to clarity of presentation. Nonetheless, we recognize that turbidity by itself could reasonably be considered as a habitat attribute. For example, it is possible that Delta Smelt experience stress in low turbidity habitat, which would in turn affect survival (likely through predation) but also in other direct ways such as lower growth and reduced egg production. However, we do not have evidence at this point to support that hypothesis.

In addition to salinity gradients, estuaries often have turbidity gradients. Turbidity is an optical property of water, which is the loss of transparency due to scattering of light by suspended particles. Typically, the upper reaches of estuaries have areas with high levels of suspended particles known as “estuarine turbidity maxima.” In many estuaries, these areas are located in or near the low salinity zone and are associated with higher numbers and enhanced growth for larvae of some species (Sirois and Dodson 2000a, b, Shoji et al. 2005). In the SFE, turbidity is largely determined by the amount of suspended inorganic sediment in the water (Cloern 1987, Ganju et al. 2007, Schoellhamer et al. 2012), although organic components can also play a role (USGS 2008). Sediment particles are constantly deposited, eroded, and resuspended, and are transported into, within, and out of the estuary. The amount of sediment that is suspended in the water column depends on the available hydrodynamic energy, which determines transport capacity, and on the supply of erodible sediment in the estuary and suspended sediments from the watershed.

In the upper SFE there are two main physical processes controlling turbidity. Suspended sediment is transported from the tributary watersheds into the system during high flows associated with winter and spring storm runoff (Schoellhamer et al. 2012). The first large storm of the rainy season often carries the highest concentrations of suspended sediment. Some portion of the transported sediment moves through the system to San Pablo and San Francisco Bay and the remainder is stored within the system as bottom sediment. During the remainder of the year, turbidity is primarily caused by interactions of this stored sediment with other environmental drivers (Schoellhamer et al. 2012). Water moving with the tides can resuspend fine sediments because of turbulence resulting from interactions between the bottom and water moving at high tidal velocities. At a larger scale, irregularities in the bottom topography may define geographic regions of greater turbulence and greater turbidity. In the upper estuary, such regions occur at a large bathymetric sill between Carquinez Strait and Suisun Bay and at another location within Suisun Bay (Schoellhamer 2001). Sediments may also be resuspended by turbulence related to wind waves. This process is mainly limited to areas with fine sediments on relatively shallow shoals where wind wave turbulence reaches the bottom. This process is most important in the shallows of Suisun, Grizzly, and Honker Bays and Liberty Island (Ruhl and Schoellhamer 2004, Warner et al. 2004, Morgan-King and Schoellhamer 2013). Thus, turbidity at any particular location is the result of several environmental drivers, including hydrology (transport from the watershed) and weather (wind and precipitation) interacting with the physical configuration of the upper SFE. Further, annual variation in these factors may have important effects. For example, during a drought there is little transport of suspended sediment and the same wind patterns during the summer may result in less turbidity than would occur after a wet year because less sediment was stored as benthic sediment during the winter. There is also evidence of longer term changes in turbidity (Schoellhamer et al. 2011, Hestir et al. 2013), along with regional differences.

In addition to the inorganic component of turbidity, organic matter (e.g., phytoplankton) also contributes to both suspended solids and the sediment load on the bed that is re-suspended with wind and wave action (McGann et al. 2013). In the SFE, phytoplankton concentration varies spatially, seasonally, and on an inter-annual scale (Cloern et al. 1985, Jassby 2008, Cloern and Jassby 2012), and is controlled by multiple factors, including benthic grazing, climate, river inflows (Jassby et al. 2002), and nutrient dynamics (Glibert et al. 2011, Parker et al. 2012, Dugdale et al. 2013), which in turn are likely to affect the organic component of turbidity. Phytoplankton dynamics are discussed in detail in the 'Food and Feeding' section (below), but it is important to note here that plankton concentration comprises part of the SFE turbidity and is significant as it relates to productivity at higher trophic levels.

Among the geographic regions of the upper SFE, the Suisun region is one of the most turbid, when the system is not being influenced by storm flows. This results from strong turbulent hydrodynamics in the Suisun region caused by strongly interacting tidal and riverine flows, bathymetric complexity, and high wind speeds, which create waves that resuspend erodible benthic sediment in the large and open shallow bays of the Suisun region. The North Delta, especially the large open expanse of Liberty Island (flooded since 1998) and the adjacent Cache Slough region are also relatively turbid. Recent evidence suggests that Liberty Island acts as a sediment sink in the winter and a sediment source for the surrounding Cache Slough complex in the summer (Morgan-King and Schoellhamer 2013).

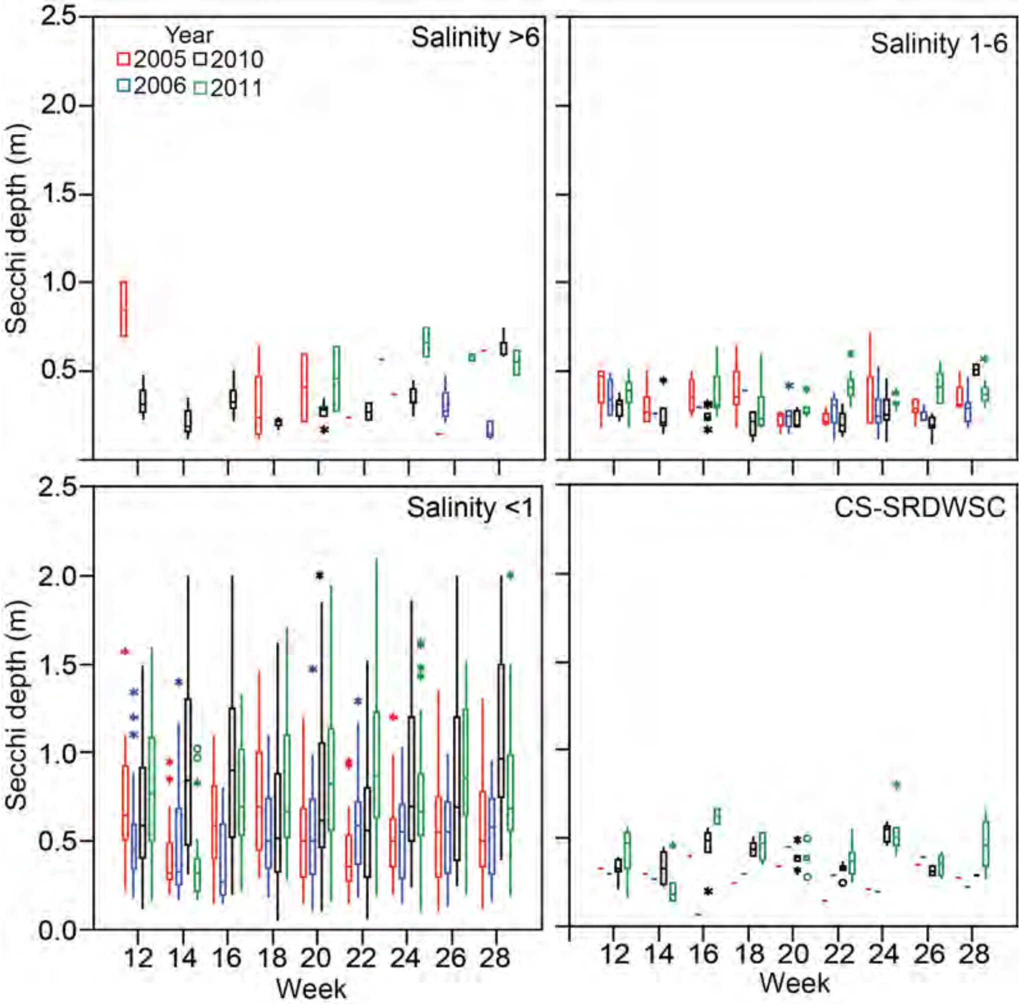
Turbidity is usually lower in the channels of the confluence of the Sacramento and San Joaquin Rivers compared to the Suisun region and North Delta region. Turbidity dynamics in the deep channels of the river confluence are driven more by riverine and tidal processes while high wind and associated sediment resuspension has little if any effect (Ruhl and Schoellhamer 2004). Turbidity is generally lowest in the south Delta (Nobriga et al. 2008). This may in part be due to sediment trapping by large, dense beds of *Egeria densa*, an invasive species of submerged aquatic vegetation (Hestir 2010). In winter/spring during the comparison years the highest Secchi disc depths (lowest turbidity) were found in the freshwater regions of the estuary (< 1 salinity), except for the Cache Slough region in the north Delta which was as turbid as the saltier regions of the estuary (Fig. 24).

There is strong evidence for an initial increase followed by a more recent long-term decline in sediment transport into the upper estuary, likely due to anthropogenic activities during the last century and a half (Schoellhamer et al. 2013, Wright and Schoellhamer 2004). Schoellhamer et al. (2013) presented a conceptual model of the effects of human activities on the sediment supplies in the SFE with four successive regimes:

1. The natural state.
2. Increasing sediment supplies due to mining, deforestation, agricultural expansion, etc.
3. Decreasing sediment supply due to sediment flushing during high flow events and sediment trapping behind dams and dikes.
4. A new altered state of low sediment supplies. The pulse of increased sediment inputs during and after the California gold rush and the more recent decline in these inputs is apparent in isotopic data from sediment cores taken in the estuary (Drexler et al. 2014).

The recent declines in sediment supplies have led to a long-term increase in water clarity in the upper Estuary (Jassby et al. 2002, Feyrer et al. 2007, Jassby 2008). Jassby et al. (2002) documented a 50% decrease in total suspended-solids concentration (TSS, a laboratory measurement of total suspended solids), approximated by suspended sediment concentration

Figure 24. **Secchi depth data collected during the 20 mm Survey. Surveys are conducted biweekly March-July. See Chapter 3: Data Analyses for explanation of boxplots.**



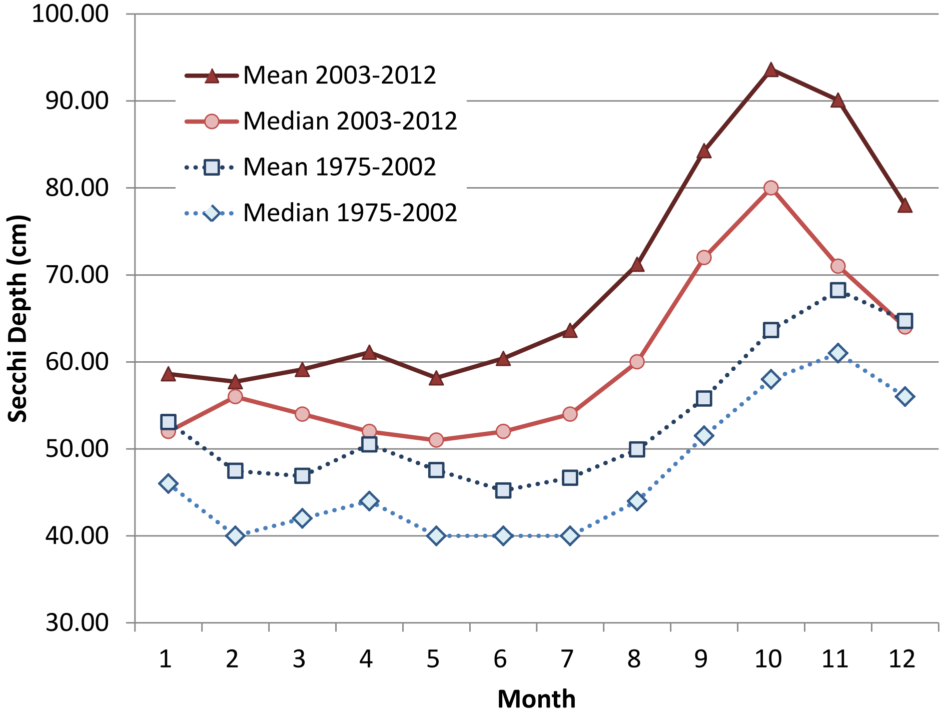
(SSC, an optical measurement done in the field for these data) in the Delta from 1975-1995. Jassby (2008) found that the downward trend continued in the decade after 1995, although at a slower pace than over the entire 1975-2005. From 1975-2005, there were significant declines in SSC of up to 6% per year at 8 of 10 Delta stations (Jassby 2008). Jassby et al. (2005) showed that TSS concentrations in the north Delta dropped sharply toward the end of the 1982–1983 El Niño-Southern Oscillation (ENSO) event, which was associated with extremely high outflows, and did not recover afterward. This step decrease after 1983 has been corroborated by further trend analyses of TSS (Hestir 2013). Following the El Niño event of 1997–1998, there was a 36% step decrease in SSC in San Francisco Bay as the threshold from transport to supply regulation was crossed as an anthropogenic erodible sediment pool was depleted (Schoellhamer 2011). Sediment trapping by dense beds of *Egeria densa* may be further reducing available sediment in the Delta (Hestir 2010). While other anthropogenic factors may have also contributed to long-term changes in turbidity (e.g., export operations; Arthur et al. 1996), quantitative analyses of the effects of these factors have not been conducted.

Before the step decline in SSC and the onset of the pelagic organism decline in the late 1990s and early 2000s (i.e. the "pre-POD" period), water transparency (roughly the opposite of turbidity) measured with a Secchi disc at all IEP EMP stations was usually highest in November and lowest in June (Fig. 25). From 2003-2012 (i.e. the "POD" period), average water transparency was not only higher (by an average of 16 cm Secchi depth) than in the previous period, but the annual dynamics also shifted forward by a month, to greatest transparency (i.e. lowest turbidity) in October and lowest transparency in May. The greatest differences in average water transparency between the pre-POD and POD periods occurred in September and October (28 and 30 cm difference between monthly averages, respectively) and the smallest differences in January-May (10 cm). While the EMP has collected turbidity data (nephelometric turbidity (NTU) measurements) since 1975, long-term fish monitoring surveys have traditionally collected Secchi disc data and only in recent years have incorporated turbidity. Therefore, Secchi disc data are presented in the majority of this report when relating Delta Smelt abundance to water clarity conditions.

Multiple field and modeling studies have established the association between elevated turbidity and the occurrence and abundance of Delta Smelt. The abundance of larval/postlarval Delta Smelt larvae was well explained by salinity and Secchi depth, a proxy for turbidity (Kimmerer et al. 2009). Sommer and Mejia (2013) and Nobriga et al. (2008) found that late-larval and juvenile Delta Smelt are strongly associated with turbid water, a pattern that continues through fall (Feyrer et al. 2007). Long term declines in turbidity may also be a key reason that juvenile Delta Smelt now rarely occur in the south Delta during summer (Nobriga et al. 2008). Thomson et al. (2010) found that turbidity (water clarity) was the only significant predictor variable that was shared by three of the four POD species; all other significant predictor variables were unique to each species. Grimaldo et al. (2009) found that the occurrence of adult Delta Smelt at the fish salvage facilities was linked, in part, with high turbidity associated with winter "first flush" events. Turbidity may also serve as a behavioral cue for small-scale (lateral and vertical movements in the water column) and larger-scale (migratory) Delta Smelt movements (Bennett and Burau 2014).

Delta Smelt are visual feeders, and feed primarily between dawn and dusk (Hobbs et al. 2006, Slater and Baxter 2014). As for all visual feeders, visual range and prey density determine feeding success of Delta Smelt. Visual range depends on size, contrast and mobility of the prey, retinal sensitivity and eye size of the visual feeder, and on the optical habitat attributes such as light scattering, absorption, and intensity (Aksnes and Giske 1993). Optical habitat attributes are affected by turbidity from suspended organic particles, such as algae and detritus, and inorganic particles, such as sand and silt. Somewhat counterintuitively, some level of turbidity appears important to the feeding success of larval Delta Smelt. Baskerville-Bridges et al. (2004a) conducted laboratory experiments in which alga densities (0, 0.5 x 10^6 cell/mL, and 2 x 10^6 cell/mL or 1, 3, and 11 NTU) and light levels (range tested: 0.01 µmoles/s x m^2, 0.3 µmoles/s x m^2, 1.9 µmoles/s x m^2) were manipulated and first-feeding success of larval Delta Smelt was quantified. They found that maximum feeding response occurred at the highest alga concentrations and light levels tested. In a subsequent experiment, when algae were removed entirely, the feeding response was very low. 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. 2004, Baskerville-Bridges et al. 2005, Werner et al. 2010b, Lindberg et al. 2013). Presumably the suspended particles provide a background of stationary particles that helps the larvae detect moving prey. Sufficient turbidity also appears to be important to reduce overall environmental stress and increase survival of larval Delta Smelt (Lindberg et al. 2013). Thus, it seems likely that turbidity is important to the feeding success and survival of larval Delta

Figure 25. Average and median Secchi depth in cm from monthly sampling at IEP Environmental Monitoring Program stations. Data are shown for the time period up to the pelagic organism decline (1975-2002) and after the decline (2003-2012).



Smelt in the wild. Recent research on juvenile Delta Smelt, however, suggests that influence of turbidity on feeding success may vary across life stages and field conditions. Hasenbein et al. (2013) exposed juveniles to varying turbidities (5-250 NTU) and observed a negative relationship between turbidity and feeding rates, with a marked decline in feeding at 250 NTU. However, feeding rates were highest at 12 NTU and stable in the 12-120 NTU turbidity range, which is likely within the range experienced by juvenile Delta Smelt in typical summer conditions in the Delta. Turbidity values of 250 NTU are generally not observed during the summer; therefore, the typical summer turbidity range in the Delta likely does not limit juvenile feeding success.

In addition to its effects on feeding, turbidity may also reduce predation risk. Based on the general recognition that fish assemblages are often partitioned between turbid-water and clear-water assemblages (Rodríguez and Lewis 1997, Whitfield 1999, Quist et al. 2004), and that turbidity can influence the predation rate on turbid-adapted fishes (Rodríguez and Lewis 1997, Gregory and Levings 1998, Quist et al. 2004), it has generally been assumed that juvenile and adult Delta Smelt are closely associated with turbidity in order to minimize their risk of predation in their generally open-water habitat. There may also be complex interactions between feeding and predation risk that are mediated by turbidity. Recent laboratory work has shown that in light (as opposed to dark) conditions, the vertical distribution of larval Delta Smelt shifts upward in the water column when turbidity is increased from clear (< 2 NTU) to 24 NTU (L. Sullivan, San Francisco State University, unpublished data), suggesting that larval Delta Smelt may use turbidity to safely forage in surface waters that may be more food-rich. Interestingly, when a predator cue (water, after containing juvenile Striped Bass for 1 hr) is added to clear water, the distribution of larval Delta Smelt becomes bimodal, with increased densities near the surface and closer to the bottom (L. Sullivan, San Francisco State University, unpublished data). Thus, while laboratory studies have demonstrated that larvae have improved feeding success at higher (but not too high, see above) turbidities, in natural settings, turbidity and predation risk may interact (e.g., Miner and Stein 1996) to affect Delta Smelt habitat choice and feeding success.

Turbidity may also be a migration cue for Delta Smelt. A recent field study investigated behavioral responses of Delta Smelt to winter "first flush" events in the Sacramento and San Joaquin Rivers near their confluence (W. Bennett, U.C. Davis, unpublished data). A first flush is defined as an increase in flow and turbidity associated with the onset of winter rain. This study found lateral turbidity gradients that changed with the tides and before and after first flush events and coincided with lateral Delta Smelt movements toward the channel during flood tides and toward the shoreline during ebb tides. The researchers concluded that this behavior likely facilitates maintaining channel position or moving upriver and cross-channel gradients in water turbidity may act as a behavioral cue. Feyrer et al. (2013) also found small-scale lateral and vertical gradients in turbidity in the lower Sacramento River just prior to a winter-time first flush event. In their study, turbidity and salinity were highest in the lower half of the water column and during flood tides and lowest during ebb tides in the center of the channel in the upper half of the water column. This coincided with observations of Delta Smelt which were more frequently caught throughout the water column during flood tides than during ebb tides when they were observed only in the lower half of the water column and sides of the channel. Feyrer et al. (2013) concluded that Delta Smelt may actively move in the water column by keying in on turbidity and salinity gradients or because of the physics underlying them.

Entrainment and Transport

The egg, larval, and juvenile stages of estuarine fishes and invertebrates along with small and weakly swimming adult stages are subject to involuntary transport (advection) by riverine and tidal flows. Entrainment is a specific case of involuntary transport. It refers to situations when altered flows misdirect and transport fish and other organisms in directions in which they would not normally travel or where they will encounter unfavorable conditions and increased risk of mortality. In this report, we use the term entraiment to specifically refer to the incidental removal of fishes and other organisms in water diverted from the estuary, primarily by CVP and SWP export pumping (Arthur et al. 1996, Grimaldo et al. 2009, Castillo et al. 2012).

Ultimately, watershed hydrology determines how much water can flow into and through the Delta; however, water flows into, within, and out of the Delta are manipulated in many ways. Water is: routed through and around artificial channels, gates, and barriers; stored in and released from reservoirs; discharged from agricultural and urban drains; and diverted with large and small pumps. Perhaps the greatest flow alterations in the Delta have taken place in Old and Middle Rivers (collectively referred to as "OMR") in the central Delta (Fig. 2). Historically, these river channels were part of the tidal distributary channel network of the San Joaquin River (Whipple et al. 2012). Today, they are a central component of the CVP and SWP water conveyance system through the Delta. Water from the Sacramento River in the north now flows through the northern Delta (down Georgiana Slough, through Three-Mile Slough and around Sherman Island) and eastern Delta (via the artificial "Delta cross-channel" and down the forks of the Mokelumne River) to OMR in the central Delta, then to the SWP and CVP. The SWP and CVP pumps are capable of pumping water at rates sufficient to cause the loss of ebb tide flows and to cause negative net flows (the advective component of flow after removal of the diffusive tidal flow component) through OMR toward the pumps (see Grimaldo et al. 2009), thus greatly altering regional hydrodynamics and water quality (Monsen et al. 2007). Under these conditions, fish and other aquatic species in the Delta may be transported toward the pumps (Arthur et al 1996, Brown et al. 1996, Moyle et al. 2010), may swim toward the pumps if they are behaviorally inclined to follow net flow (Grimaldo et al. 2009), or may move toward the pumps if they are employing tidal surfing behavior (Sommer et al. 2011).

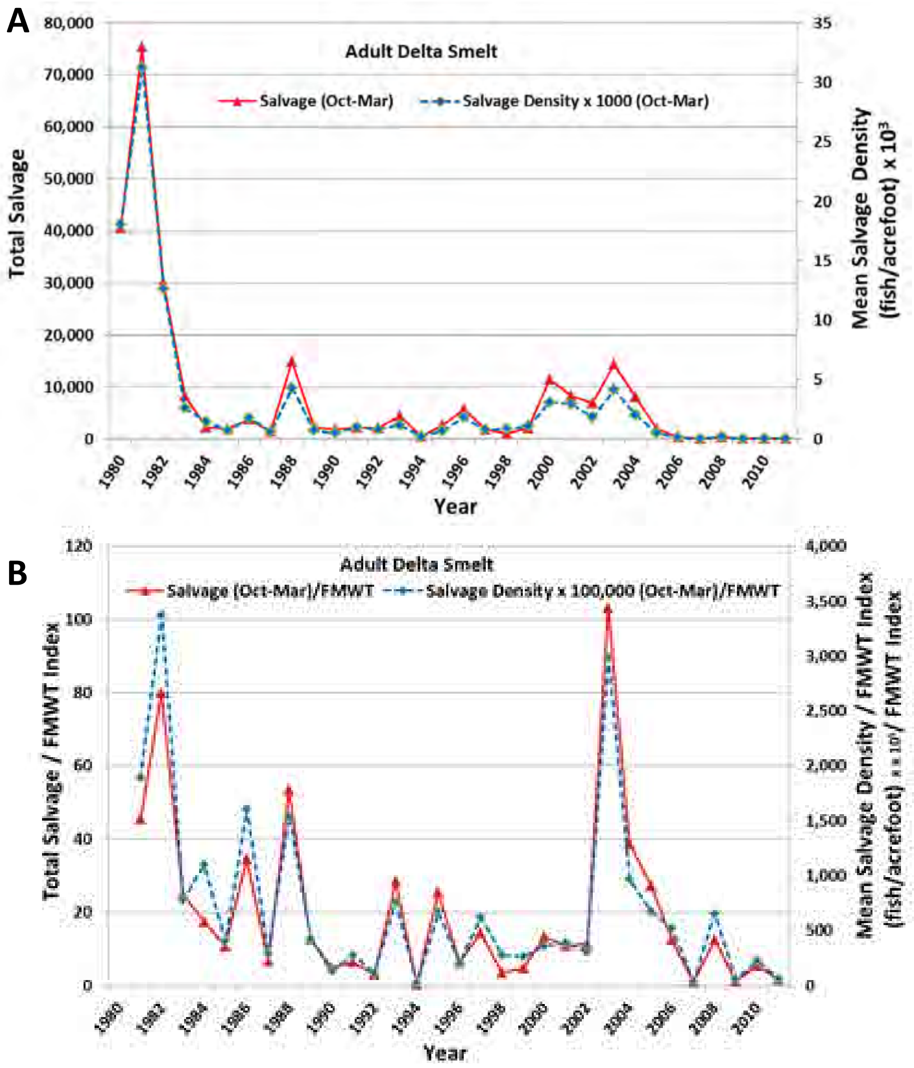
The SWP and CVP have large fish salvage facilities intended to reduce fish loss from the system due to entrainment - the State Skinner Fish Protective Facility (SFPF) and the federal Tracy Fish Collection Facility (TFCF). The SFPF and TFCF are located at the intakes to the State and federal export pumps on Old River in the southwestern Delta (Fig. 2). Both facilities have fish directing louvers and collecting screens that are used to capture and collect fish before they reach the pumps. The "salvaged" fish are then trucked to and released back into the western Delta. A variable fraction of these fish survive the capture, handling, trucking and release process (Miranda et al. 2010a,b, Aasen 2013, Afentoulis et al. 2013, Morinaka 2013a). The number of salvaged fish is monitored and reported as an index of SWP and CVP salvage and entrainment losses (Morinaka 2013b, more information and data available at http://www.dfg.ca.gov/delta/apps/salvage/Default.aspx). The SWP differs from the CVP in having a regulating reservoir, Clifton Court Forebay that temporarily stores water from Old River to improve operations of the SWP pumps. A change in the location of SWP water diversion from Italian Slough to Old River through CCF in 1969 may have led to a substantial increase in pre-screen losses at the SWP (Heubach ca. 1973, Kano 1990).

Fish have been salvaged since 1958 at the TFCF and since 1968 at SFPF, and the quality of the historical salvage data has improved over time. Delta Smelt salvage data is available since May 1979 for both the TFCF and SFPF (ftp://ftp.delta.dfg.ca.gov/salvage/). Juveniles less than 30 mm fork length are less efficiently captured in the salvage facilities (Kimmerer 2008, Morinaka 2013a) and Delta Smelt larvae less than 20 mm fork length have not been reported in the salvage data, although entrainment losses of Delta Smelt larvae have been calculated to be substantial under some circumstances (Kimmerer 2008). Development of a quantitative monitoring methodology for entrained Delta Smelt larvae at the CVP and SWP was recognized as necessary to refine triggers for protective actions (USFWS 2008). The current methodology for monitoring larval Delta Smelt at the TFCF and SFPF has provided presence-absence data since 2008 (Morinaka 2013b). Improved methods for sampling fish larvae have been reported at the TFCF (Reyes et al. 2012).

Despite these caveats salvage of Delta Smelt has been used as a rough index of entrainment losses. Delta Smelt salvage data since 1993 is considered more reliable than salvage data from earlier years. The difference in reliability is due to a change in count frequency from twice a day (0100 and 1300) from July 1978 to July 1992 to every two hours thereafter and an increased focus on proper identification of Delta Smelt following its State and federal listings as threatened (Morinaka 2013b).

Similar to the TNS and FMWT results for Delta Smelt, Delta Smelt salvage has declined dramatically since the beginning of this time series (Fig. 26). This is similar to trends for Chinook Salmon and Striped Bass salvage (not shown), but opposite to trends for Largemouth Bass and Bluegill (*Lepomis macrochirus*) salvage (Fig. 27), two species that may be benefiting from conditions resulting from an apparent ecological regime shift (Baxter et al. 2010). The ratio of Delta Smelt salvage divided by the previous year's FMWT index has been used as a simple indicator of relative interannual entrainment losses. For adult (December-March) salvage, this ratio has been variable over time, but particularly high in the first three years of this time series (1980-1982, with 1982 being a wet year) and again during the beginning of a series of drought years in 1989 and in the fairly dry "POD" years 2003-2005 (Fig. 26). Current management

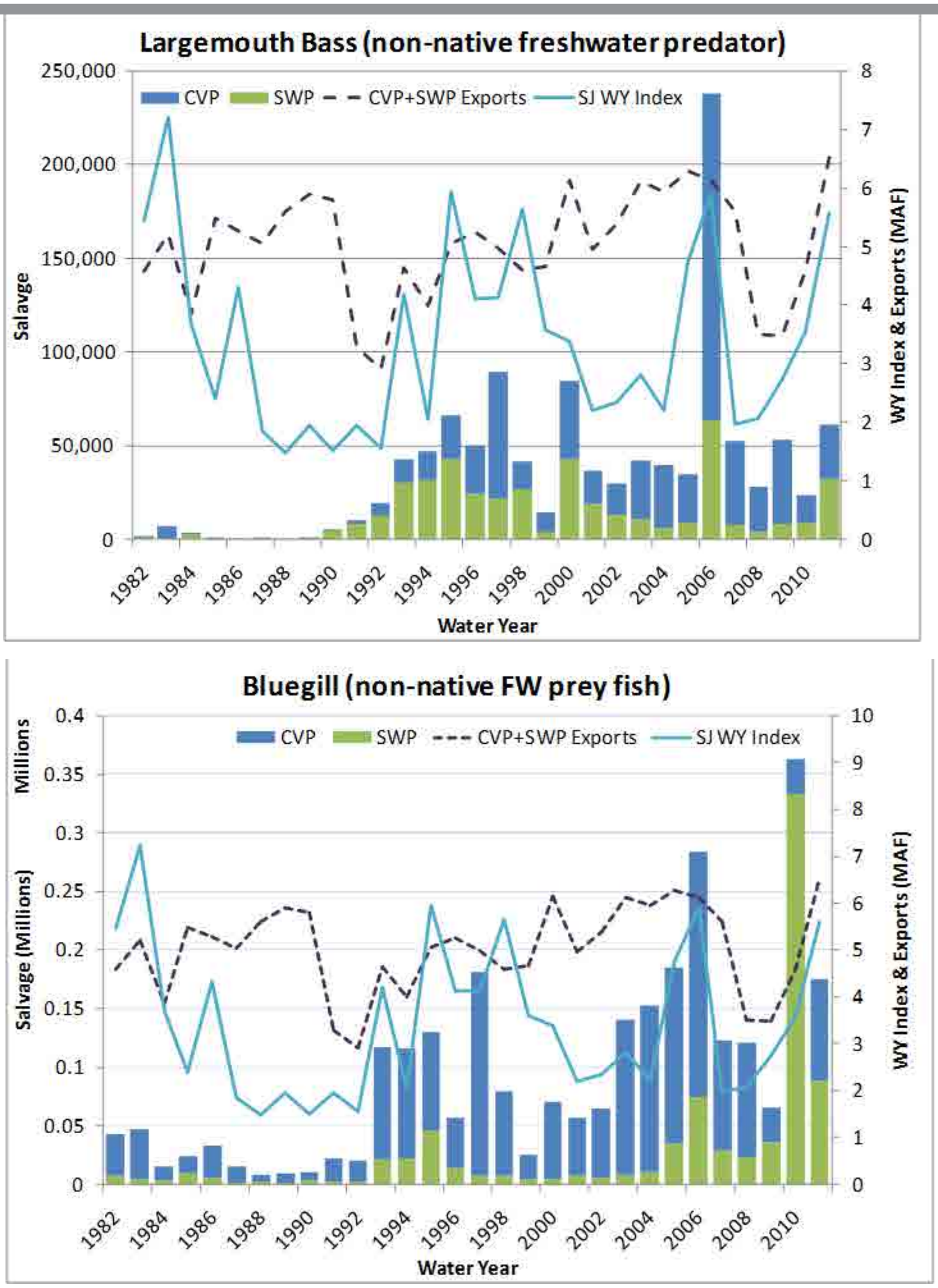
Figure 26. **A: Total reported October-March salvage for adult Delta Smelt and the corresponding mean salvage density based on the total monthly salvage and water volume exported by CVP and SWP. B: Both salvage and salvage density standardized by the Fall Midwater Trawl (FMWT) index for the previous year.**



provisions to protect Delta Smelt (USFWS 2008) are aimed at keeping this ratio at no more than the average during the period of 2006-2008.

Delta Smelt were salvaged nearly year-round in the beginning of this time series. Delta Smelt salvage since 2005 has occurred mostly from January through June, with substantial decline of May-June juvenile salvage since the mid 2000s (Fig. 28) and virtual disappearance of older juveniles from July-August salvage since the year 2000 (Fig. 29) and subadults since the early 1990s (Fig. 30). These patterns coincide with the near disappearance of Delta Smelt from the central and southern Delta in the summer (Nobriga et al 2008) and in the south Delta in the fall (Feyrer et al. 2007). Historically, adult and larval-juvenile (> 20 mm FL) Delta Smelt salvaged were not separately recorded and reported, but based on length measurements of a subset of salvaged fish, adults were predominantly salvaged between December and March or April

Figure 27. **Annual time series of Largemouth Bass (top graph) and Bluegill (bottom graph) salvage at the CVP (blue bars) and SWP (green bars) fish protection facilities. Also shown are the annual San Joaquin Valley Water Year Index (SJWY Index) (blue line) and the combined annual (water year) SWP and CVP water export volume (purple line; MAF, million acre feet).**



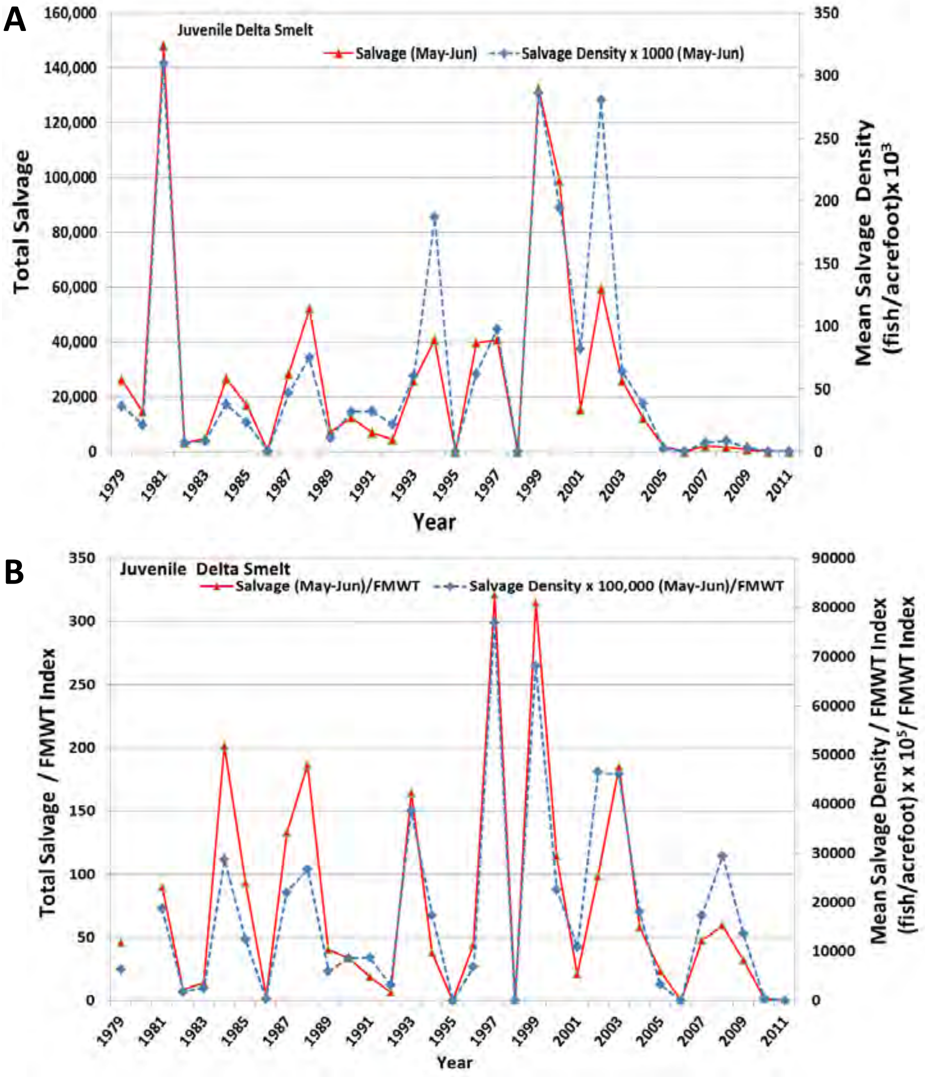
Largemouth Bass (non-native freshwater predator)

Bluegill (non-native FW prey fish)

and most Delta Smelt larvae and juveniles were historically salvaged from April through July (Kimmerer 2008, Grimaldo et al. 2009).

Salvage data are routinely used to track and manage incidental take at the SWP and CVP and have been used to explore factors affecting entrainment and to estimate the effects of the SWP and CVP on Delta fishes. For example, Grimaldo et al. (2009) found that OMR flows and

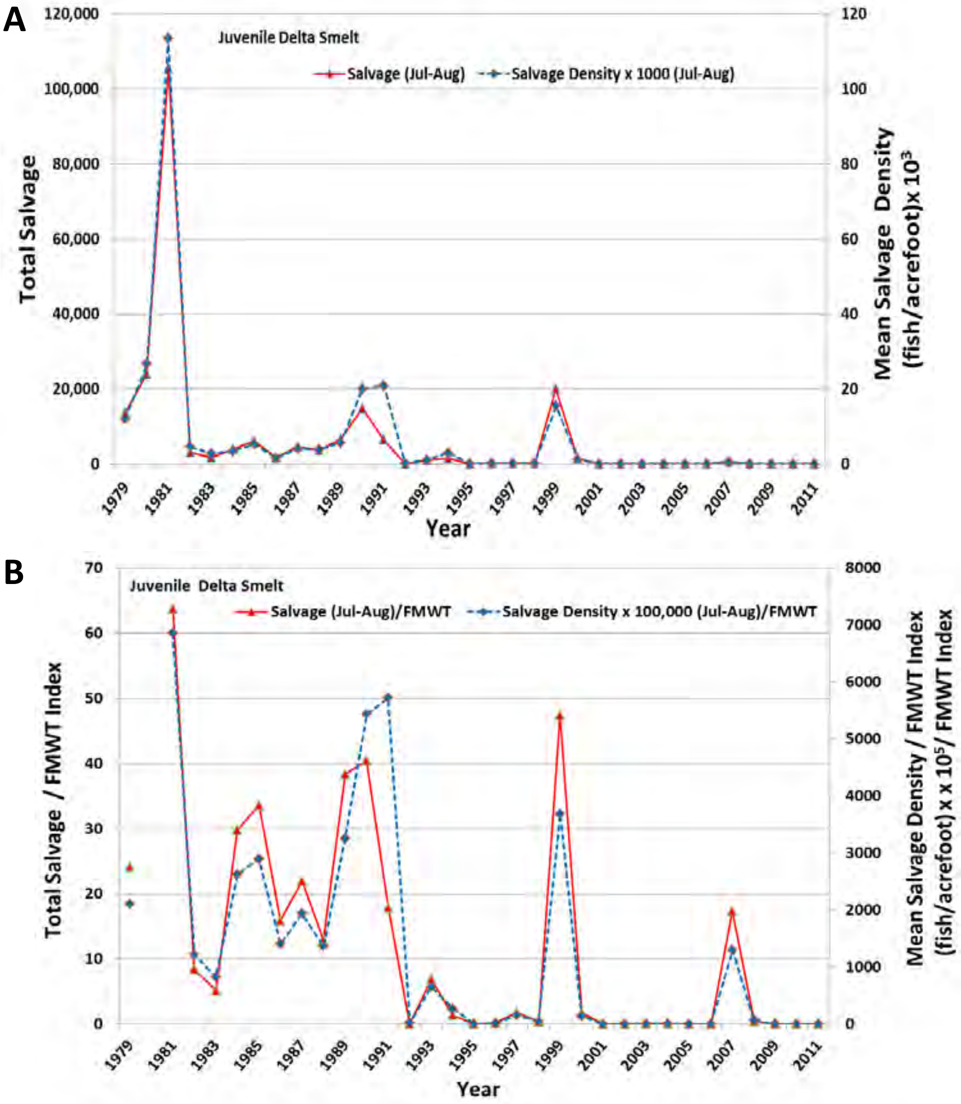
Figure 28. **A: Total reported May-June salvage for juvenile Delta Smelt and the corresponding mean salvage density based on the total monthly salvage and water volume exported by CVP and SWP. B: Both salvage and salvage density standardized by the Fall Midwater Trawl (FMWT) index for the previous year.**



turbidity account for much of the intra-annual variability in the salvage for juvenile and adult Delta Smelt.

It is important to remember, however, that salvage is only a very rough indicator of Delta Smelt entrainment. Based on mark-recapture experiments using cultured Delta Smelt, salvage was a very small fraction of total entrainment losses because of major pre-screen losses and low fish facility efficiency (Castillo et al. 2012). Experimental studies with cultured Chinook Salmon, Steelhead (*Oncorhynchus mykiss*), and Striped Bass have consistently shown that a large fraction (63% to 100%) of the entrained fish are not salvaged due to pre-screen losses and capture inefficiencies at the SWP fish facility (Brown et al. 1996, Gingras 1997, Clark et al. 2009). In addition, a mark–recapture test using field collected juvenile Chinook Salmon in CCF resulted in only 0.32% of the fish being salvaged (see Castillo et al. 2012). Pre-screen losses are generally

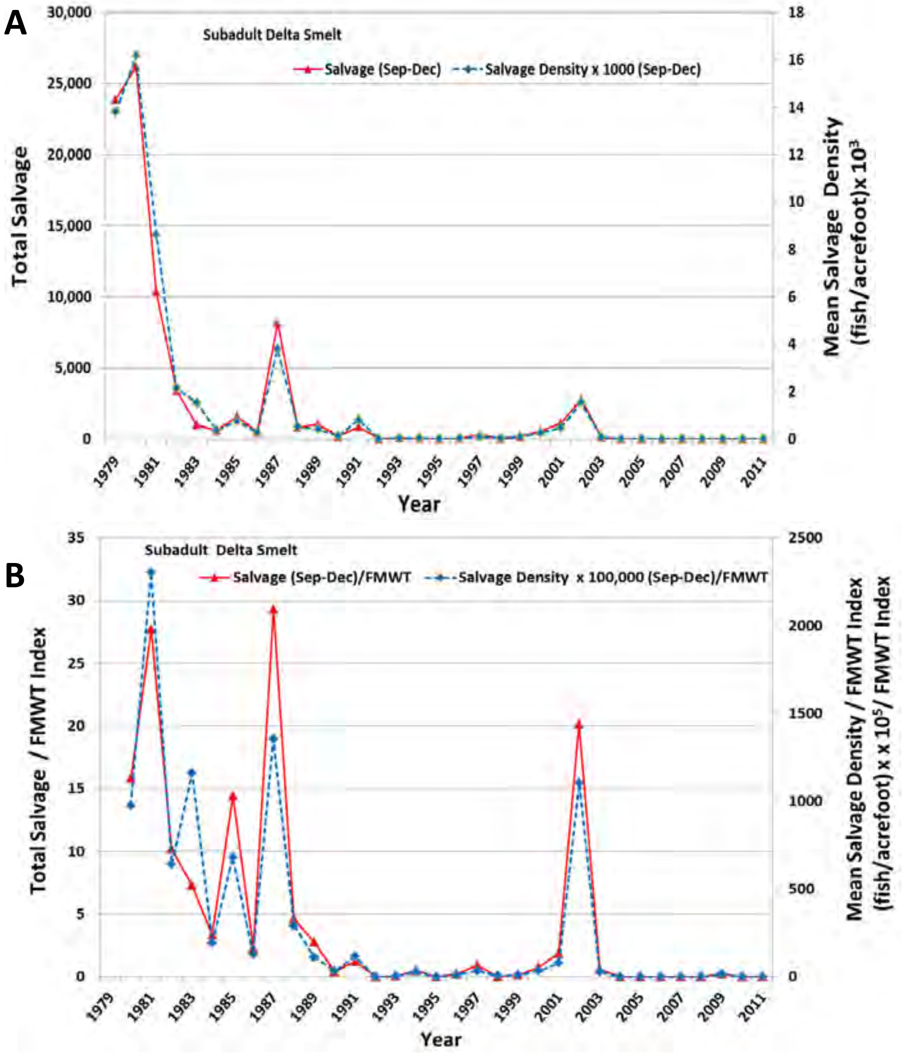
Figure 29. A: Total reported July-August salvage for juvenile Delta Smelt and the corresponding mean salvage density based on the total monthly salvage and water volume exported by CVP and SWP. B: Both salvage and salvage density standardized by the Fall Midwater Trawl (FMWT) index for the previous year.



attributed to increased predation and other unfavorable habitat conditions near the SWP and CVP pumps (e.g. Kano 1990, Brown et al. 1996, Gringas and McGee 1997, Clark et al. 2009, Castillo et al. 2012). For juvenile and adult Delta Smelt, Castillo et al. (2012) found that 94.3% to 100% of marked fish groups released into the SWP CCF were never salvaged and that salvage of marked fish decreased as the distance from the release site to SFPF increased and as residence time in CCF increased.

Large pre-screen losses of Delta Smelt in CCF are likely due to increased predation, especially when Delta Smelt spend a relatively long time in the reservoir in the presence of predators. MacWilliams and Gross (2013) used a particle tracking model to estimate residence time of passive particles, which can be considered surrogates for weakly swimming Delta Smelt. In 21-

Figure 30. **A: Total reported July-August salvage for sub-adult Delta Smelt and the corresponding mean salvage density based on the total monthly salvage and water volume exported by CVP and SWP. B: Both salvage and salvage density standardized by the Fall Midwater Trawl (FMWT) index for the same year.**



day simulations with the three-dimensional (3D) hydrodynamic model UnTRIM, MacWilliams and Gross (2013) found that the time particles spend in CCF varies greatly with wind and SWP operating conditions. They estimated transit times for passive particles (e.g., larval Delta Smelt) from the radial gates to the SFPF of 4.3 days under moderate export conditions (average daily SWP export rate of 2,351 cfs) and 9.1 days under low export conditions (689 cfs). The CVP does not have a regulating reservoir in the Delta and CVP pre-screen losses in the river channels leading to the TFCF are likely different from SWP pre-screen losses, but there are no studies quantifying these differences.

In general, Delta Smelt salvage increases with increasing net OMR flow reversal (i.e., more negative net OMR flows) and when turbidity exceeds 10-12 NTU (USFWS 2008, Grimaldo et al. 2009). Based on field and salvage data, Kimmerer (2008) calculated that from near 0% to 25% of larval-juvenile and 0% to 50 % of the adult Delta Smelt population can be entrained at the CVP and SWP annually, in years with periods of high exports. Although methods to calculate proportional loss estimates have since been debated (Kimmerer 2011, Miller 2011), a number of modeling efforts suggest that entrainment losses can adversely affect the Delta Smelt population (Kimmerer 2011, Maunder and Deriso 2011, Rose et al. 2013a, b).

High winter entrainment of Delta Smelt has been suspected as a contributing cause of both the early 1980s (Moyle et al. 1992) and the POD-era declines of Delta Smelt (Baxter et al. 2010). In addition to entraining Delta Smelt, water exports may likely also have indirect effects on Delta Smelt by contributing to adverse alterations of their habitat, for example, by changing Delta outflow and the size and location of the LSZ (see above) or by entraining food organisms (Jassby et al. 2002). The magnitude of these indirect effects of water exports on the Delta Smelt population has, however, not yet been quantified.

Delta Smelt are most vulnerable to entrainment when, as adults, they move from brackish water into fresh water, or as larvae, when they move from freshwater in the southern and central Delta into the brackish water of Suisun Bay. While some Delta Smelt live year-round in fresh water far from the CVP and SWP, most rear in the low-salinity regions of the estuary, also at a relatively safe distance from the SWP and CVP pumps. The timing, direction and geographic extent of the spawning movements of adult Delta Smelt affect their entrainment risk (Sweetnam 1999, Sommer et al. 2011a). Unlike the years prior to the 1990s, when high salvage of adult and juvenile Delta Smelt occurred at high, intermediate or low export levels, the risk of entrainment for fish that move into the central and south Delta is currently highest when net Delta outflow is at intermediate levels (~20,000 to 75,000 cfs) and OMR flow is more negative than -5000 cfs (USFWS 2008). In contrast, when adult Delta Smelt move upstream to the Sacramento River and into the Cache Slough region or do not move upstream at all, entrainment risk is appreciably lower. As explained later in this report, adult Delta Smelt may not move very far upstream during extreme wet years because the region of low salinity habitat becomes fresh and suitable for spawning (e.g., Suisun Bay or Napa River).

Transport mechanisms are most relevant to larval fishes, which have comparatively little ability to swim or otherwise affect their location. Dispersal from hatching areas to favorable nursery areas with sufficient food and low predation is generally considered one of the most important factors affecting the mortality of fish larvae (Hjort 1914, Hunter 1980, Anderson 1988, Leggett and Deblois 1994). Larvae of various smelt species exhibit diverse behaviors to reach and maintain favorable position within estuaries (Laprise and Dodson 1989, Bennett et al. 2002). Such nursery areas provide increased feeding success, growth rates and survival (Laprise and Dodson 1989, Sirois and Dodson 2000a, b, Peterson 2003, Hobbs et al. 2006). Until recently it was thought that larval Delta Smelt were transported from upstream hatching areas to downstream rearing areas, particularly the shallow productive waters of Suisun Bay (Moyle et al. 1992). Spring distributions of post-larval and small juvenile Delta Smelt support this view (Dege and Brown 2004). The distributions of these life stages were centered upstream of X2, but approached X2 as fish aged. These distributions could be displaced, and shifted up or down estuary with outflow and the shifting position of X2 (Dege and Brown 2004). More recent evidence suggests, however, that the timing and extent of downstream movement by young Delta Smelt is more variable than previously thought and that some may remain in upstream areas throughout the year (Sommer et al. 2011a, Contreras et al. 2011, Merz et al. 2011, Sommer and Mejia 2013).

Adult spawning site selection affects the potential importance of transport and entrainment to larvae. The risk of larval entrainment appears to increase with proximity to the south Delta export pumps (Kimmerer and Nobriga 2008). Larvae hatching in the San Joaquin River channel from

Big Break upstream to the city of Stockton and tidal channels south of these locations, can be affected by several interacting processes. Flows from the San Joaquin, Calaveras, Mokelumne and Cosumnes rivers act to cause net downstream flow, whereas export levels at the south Delta pumps act to reverse net flows in the lower San Joaquin River. High export rates can create negative flows past Jersey Point on the lower San Joaquin River ("Qwest," see Dayflow documentation: http://www.water.ca.gov/dayflow/output/Output.cfm) and negative OMR flows (Fig. 31). Since the onset of the POD in 2002, positive average monthly OMR flows have only occurred in 9 months (6%) during the wettest years and average monthly Qwest flows were negative in just under half (49%) of all months (Fig. 31). Tidal conditions can also act in favor of downstream transport or entrainment depending upon whether the Delta is filling or draining in response to the fortnightly spring-neap cycle (Arthur et al. 1996). The combination of high export and low inflow can create very asymmetrical tides in OMR that covary with net negative flow resulting in stronger floods compared to ebbs, which may also contribute to fish entrainment.

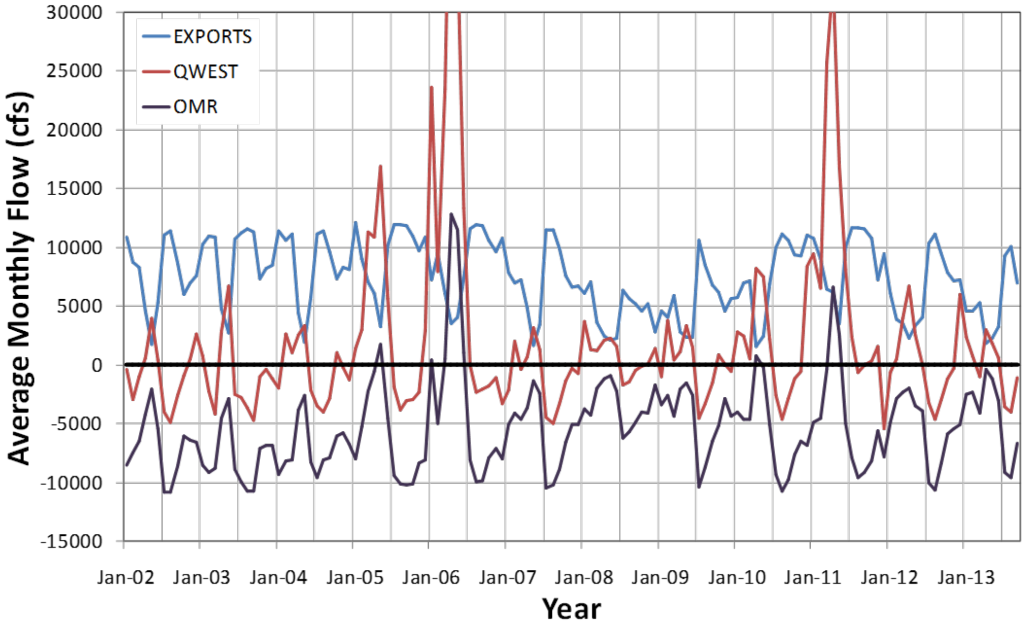
Predation Risk

Small planktivorous fishes, including osmerids, serve as prey for larger fishes, birds and mammals. As prey, they have the critically important trophic function of transferring energy to higher trophic levels. Consequently, they are often subjected to intense predation pressure (Gleason and Bengsten 1996, Jung and Houde 2004, Hallfredsson and Pedersen 2009). Prey fish populations compensate for high mortality through high reproductive rates, including strategies such as repeat spawning by individuals and rapid maturation (Winemiller and Rose 1992, Rose et al. 2001). Predation can be a dominant source of mortality for fish larvae, along with starvation and dispersion to inhospitable habitats (Hjort 1914, Hunter 1980, Anderson 1988, Leggett and Deblois 1994).

Since predation is a natural part of functional aquatic ecosystems, predators are likely not responsible for long-term declines in populations of prey fishes, such as Delta Smelt, without some additional sources of stress that disrupt the predator-prey relationship (Nobriga et al. 2013). Predation may become an issue when established predator-prey relationships are disrupted by habitat change or species invasions (Kitchell et al. 1994). As described in Chapter 1, the SFE has been extensively modified (Nichols et al. 1986, Cohen and Carlton 1998, Whipple et al. 2012, Cloern and Jassby 2012) so disrupted relationships between predators and prey are certainly plausible. For example, prey may be more susceptible to predation if they are weakened by disease, contaminants, poor water quality, or starvation. Similarly, the creation of more "ambush habitat" (e.g. structures, weed beds), declines in turbidity levels, or the introduction of a novel piscivore also may dramatically shift the existing predator-prey relationships (Ferrari et al. 2014). All of these changes have in fact taken place in the estuary, especially in the central and south Delta (Feyrer and Healey 2003, Nobriga et al. 2005, Brown and Michniuk 2007).

Virtually all fishes of appropriate size will feed on fish larvae when available and predation is theoretically maximal when larvae lengths are 10% of the length of the predator (Paradis et al. 1996). Presently, Mississippi Silverside (*Menidia audens*) is thought to be the most substantial predator of Delta Smelt larvae (Bennett and Moyle 1996, Bennett 2005, Baerwald et al. 2012). Juvenile and adult Delta Smelt have also been reported from the stomach contents of Striped Bass (Stevens 1963, Stevens 1966, Thomas 1967), White Catfish (*Ictalurus catus*) and Black Crappie (*Pomoxis nigromaculatus*) (Turner 1966a,b). Stevens (1963) reported "freshwater smelt" to be a very common component of Striped Bass stomach contents (nearly 100% frequency of occurrence in fifteen stomachs with food) on the Sacramento River near Paintersville Bridge

Figure 31. Flows in cubic feet per second for Qwest (positive values are seaward), Old and Middle River (OMR) (positive values are seaward), and total exports for years since the beginning of the pelagic organism decline (POD). Maximum monthly average Qwest values in 2006 and 2011 omitted to improve graph display, values are 50,086 cfs in April 2006, 35,477 in May 2006, and 32,884 cfs in April 2011 (Qwest and Export data are from 2013 Dayflow, OMR data are from USGS).



during March-April 1963. During 1963-1964, Stevens (1966) also evaluated seasonal variation in the diets of juvenile Striped Bass throughout the Delta; only age 2 and age 3 Striped Bass contained more than trace amounts of Delta Smelt. The highest reported predation on Delta Smelt was 8% of the age 2 Striped Bass diet by volume during the summer. Thomas (1967) reported on spatial variation in Striped Bass diet composition based on collections throughout the SFE and the Sacramento River above tidal influence. The field collections occurred from 1957-1961; data were collected on age 1 and older Striped Bass but data were only summarized as all ages combined. Delta Smelt accounted for 8% of the spring diet composition and about 16% of the summer diet composition in the Delta.

Several authors tested hypotheses about inverse correlations between estimates of adult and juvenile Striped Bass abundance and indices of Delta Smelt relative abundance or survival (Mac Nally et al. 2010, Thomson et al. 2010, Maunder and Deriso 2011, Miller et al. 2012, Nobriga et al. 2013). None of these statistical analyses has found evidence for the expected inverse correlation. Modeling studies indicate that Striped Bass predation rates on prey are affected by temperature and predator abundance (mostly the latter; Loboschefsky et al. 2012). However, the links between prey abundance and predator abundance vary from strong to non-existent, depending on the strength of their interaction in the food web (Essington and Hansson 2004). It is not currently known if changes in juvenile Striped Bass abundance correspond with changes in population-level or per capita Striped Bass predation rate on Delta Smelt (Nobriga et al. 2013).

Recent modeling efforts show that Delta Smelt declines are negatively associated with metrics assumed to reflect the abundance of predators in the estuary (Maunder and Deriso 2011, Miller et al. 2012). These metrics are composites of the relative abundance of Mississippi Silverside, Largemouth Bass and other centrarchids; species that are potential predators of concern because of their increasing abundance (Fig. 27; Bennett and Moyle 1996, Brown and Michniuk 2007, Thomson et al. 2010), and because of inverse correlations between Largemouth Bass abundance and Delta Smelt abundance (Nobriga and Feyrer 2007, Thomson et al. 2010, Maunder and Deriso 2011). These correlations could represent predation on Delta Smelt by Largemouth Bass, or alternatively, the very different responses of the two species to changing habitat within the Delta (Moyle and Bennett 2008). Current data suggest that Largemouth Bass populations have expanded as the SAV *Egeria densa* has expanded and have come to dominate parts of the Delta (Brown and Michniuk 2007). *E. densa* and Largemouth Bass are particularly prevalent in the central and southern Delta (Brown and Michniuk 2007) and Largemouth Bass may contribute to the pre-screen losses of Delta Smelt entrained into the SWP and CVP export pumps (see above). Largemouth Bass will readily eat Delta Smelt when the opportunity exists (Ferrari et al. 2014). However, there is little evidence that Largemouth Bass are major consumers of Delta Smelt due to low spatial co-occurrence (Nobriga et al. 2005, Baxter et al. 2010; L. Conrad, California Department of Water Resources, unpublished data). Thus, the inverse correlations between these species may not be mechanistic. Rather, they may reflect adaptation to, and selection for, different environmental conditions.

As noted above, predation on fish larvae can also be an important source of mortality. Juvenile and small adult fishes of many species will consume fish larvae when they are available. Major predators of the eggs and larvae of nearshore coastal and pelagic estuarine forage fishes can include invertebrates (DeBlois and Leggett 1993) and numerous small fishes not typically thought of as “piscivorous” (Johnson and Dropkin 1992), including adults of their own species (Takasuka et al. 2003). Bennett and Moyle (1996) and Bennett (2005) noted this and specifically identified Mississippi Silversides (hereafter, Silversides) as potential predators on Delta Smelt larvae. These authors also documented increases in the Silverside population from the mid-1970s through 2002. Consumption of Delta Smelt larvae by Silversides in the Delta was recently verified using DNA techniques (Baerwald et al. 2012). Larval predation is discussed in more detail in the next Chapter.

Contaminants

Fish are particularly sensitive to alterations in the chemical composition of the natural aquatic environment, as these changes can have significant impacts on their behavioral and physiological systems (Radhaiah et al. 1987). Chemical alterations can be the result of natural processes, for example the changes in local water quality associated with tidal water movements or natural biogeochemical processes, or they can be caused by pollution from watershed- or land-based sources of nutrients, such as nitrogen compounds, and contaminants, such as pesticides, metals, and contaminants of emerging concerns (CECs). The movement of contaminants through aquatic ecosystems is complex and dynamic, and many contaminants are difficult to detect and expensive to monitor (Scholz et al. 2012).

Portions of the SFE are listed as “impaired” on California’s 303(d) list of Impaired Water Bodies due to metals, pesticides, legacy pollutants, and nutrients that exceed established water quality objectives (SWRCB 2010). In particular, the entire SFE has been listed as impaired due to pollution with metals, such as mercury and selenium, and pesticides such as chlorpyrifos, DDT (Dichlorodiphenyltrichloroethane), and diazinon. The entire Delta, but not the bays of the SFE, is also listed for observed toxicity to aquatic organisms. In addition, the Stockton Ship Channel in the southeastern Delta is listed for enrichment with nutrients, organic compounds, and low dissolved oxygen levels; Old River in the south-central Delta is listed for elevated salinity (electrical conductivity; EC) and total dissolved solids (TDS). Delta Smelt are likely exposed to a variety of these contaminants throughout their life cycle; however, the frequency and magnitude of the effects of contaminants on Delta Smelt health and reproduction are not very well understood in the SFE (Johnson et al. 2010, Brooks et al. 2012). The following sections describe the potential effects of key contaminants on Delta Smelt.

Pesticides

Pesticides produce many physiological and biochemical changes in freshwater organisms through their influence on the activities of several enzymes (Khan and Law 2005). Specifically, pesticides can have an adverse effect on hormones or other chemical messengers important to the health of an individual. Previous work has shown that chronic exposure to low levels of pesticides may even have a more adverse effect on fish than a single acute exposure to high levels. Chronic exposures were associated with changes in behavior and physiology that could influence survival and reproduction of wild fish (Ewing 1999). Biochemical and physiological stresses induced by exposure to pesticides can result in metabolic disturbances, retardation of growth, as well as reduction in longevity and fecundity (Murty 1986).

Pesticides are among the key contaminants believed to have contributed to the Delta Smelt decline (Johnson et al. 2010, Brooks et al. 2012, NRC 2012). Because pesticide concentrations in surface water are typically highest during the winter and spring, pesticides are most likely to affect the adult and larval life stages; however, effects may occur during any life stage as pesticides are seasonally and geographically widespread (Kuivila and Hladik 2008). Kuivila and Moon (2004) found that peak densities of larval and juvenile Delta Smelt sometimes coincided in time and space with elevated concentrations of dissolved pesticides in the spring. These periods of co-occurrence lasted for up to 2–3 weeks. While concentrations of individual pesticides were lower than would be expected to cause acute mortality, little is known of the sublethal effects of pesticides on Delta Smelt. Although little evidence exists for acute effects of pesticides on fish or invertebrates, several studies have documented sublethal effects on fish health (Werner et al. 2008, Werner et al. 2010a, Werner et al. 2010b).

Herbicides and fungicides were among the most commonly detected classes of pesticides observed in water and sediment in the Delta and are also found in fish tissue (Orlando et al. 2013, Smalling et al. 2013). Herbicides are known to affect primary producers, while insecticides can affect invertebrate prey species (e.g., Brander et al. 2009, Weston et al. 2012), which could lead to contaminant-mediated food limitation for Delta Smelt. Fungicides have been found to cause endocrine disruption in fish, including reduced fecundity (Ankley et al. 2005). Recent work has shown that the insecticide esfenvalerate affects swimming behavior of exposed larval Delta Smelt (Connon et al. 2009). It was also found to alter the expression of genes involved in neuromuscular activity and immune response, detoxification, and growth and development (Connon et al. 2009). Additionally, insecticides are known to affect predator-prey relationships for fish, as well as lead to endocrine disruptions (Scholz et al. 2000, Junges et al. 2010, Relyea and Edwards 2010, Riar et al 2013, Forsgren et al. 2013). Contamination of aquatic systems by pyrethroid insecticides was recently found to lead to genetic point mutations in the nontarget, aquatic amphipod *Hyalella azteca*, resulting in differences in pyrethroid sensitivity. Wild populations of *H. azteca* collected from areas with high sediment concentrations of pyrethroids exhibited remarkable resistance to pyrethroids compared to laboratory cultures and the observed resistance was highly coupled to the presence of a genetic mutation. The LC50s (concentration that is lethal to 50% of the exposed population) of previously-exposed wild populations were up to two orders of magnitude greater than LC50s of laboratory cultures. Moreover, the presence of a genetic mutation was detected in 100% of *H. azteca* that survived exposure to high pyrethroid concentrations. The development of such resistance can result in costs to genetic and biological diversity, including reduced fitness, and may lead to impacts to the food web (Weston et al. 2013). The presence of such resistance and genetic mutations in Delta Smelt as a result of pyrethroids or other pesticide exposure has not been investigated

It is also important to note that environmental factors such as temperature and salinity affect pesticide toxicity in fish (Coats et al. 1989, Lavado et al. 2009). For that reason, seasonal variation in environmental factors may result in greater risk to certain life stages. The results above are for dissolved pesticides; pesticides may also be bound to sediments, representing another possible mechanism of exposure. Pesticides, such as pyrethroids and organochlorines, that strongly bind to sediment may be particularly important to the adult and larval life stage of Delta Smelt as these life stages occur during the winter and spring, when rain events (including the “first flush”) transport sediment and associated contaminants into the Delta; however, as the mechanisms that influence the desorption rates of pesticides are complex (e.g., temperature, contact time, pesticide) (e.g., Xu et al. 2008, Cornelissen et al. 1998), exposure rates for Delta Smelt lifestages are likely multifaceted and difficult to predict.

Ammonia and Ammonium

Agricultural operations, wastewater treatment plant effluent, and other sources contribute to the accumulation of nutrients in the Delta. Nutrients, such as ammonium (a cation) and ammonia (its toxic, unionized form) are of particular concern in the Delta, as they can have significant negative effects on Delta Smelt and their habitat. Ammonium is increasingly converted into ammonia as pH rises. Delta Smelt spawning and larval nursery areas in the northern Delta are at particular 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. 2011a). However, effects of nutrients such as ammonia/um are likely at all Delta Smelt life stages, as nutrients are discharged throughout the Delta year-round.

Recent work demonstrated that Delta Smelt exposed to ammonia exhibited membrane destabilization, which may lead to increased membrane permeability as well as increased susceptibility to synergistic effects of multi-contaminant exposures (Connon et al. 2011a, Hasenbein et al. 2013b); however, the concentrations of ammonia used in these studies were higher than the concentrations typically experienced by Delta Smelt in the wild. In other fish species, sublethal concentrations of ammonia/um have also led to histological effects such as gill lamellae fusions and deformities (Benli et al. 2008). Other work has also shown that neurological and muscular impacts of ammonia/um resulted in slowed escape response and subsequent mortality (McKenzie et al. 2008).

Metals and Other Elements of Concern

Historic mining sites, industrial and domestic wastewater discharges, and agricultural runoff are largely responsible for the presence of metals and other elements of concern in the Delta. Metals of particular importance in the Delta include copper and mercury; selenium is a trace element of concern. Delta Smelt exposed to copper exhibited reduced swimming velocities and suffered digestive and neurological effects (Connon et al. 2011b). Other sublethal effects on fish caused by exposure to 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 be particularly important to the adult and larval life stages, since sediment is transported with significant rain events, including the "first flush."

Contaminants of Emerging Concern

Contaminants of emerging concern (CECs) such as pharmaceuticals, hormones, personal care products, and industrial chemicals are of increasing concern because they are widespread in the aquatic environment, biologically active, and are relatively unregulated (Kolpin et al. 2002, Pal et al. 2010). The California State Water Resources Control Board is currently investigating CECs in the Delta (http://www.sccwrp.org/ResearchAreas/Contaminants/ContaminantsOfEmergingConcern/ EcosystemsAdvisoryPanel.aspx). CECs originate from many sources including industrial and domestic wastewater. They are responsible for a myriad of sublethal effects in fish including endocrine disruption, changes in gene transcription and protein expression, and morphological and behavioral changes (Brander 2013). Though the effects of CECs have been well studied in other fish species, the extent to which they influence Delta Smelt remains unclear.

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

The PAHs and PCBs found in the Delta are largely from urban and industrial sources. PAHs are formed during the incomplete burning of coal, oil, gas, garbage, and other organic substances. PCBs are synthetic organic chemicals that were used in many industrial and commercial applications. PCBs were banned in 1979, but continue to persist in the environment. PAHs and PCBs bind strongly to sediment and therefore are likely to be associated with the "first flush" and may be particularly important to the adult and larval life stages of Delta Smelt. Almost all sediments sampled in the Delta in 2006 contained PAHs (mean concentration of 0.3 parts per million in Suisun Bay) and PCBs (mean concentration of 0.8 parts per million in Suisun Bay) (SFEI 2007). Studies have found PAHs and PCBs in surface water, with concentrations in excess of established water quality objectives (Thomson et al. 2000, Oros et al. 2006). Both PCBs and PAHs can cause endocrine disruption in fish (Brar et al. 2010, Nicolas, 1999); however, specific impacts on Delta Smelt have not been documented.

Contaminant Mixtures

While the individual effects of the aforementioned contaminants can be severe, recent work has demonstrated that the interaction of the contaminants within mixtures can have both synergistic and antagonistic effects, exacerbating potential impacts on fish physiology (e.g., Jordan et al. 2012). There is increasing evidence that compounds in mixtures show adverse effects at concentrations at which no effects were observed for single toxicants (e.g., Baas et al. 2009, Silva et al. 2002, Walter et al. 2002). For example, recent work on Mississippi Silversides has demonstrated that contaminant mixtures resulted in endocrine disruptions such as varied expression of mRNA levels for estrogen-responsive genes, reduced mean gonadal somatic indices (GSI), testicular necrosis, and biased sex ratios (Brander et al. 2013). Studies have also shown that mixtures can affect predator-prey interactions (Relyea and Edwards 2010) and cause liver abnormalities (Sacramento Splittail, *Pogonichthys macrolepidotus*; Greenfield et al. 2008). Other work on Striped Bass has demonstrated that contaminant mixtures can be maternally-transferred to fish eggs, resulting in larvae with impaired growth and abnormal brain and liver development (Ostrach et al. 2008).

Due to the unpredictability of their effects on organisms, the synergistic effects of contaminant mixtures have received a great deal of attention both within pharmacology and environmental sciences (Arnold et al. 1996, Ashby et al. 1997, Berenbaum 1989, Greco et al. 1995, Liang and Lichtenstein 1974). Currently, one of the greatest challenges in chemical mixture research is how to deal with the infinite number of combinations of chemicals and other stressors, as well as their interactive effects, on organisms (Baas et al. 2010). Additional challenges also exist trying to relate lab-based findings to wild populations for studies examining the effects of individual contaminants and contaminant mixtures on organisms using exposure concentrations that are environmentally representative. Therefore, while the potential for exposure to contaminant mixtures in all Delta Smelt life stages is highly probable, any specific effects of such interactions on Delta Smelt remain unknown.

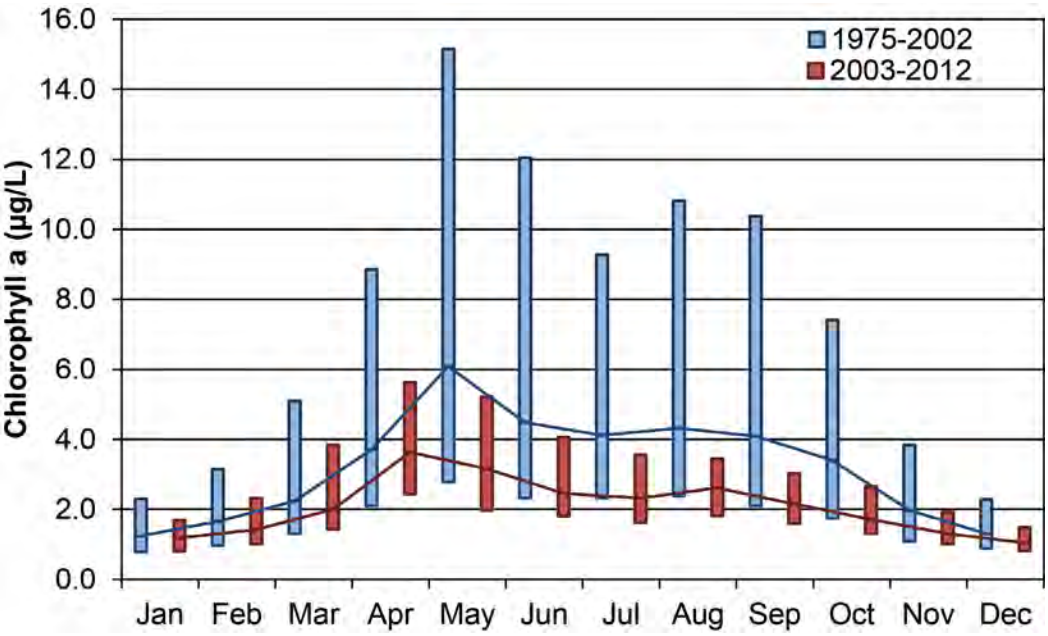
Food and Feeding

The presence of food is, obviously, a critical habitat attribute for any organism; however, the factors determining the quantity and quality of available food can be quite complex. In this section, we begin with a brief review of information about trophic processes in the upper SFE. We then discuss the available data on prey consumed by Delta Smelt. Finally, we provide a review of information on factors possibly affecting abundance and quality of food organisms.

Estuaries are commonly characterized as highly productive nursery areas for a suite of organisms. Productivity of estuarine ecosystems is often fueled by detritus-based food webs. In the SFE, much of the community metabolism in pelagic waters does result from microbial consumption of organic detritus. However, evidence suggests that metazoan production in pelagic waters is primarily driven by phytoplankton production (Sobczak et al. 2002, 2005, Mueller-Solger et al. 2002, 2006, Kimmerer et al. 2005). Protists (flagellates and ciliates) consume both microbial and phytoplankton prey (Murrell and Hollibaugh 1998, York et al. 2010) and are an additional important food source for many copepod species in the estuary (Rollwagen-Bollens and Penry 2003, Bouley and Kimmerer 2006, Gifford et al. 2007, McManus et al. 2008). However, the conversion of dissolved and particulate organic matter to microbial biomass and then to zooplankton is a relatively slow and inefficient process. Shifts in phytoplankton and microbial food resources for zooplankton might favor different zooplankton species. Moreover, phytoplankton production and biomass in the SFE is low compared to many other estuaries (e.g., Jassby et al. 2002, Kimmerer et al. 2005, Wilkerson et al. 2006, Cloern and Jassby 2012). The recognition that phytoplankton production might impose limits on pelagic fishes, such as Delta Smelt, through food availability has led to intense interest in factors affecting phytoplankton production and species composition and in management actions aimed at enhancing high-quality phytoplankton production. In addition, there is a major need to understand other trophic pathways given the observation that larger Delta Smelt periodically can take advantage of epibenthic prey (see below).

Phytoplankton biomass (measured as chlorophyll-*a*) has been routinely monitored in the estuary since the 1970s. The 1975-2012 median chlorophyll-*a* concentration across all IEP EMP stations is 2.8 µg/L (n = 13482, interquartile range (IQR) = 5 µg/L). Seasonally, the highest chlorophyll-*a* concentrations tend to be observed in May and June and the lowest concentrations in December and January (Fig. 32). Regionally, monitoring stations in the South Delta/San Joaquin River usually have the highest chlorophyll-*a* concentrations. There has been a well-documented long-term decline in phytoplankton biomass (chlorophyll-*a*) and primary productivity (estimated from measurements of chlorophyll-*a* and of water column light utilization efficiency) to very low levels in the Suisun Bay region and the lower Delta (Jassby et al. 2002). Jassby et al. (2002) detected a 47% decline in June–November chlorophyll-*a* and a 36% decline in June–November primary production between the periods 1975–1985 and 1986–1995. Jassby (2008) updated the phytoplankton analysis to include the more recent data (1996–2005) from the Delta and Suisun Bay. Jassby (2008) confirmed a long-term decline in chlorophyll-*a* from 1975 to 2005 but also found that March–September chlorophyll-*a* had an increasing trend in the Delta from 1996 to 2005. Suisun Bay did not exhibit any trend during 1996–2005. A similar pattern was noted for primary production in the Delta. These chlorophyll-*a* patterns continued to hold through 2008 according to a more recent study by Winder and Jassby (2011). In the most recent decade (2003-2012), the median chlorophyll-*a* concentration across all IEP EMP stations was 2 ug/L (n = 2620, IQR = 2 ug/L), compared to the 1975-2002 median chlorophyll-*a* concentration of 3 ug/L (n = 10862, IQR = 6 ug/L) (Fig. 32). Most of the decrease was due to declines during May-October and especially the near-elimination of the formerly common "spring bloom" of phytoplankton in May (Fig. 32). In summary, phytoplankton biomass and production in the Delta and Suisun Bay seem to have reached a low point by the end of the 1987–1994 drought. While they recovered somewhat in the Delta, chlorophyll-*a* stayed consistently low in Suisun Bay through the POD years.

Figure 32. **Interquartile ranges (boxes) and medians (lines) for chlorophyll-*a* measured monthly at all IEP EMP stations from 1975-2002 (blue) and 2003-2012 (red). Data from http://www.water.ca.gov/bdma/.**



A major reason for the long-term phytoplankton reduction in the upper SFE after 1985 is benthic grazing by the invasive overbite clam (*Potamocorbula amurensis* also known as *Corbula amurensis*) (Alpine and Cloern 1992), which became abundant by the late 1980s (Kimmerer 2002). The overbite clam was first reported from San Francisco Estuary in 1986 and it was well established by 1987 (Carlton et al. 1990). Prior to the overbite clam invasion, the invasive Asiatic freshwater clam (*Corbicula fluminea*) (introduced in the 1940s) colonized Suisun Bay during high flow periods and the estuarine clam *Mya arenaria* (also known as *Macoma balthica*, an earlier introduction) colonized Suisun Bay during prolonged (> 14 month) low flow periods (Nichols et al. 1990). Thus, there were periods of relatively low clam grazing rates while one species was dying back and the other was colonizing, resulting in neither reaching high abundances. The *P. amurensis* invasion changed this formerly dynamic clam assemblage because *P. amurensis*, which is tolerant of a wide range of salinity, can maintain large, permanent populations in the brackish water regions of the estuary. *P. amurensis* biomass and grazing usually increase from spring to fall which contributes to the reduction in phytoplankton biomass from May to October relative to historical levels. In addition, the grazing influence of *P. amurensis* extends into the freshwater Delta beyond the clam's typical brackish salinity range, presumably due to tidal dispersion of phytoplankton-depleted water between regions of brackish water and fresh water (Kimmerer and Orsi 1996, Jassby et al. 2002).

Phytoplankton production in the SFE has been considered primarily light-limited because nutrient concentrations commonly exceed concentrations limiting primary production. According to some recent work, shifts in nutrient concentrations and ratios may, however, also contribute to the phytoplankton reduction and changes in algal species composition in the SFE. Nutrients may also play a larger role in regulating phytoplankton dynamics in the estuary as the estuary clears and light availability increases (see turbidity section above).

While phosphorus (total phosphorous and soluble reactive phosphorous) concentrations declined in the Delta and Suisun Bay region over the last few decades, nitrogen (total nitrogen and ammonium) concentrations increased. These changes have been attributed to the operation of the Sacramento Regional Wastewater Treatment Plant (SRWTP), a large secondary treatment facility that was completed in 1984 (VanNieuwenhuyse 2007, Jassby 2008). As stated previously, ammonia has two forms, un-ionized ammonia (NH_3) which is toxic to aquatic organisms and the ammonium ion (NH_4+) which is considerably less toxic to animals and an important nutrient for plants and algae (Thurston et al. 1981). Ammonia exists in equilibrium between the two forms dependent primarily on the pH of the water, but also temperature, with increases in pH and temperature favoring the un-ionized form (Thurston et al. 1981). Dugdale et al. (2007) and Wilkerson et al. (2006) found that high ammonium concentrations prevented the formation of diatom blooms but stimulated flagellate blooms in the lower estuary. They propose that this occurs because diatoms preferentially utilize ammonium in their physiological processes even though it is used less efficiently and at high concentrations ammonium can prevent uptake of nitrate (Dugdale et al. 2007). Thus, diatom populations must consume available ammonium before nitrate, which supports higher growth rates, can be utilized or concentrations of ammonium need to be diluted. A recent independent review panel (Reed et al. 2014) found that there is good evidence for preferential uptake of ammonium and sequential uptake of first ammonium and then nitrate, but that a large amount of uncertainty remains regarding the growth rates on ammonium relative to nitrate and the role of ammonium in suppressing spring blooms.

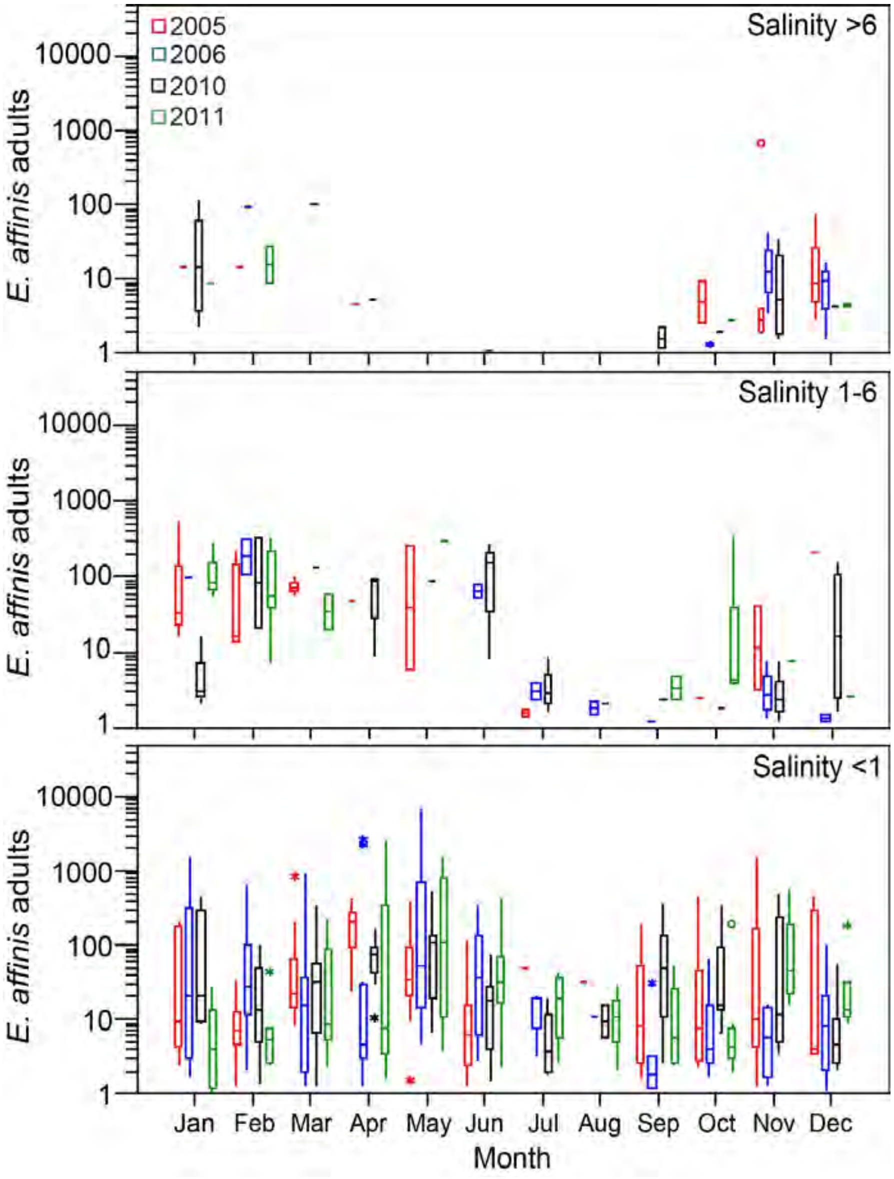
Glibert (2012) analyzed long-term data (from 1975 or 1979 to 2006 depending on the variable considered) from the Delta and Suisun Bay and related changing forms and ratios of nutrients, particularly changes in ammonium, to declines in diatoms and increases in flagellates and cyanobacteria. Similar shifts in species composition were noted by Brown (2009), with loss of diatom species, such as *Thalassiosira sp*., an important food for calanoid copepods, including *Eurytemora affinis* and *Sinocalanus doerri* (Orsi 1995). More recently, Parker et al. (2012) found that the region where blooms are suppressed extends upstream into the Sacramento River to the SRWTP, the source of the majority of the ammonium in the river (Jassby 2008). Parker et al. (2012) found that at high ambient ammonium concentrations, river phytoplankton cannot efficiently take up any form of nitrogen including ammonium, leading to often extremely low biomass in the river. A study using multiple stable isotope tracers (Lehman et al. 2014) found that the cyanobacteria *M. aeruginosa* utilized ammonium, not nitrate, as the primary source of nitrogen in the central and western Delta. In 2009, the ammonia concentration in effluent from SRWTP was reduced by approximately 10%, due to changes in operation (K. Ohlinger, Sacramento Regional County Sanitation District, personal communication). In spring 2010 unusually strong spring diatom blooms were observed in Suisun Bay that co-occurred with low ammonia concentrations (Dugdale et al. 2013).

Jassby (2008) suggested the following comprehensive explanation for his observations. Phytoplankton production in the lower Delta is associated with flow and residence time; however, other factors introduce a substantial degree of interannual variability. Benthic grazing by *C. fluminea* is likely a major factor as grazing can exceed rates of primary production (Lucas et al. 2002, Lopez et al. 2006) and are abundant year round at some locations in the Delta (Fuller 2012). Current data are inadequate to estimate the overall magnitude of the grazing effect of *C. fluminea*. In Suisun Bay, benthic grazing by *P. amurensis* is a controlling factor that keeps phytoplankton at low levels. Thus, metazoan populations in Suisun Bay are dependent on importation of phytoplankton production from the upstream portions of the Delta. Upstream Delta phytoplankton can be lost via exports and within-Delta depletion; Cloern and Jassby (2012) reported phytoplankton losses equivalent to 30% of the primary production in the Delta. Ammonium concentrations and water clarity have increased; however, these two factors should have opposing effects on phytoplankton production. These factors likely also contribute to variability in the interannual pattern but the relative importance of each is unknown. The interactions among primary production, grazing, and transport time can be complex (Lucas et al. 2002, 2009a,b, Lucas and Thompson 2012).

The changes in phytoplankton production and invasion and establishment of the overbite clam *P. amurensis* were also accompanied by a series of major changes in consumers (Winder and Jassby 2011). Many of these changes likely negatively influenced pelagic fish production, including Delta Smelt. The quantity of food available to Delta Smelt is a function of several factors, including but not limited to seasonal trends in prey abundance and prey species specific salinity tolerances, which influence distribution (Kimmerer and Orsi 1996, Hennessy and Enderlein 2013). Seasonal peaks in abundance vary among calanoid copepods consumed as prey by Delta Smelt, *E. affinis* in April-May (Fig. 33), *P. forbesi* in July (Fig. 34), and *A. sinensis* in Sep-Oct (Fig. 35). Upstream, the calanoid copepod *S. doerrii* is most abundant May-June (Fig. 36). The seasonal trend in cladocerans (Fig. 37) and mysid (Fig. 38) prey are similar, being most abundant in summer.

From March through June, larval Delta Smelt rely heavily on first juvenile, then adult stages of the calanoid copepods *Eurytemora affinis* and *Pseudodiaptomus forbesi*, as well as cladocerans (Nobriga 2002, Hobbs et al. 2006, Slater and Baxter 2014), and *Sinocalanus doerrii* (Fig. 39). Nobriga (2002) found that Delta Smelt larvae expressed positive selection for *E. affinis* and *P. forbesi*, consuming these prey species in greater proportion than available in the environment. Such selection was not noted for other zooplankton prey. Regional differences in food use occur,

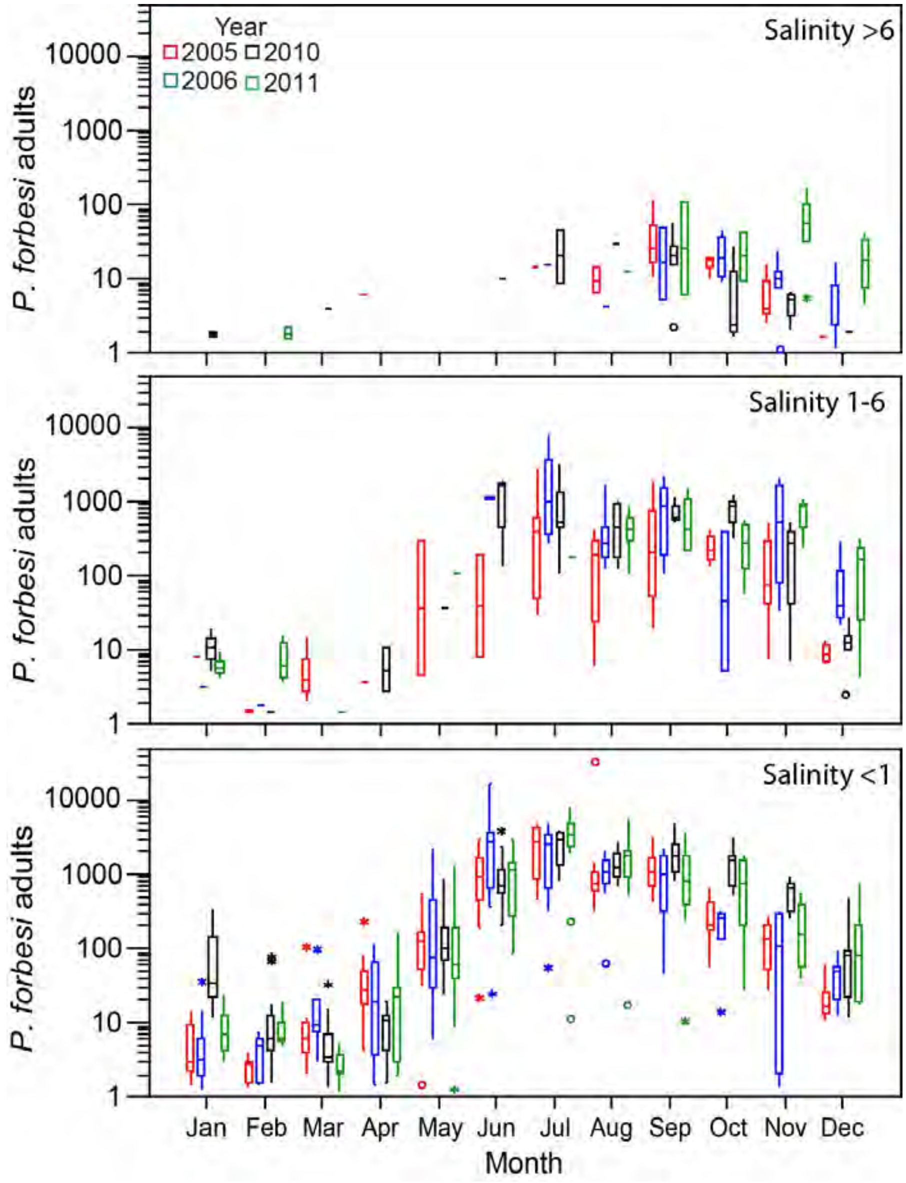
Figure 33. **Density (number/m^3) of adult *Eurytemora affinis* (*E. affinis*) by month for three salinity ranges. Each month 16 stations were sampled across all salinity ranges. Horizontal lines represent single samples within a salinity range and boxes without whiskers indicate 2 samples within a salinity range. Data from the IEP Zooplankton Study index stations. See Chapter 3: Data Analyses for explanation of boxplots.**



with *E. affinis* and *P. forbesi* being major prey items downstream in the LSZ with a transition to *S. doerrii* and cyclopoid copepods as major prey items upstream into the Cache Slough-Sacramento River Deepwater Ship Channel (CS-SRDWSC) (Fig. 39).

Juvenile Delta Smelt (June-September) rely extensively on calanoid copepods such as *E. affinis* and *P. forbesi*, especially in freshwater (salinity < 1) and CS-SRDWSC but there is great variability among regions (figs. 40-43). Larger fish are also able to take advantage of mysids,

Figure 34. Density (number/m^3) of adult *Pseudodiaptomus forbesi* (*P. forbesi*) by month for three salinity ranges. Each month 16 stations were sampled across all salinity ranges. Horizontal lines represent single samples within a salinity range and boxes without whiskers indicate 2 samples within a salinity range. Data from the IEP Zooplankton Study index stations. See Chapter 3: Data Analyses for explanation of boxplots.



cladocerans, and amphipods (Moyle et al. 1992, Lott 1998, Feyrer et al. 2003, Steven Slater, California Department of Fish and Wildlife, unpublished data) (Figs. 34-37). The presence of several epibenthic species in diets therefore indicates that food sources for this species are not confined to pelagic pathways. Such food sources may be especially important in regions of the estuary where there is extensive shoal habitat such as Liberty Island (Steven Slater, California Department of Fish and Wildlife, unpublished data).

Figure 35. **Density (number/m³) of adult *Acartiella sinensis* (*A. sinensis*) by month. Each month 16 stations were sampled across all salinity ranges. Horizontal lines represent single samples within a salinity range and boxes without whiskers indicate 2 samples within a salinity range. Data from the IEP Zooplankton Study index stations. See Chapter 3: Data Analyses for explanation of boxplots.**

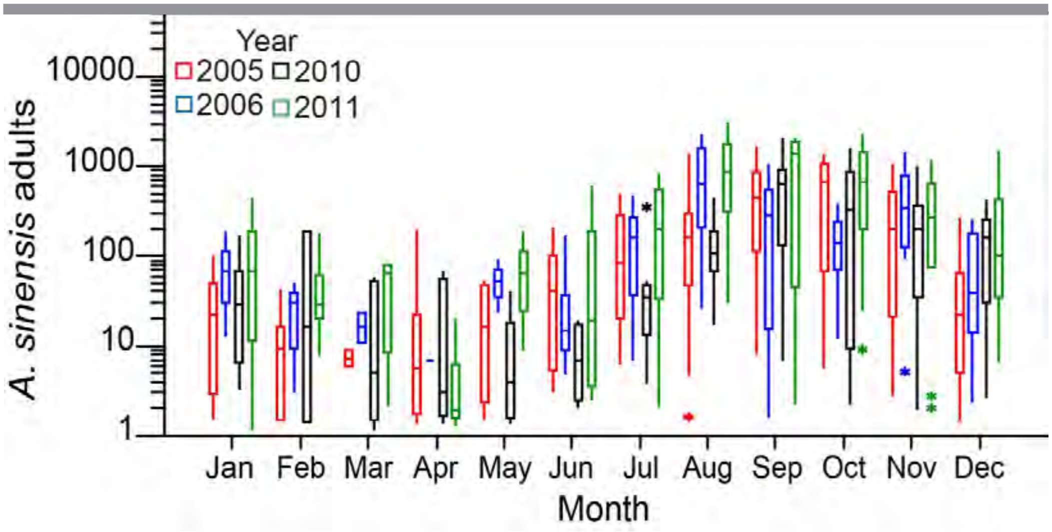
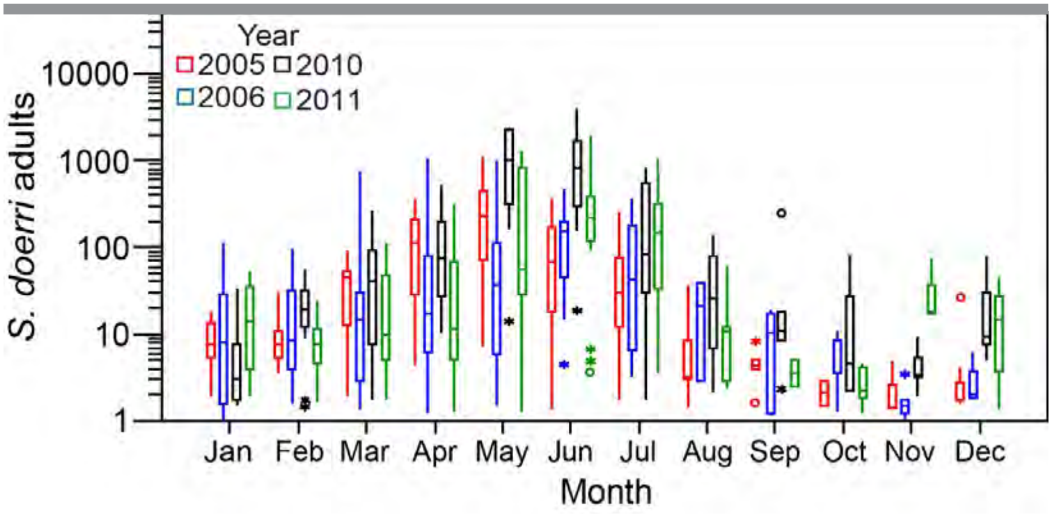


Figure 36. **Density (number/m³) of adult *Sinocalanus doerrii* (*S. doerri*) by month. Each month 16 stations were sampled across all salinity ranges. Horizontal lines represent single samples within a salinity range and boxes without whiskers indicate 2 samples within a salinity range. Data from the IEP Zooplankton Study index stations. See Chapter 3: Data Analyses for explanation of boxplots.**



Subadult Delta Smelt (September through December) prey items are very similar to those of juvenile Delta Smelt but with increased variability in diet composition (Moyle et al. 1992, Lott 1998, Steven Slater, California Department of Fish and Wildlife, unpublished data) (Figs. 40-43) coinciding with the seasonal decline in pelagic zooplankton, such as *P. forbesi* (Fig. 34) and mysids (Fig. 38). Food habits of adult Delta Smelt during the winter and spring (January-May) have been less well documented (Moyle et al. 1992). In 2012, diet of adults in the LSZ and

Figure 37. Density (number/m^3) of all cladoceran taxa by month. Each month 16 stations were sampled across all salinity ranges. Horizontal lines represent single samples within a salinity range and boxes without whiskers indicate 2 samples within a salinity range. Data from the IEP Zooplankton Study index stations. See Chapter 3: Data Analyses for explanation of boxplots.

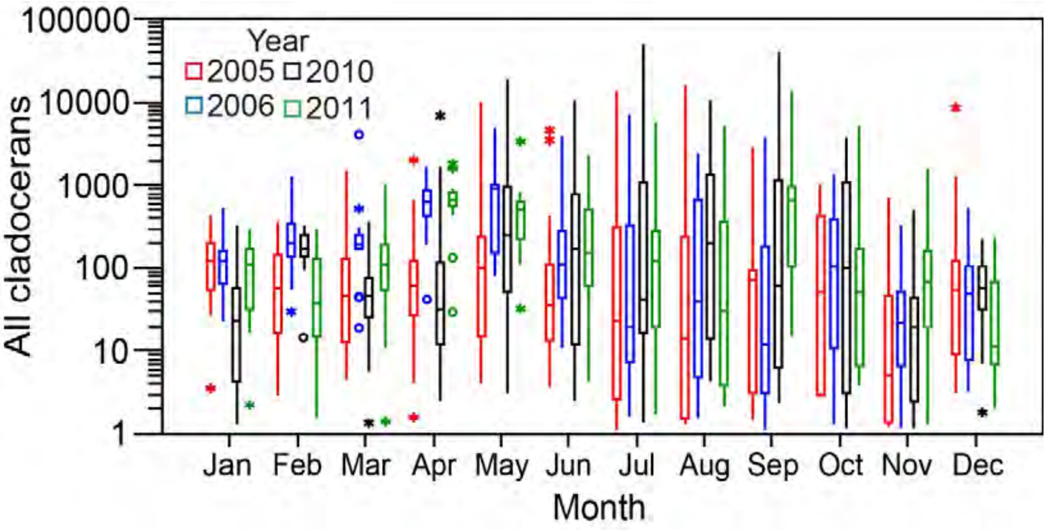
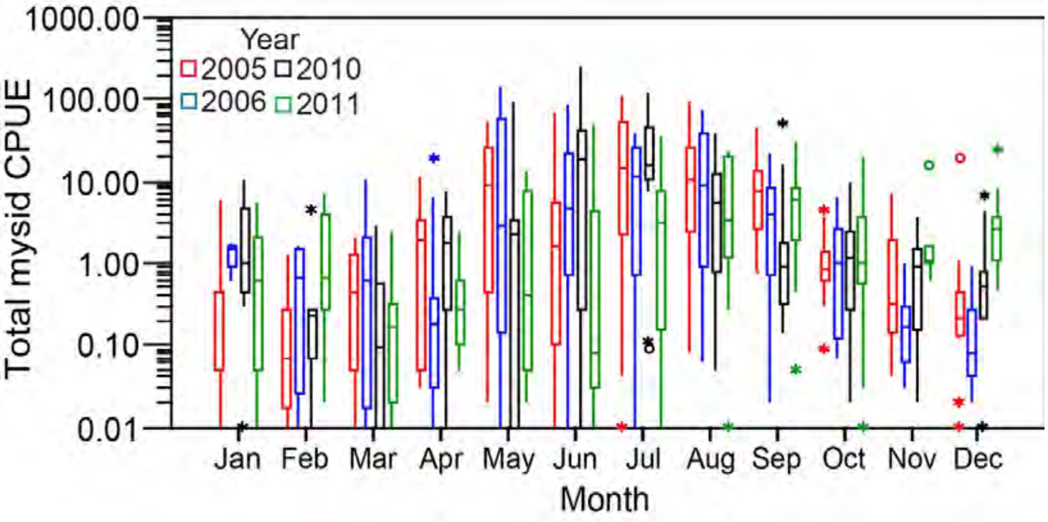


Figure 38. Density (number/m^3) of all mysid shrimp taxa by month. Each month 16 stations were sampled across all salinity ranges. Horizontal lines represent single samples within a salinity range and boxes without whiskers indicate 2 samples within a salinity range. Data from the IEP Zooplankton Study index stations. See Chapter 3: Data Analyses for explanation of boxplots.



< 1 ppt were found to include cyclopoid copepods, other than *Limnoithona* spp., with a mix of larger prey types, amphipods, cladocerans, cumaceans, and larval fish and in CS-SRDWSC the calanoid copepod *S. doerrii* continued to be a large portion of the diet (Steven Slater, California Department of Fish and Wildlife, unpublished data) (Fig. 44). Larval fish found in stomachs of Delta Smelt in the higher salinity areas were primarily Pacific Herring (*Clupea pallasii*), with

some Longfin Smelt, and Prickly Sculpin (*Cottus asper*) in the Sacramento River and CS-SRDWSC region; no Delta Smelt larvae were found in the stomachs of adults (Steven Slater, California Department of Fish and Wildlife, unpublished data).

The large proportion of benthic amphipods, cumaceans, and some cladocerans (*Camptocercus* spp.) in the diet is a notable change from Delta Smelt diet in the 1970s. Delta Smelt diets historically did include amphipods, notably *Corophium* spp. (Moyle et al. 1992), yet it was a small fraction of a mostly pelagic based diet. The considerable use of benthic invertebrates for food in recent years is believed to be in large part due to food limitation associated with the long-term decline and changes in composition of the pelagic food web (Slater and Baxter 2014). The quality of benthic invertebrates as food is not currently understood, but amphipods are lower in energy (calories per gram) than copepods (Cummins and Wuychek 1971, Davis 1993) and mysids (Davis 1993).

As noted previously, the changes in phytoplankton production and phytoplankton species abundances observed and the invasion of *P. amurensis* may have had important consequences for consumer species preyed upon by Delta Smelt. For example, there has been a decrease in mean zooplankton size (Winder and Jassby 2011) and a long-term decline in calanoid copepods, including a major step-decline in the abundance of the copepod *E. affinis*. These changes are possibly due to predation by the overbite clam (Kimmerer et al. 1994) or indirect effects of clam grazing on copepod food supply. Predation by *P. amurensis* may also have been important for other zooplankton species (Kimmerer 2008). Northern Anchovy *Engraulis mordax* abandoned the low salinity zone coincident with the *P. amurensis* invasion, presumably because the clam reduced planktonic food abundance to the point that occupation of the low-salinity waters was no longer energetically efficient for this marine fish (Kimmerer 2006). Similarly, Longfin Smelt *Spirinchus thaleichthys* shifted its distribution toward higher salinity in the early 1990s, also presumably because of reduced pelagic food in the upper estuary (Fish et al. 2009). There was also a decline in mysid shrimp (Winder and Jassby 2011), including a major step-decline in 1987–1988, likely due to competition with the overbite clam for phytoplankton (Orsi and Mecum 1996). Mysid shrimp had been an extremely important food item for larger fishes like Longfin Smelt and juvenile Striped Bass (Orsi and Mecum 1996), and may be consumed by larger Delta Smelt (Moyle et al. 1992). The decline in mysids was associated with substantial changes in the diet composition of these and other fishes, including Delta Smelt (Feyrer et al. 2003, Bryant and Arnold 2007). The population responses of Longfin Smelt and juvenile Striped Bass to winter–spring outflows changed after the *P. amurensis* invasion. Longfin Smelt relative abundance was lower per unit outflow after the overbite clam became established (Kimmerer 2002b). Age-0 Striped Bass relative abundance stopped responding to outflow altogether (Sommer et al. 2007). One hypothesis to explain these changes in fish population dynamics is that lower prey abundance reduced the system carrying capacity (Kimmerer et al. 2000, Sommer et al. 2007).

In addition to a long-term decline in calanoid copepods and mysids in the upper Estuary, there have been numerous copepod species introductions (Winder and Jassby 2011). *P. forbesi*, a calanoid copepod that was first observed in the estuary in the late 1980s, has replaced *E. affinis* as the most common Delta Smelt prey during the summer. It may have a competitive advantage over *E. affinis* due to its more selective feeding ability. Selective feeding may allow *P. forbesi* to utilize the remaining high-quality algae in the system while avoiding increasingly more prevalent low-quality and potentially toxic food items such as *M. aeruginosa* (Mueller-Solger et al. 2006, Ger et al. 2010a). After an initial rapid increase in abundance, *P. forbesi* declined somewhat in abundance from the early 1990s in the Suisun Bay and Suisun Marsh regions but maintained its abundance, with some variability, in the central and southern Delta (Winder and Jassby 2011).

Figure 39. **Percentage by weight of prey types found in the digestive tracts of larval and young juvenile Delta Smelt (≤ 20 mm fork length) collected from 1-6 ppt, < 1 ppt, and Cache Slough-Sacramento River Deepwater Ship Channel (CS-SRDWSC) in A) 2005, B) 2006, C) 2010, and D) 2011. Number of digestive tracts examined are shown above the columns. Mean fork length (mm) of Delta Smelt is also shown.**

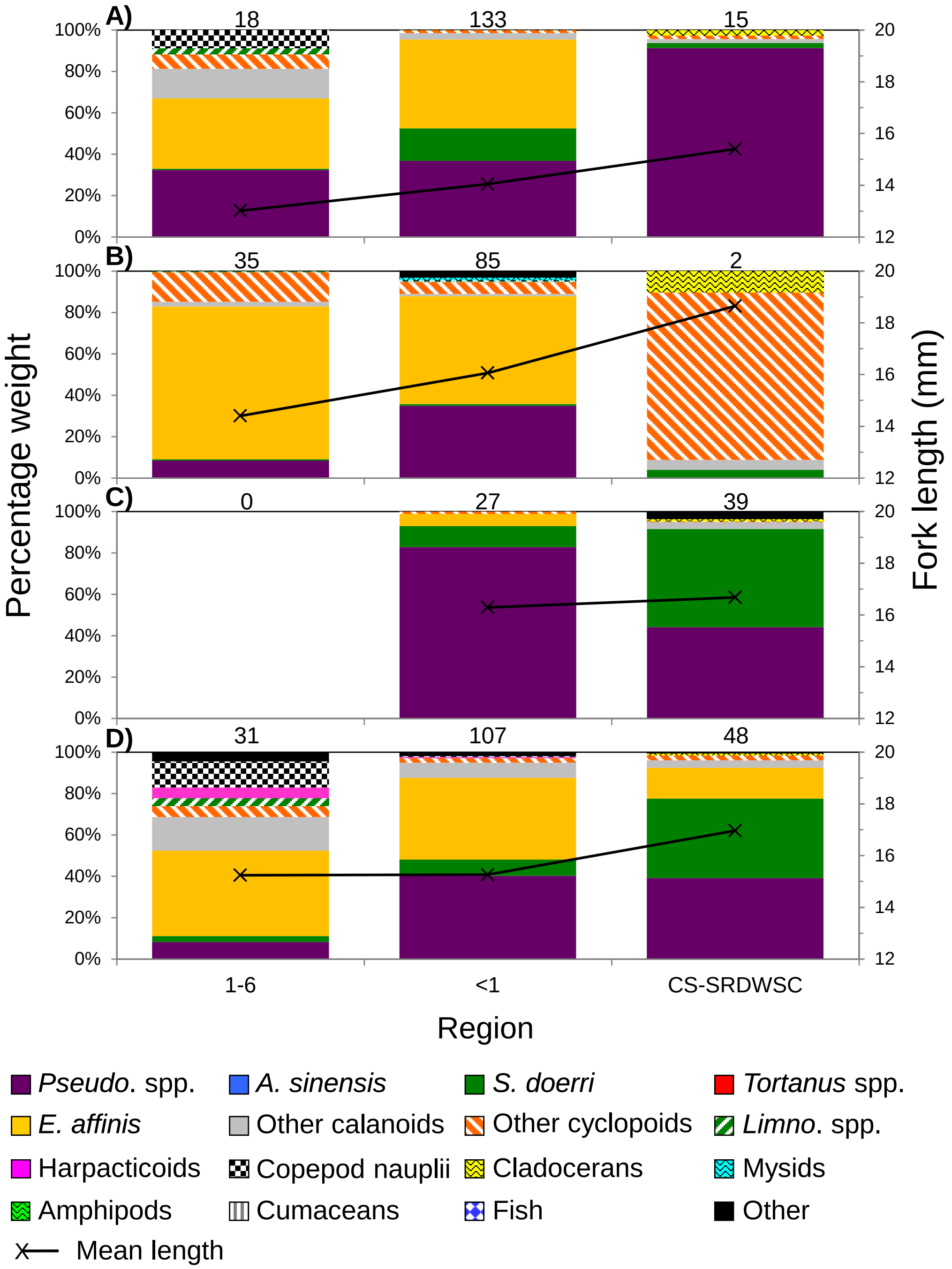


Figure 40. **Percentage by weight of prey types found in stomachs of age-0 Delta Smelt collected from > 6 ppt during April through December in A) 2005, B) 2006, C) 2010, and D) 2011. Number of stomachs examined are shown above the columns. One fish examined in August 2006 had an empty stomach. Mean fork length (mm) of Delta Smelt is also shown.**

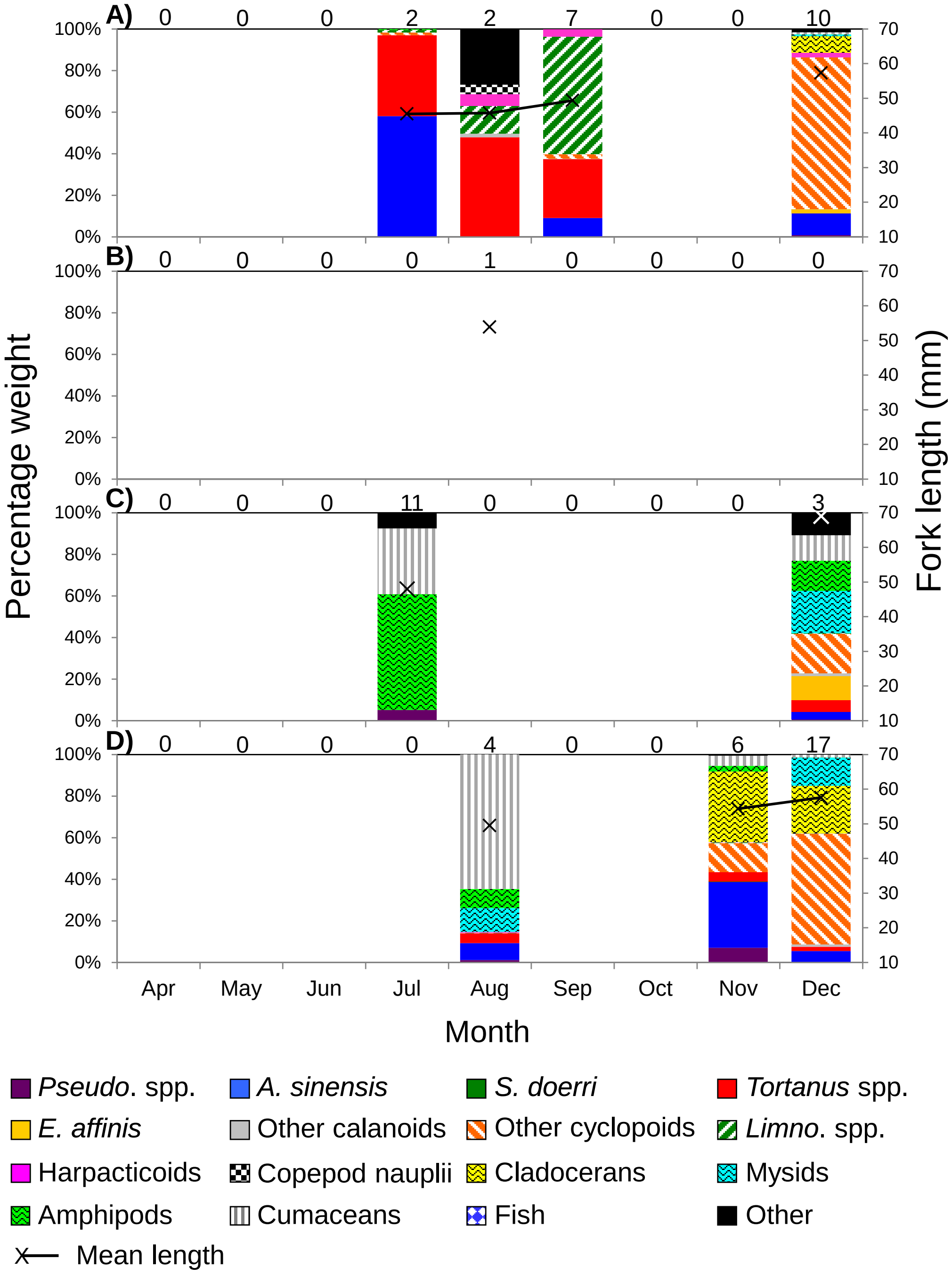


Figure 41. **Percentage by weight of prey types found in stomachs of age-0 Delta Smelt collected from 1-6 ppt during April through December in A) 2005, B) 2006, C) 2010, and D) 2011. Number of stomachs examined are shown above the columns. Mean fork length (mm) of Delta Smelt is also shown.**

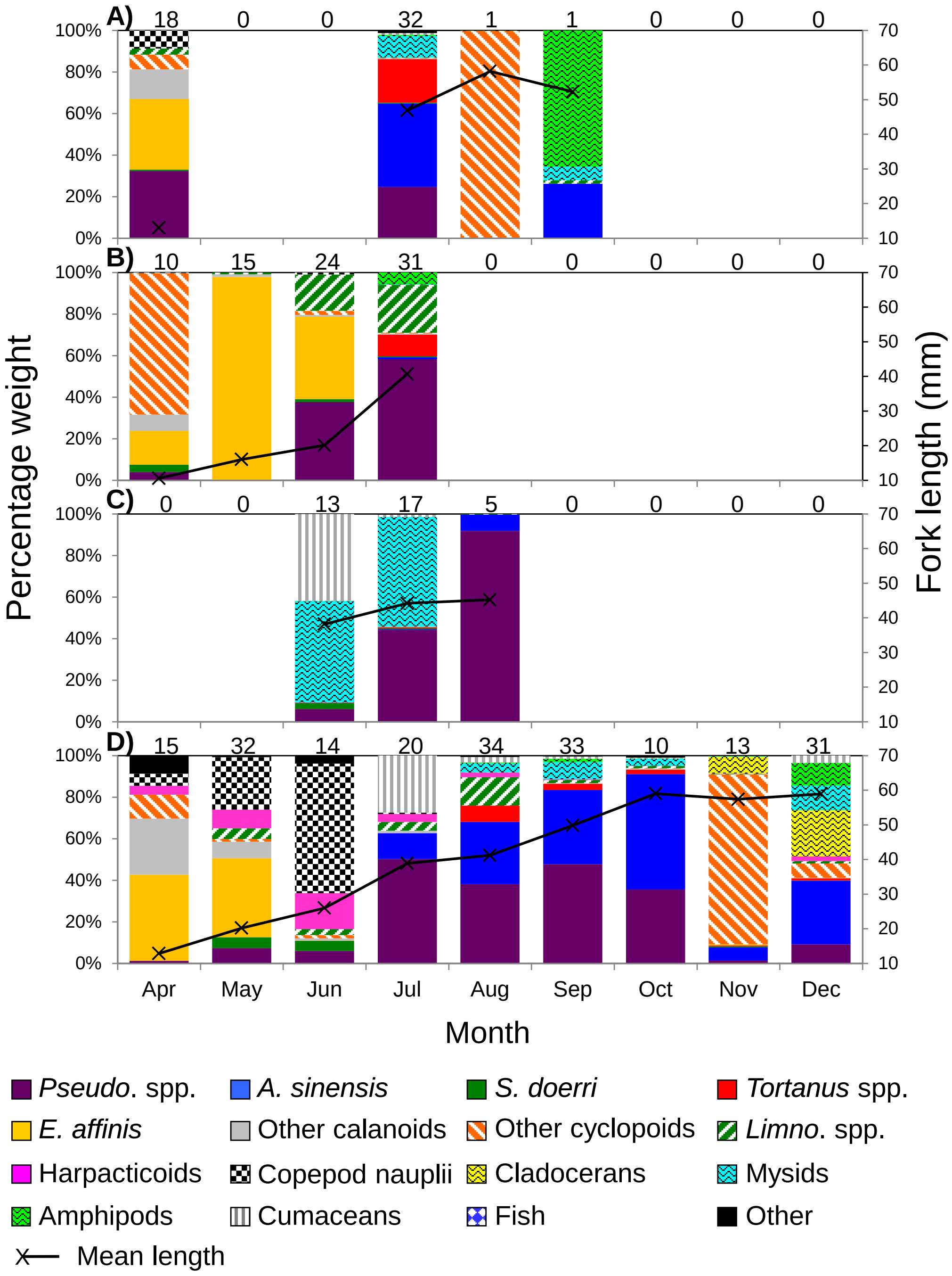


Figure 42. **Percentage by weight of prey types found in stomachs of age-0 Delta Smelt collected from < 1 ppt during April through December in A) 2005, B) 2006, C) 2010, and D) 2011. Number of stomachs examined are shown above the columns. Mean fork length (mm) of Delta Smelt is also shown.**

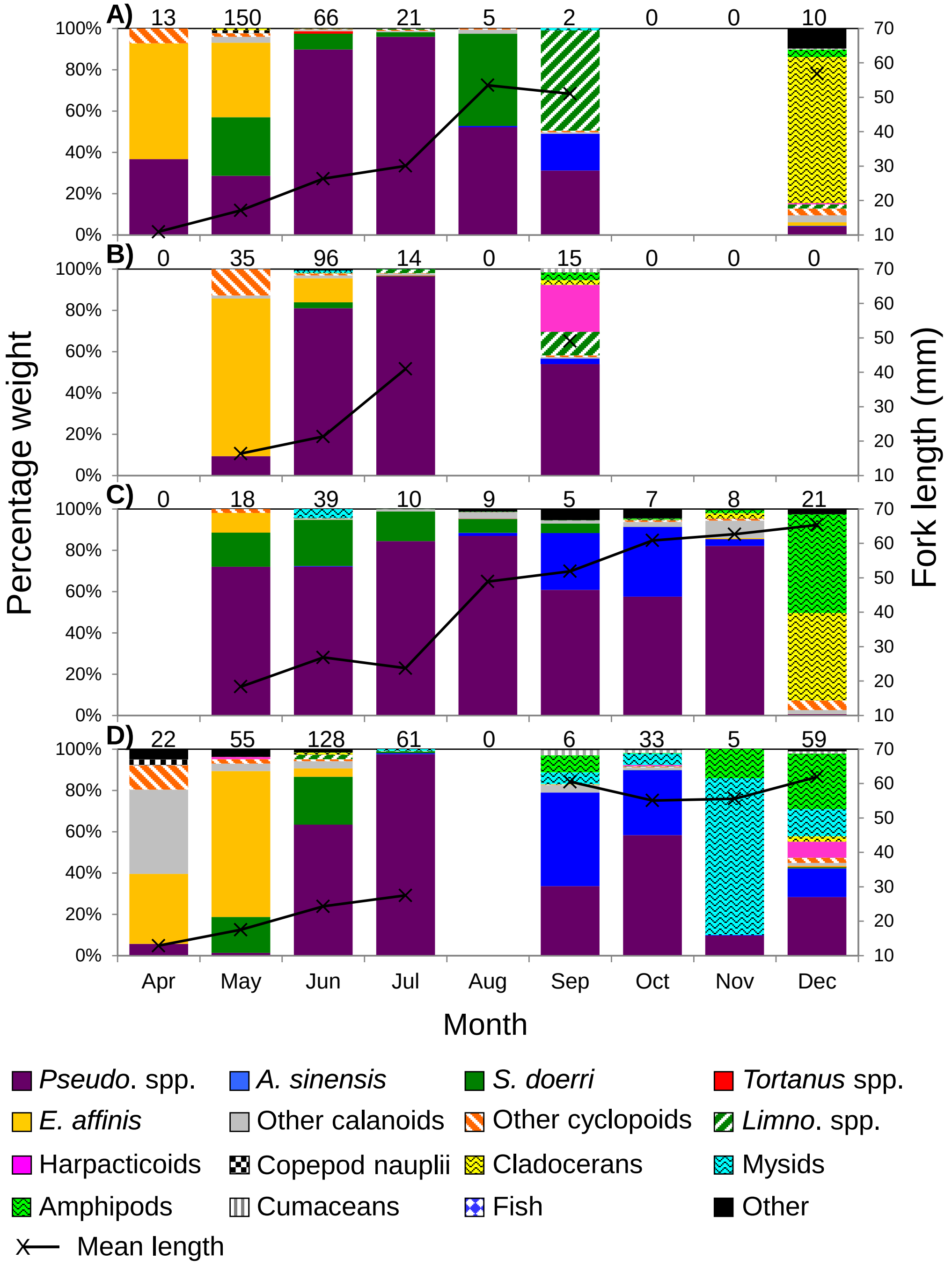


Figure 43. **Percentage by weight of prey types found in stomachs of age-0 Delta Smelt collected from Cache Slough-Sacramento River Deepwater Ship Channel (CS-SRDWSC) during April through December in A) 2005, B) 2006, C) 2010, and D) 2011. Number of stomachs examined are shown above the columns. Mean fork length (mm) of Delta Smelt is also shown.**

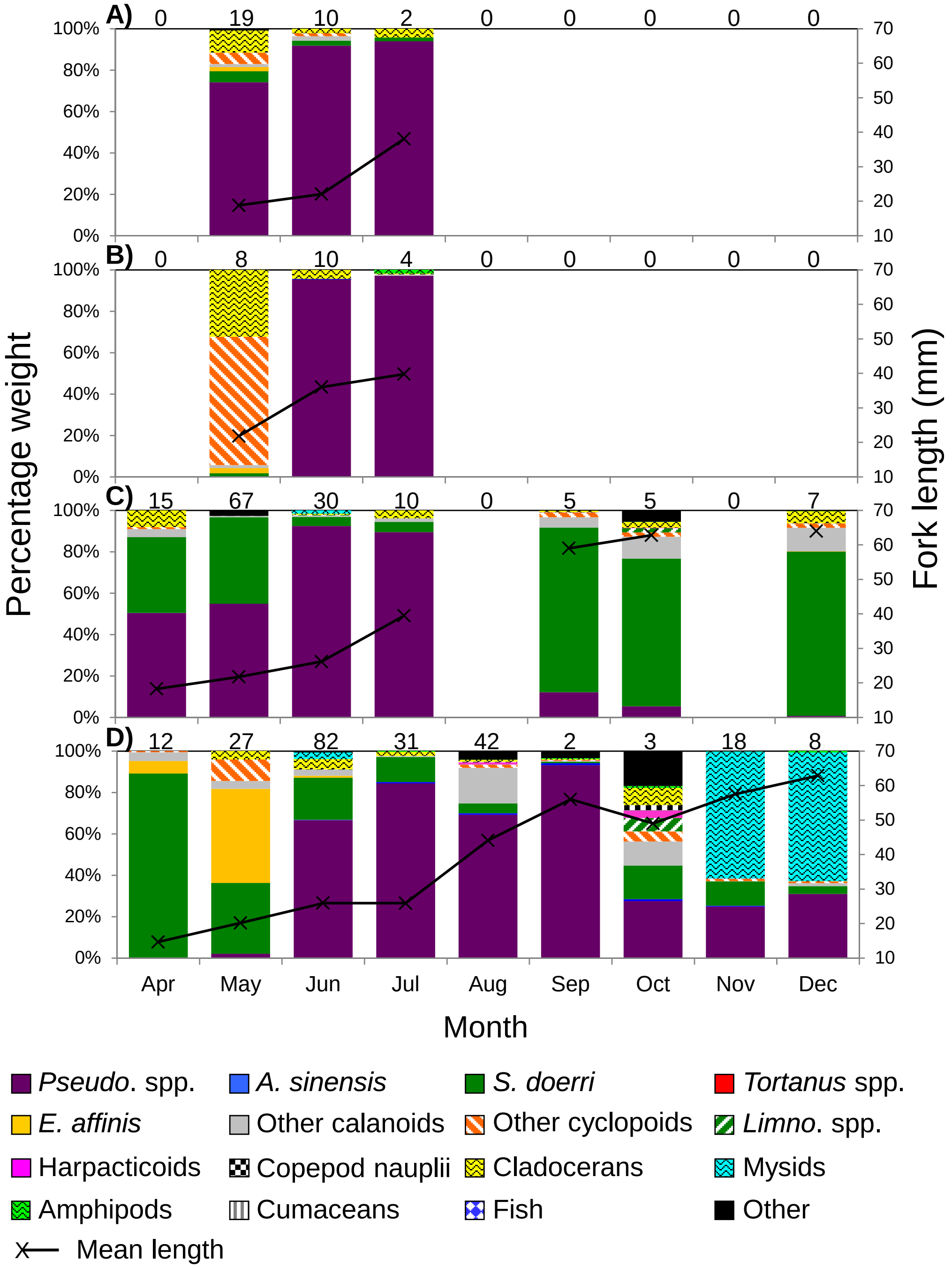
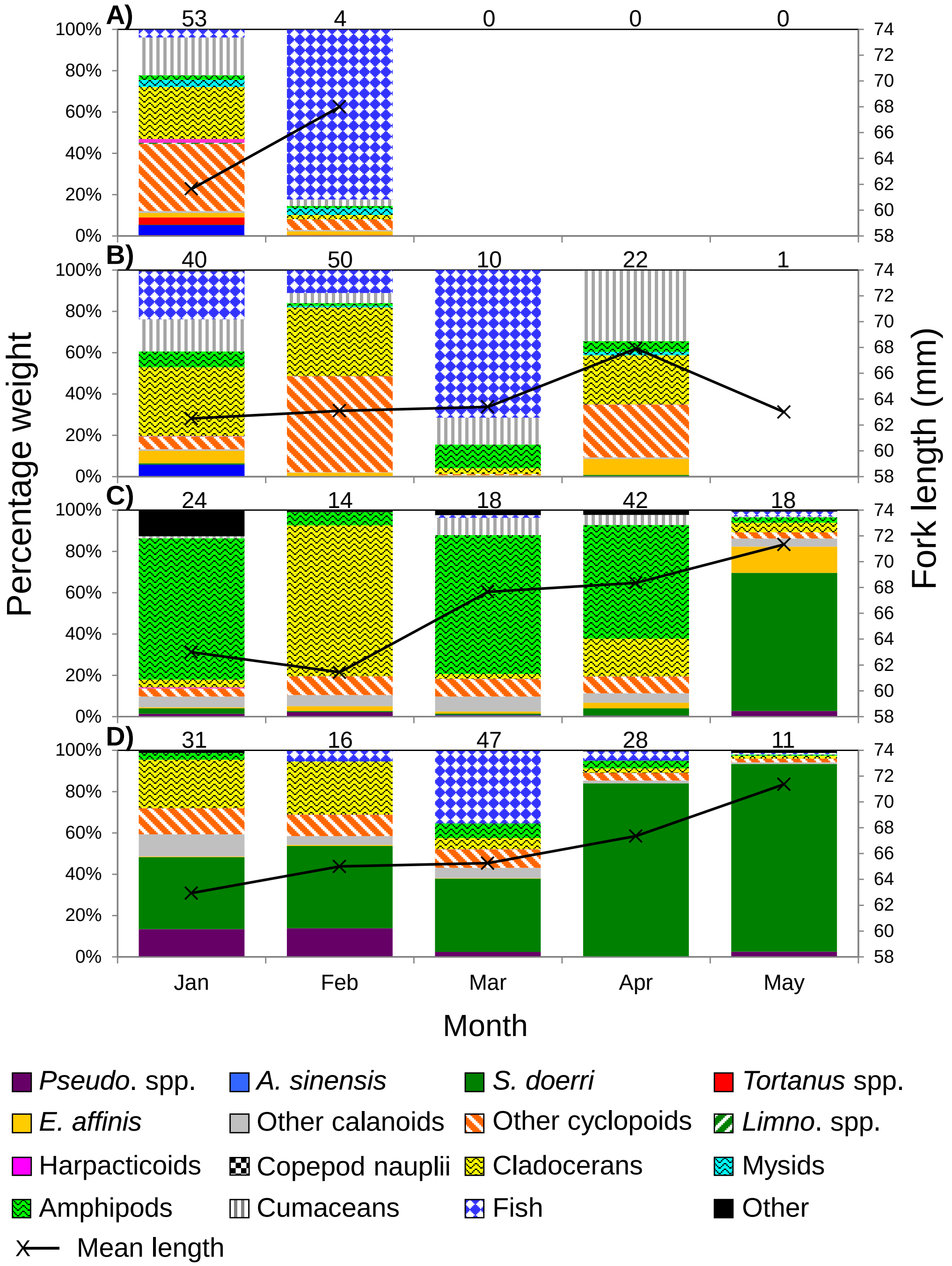


Figure 44. **Percentage by weight of prey types found in stomachs of adult Delta Smelt collected in 2012 during January through May from A) > 6 ppt, B) 1-6 ppt, C) < 1 ppt, and D) Cache Slough-Sacramento River Deepwater Ship Channel (CS-SRDWSC). Number of stomachs examined are shown above the columns. One fish examined from 1-6 ppt in May had an empty stomach. Mean fork length (mm) of Delta Smelt is also shown.**



Although substantial uncertainties about mechanisms remain, the decline of *P. forbesi* in the Suisun region may be related to increasing recruitment failure and mortality in this region due to competition and predation by *P. amurensis*, contaminant exposures, and entrainment of source populations in the Delta (Mueller-Solger et al. 2006, Winder and Jassby 2011, Durand 2010).

The abundance of a more recent invader, the cyclopoid copepod *Limnoithona tetraspina*, significantly increased in the Suisun Bay region beginning in the mid-1990s. It is now the most abundant copepod species in the Suisun Bay and confluence region of the estuary (Bouley and Kimmerer 2006, Winder and Jassby 2011). Gould and Kimmerer (2010) found that it grows slowly and has low fecundity. Based on these findings they concluded that the population success of *L. tetraspina* must be due to low mortality and that this small copepod may be able to avoid visual predation to which larger copepods are more susceptible. It has been hypothesized that *L. tetraspina* is an inferior food for pelagic fishes including Delta Smelt because of its small size, generally sedentary behavior, and ability to detect and avoid predators (Bouley and Kimmerer 2006, Gould and Kimmerer 2010). Nevertheless, this copepod has been found in the guts of Delta Smelt when *Limnoithona* spp. occurrs at extremely high densities relative to other zooplankton (Slater and Baxter 2014). Recent experimental studies addressing this issue suggest that larval Delta Smelt will consume and grow on *L. tetraspina*, but growth is slower than with *P. forbesi* (Kimmerer et al. 2011). It remains unclear if consuming this small prey is energetically beneficial for Delta Smelt at all sizes or if there is a breakpoint above which larger Delta Smelt receive little benefit from such prey. *Acartiella sinensis*, a calanoid copepod species that invaded at the same time as *L. tetraspina*, also reached considerable densities in Suisun Bay and the western Delta over the last decade (Hennessy 2010), although its suitability as food for pelagic fish species remains unclear.

Preliminary information from studies on pelagic fish growth, condition, and histology provide additional evidence for food limitation in pelagic fishes in the estuary (IEP 2005). In 1999 and 2004, Delta Smelt growth was low from the Sacramento-San Joaquin confluence through Suisun Bay relative to other parts of the system. Delta Smelt collected in 2005 from the Sacramento-San Joaquin confluence and Suisun Bay also had high incidence of liver glycogen depletion, a possible indicator of food limitation (Bennett et al. 2008). As previously noted, warm water temperatures during the summer period may have exacerbated lack of food by raising the metabolic rate of Delta Smelt. Based on data for histopathology, date of birth from otoliths, and growth rates from otoliths of Delta Smelt in 2005, Bennett et al. (2008) proposed a novel strategy for Delta Smelt survival in 2005. Natural selection appeared to favor individuals with a specific set of characters, including relatively slow larval development, but faster than average juvenile growth in July. Water temperatures in July typically include the annual maximum (Fig. 16). The salinity field can also change rapidly as freshwater flow out of the Delta changes. Many of these fish surviving into the pre-adult stage had also hatched earlier in the spawning season (i.e., before May).

For many fishes, success at first feeding is believed to be critical to larval survival and a major cause of year-class variability (e.g., “critical period hypothesis,” Hjort 1914, Leggett and DeBlois 1994). In Rainbow Smelt *Osmerus mordax* a related smelt species, calculated larva mortality rates were related to feeding conditions at first feeding that varied on a predictable cycle of 15 days associated with tide and photoperiod (Sirois and Dodson 2000b). In feeding experiments, copepod evasion behavior affected capture by larval Striped Bass, and *E. affinis* was among the more easily captured species (Meng and Orsi 1991). There has been a long-term decline in calanoid copepods in the upper estuary, particularly in the Suisun Region (Winder and Jassby 2011), potentially reducing feeding success, growth and thereby survival. Currently, *E. affinis* abundance peaks in spring (Hennessy 2010, 2011) coincident with hatching of Delta Smelt. *E. affinis* abundance has been negatively related to X2 since the overbite clam invasion (Kimmerer 2002b). When X2 is “high” outflow is low and *E. affinis* densities are low. These lines of evidence suggest that the first feeding conditions may improve in springs with higher outflow.

Changes in the quality and quantity of available prey may have contributed to the observed reduction in the mean size of Delta Smelt in fall since the early 1990s (Sweetnam 1999, Bennett 2005); however, mean size subsequently increased. The importance of food resources as a driver is supported by Kimmerer (2008), who showed that Delta Smelt survival from summer to fall is correlated with biomass of copepods in the low salinity zone, the central 50% of the summer Delta Smelt distribution. Other variations of this correlation were shown by Maunder and Deriso (2011) and Miller et al. (2012). Miller et al. (2012) have tested for an explicit influence of prey density during the fall. Miller et al. (2012) found a stronger correlation between Delta Smelt abundance during the fall and prey density during the fall than for prey density during the summer.

Harmful algal blooms

Periodic blooms of the toxic blue-green alga *Microcystis aeruginosa* during late summer, most commonly August and September are an emerging concern for Delta Smelt (Lehman et al. 2005, Lehman et al. 2013). Although this harmful algal bloom (HAB) typically occurs in the San Joaquin River away from the core summer distribution of Delta Smelt, some overlap is apparent during blooms and as cells and toxins are dispersed downstream after blooms (Baxter et al. 2010). Density rankings of *Microcystis* at TNS stations were highest in the south Delta, east Delta and lower San Joaquin River regions; yet *Microcystis* distribution may be expanding north over time (Morris 2013). Moreover, studies by Lehman et al. (2010) suggest that Delta Smelt likely are exposed to microcystins, which may degrade their habitat and perhaps affect the distribution of Delta Smelt (Baxter et al. 2010). For example, these HABs are known to be toxic to another native fish of the region, Sacramento Splittail (Acuña et al. 2012a) and the alien Threadfin Shad (Acuña et al. 2012b). Histopathology evidence from Lehman et al. (2010) suggested the health of two common fish in the estuary, Striped Bass, and Mississippi Silversides, was worse at locations where microcystin concentrations were elevated.

Indirect effects are also likely as *Microcystis* blooms are toxic to copepods that serve as the primary food resources of Delta Smelt (Ger et al. 2009, 2010a,b). Ger et al. (2009) determined toxicity of one form of microcystin (LR) to two species of calanoid copepods, *E. affinis* and *P. forbesi*, which are important as food to Delta Smelt. They found that, although the copepods tested were relatively sensitive to microcystin-LR compared to other types of zooplankton, ambient concentrations in the Delta were unlikely to be acutely toxic. However, chronic effects were not determined and Lehman et al. (2010) found that *Microcystis* may indeed contribute to changes in phytoplankton, zooplankton and fish populations in the Delta.

Factors that are thought to cause more intensive *Microcystis* blooms include warmer temperatures, lower flows, high nitrogen levels, and relatively clear water (Lehman et al. 2005, Baxter et al. 2010, Lehman et al. 2013, Morris 2013). These conditions occur during dry years in the SFE. Both *Microcystis* abundance and microcystin concentrations have been greater in recent years with dry year conditions (Lehman et al. 2013). These factors can also interact. For example, low flows can provide less dilution of ammonium from wastewater treatment plants (Jassby and Van Nieuwenhuyse 2005, Dugdale et al. 2012, Dugdale et al. 2013) and *Microcystis* can readily utilize ammonium as a primary nitrogen source during blooms (Lehman et al. 2013). The intensity and duration of *Microcystis* blooms are expected to increase over the long-term, along with any negative impact on aquatic organisms, due to increased frequency of drought conditions associated with climate change (Lehman et al. 2013).

Chapter 5: Updated Conceptual Models for Delta Smelt

In this Chapter we transfer the information on drivers and Delta Smelt responses reviewed and presented in Chapter 4 into the conceptual model framework established in Chapter 3. The Delta Smelt general life cycle conceptual model recognizes the pervasive, year-round importance of the tier 1 landscape attributes and the seasonal importance of the various tier 2 environmental drivers and tier 3 habitat attributes to the tier 4 life stage transitions of Delta Smelt in the four tier 5 "transition seasons" (Fig. 45). Some habitat attributes – food, toxicity, and predation – affect life stage transitions in all seasons, while other habitat attributes – temperature, entrainment and transport, size and location of the low salinity zone, and harmful algal blooms – affect some life stage transition more than others. Clearly, adequate food must be available at all life stages for Delta Smelt to survive. Toxicity is included during all seasons because we know that contaminants of various types are present throughout the year; however, little is known about the direct or indirect effects of contaminants at ambient concentrations on individual Delta Smelt or the population as a whole. Predation is included in all seasons because we recognize that predation is likely the ultimate cause of mortality for most individual fish; however, responses of Delta Smelt to other habitat attributes and environmental drivers such as food availability and turbidity can modify predation risk.

The mechanistic linkages between landscape attributes, environmental drivers, habitat attributes and Delta Smelt responses in the four life stage seasons are depicted as one-way arrows in four new "life stage transition" conceptual models (Figs. 46-49). As mentioned in Chapter 3, the life stage transition conceptual models are nested components of the general life cycle conceptual model (Fig. 8). Each life stage transition conceptual model (Figs. 46-49) includes the habitat attributes hypothesized to affect the transition of Delta Smelt from one life-stage to the next. Hypotheses selected for detailed consideration in Chapter 7 are indicated by "H" in the diagrams. The models also show the landscape attributes and environmental drivers. While the models include many linkages among individual landscape attributes, environmental drivers, and habitat attributes, they do not include linkages between individual habitat attributes and the specific biological processes (growth, survival, reproduction) underlying the life stage transitions. The primary reason for this simplification is that the available data are generally inadequate to fully describe and differentiate among specific functional relationships and mathematical modeling that could help estimate them is beyond the scope of this report. Instead, the combined effects of all habitat attributes on the life stage transition probability are depicted by one upward arrow in each life stage transition conceptual model. This does not imply, however, that all habitat attributes have an equal role in determining life stage transition probability and population success or that the role of each habitat attribute remains constant from year to year.

In the remainder of this Chapter we briefly describe the linkages and associated hypotheses depicted in each of the life stage transition conceptual model diagrams (figs. 46-49). These

Figure 45. Delta Smelt general life cycle conceptual model.

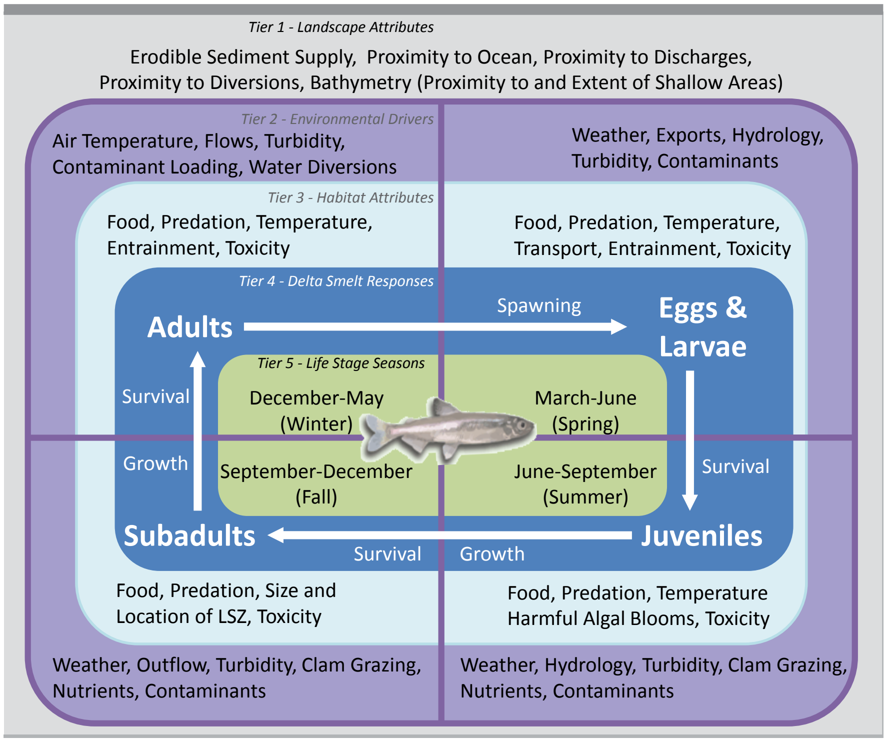


Figure 46. Conceptual model of drivers affecting the transition from Delta Smelt adults to larvae. Hypotheses addressed in Chapter 7 are indicated by the "H-number" combinations.

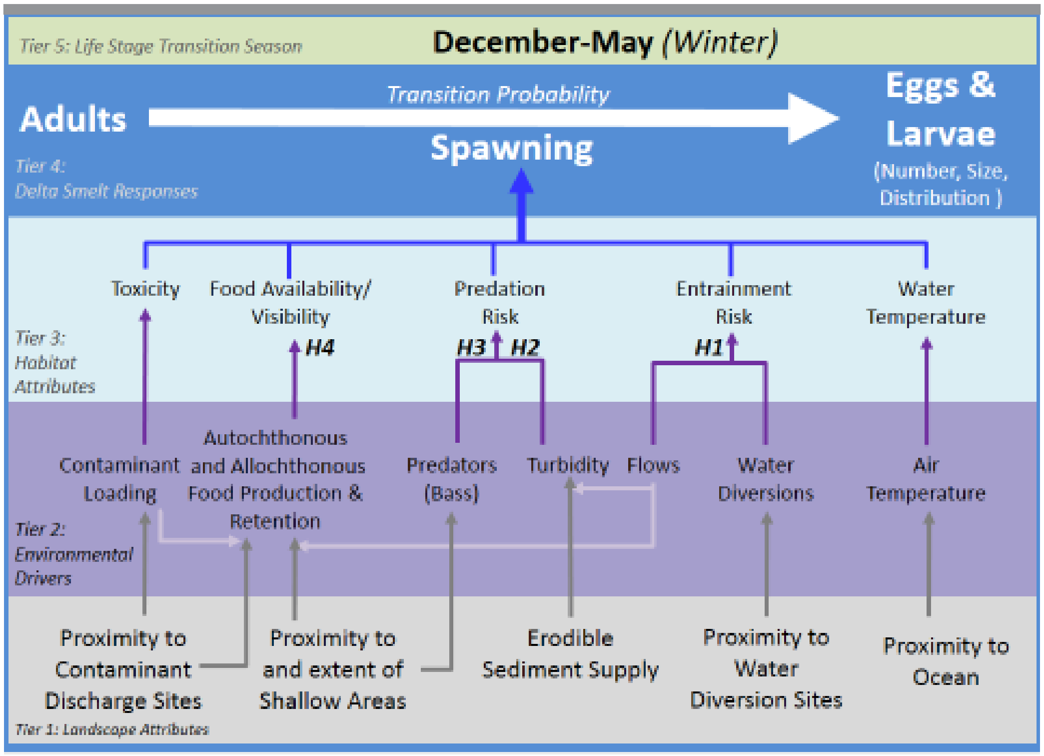


Figure 47. Conceptual model of drivers affecting the transition from Delta Smelt larvae to juveniles. Hypotheses addressed in Chapter 7 are indicated by the “H-number” combinations.

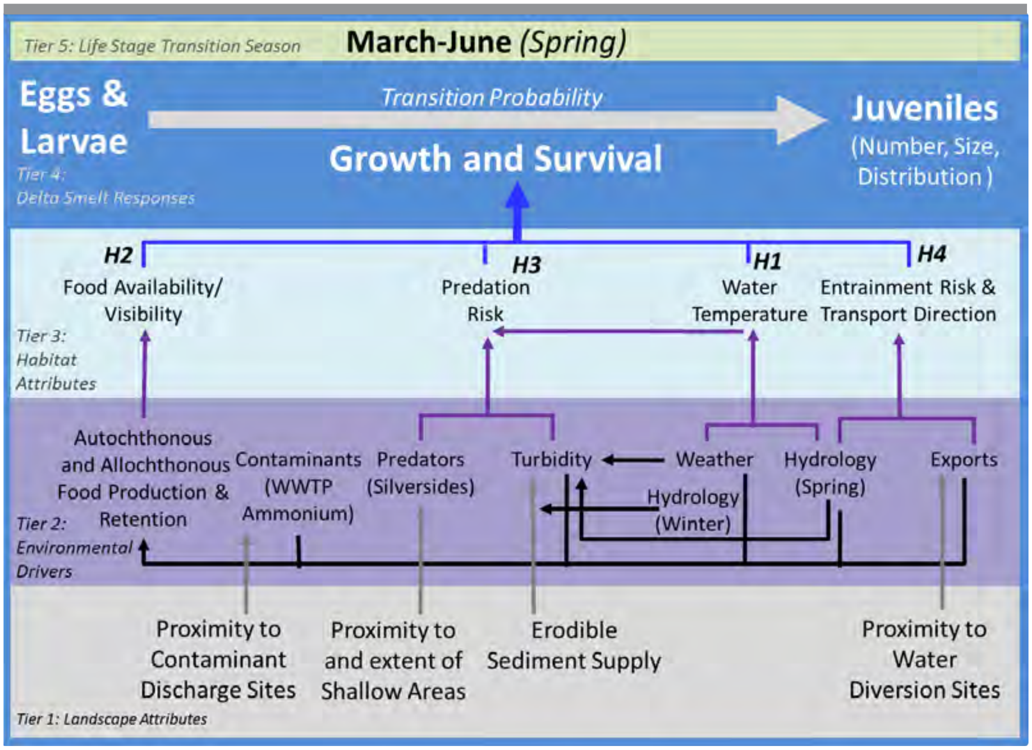


Figure 48. Conceptual model of drivers affecting the transition from Delta Smelt juveniles to subadults. Hypotheses addressed in Chapter 7 are indicated by the “H-number” combinations.

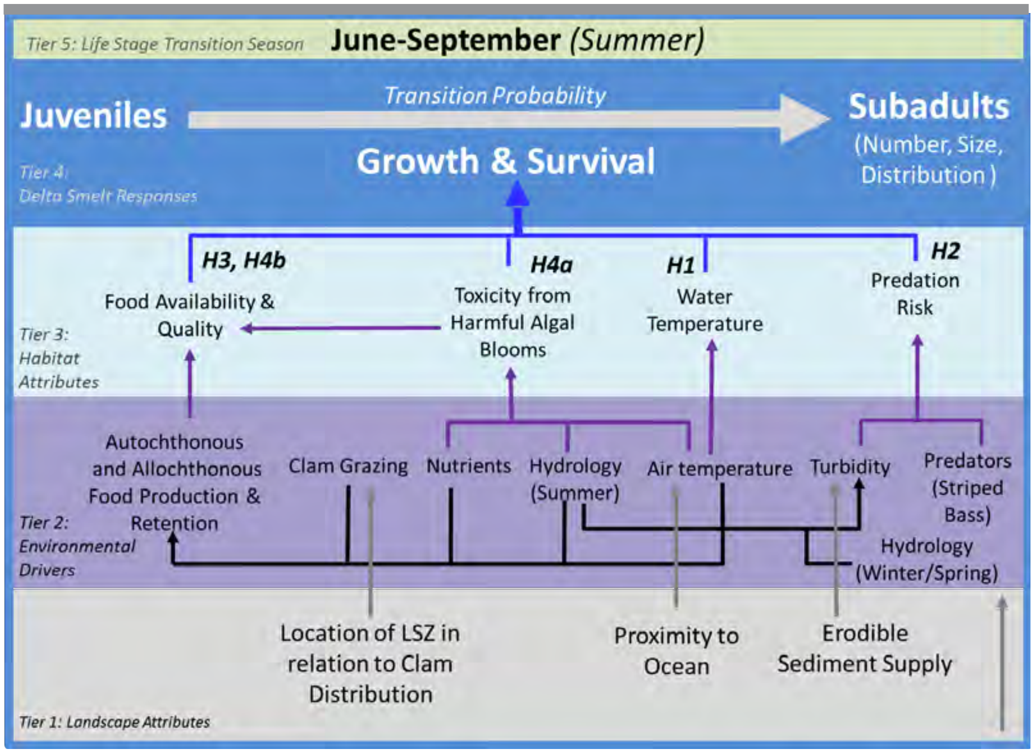
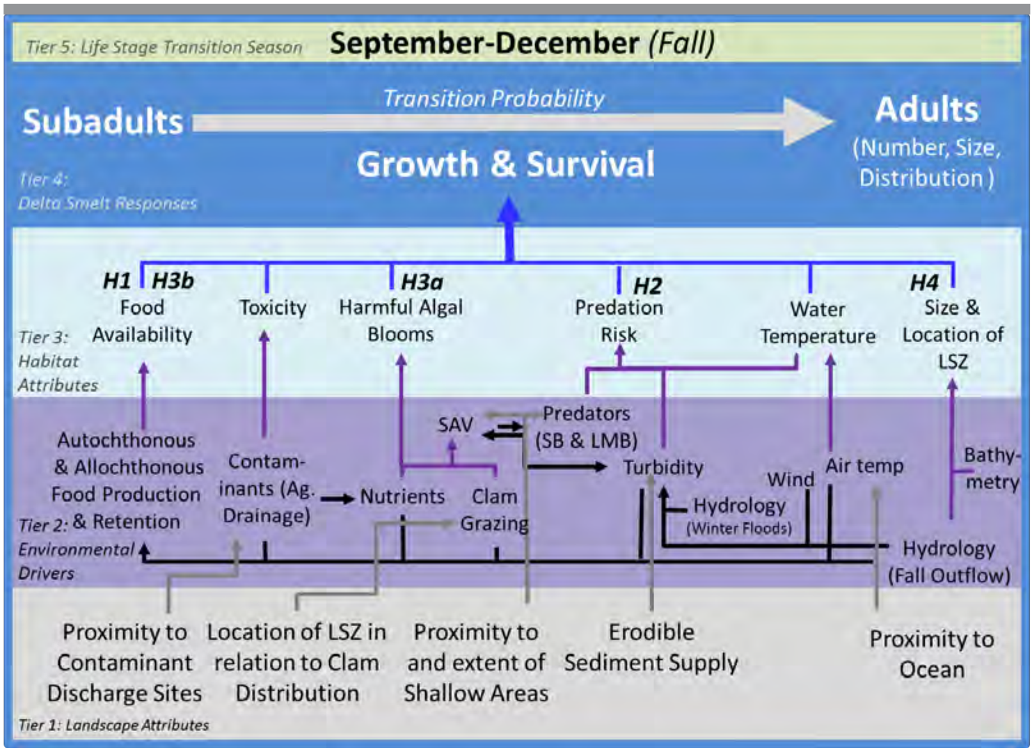


Figure 49. **Conceptual model of drivers affecting the transition from Delta Smelt subadults to adults. Hypotheses addressed in Chapter 7 are indicated by the "H-number" combinations.**



hypotheses are stated and addressed in more detail in Chapter 7. All hypotheses focus on the life stage that is transitioning to (i.e. occurs prior to) the next life stage, for example, adults but not eggs and larvae, larvae and post-larvae but not juveniles, and so on. That said, it is important to remember that all life stages overlap and all transitions except for the transitions from adults to eggs and from eggs to freshly hatched larvae are gradual, not abrupt, and delineations of life stages are somewhat arbitrary (see Chapter 3).

The life stage conceptual model for the transition of adult Delta Smelt to eggs and larvae (Fig. 46) includes 5 habitat attributes. Because of the lack of information about specific contaminant effects on Delta Smelt noted above, there are no specific hypotheses regarding the effects of contaminants and possible direct or indirect toxicity on Delta Smelt, but based on the information discussed in Chapter 4, the model does recognize that effects on Delta Smelt or its food supply may be occurring. Food availability and visibility are hypothesized to be important with respect to providing nutrition that allows Delta Smelt to grow into healthy, large adults that can produce a large numbers of high quality eggs as well as multiple clutches of eggs over the spawning season. The availability of food is considered dependent on both food production and the availability of such food to the fish. There are two hypotheses related to predation risk. The first is that turbidity, created by the interaction of high winter and spring flows with the erodible sediment supply in the watershed and within the Delta, influences the vulnerability of Delta Smelt to predators that co-occur with them. The second is that Delta Smelt behaviors that bring Delta Smelt close to channel edges may increase their vulnerability to Largemouth Bass, which generally occupy nearshore and vegetated habitats such as SAV beds. Entrainment risk in this life stage transition conceptual model is focused on adults. Entrainment of adults would reduce the reproductive potential of the population. Entrainment risk depends on the distribution of the adult Delta Smelt in relation to water diversions, and the magnitudes of water diversions and flows. Delta water temperature determines the beginning and duration of the spawning season (hereafter "spawning window").

The life stage conceptual model for the transition of Delta Smelt eggs and larvae to juveniles includes 4 habitat attributes (Fig. 47). Food production and availability is important for the survival of larvae to juveniles. Food quantity is dependent on multiple interacting factors. Turbidity is important for early feeding by delta smelt larvae. Predation risk focuses on predation of Mississippi Silversides on Delta Smelt larvae because of recent evidence that such predation occurs. Predation risk is hypothesized to depend on co-occurrence of the two species, with Mississippi Silverside generally being associated with shallower waters, turbidity, which decreases the effectiveness of predators, and water temperature, which affects energy requirements of predators (hunger level). In addition to its effect on predator bioenergetics, water temperature is hypothesized to affect the length of the spawning season (spawning window). If food availability is sufficient, then a longer spawning window may allow the adult population to produce multiple clutches of eggs, resulting in more young. This hypothesis could arguably be included in the previous life stage transition conceptual model, but considering it here allows for consideration of predation on larvae in the context of the time period over which larvae are being produced. Larvae are also at risk of entrainment or transport to unfavorable areas. The magnitude of this risk is hypothesized to depend on an interaction of spring hydrology and water exports. As indicated by numerous arrows, winter and spring hydrology affect Delta Smelt spawning and larval rearing habitat in many ways. We thus also include a more general hypothesis about the hydrological effects on Delta Smelt larval abundance and recruitment.

The life stage conceptual model for the transition of Delta Smelt juveniles to subadults includes 4 habitat attributes (Fig. 48). In addition, there is a stand-alone hypothesis dealing with population dynamics. Juvenile growth and survival is hypothesized to depend on availability and quantity of food. Food production during this summer period is hypothesized to involve complex interactions of clam grazing, nutrients, hydrology and harmful algal blooms. The probability of observing a harmful algal bloom is hypothesized to be a function of the same factors but with temperature playing an important role. Harmful algal blooms may also affect Delta Smelt directly through production of toxic microcystins. Summer water temperatures are hypothesized to have a very direct effect on juvenile Delta Smelt with water temperatures hypothesized to reach stressful levels, affecting their bioenergetics and the area of suitable habitat. The transition probability hypothesis is that at the currently small population sizes, survival from juvenile to subadult is density independent, meaning independent of the number of individuals present (see Chapter 6 for details).

The life stage conceptual model for the transition of Delta Smelt subadults to adults includes 6 habitat attributes (Fig. 49). As for the previous conceptual model, there is a stand-alone hypothesis dealing with population dynamics. As in the previous conceptual model, growth and survival are hypothesized to depend on food availability and food production and availability depends on interactions of a variety of landscape attributes and environmental drivers. Toxicity is recognized as potentially important but no specific hypotheses have been tested. Harmful algal blooms may still be present with hypothesized direct effects on Delta Smelt subadults and indirect effects on their food. Predation risk on subadult Delta Smelt is hypothesized to depend on co-occurrence of Delta Smelt with the two most likely predators, Largemouth Bass and Striped Bass. Largemouth Bass occurrence is linked with that of SAV and the vulnerability of prey to both predators is affected by turbidity and bioenergetics. Water temperature is mainly hypothesized to have an effect through bioenergetics because water temperature becomes less stressful than in the summer. In this conceptual model the size and location of the LSZ is considered both a landscape attribute and a habitat attribute. In the earlier conceptual models, the LSZ was mainly viewed as a landscape attribute that interacted with other landscape attributes and environmental drivers to create habitat attributes. In this conceptual model the size and position of the LSZ is hypothesized to have certain characteristics that directly determine habitat quantity and quality for Delta Smelt. The transition probability hypothesis is that at the currently small population sizes, survival from subadult to adult is density independent, meaning independent of the number of individuals present (see Chapter 6 for details).

Chapter 6: Delta Smelt Population Biology

This Chapter consists of two main parts. In the first part, we introduce general concepts in population biology that are utilized in the following sections of this Chapter and to generally describe Delta Smelt population dynamics. Explaining these concepts and population trends now is intended to reduce repetitive text in the remaining sections and to reduce possible confusion for readers unfamiliar with the concepts. The concepts are discussed specifically in the context of Delta Smelt.

In the second part of this Chapter, we review information about the life history and population trends of each Delta Smelt life stage represented in our conceptual models, starting with adults. While we describe trends over the entire available time series for each life stage, we pay particular attention to differences in Delta Smelt abundance and life stage transitions between the two most recent wet years, 2006 and 2011. Our working assumption is that these differences should be attributable to differing habitat conditions and, in some cases, management actions. Differences in habitat conditions between these two years will be further explored in Chapter 7.

Population Biology

Recruitment is the addition of new individuals to a population through reproduction or immigration. In fisheries science, the term recruitment was first used by Ricker (1954) to describe the addition of fish of a new generation to a fish population, in other words, the number of young surviving to a particular age or life stage. We use the term recruitment to refer to production of larvae, juveniles, subadults, or adults by adults of the previous generation. Relationships between numbers of spawning fish or other measures of potential spawning stock (e.g., numbers of subadult or mature prespawning fish) and the numbers of fish of a given age or life stage in the subsequent generation are known as stock-recruitment relationships.

Stock-recruitment relationships have been described for many species and are a central part of the management of commercially and recreationally fished species (Myers et al. 1995, Touzeau and Gouze 1998). Different forms of stock-recruitment relationships are possible, including density-independent, density-dependent, and density-vague types. The density-independent type occurs when the current size of the population has little or no effect on the number of recruits (except possibly when stock size is extremely low). This type of population growth is rare in fish populations and occurs when environmental factors largely determine the survival and number of recruits (e.g., the Longfin Smelt outflow abundance relationship; see Myers 1998). Density dependence occurs when the current population size affects survival and abundance of recruits and thus population growth. In such populations, within the lower range of stock size, the number of recruits is strongly and positively related to stock size. At some point as stock size increases, competition for food (or some other limiting factor) between the adult population and recruits affects survival and abundance of recruits; cannibalism is another means by which recruitment can be affected by stock size. Thus, the growth and survival of the recruit population strongly depends on the density of the stock population. In reality it's difficult to determine which type of response is occurring (e.g., Myers and Barrowman 1996). Moreover, a predominantly annual fish, such as Delta Smelt, is predicted to conform poorly to models that assume density-dependent recruitment (Winemiller 2005), which appears to be the case (e.g., Rose et al. 2013).

The idea of density dependence is related to the idea of carrying capacity. The carrying capacity of an ecosystem is the number of individuals of all species that can be supported by the available resources. In reality it can be very difficult to apply this idea to a single species in an ecosystem because of the complex relationships among species and the seasonal, annual, and other changes in resource availability. The density vague type of population growth refers to situations where there is not a statistically demonstrable stock-recruitment relationship observable in available data.

In density-dependent stock-recruitment relationships, the factors causing the density dependence can operate at various points in the life cycle of the new generation. For some species, the concept of density dependence is separated into two concepts. In this formulation, density-dependent stock recruitment is limited to the direct effects of the adult stock on recruitment of the next generation, as described above. For example, if a large spawning stock has a limited spawning area, as in the case of salmonids, then successive waves of female spawners are known to re-excavate previous nests while building their own, substantially increasing mortality of the eggs. Density dependence could also occur at the larval or juvenile stage if adults are predatory and feed on young, or if adults are in direct competition for food or space with young. The second concept of density-dependent survival is often inextricably linked to density-dependent stock-recruit relationships because the mechanisms causing declines in recruits at high stock levels are unknown. In density-dependent survival, the abundance of young affects their own survival.

In the case of Delta Smelt, density dependent survival could occur if many of the larvae starved because of insufficient food supplies due to competition with other Delta Smelt larvae, or other species. Because many Delta Smelt die after their first spawning, density-dependent survival is certainly the dominant mechanism for the species and for the remainder of this report the direct effects of adults on survival of eggs and larvae are assumed to be minimal. If resources were sufficient for larvae and juvenile fish to survive in large numbers, the surviving subadults might overwhelm food sources (i.e., surpass carrying capacity), resulting in low survival and poor reproductive output. Thus, it is important to understand species ecology and survival between life stages to understand how density dependence is affecting a population. This is particularly important for fishes in estuaries where environmental factors can create large variation in habitat size and food web productivity from season to season and year to year, thus affecting carrying capacity and the potential for density-dependent survival.

Density-independence is more straightforward. In this case, the population is controlled by factors unrelated to the density of the population. For example, high water temperatures will affect individual fish, whether the population is large or small. In reality, populations can be affected by both density-dependent and density-independent factors at different times. This interaction is the basis for the idea of compensatory density dependence. In this formulation, a population is governed by density independent factors when population size is small. As the population increases and approaches the carrying capacity, density-dependent factors become important and the population growth rate declines. Fluctuations in carrying capacity, as noted above, are an added complication. Again, it is essential to understand the ecology of the species and survival between life stages to understand the relative importance of density dependent and density independent factors.

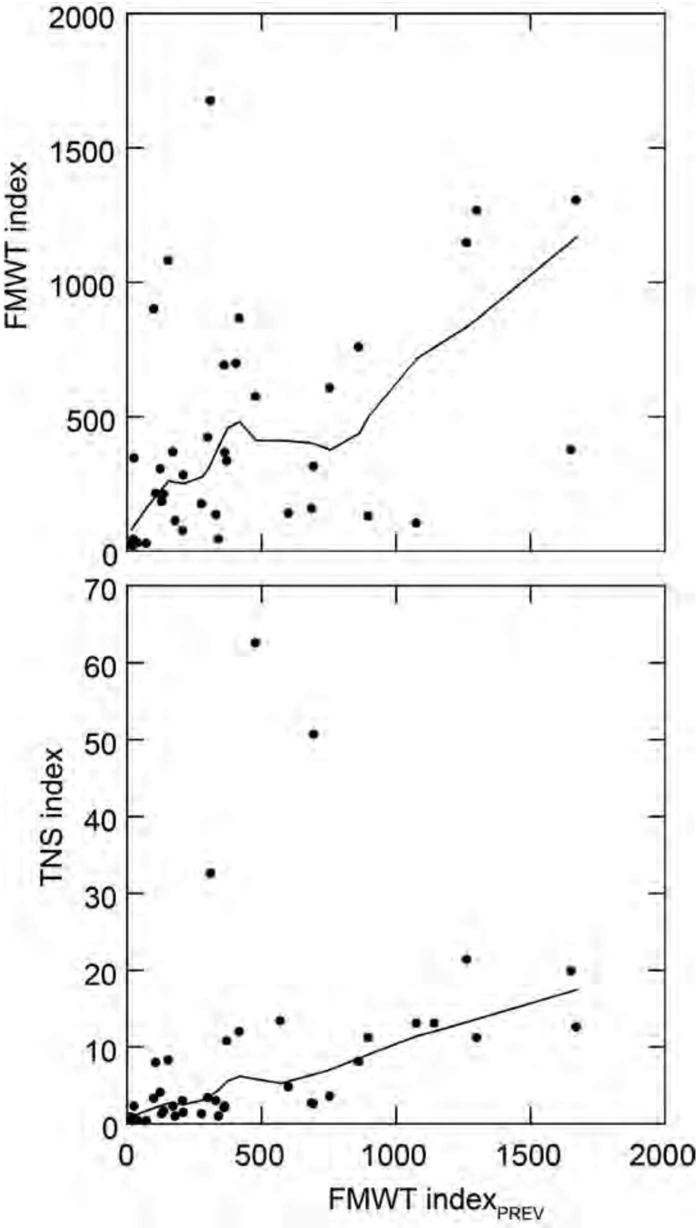
Unfortunately, Delta Smelt were never of sufficient interest as a commercial or recreational species to warrant development of stock-recruitment models until they were listed. Data now used to develop stock-recruitment models for Delta Smelt started becoming available after the initiation of fisheries studies and monitoring surveys in the late 1950s (TNS initiated 1959; FMWT initiated 1967) in association with the planning and operation of the CVP and SWP. These IEP fish monitoring surveys were designed to produce relative abundance indices or catch-per-unit-effort (CPUE, e.g., number per trawl) that could be used to monitor trends in abundance over time. More recently, annual abundance indices based on these surveys have also been incorporated into stock-recruit relationships (e.g., Moyle et al. 1992, Sweetnam and Stevens 1993, Miller 2000, Bennett 2005, Maunder and Deriso 2011). Neither of these early IEP fish monitoring surveys (TNS, FMWT) were specifically designed to monitor Delta Smelt, but instead targeted primarily the commercially and recreationally more important Striped Bass. As researchers began using TNS and FMWT indices for Delta Smelt analyses, they began investigating how the indices performed and means to improve them (see Wadsworth and Sommer 1996, Miller 2000, Newman 2008). This work is ongoing and also includes similar investigations for the newer SKT (initiated in 2002) and 20 mm survey (initiated in 1995) monitoring surveys.

The two stock-recruitment relations based on the longest data records include the relationsip of the FMWT abundance index with the FMWT adundance index in the previous year and the relationship of the TNS abundance index with the FMWT adundance index in the previous year (Fig. 50). Because of the large changes that have occurred in the Delta ecosystem, including the invasion by *P. amurensis* and the POD, these plots can be difficult to interpret because carrying capacity is assumed to have changed (Bennett 2005, Kimmerer et al. 2000, Sommer et al. 2007). It does appear that there is much more variability associated with the FMWT relationship compared to the TNS relationship. This might indicate variable survival between the juvenile and subadult life stage.

In any form of a stock-recruitment model, there is a point at which low adult stock will result in low juvenile abundance and subsequent low recruitment to future adult stocks. This can occur even under favorable environmental conditions while the stock “rebuilds” itself. From a stock-recruitment perspective, the recent low abundance of Delta Smelt is of particular concern. Since about 2002, the current population is smaller than at any time previously in the record, with the exception of the 2011 year class. This strong year class suggests that Delta Smelt have yet to reach low levels where the stock will need years to rebuild, at least to pre-POD levels (Fig. 3).

In addition to their use in exploring stock-recruitment relationships, ratios of annual Delta Smelt abundance indices can also be used to obtain rough estimates of relative annual recruitment and survival rates (figs. 51 and 52). As for the stock-recruitment relationships these recruitment and survival indices should be interpreted with caution given the large changes that have taken place in the Delta and the absence of estimates of variability for the indices. The main utility of these

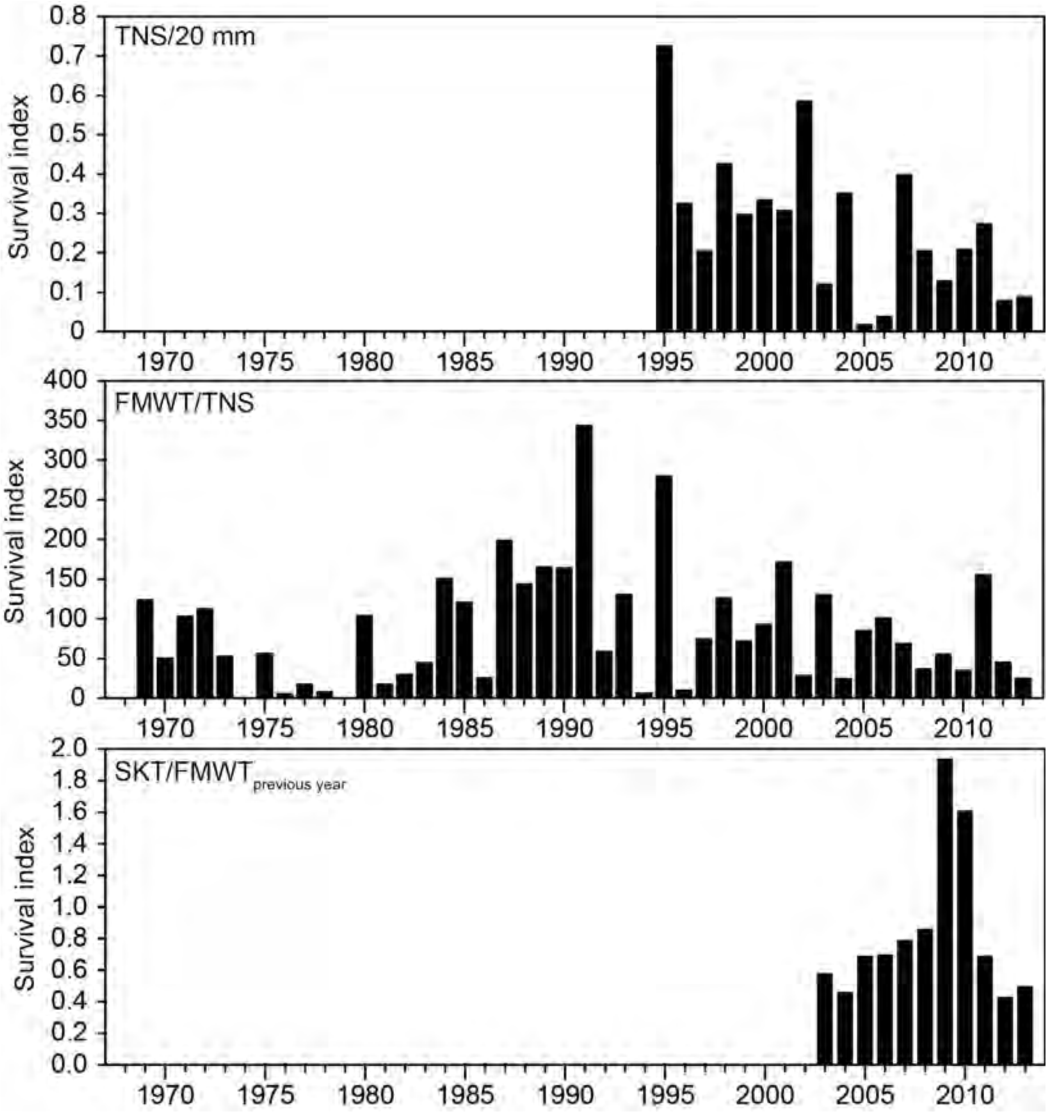
Figure 50. Scatterplots and LOWESS splines depicting the relationship of the Fall Midwater Trawl index of Delta Smelt relative abundance (FMWT) (1968-2012) and Summer Townet Survey (TNS) (1969-2012) with the FMWT in the previous year.



indices is identifying years with relatively high or low survival for a specific life stage transition or life stage transitions with differences in annual variability.

Here, we use the ratios of abundance indices for different life stages of the same generation as indices of survival (survival indices, Fig. 51) and the ratios of current to preceding year abundance indices as indices of recruitment (recruitment indices, Fig. 52). For the density-independent case, recruitment rate is independent of the size of the adult population. The number

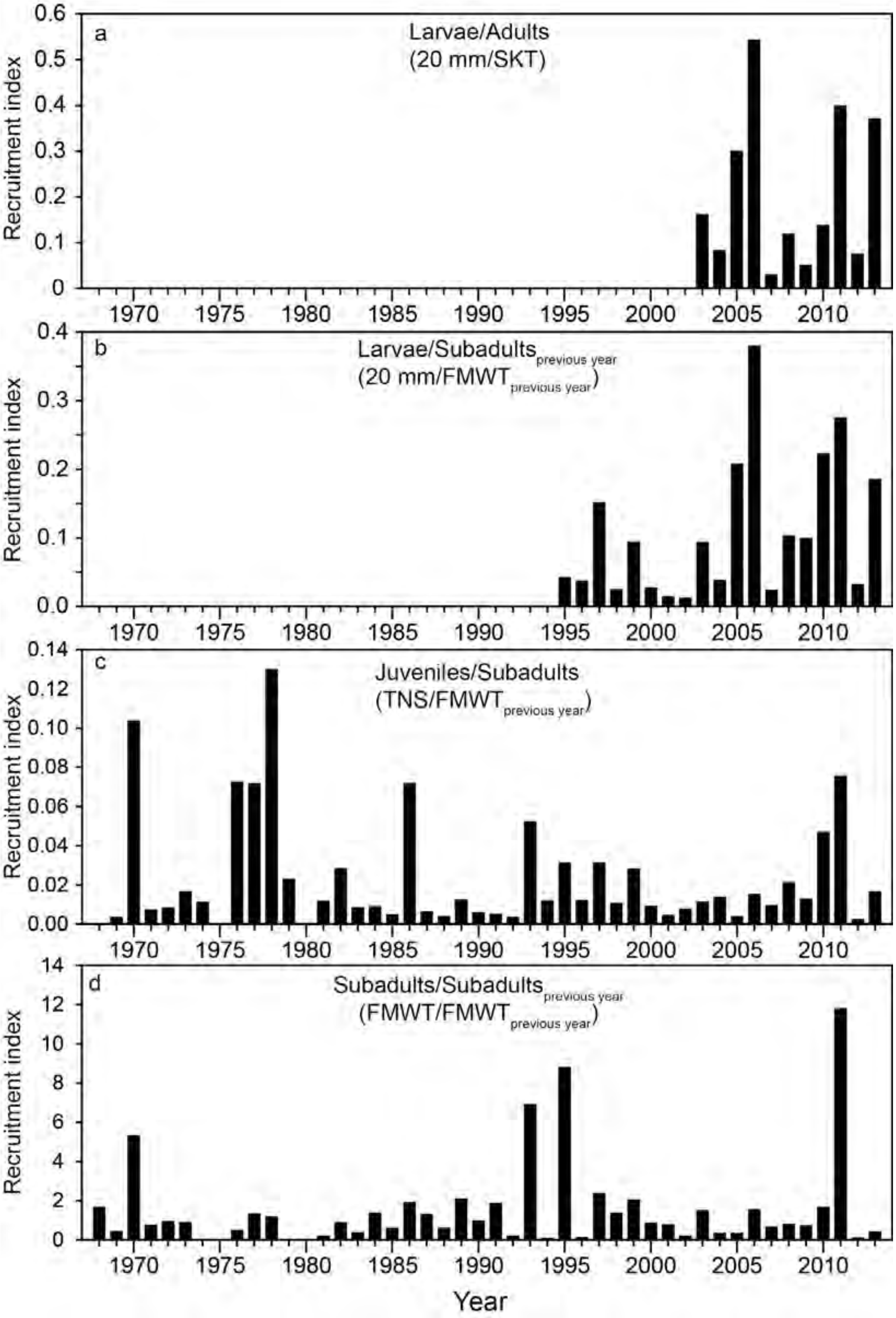
Figure 51. Stage to stage survival indices based on data from Summer Townet Survey (TNS), Fall Midwater Trawl (FMWT), and Spring Kodiak Trawl (SKT).



of recruits produced is the product of recruitment rate and the size of the adult population. For this report, we assume that the estimates have sufficiently low and comparable uncertainty to provide worthwhile interpretations, as long as caution is exercised. It is also important to remember that abundance, survival, and recruitment index values are only meaningful in a relative, not in an absolute sense.

The annual stage to stage survival indices from larvae to juveniles, subadults, and adults are shown in Figure 51. The relative recruitment rates from adults and subadults in one year to larvae, juveniles, and subadults the next year are shown in Figure 52. We recognize that a life cycle model with environmental covariates is needed to fully assess the combined effects of stock-recruitment and stage-to-stage survival indices on Delta Smelt population dynamics. Nevertheless, examination of the recruitment and survival index data sets reveal several interesting patterns for the POD period (2003-2013).

Figure 52. Delta Smelt recruitment indices based on the annual adult, larval, juvenile, and subadult abundance indices provided by the Spring Kodiak Trawl (SKT, adults), 20 mm Survey (20 mm, larvae), Summer Townet Survey (TNS. juveniles), and Fall Midwater Trawl (FMWT, subadults).



First, interannual variability in these stock and survival indices declines from larval recruitment (coefficient of variation (CV): 92%), to subsequent larvae to juvenile survival (CV: 67%), juvenile to subadult survival (CV: 43%), to subadult to adult survival (CV: 38%). This result is consistent with expected highly dynamic patterns of recruitment and survival for an annual opportunistic species such as Delta Smelt. The pattern of reduced variability in survival for larger fish suggests that older fish may no longer be vulnerable to some forms of mortality affecting earlier life stages either because a factor is no longer important when larger fish are present (e.g., effect of summer high water temperatures on juveniles) or that larger fish escape some forms of mortality (e.g., larger fish are no longer eaten by the large variety of predators able to consume larvae).

Second, the patterns of adult and larval abundance (Fig. 3) and adult to larvae recruitment (Fig. 52a) suggest: (1) even a small adult Delta Smelt stock can produce a large number of larvae under the right habitat conditions; but (2) larval recruitment is not a good predictor of juvenile survival and subsequent adult stock size. In other words, good larval recruitment sets the stage for population recovery, but good survival through subsequent life stage transitions is needed to realize its potential.

Third, there are clear contrasts in Delta Smelt responses between the two wet years 2006 and 2011 (the years of particular interest in this report) (Figs. 51 and 52). Since the initiation of the SKT survey for adult Delta Smelt in 2002 (indices calculated beginning in 2003), the recruitment of larvae from adults was greatest in the two wet years 2006 and 2011 (Fig. 52a) compared to the other, drier years in the time series, but in 2006 very strong adult to larvae recruitment was followed by very poor larvae to juvenile survival in the summer (Fig. 51a) and only average survival in the fall (Fig. 51b) and winter (Fig. 51c). This led to low abundance of the subsequent life stages of the 2006 cohort. Survival from larvae to juveniles and subadults was much better in 2011 and, along with good recruitment, led to the highest juvenile and adult abundance indices since the onset of the POD (Fig. 3). In other words, good recruitment set the stage for population recovery in both recent wet years, but a substantial abundance increase was realized only in 2011. Unfortunately the 2011 abundance increase was short-lived; it was immediately followed by poor recruitment and survival in 2012 and abundance indices for the 2012 and 2013 cohorts were once again at the low levels typical for the POD period (Fig. 3). Several consecutive years of good recruitment and survival are likely needed for a more sustained increase of the Delta Smelt population abundance to pre-POD abundance levels. Population declines such as the decline experienced by Delta Smelt do not only reduce the number of individuals, but can also reduce the genetic diversity present in the population. While the 2011-2012 data suggest that recovery of Delta Smelt abundance can still be fairly rapid via high larval recruitment followed by good survival (Figs. 51 and 52) recovery of genetic diversity is a much slower process which is an important conservation concern (Fisch et al. 2011).

Small Delta Smelt population size affects the effective population size (*Ne*), a measure of the genetic properties of a population and the abundance at which significant genetic diversity is lost due to inbreeding (Falconer and Mackay 1996, Schwartz et al. 2007, Antao et al. 2010). In many species *Ne* may be orders of magnitude smaller than the census population size (*N*) and low *Ne*/*N* ratios indicate the population may be in danger of losing genetic variability, potentially resulting in reduced adaptability, population persistence, and productivity (Hauser et al. 2002). For Delta Smelt, Fisch et al. (2011) detected a genetic bottleneck in each of four sampling years (2003, 2005, 2007 and 2009) and observed a significant decline in effective population size between sampling years 2003 and 2007 (Fisch et at. 2011). The genetic signal of the decline in *Ne* is corroborated by the observed abundance index declines and support the hypothesis that decreases in *Ne* and allelic richness have likely occurred over the last few decades (Fisch et al. 2011). Genetic changes within the Delta Smelt population deserve continued evaluation with respect to changes in population size.

In addition, Delta Smelt recruitment and the fecundity of adult Delta Smelt likely vary substantially from year to year (Rose et al. 2013b). Delta Smelt fecundity is a function of female size (Bennett 2005, Lindberg et al. 2013). The mean size of adult Delta Smelt declined in the early 1990s (Sweetnam 1999), possibly due to changes in the food web (see Chapter 4), but substantially recovered in the late 2000s. Another possible reason is that in some recent years, there may have been selection for smaller, late-spawned larvae as a result of export pumping schedules (Bennnett 2011). For example, Bennett (2011) proposed that high export pumping in late winter may have resulted in high entrainment mortality of offspring from larger, fitter, early spawning females, which produced larger, fitter offspring (Bennett 2011). Further, Bennett et al. (2008) and Bennett (2011) posited that curtailment of export pumping in mid-April related to the Vernalis Adaptive Management Program (VAMP), allowed for greater survival of later-spawned, smaller larvae. The major concern is that these smaller later-spawned larvae have less opportunity to grow to large adult size, especially when food is scarce. If correct, the combined effects of export pumping and food supply on Delta Smelt growth and size could have a nonlinear impact on overall fecundity and population success. This is corroborated by the results from individual-based modeling which showed that growth in fall-winter and the subsequent number of eggs produced per adult were the most important factor determining the success of the next generation (Rose et al. 2013b). Moreover, repeated losses of early-spawned larvae could potentially have a negative effect on expression of this important phenotype and result in eventual loss of genetic variability in the population, and contribute to the genetic bottlenecks reported by Fisch et al. (2011).

Given the unprecedented low abundance of Delta Smelt since 2002 (Fig. 3, summer and fall), serious consideration should be given to evaluation of Allee effects. Allee effects occur when reproductive output per fish declines at low population levels (Berec et al. 2006). In other words, below a certain threshold the individuals in a population can no longer reproduce rapidly enough to replace themselves and the population, exhibiting inverse density dependence, spirals to extinction. For Delta Smelt, possible mechanisms for Allee effects include processes directly related to reproduction and genetic fitness such as difficulty finding mates, genetic drift, and inbreeding (Gascoigne et al. 2009), although none of these effects have been documented yet in Delta Smelt (Fisch et al. 2011). Other mechanisms related to survival such as increased vulnerability to predation (Gascoigne and Lipcius 2004) are also possible. While theoretical work suggests that Allee effects might be common in nature, empirical evidence for Allee effects in natural populations of fishes remains relatively sparse (Myers et al. 1995, Liermann and Hillborn 1997), possibly because they are often masked by measurement errors (Gregory et al. 2010). Recent meta-analytical work by Keith and Hutchings (2012) suggests that Allee effects in marine fish species might be more common than previously thought. But even in the absence of “true” Allee mechanisms, small population size (Hutchings 2013) can produce an emergent Allee effect and prevent recovery of collapsed fish populations even when threats are reduced (Kuparinen et al. 2012). This may be one of the reasons why recovery of many collapsed fish populations remains slow despite large reductions in fishing (Pauly et al. 1998, Hutchings et al. 2010). This finding challenges the traditional fisheries management view that depleted populations will grow and recover rapidly when fishing pressure is relaxed (Hilborn and Walters 1992). In addition, the interactive effects of multiple Allee effects may have important implications for species conservation, but have not yet been well explored in ecology (Berec et al. 2006).

Compensatory density dependence predicts that a fish's population growth or survival rates can increase when abundance is low and decrease if abundance increases beyond a carrying capacity (Rose et al. 2001). If compensatory density dependence occurred in 2011, Delta Smelt survival would be expected to increase as long as the carrying capacity of the environment was not exceeded. Therefore, the sudden increase in subadult abundance in 2011 is consistent with the higher survival predicted by compensatory density dependence at low population abundance coupled with widespread availability of good habitat conditions throughout the year. Among the remaining comparison years, both 2005 and 2006 show evidence of compensatory recruitment to larvae (Fig. 52a). Adult abundance was moderately high in 2005, but low in 2006 and 2010 (Fig. 3). As predicted by compensatory density dependence processes, the recruitment index to larvae was higher in 2006 than in 2005. However, low adult abundance in 2010 did not give way to a similarly high recruitment index (Fig. 52a). In addition, the relatively high recruitment index in 2006 did not result in a higher larval abundance index compared to 2005 (Fig. 3). These inconsistences, combined with a small number of comparison years, prevent any firm conclusion regarding compensatory recruitment or survival.

Similarly, if compensatory density-dependent survival was important we might expect larva to juvenile survival to be lower when larva production per adult was higher assuming similar adult populations. This was not the case for 2006, 2010, and 2011, which had relatively similar values for the SKT abundance index (figs. 3). In 2006, larval survival was low with high larval production per adult, and 2010 and 2011 had very similar larval survivals with similar adult abundances. Finally, in 2011, the highest population of juveniles led to the highest population of subadults and adults (2012 SKT), which argues against compensatory density-dependent survival. These comparisons argue against strict compensatory density dependence operating within the POD years. It seems more likely that population dynamics are driven by density independent relationships with factors such as summer water temperatures and resource availability (fluctuations in carrying capacity); however, the evidence is not conclusive. In particular, we do not understand how carrying capacity fluctuates over seasons and years or how other factors, such as predation, affect carrying capacity (Walters and Juanes 1993; Walters and Korman 1999).

Adults

Life History

The Delta Smelt is generally considered a diadromous seasonal reproductive migrant, and in the winter, many adult Delta Smelt move upstream into fresh water for spawning (Moyle et al. 1992, Bennett 2005, Sommer et al. 2011). These movements may be a specific change in behavior in response to one or more environmental cues, for example, to the rapid and often dramatic environmental changes during winter first flush periods (Sommer et al. 2011, Bennett and Burau 2014). Focused, fixed-station sampling in the winters of 2009-10 and 2010-11 revealed higher catch of Delta Smelt at higher turbidity levels, as well as an asymmetry in probability of catch with respect to tidal phase; catch was highest in the channels during flood tide, but highest near the shoreline during ebb tides (Bennett and Burau 2014). This change in horizontal channel position with respect to tidal direction has recently been confirmed by a second study in the fall of 2012 that used the "SmeltCam," an underwater video camera attached to the cod-end of the FMWT net to detect Delta Smelt (Feyrer et al. 2013). This study demonstrated that during flood tides, Delta Smelt were relatively abundant throughout the water column, but less abundant during ebb tides, and found only in the lower portion of the water column and closer to shorelines. This asymmetry in catch supports the idea of a “tidal surfing” behavior during migration that may minimize energetic costs of upstream movement and allow Delta Smelt to follow favorable conditions with respect to turbidity and salinity (Feyrer et al. 2013). Variations of this behavior would allow fish to maintain position in the channel (stay on the edge during flood or ebb tide) or move downstream (move into the channel on ebb tide).

It is also possible that Delta Smelt movements do not represent a change in behavior; rather, fish are simply expanding their foraging or refuge distribution to habitat upstream when it becomes turbid or otherwise more suitable during and after the first flush period (Murphy and Hamilton 2013). The specific mechanism for the seasonal change in distribution, however, may be more a matter of terminology than of ecological relevance for a fish with as small a home range as Delta Smelt. Here, we acknowledge the existence of both possibilities, but will use the term “spawning migration” to simply refer to a directed movement upstream or downstream occurring prior to and during the spawning season. Using this definition, this seasonal change counts as a migration since it represents a relatively predictable and substantial change in distribution that has adaptive value including potential spawning, foraging and refuge functions (Lucas and Bara 2001).

The Delta Smelt spawning migration from their low-salinity rearing habitat into freshwater usually occurs between late December and late February, typically during first flush periods when inflow and turbidity increase on the Sacramento and San Joaquin Rivers (Grimaldo et al. 2009, Sommer et al. 2011a). Increased catches of Delta Smelt in the Delta Juvenile Fish Monitoring Program’s Chipps Island Trawl Survey and at the south Delta salvage facilities are unimodal in most years and occur within a couple of weeks of first flush events, suggesting that adult Delta Smelt are responding to environmental changes and migrating rapidly upstream once the first flush occurs (Grimaldo et al. 2009, Sommer et al. 2011a). However, spawning migrations are not always upstream. During occasional periods of very high river flows that spread freshwater habitat throughout much of the estuary, some Delta Smelt “migrate downstream” from rearing habitats in Suisun Bay and the Delta to freshwater spawning habitats as far west as the Napa River (Hobbs et al. 2007). Also under high flow conditions, it is possible that some Delta Smelt may not migrate in any direction; if their brackish-water rearing habitat becomes fresh, they can presumably spawn in suitable areas nearby. In addition, there is a small subset of the population that appears to remain in the Cache Slough complex year around; these fish presumably stay in the region for spawning (Sommer et al. 2011).

Osmerids generally spawn in shallow waters (Moulton 1974, Murawski et al. 1980, Hirose and Kawaguchi 1998, Martin and Swiderski 2001, Bennett 2005). It is believed that Delta Smelt spawn over sandy substrates in shallow areas based on the observation that first hatch larvae are collected in high concentrations in areas near expansive sandy shoals (Bennett 2005, L. Grimaldo, U.S. Bureau of Reclamation, unpublished data); confirmation of this hypothesis has not been verified through egg collections or observations of spawning adults, except in mesocosm studies (J. Lindberg, U.C. Davis, unpublished data). Pilot studies to identify egg deposition areas have been conducted by the IEP but these efforts were unsuccessful; it is unknown whether it was due to the method used, locations selected, or because of the low probability of detecting eggs from a relatively rare species.

The Delta Smelt is an opportunistic strategist (Nobriga et al. 2005). Opportunistic strategists are characterized by their short life spans, but high intrinsic rates of population increase driven by rapid maturation and repeat spawns over a protracted spawning season (Winemiller and Rose 1992). The importance of per capita fecundity to the success of the Delta Smelt population was recently highlighted in an individual-based modeling study (Rose et al. 2013a,b). In culture, Delta Smelt can spawn up to four times per year depending on water temperature (J. Lindberg, U.C. Davis, unpublished data). Recent evidence indicates that Delta Smelt can spawn multiple times in the wild if water temperatures stay cool in the later winter and early spring (Wang 2007, L. Damon, CDFW, written comm. 2013). The ability of Delta Smelt to spawn multiple times in the wild could substantially increase per capita fecundity over previous estimates for individuals of a specific size. It could also be a contributing factor to the large interannual variability in adult to larvae recruitment (Fig. 52a).

Population Trends

Adult Delta Smelt are monitored by the Spring Kodiak Trawl (SKT) survey which was initiated by CDFW (then CDFG) in 2002 and runs from January to May each year (Honey et al 2004). An indexing method was recently developed by CDFW for the SKT survey, allowing for year to year comparisons as well as comparisons with the abundance indices for other life stages (Fig. 3). The SKT index time series used in this report comprises 11 annual indices, from 2003 to 2013; no index is available for 2002. Each index represents the abundance of adult fish hatched in the previous calendar year that survive to spawn at the beginning of the next calendar year. The highest SKT index on record occurred in 2012 (147), as a result of the high 2011 abundance of younger fish, and the lowest in 2006 (18). Of the four comparison years, 2005 had the highest SKT index (51), followed by 2010 (27) and 2011 (20) and then 2006 (18). While the SKT index was thus lower in the two wet years than in the two drier years, the SKT index increased substantially in each of the years following the two wet years; however it increased only 2-fold from 2006 to 2007 while it increased 7-fold from 2011 to 2012 (Fig. 3). It is also possible that the SKT is less effective during very high flow events. Delta outflow at times exceeded 200,000 cfs in winter 2011 and 300,000 cfs in winter 2006. These high flow events might have contributed to the low SKT indices in these two wet years, if Delta Smelt remained near shore to avoid displacement or moved into San Pablo Bay with the LSZ. In both cases they would be outside of SKT sampling range. Further evaluations are needed, however, to investigate and quantify this hypothesized effect.

The annual adult Delta Smelt abundance indices track the annual abundance indices of sub-adults calculated from the previous years’ FMWT survey closely (Fig. 53; see also Kimmerer 2008). The relationship is particularly strong at higher fall abundance indices (FMWT index > 50), with more variability at lower abundance indices. Before the POD decline in 2002, all Delta Smelt FMWT indices were greater than 50 (Fig. 3). Thus, the FMWT might provide a useful surrogate for estimating long-term abundance trends in the adult Delta Smelt population prior to the initiation of the SKT survey in 2002, but great caution is warranted with the approach because this hindcasting would rest on only four data points with high leverage (2003-2005, 2012) and assume stable subadult to adult survival relationships and habitat conditions, neither of which is likely true. Moreover, the Kodiak trawl more efficiently captures Delta Smelt than the FMWT net. The SKT survey was set up to target Delta Smelt, while the FMWT survey was designed to monitor young Striped Bass, which tend to be larger than Delta Smelt during fall; however, there is no reason to expect the difference in capture efficiency to affect the relationship, unless such differences were a function of population size (i.e., efficiency was different above and below FMWT = 50). The utility of the FMWT as a descriptor of long-term adult population trends in the absence of long-term data from the SKT will benefit from ongoing IEP efforts to quantitatively estimate the efficiency of the FMWT and to compare efficiencies of different trawling gear and protocols. While survival from subadults in the fall (FMWT) to adults in the winter and spring (SKT) (Fig. 53) has been more stable than adult to larvae recruitment and survival between other life stages (Figs. 51 and 52), it nevertheless shows some variability, especially when abundance is low. These data suggest that at least in the POD decade, adult numbers appear largely driven by juvenile abundance and the influence of changes in winter-time habitat attributes is less important and relatively stable from year to year.

The number of adult spawners affects population dynamics through production of eggs. Potential reproductive output is proportional to the number of adult female spawners, the clutch size for females of a specific size, and the number of egg clutches produced by each female. Although egg production in the wild has not yet been documented, we can evaluate the relationship of the SKT adult population index to the 20 mm Survey abundance index (Fig. 54). This relationship does not appear to be strong during the POD period (linear regression, $P > 0.05$). This suggests that egg production or subsequent hatching of eggs and survival of larvae and thus overall recruitment of larvae from the previous generation's adults is affected by other factors than adult population size. Hypotheses about the effects of habitat attributes in our conceptual model on adult growth and fecundity and recruitment of young are explored in Chapter 7.

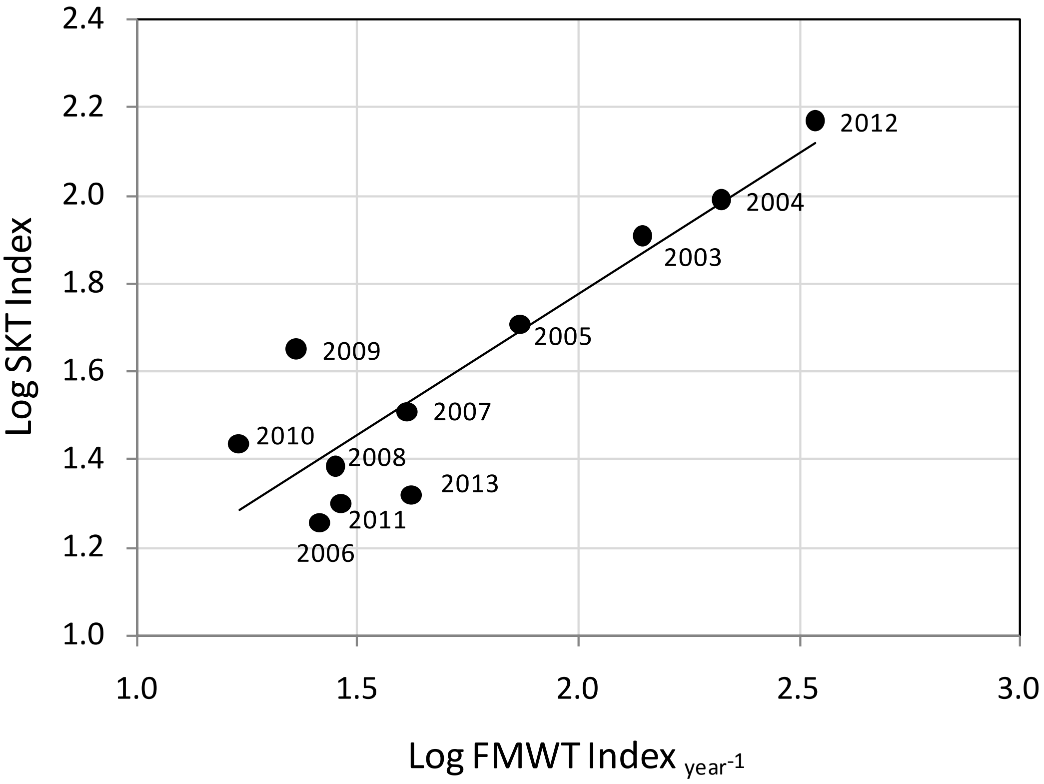
Clutch sizes of fish collected in the SKT were not measured, but annual fork lengths of Delta Smelt collected in the SKT did not vary greatly (Fig. 55). It does not appear that clutch size should have varied much in the POD years, including the four comparison years 2005-6 and 2010-11, with 2003 as the exception where the median length was greater than 70 mm standard length (Fig. 55). For Delta Smelt, which are now considered seasonal indeterminant spawners (i.e., they spawn multiple times), total reproductive output of an individual female should vary with: 1) size at the onset of the spawning window because batch fecundity is a function of size (Bennett 2005, CDFW unpublished data), 2) length of the spawning window, which is the number of days with suitable water temperatures for spawning (see larvae section below) and determines the number of batches possible; and 3) growth during the spawning window, which can potentially improve batch fecundity over time (see larval section below). Obviously, reproductive output will be higher in years when adult females are larger, abundances are higher, and the spawning window is prolonged such that multiple clutches are produced. Note that maximum reproductive output of the adult population at the beginning of spawning is not often realized due to mortality arising from density-dependent (e.g., food limitation or predation) or density-independent (e.g., entrainment, contaminants) mechanisms. According to Bennett (2011), larvae from bigger, early-spawning females may be disproportionally lost to CVP and SWP entrainment. In this report, we consider years when there are bigger females and/or a higher spawning stock size to be better in terms of reproductive potential than years when adult female size and spawning stock are smaller.

Larvae

Life History

Adult Delta Smelt, through their selection of spawning sites and spawn timing, largely determine the early rearing habitat and environmental conditions encountered by larvae. Given the Delta Smelt's annual life cycle, small size at maturity, relatively low fecundity, and small egg size compared to other fishes, life history theory suggests that parental care, here limited to selection of spawning sites and spawn timing, should be an important factor in reproductive success (Winemiller and Rose 1992). Since eggs have not been detected routinely in the wild, spawning and early rearing habitat locations are inferred from collection of ripe adults and early stage

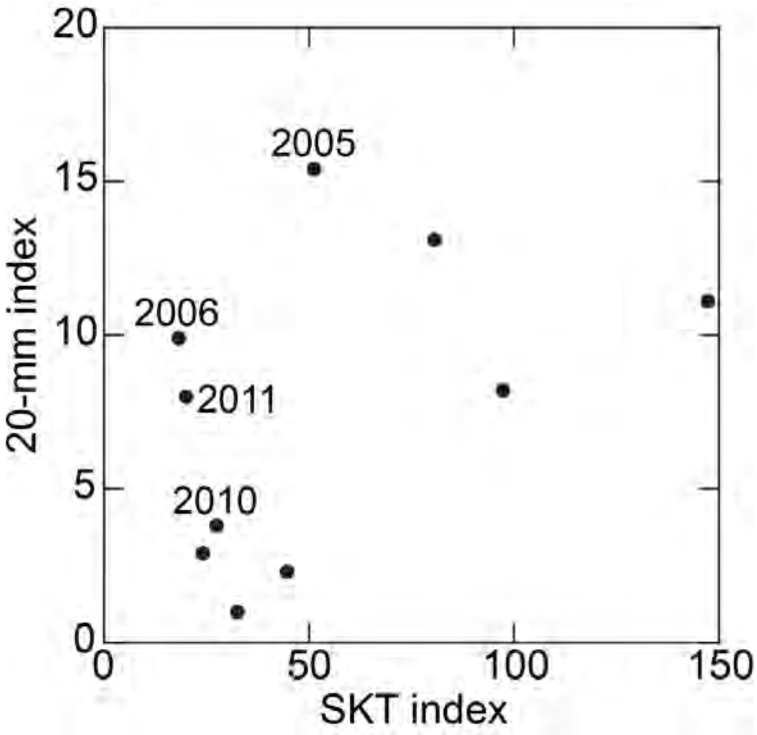
Figure 53. Relationship of annual indices of Delta Smelt abundance from the Spring Kodiak Trawl (SKT) and Fall Widwater Trawl (FMWT) from the previous year. Year labels correspond to the year of the SKT. The linear regression with all index values log-transformed to address non-normal distributions in the raw data is: Log SKT Index = 0.4997 + 0.6381(Log FMWT Index Year^{1}), n = 11, p < 0.001, R^{2} = 0.79.



larvae, which occur from the Delta margins through eastern Suisun Bay (see: http://www.dfg.ca.gov/delta/projects.asp?ProjectID=SKT; Wang 1986, 1991, 2007). In culture, Delta Smelt begin spawning as water temperatures increase to 10-12 °C, at which time individual females accompanied by several males select appropriate water velocities and release gametes close to the substrate from dusk to dawn (Baskerville-Bridges et al. 2004b). In lab experiments, females deposited significantly more eggs on sand and gravel substrates as compared to other substrates offered for egg deposition (J. Lindberg, U.C. Davis, unpublished data). Based on periodicity in egg deposition in culture, Bennett (2005) proposed that spawning likely coincides with peak tidal currents (i.e., spring tides), which would result in hatching near neap tides. Such a strategy would limit the initial tidal dispersal of larvae.

In culture, larvae hatch after an 11-13 day incubation period at 14.8-16.0 °C and begin a short period of buoyancy (or positive phototaxis; Baskerville-Bridges et al. 2004b) prior to slowly settling to the bottom (Mager et al. 2004). After this buoyant period, Mager et al. (2004) found that larvae were demersal unless actively swimming to feed, which occurred only during daylight hours. Exogenous feeding begins at 5-6 days post-hatch as the last of the yolk sac is absorbed; the lipid globule is absorbed at 10 days (Mager et al. 2004) providing some nutritional reserve if feeding conditions are poor. Larvae probably remain somewhat bottom oriented until swim

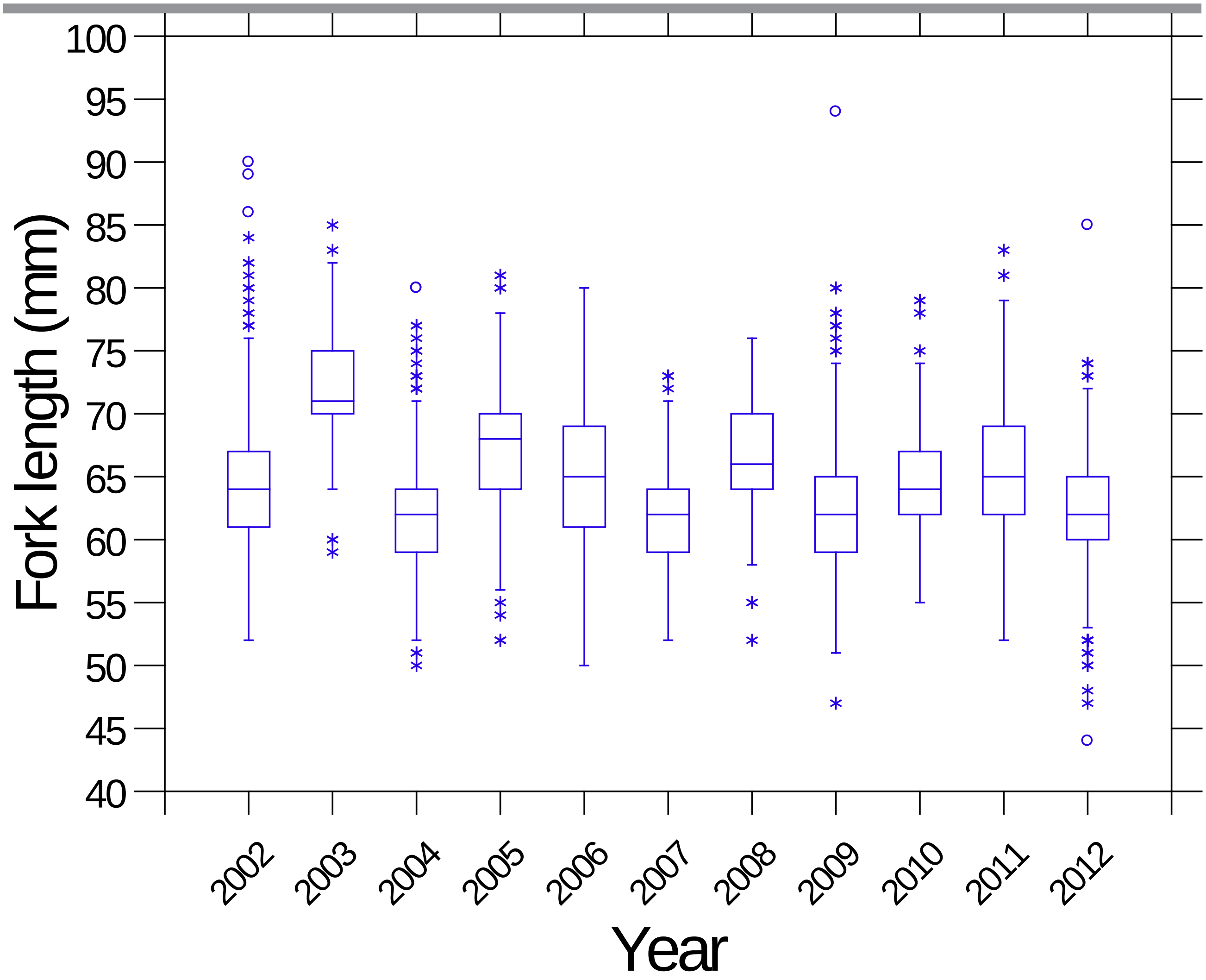
Figure 54. **Plot of the Spring Kodiak Trawl (SKT) adult abundance index against the 20 mm Survey larval abundance index 2003-2012. The comparison years of 2005, 2006, 2010, and 2011 are labeled.**



bladder and fin development are complete at about 65 days of age and about 20 mm TL (Mager et al. 2004, Baskerville-Bridges et al. 2004b), at which time they can fully control their buoyancy and efficiently use tidal and river currents to migrate. The center of distribution for Delta Smelt larvae and young juveniles is generally downstream of the spawning habitat, but upstream of and varying in association with X2 during spring (Dege and Brown 2004).

Early larval stages of Delta Smelt (4-15 mm) tended to be poorly collected by gear previously used in historical SFE egg and larval surveys (Striped Bass Egg and Larva Survey; sled-mounted 500 micron mesh net with 0.38 m^2 mouth area), but with growth and development greater proportions of the population become vulnerable. This observation led to a sampling gear change in the mid-1990s from the historical egg and larval gear to new gear targeting more vulnerable post-larvae and early juvenile Delta Smelt (i.e., 20 mm Survey). The improved catch and distribution information resulting from this change has since proven valuable to the management of Delta Smelt, and the 20 mm Survey results are now considered essential information (USFWS 2008). In the mid-2000s, an abundance index was developed from 20 mm data (Gleason and Adib-Samii 2007) that has since been used to index abundance trends of larvae in spring (e.g., Hieb et al. 2005, Contreras et al. 2011). We use 20 mm Survey abundance indices as one Delta Smelt end-point to evaluate the support for our hypotheses concerning the environmental drivers and habitat attributes responsible for abundance and survival of larvae.

Figure 55. **Median fork length (mm) of Delta Smelt collected in January and February by the Spring Kodiak Trawl by year, 2002-2012. See Chapter 3: Data Analyses for explanation of boxplots.**



Population Trends

The highest larval abundance indices on record occurred in the late 1990s, shortly after the initiation of the 20 mm survey in 1995. The lowest larval abundances were observed in 2007-2010 (Fig. 3). In 2011, larval abundance improved substantially from the recent minimum in 2007, and achieved levels comparable to those earlier in the 2000s (Fig. 3). Although 2011 larval abundance compared favorably to that of 2010, it remained below levels of 2005 and 2006. Thus, the modest larva abundance in 2011 did not appear sufficient to explain the high FMWT index observed in 2011 (Fig. 3). As explained above, larval abundance does not track the abundance of the parent generation very well (Fig. 54). In contrast, subsequent life stages of the same cohort track larval abundance and abundance relationships of larvae (log 20 mm index) with juveniles (log TNS index) and subadults (log FMWT index) in the same year are statistically significant (Fig. 56). However, the linear regression based on the FMWT explains less variance than the linear regression based on the TNS suggesting more variability in the abundance of the older life stages. This suggests that factors affecting juvenile mortality rates also play an important role in eventual recruitment.

Juveniles

Life History

During summer, juvenile Delta Smelt primarily rear in the west Delta, Suisun Bay, and Cache Slough complex (Moyle 2002, Bennett 2005, Merz et al. 2011, Sommer and Mejia 2013). As in late spring and fall, the center of distribution of the fish occurs in the low salinity zone, with the exception of the Cache Slough complex. The degree to which the fish use particular geographic areas depends on salinity, temperature, and turbidity (Nobriga et al. 2008); other factors that may affect their summer distribution include *Microcystis* distribution, and possibly prey density, bathymetric features, or other water quality constituents. As noted previously, Delta Smelt used to be common in the central and south Delta during the summer months, but this is no longer the case (Nobriga et al. 2008).

Population Trends

Relative abundance of juvenile Delta Smelt is presently indexed by the Summer Townet Survey (TNS). The survey was not designed specifically to measure Delta Smelt abundance and catches are low (Honey et al. 2004). Nonetheless, patterns in the annual abundance index provide a useful basic measure of population trends.

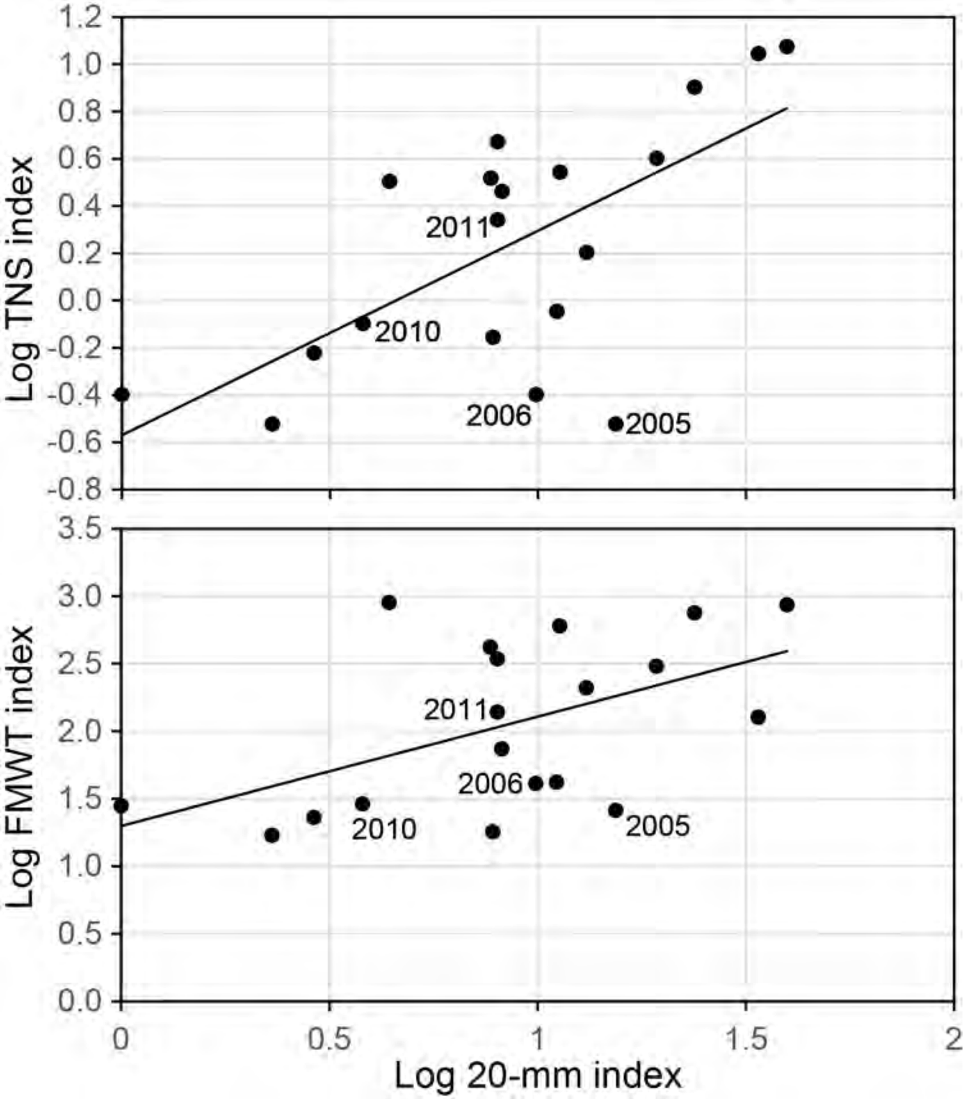
The TNS index rebounded substantially in 2011, but declined to a value consistent with low recent year indices in 2012 (Fig. 3). This pattern of persistently low abundance is consistent with the POD, which began over a decade ago (Sommer et al. 2007, Thomson et al. 2010). During the last decade, TNS abundance indices were especially low from 2005-2009 (Fig. 3). The onset of the 2005-2009 period of low juvenile abundance was characterized by extremely low larvae to juvenile survival in 2005 and 2006 (Fig. 51). Larval survival to juveniles recovered somewhat in the following years, but TNS indices stayed low (Fig. 3). Historically (e.g., early 1970s), high levels of Delta Smelt abundance during summer apparently allowed density dependent effects to occur between summer and fall in some years; this conclusion was still supported after the species declined in the early 1980s, but the apparent carrying capacity was lower (Bennett 2005). The available trawl data suggest that this trend of declining carrying capacity has continued as suggested by the very low Fall Midwater Trawl indices produced by a range of juvenile TNS abundance levels, during the POD years (Fig. 57).

Subadults

Life History

During fall, subadult Delta Smelt primarily rear in the western Delta, Suisun Bay, and Cache Slough complex (Moyle 2002, Bennett 2005, Sommer and Mejia 2013). The center of distribution is in the low-salinity zone (Sommer et al. 2011), with the exception of the Cache Slough complex. The degree to which the fish use particular geographic areas depends on salinity and turbidity (Feyrer et al. 2007). Other factors that may affect their distribution during the fall include *Microcystis* distribution and water temperature in the early fall (September-October), and possibly prey density.

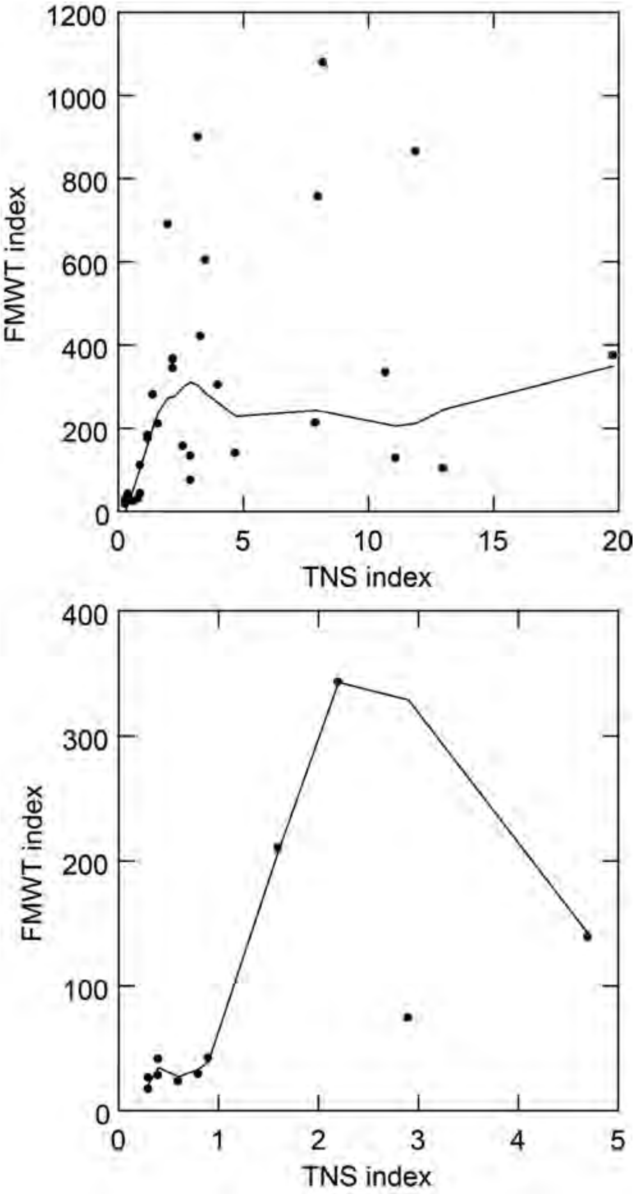
Figure 56. **Relationship of annual index of Delta Smelt abundance from the 20 mm survey (20 mm) with the annual indices from the summer townet survey (TNS) and fall midwater trawl survey (FMWT). Year labels correspond to the comparison years of interest. The linear regressions with all index values log-transformed to address non-normal distributions in the raw data are: Log 20 mm index = 0.57 + 0.87(Log TNS index), n = 19, $p < 0.05$, $R^2 = 0.44$ and Log 20 mm index = 1.30 + 0.81(Log FMWT index), n = 19, $p < 0.05$, $R^2 = 0.27$.**



Population Trends

Population trends for subadult Delta Smelt are presently indexed by the FMWT. Like the TNS, the FMWT was not designed specifically to measure Delta Smelt relative abundance and catches are low (Honey et al. 2004, Newman 2008). The data are nonetheless a useful basic measure of population trends, except perhaps at very low abundance (i.e., FMWT index values less than about 50; Fig. 53). However, the general agreement between the FMWT and subsequent Spring Kodiak Trawl (SKT) sampling (Fig. 53), suggests that FMWT results are a reasonable indicator

Figure 57. **Plots of fall midwater trawl (FMWT) abundance index as a function of summer townet survey (TNS) abundance index for 1982-2013 and 2003-2013. Note the very different scales for both axes. Lines are LOWESS smooths.**



of general trends in abundance of adult Delta Smelt.

The FMWT index rebounded substantially in 2011, but declined to a value consistent with low recent-year indices in 2012 (Fig. 3). During the last decade, FMWT indices were especially low from 2005-2010 (Fig. 3). After the rebound in 2011, the index went back to a lower level similar to the 2005-2010 period. Since 2003, the juvenile to subadult survival index was lowest in 2004. During the four comparison years, the juvenile to subadult survival index was lowest in 2010, but relatively high in the other three years and highest in 2011 (Fig. 51).

Historically, high levels of Delta Smelt abundance during summer apparently resulted in density-dependent mortality between summer and fall in some years (Bennett 2005). This conclusion was still supported after the species declined in the early 1980s, but the apparent carrying capacity, meaning the magnitude of the FMWT index relative to the TNS index, was lower (Fig. 57). The available FMWT data suggest that these trends of density-dependent mortality during the summer-fall and declining carrying capacity have continued (Fig. 57). The close correlation of the FMWT and SKT (Fig. 53) indicates that the factors likely affecting survival of Delta Smelt to the adult spawning population operate earlier in the life cycle (i.e., between the egg and subadult life stages). Additional mortality certainly occurs between the FMWT and SKT but the lack of variability around the regression line suggests there is not a lot of variability in the rate of that mortality. Thus, the relative annual spawning stock appears to be largely determined by fall of the birth year.