

Pelagic Organism Decline Progress Report: 2007 Synthesis of Results

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January 15, 2008

Executive Summary

Abundance indices calculated by the Interagency Ecological Program (IEP) through 2007 suggest recent marked declines in four pelagic fishes in the upper San Francisco Estuary (the Delta and Suisun Bay). These fishes include delta smelt which is listed under State and federal Endangered Species acts and the longfin smelt, which has been proposed for protection under those acts. Although several species show evidence of long-term declines, the recent low levels were unexpected given the relatively moderate winter-spring flows of the past several years.

In response to these changes, the IEP formed a Pelagic Organism Decline (“POD”) work team to evaluate the potential causes. The major findings through 2007 were synthesized using two conceptual modeling approaches. A basic conceptual model was developed that included the following major components: 1) *previous abundance levels*, which describes how continued low abundance of adults leads to juvenile production; 2) *habitat*, which describes how water quality variables (including contaminants and toxic algal blooms) affect estuarine species; 3) *top-down effects*, which posits that predation and water project entrainment affect mortality rates; and 4) *bottom-up effects*, which focuses on food web interactions in Suisun Bay and the west Delta. Our second set of conceptual models focused on temporal and species-specific interactions of these stressors. Towards this end, we developed individual conceptual models for each species that incorporate seasonal and geographic variability in how stressors act upon a species. We also began to consider how stressors may interact in their effects on each species.

Many studies initiated by the POD or initiated by others that will provide important POD information are still in progress. We provide preliminary results from these studies whenever possible, but peer-reviewed products will not be available for some time to come. Readers should be cautious when evaluating the relative importance of the hypotheses presented in this report. Hypotheses not based on peer-reviewed literature should be viewed with more skepticism but they represent the newest thinking on POD issues and may become new areas of research. Highlights of new work completed or ongoing since the previous POD progress report in 2005, organized by major components of the basic conceptual model, include:

1. ***Previous abundance.*** Recent analyses highlight that stock-recruitment mechanisms and survival among life stages have changed from what was found in earlier pre-POD work. Striped bass, longfin smelt, and threadfin shad previously were able to recover from low abundances, but now show limited resilience. Delta smelt now seem to exhibit a significant stock-recruitment relationship possibly because adult abundance is exceptionally low, so summer survival is a less important factor than it may have been in controlling the population abundance.

2. **Habitat.** New analyses of water quality data collected concurrently with fish data highlight the importance of Secchi depth (i.e., water clarity or turbidity), specific conductance (a surrogate for salinity), and water temperature. These relationships vary with season for the three POD species inhabiting the Delta for which data were analyzed. These results have focused new discussion about what constitutes “good habitat” for pelagic fishes. Some incidences of contaminant effects have been observed in bioassay tests of Delta waters; however, the significance of these results for POD fishes or other Delta species needs to be determined.

3. **Top-down.** Striped bass and largemouth bass are probably the major predators on larger fishes in the Delta. The importance of striped bass as a predator on fishes is well known and there is no indication of a major change during the POD years. Largemouth bass has become more abundant concurrent with the invasion of the aquatic macrophyte *Egeria densa*, which has increased habitat for largemouth bass and other invasive species. Although the increase in largemouth bass seems an unlikely single cause for the POD declines, the increase may be an important contributing factor and will likely make recovery more difficult. Entrainment at the CVP and SWP pumps also seems to be an unlikely single cause of POD but may be important in some years for some species. Removal of pre-spawning delta smelt may be especially important. Recent analyses have focused on the importance of reverse flows in Old and Middle rivers and the possible importance of turbidity as an environmental trigger for upstream migration of delta and longfin smelt.

4. **Bottom-up.** The importance of co-occurrence of fish with food continues to be a key area of interest. Much of this discussion focuses on food resources for delta smelt. Overall, total biomass of zooplankton has not changed substantially in delta smelt summer habitat; however species composition has changed. New work is focusing on which zooplankton are available to delta smelt (i.e., can delta smelt catch them) and if there are differences in energetic profitability among prey (i.e., does it take more energy to catch.)

The integration of information that has occurred as a result of preparing this progress report has suggested several areas of research for new or augmented ongoing studies. These areas of research will be highlighted in the 2008 POD workplan which is in preparation.

Introduction

The San Francisco Estuary has been an area of intense interest to humans for many thousands of years because of the ecosystem services it provides. Native Americans exploited the rich food resources available. With the settlement of Europeans, exploitation of resources broadened and accelerated particularly in the mid-1800s. Draining of wetlands for agriculture and urbanization combined with development of an extensive infrastructure for water management and other human activities have been accompanied by declines in nearly all species of native fish (Moyle 2002; Brown and Moyle 2005). The construction and operation of two large water projects, the federal Central Valley Project (CVP), and the State Water Project (SWP) have been especially important. The potential negative effects of these projects on important fisheries were recognized and extensive efforts were made to mitigate the expected effects. Salmon hatcheries were established below some dams and extensive fish screening facilities were established at the pumping facilities in the Delta (Brown et al. 1996). Despite these efforts, populations of important fish species continued to decline in the San Francisco Estuary and its watershed, culminating in listings of a number of species in the 1990s, including winter-run and spring-run Chinook salmon *Oncorhynchus tshawytscha*, Central Valley steelhead *O. mykiss*, delta smelt *Hypomesus transpacificus*, and Sacramento splittail *Pogonichthys macrolepidotus*.

The four primary pelagic fishes of the upper estuary (delta smelt, longfin smelt *Spirinchus thaleichthys*, striped bass *Morone saxatilis*, threadfin shad *Dorosoma petenense*), have shown substantial variability in their populations, with evidence of long-term declines for the first three of these species (Kimmerer et al. 2000; Bennett 2005; Rosenfeld and Baxter 2007). For the three declining species, a substantial portion of the abundance patterns has been associated with variation of outflow in the estuary. However, Fall Midwater Trawl abundance indices for these four pelagic fishes began to decline sharply around 2000, despite relatively moderate hydrology which typically supports at least modest fish production (Sommer et al. 2007). The situation deteriorated over the next several years; abundance indices for 2002-2006 included record lows for delta smelt and age-0 striped bass, and near-record lows for longfin smelt and threadfin shad. By 2004, these declines became widely recognized and discussed as a serious management issue, and collectively became known as the *Pelagic Organism Decline (POD)*.

In response to the POD, the Interagency Ecology Program (IEP) formed a study team in 2005 to evaluate the potential causes of the decline (Sommer et al. 2007). The team organized an interdisciplinary, multi-agency effort including staff from California Department of Fish and Game, California Department of Water Resources, Central Valley Regional Water Quality Control Board, U.S. Bureau of Reclamation, U.S. Environmental Protection Agency, U.S. Geological Survey, California Bay Delta Authority, San Francisco State University, and the University of California at Davis. The study was based on a basic conceptual model of the decline, which continues to be updated and revised as new results are available.

Purpose

The major goal of this report is to synthesize the information collected by the POD investigation. Our approach to synthesize this information is to revise our previous general conceptual model (Sommer et al. 2007) and introduce new conceptual models for each of the POD species: delta

smelt, striped bass, longfin smelt, and threadfin shad. The information used in the synthesis is based primarily on information collected through August 2007. We also introduce important new information from fall 2007 (highlighted in *italics*) to reflect the fact that important additional progress has been made in recent months. These newer results are primarily included in the discussions of conceptual models for individual fish species.

Because the POD involves multiple species in a highly variable and heavily-modified environment with multiple and often interacting stressors, we relied on a *weight of evidence* approach (Burkhardt-Holm and Scheurer 2007) to interpret the results from the large number of POD studies. Using this approach, we examined the multiple types of evidence to develop plausible linkages within our conceptual models. This approach was especially important in the development of the four “species models.” As an outcome of this approach, the present synthesis of the POD results focuses on the linkages within the conceptual models and their contributions to the overall “POD story” and the individual “fish species stories” rather than providing in-depth examinations of relationships between individual stressors and fish abundance.

Many of the POD studies have not been completed or fully evaluated and we wish to emphasize that our conceptual models represent works in progress. Hence, this progress report will be followed by a more complete data synthesis in 2008. This report is the first of two synthesis reports resulting from a new collaboration of the Interagency Ecological Program (IEP) with the National Center for Ecological Analysis and Synthesis (NCEAS). The present report is primarily a product of the IEP POD management team with input from the NCEAS-POD steering committee. The NCEAS-POD steering committee and work groups will take a larger role in developing the 2008 synthesis report.

This report is divided into several major sections. We first provide some basic background on the POD fishes and review the history of the POD. Second, we present a general conceptual model for the POD. This is basically an update of the conceptual model in the 2005 report. Finally, we develop more detailed conceptual models for each of the POD fishes.

This report has the same limitations as earlier reports from the POD management team. Specifically, many studies initiated by the POD or initiated by others that will provide important POD information are still in progress. Preliminary results from these studies are provided whenever possible, but peer-reviewed products from these studies may not be available for some time to come. We encourage readers to be cautious when evaluating the relative importance of the hypotheses presented in this report. Hypotheses not based on peer-reviewed literature should be viewed with more skepticism. We present them because they represent the newest thinking on POD issues and may become new areas of research. Descriptions of completed, ongoing and new POD-related studies are being compiled in the 2008 POD workplan.

Background

One of the interesting features of the POD fish declines is that the declining fish species have many differences in their individual life histories. We briefly review the general life history of each species based on descriptions in Moyle (2002) as background for understanding the

remainder of the report. Readers are referred to Moyle (2002) and the papers cited in the remainder of the report for additional details.

Delta smelt is a slender-bodied fish typically reaching 60-70 mm standard length (SL) with a maximum size of about 120 mm SL. Delta smelt is endemic to the upper San Francisco Estuary, primarily the Delta and Suisun Bay. Delta smelt is generally associated with the low salinity zone locally indexed by X2, which is the location of the 2 psu isohaline measured near the bottom of the water column (Jassby et al. 1995). Delta smelt feed primarily on planktonic copepods, cladocerans, and amphipods. Delta smelt is basically an annual species and spawn in freshwater in the Delta. Upstream migration generally occurs in the late fall or early winter with most spawning taking place from early April through mid-May. Larval delta smelt move downstream with the tides until they reach favorable rearing habitat. A very small percentage of delta smelt is believed to spawn as 2-year olds. Delta smelt was listed as a threatened species by both the federal and state governments in 1993. The species was recently proposed for endangered status.

Longfin smelt typically reach 90-110 mm SL with a maximum size of 120-150 mm SL. In the San Francisco Estuary, longfin smelt generally occur in Suisun, San Pablo, and San Francisco bays as well as in the Gulf of the Farallones, just outside San Francisco Bay. Longfin smelt is anadromous and spawn in the Delta in freshwater. Longfin smelt spawn at 2-years of age. A few female smelt may live a third year but it is not certain if they spawn again. Most spawning takes place from February through April. The larval longfin smelt move downstream with the tides until they reach favorable rearing habitat near X2 and, later, downstream into Suisun and San Pablo bays. Larger longfin smelt feed primarily on opossum shrimps *Neomysis mercedis* and *Acanthomysis* spp. Copepods and other crustaceans can also be important food items, especially for smaller fish. Although other populations of longfin smelt occur on the Pacific Coast, the San Francisco Estuary population was recently proposed for listing under the state and federal Endangered Species acts as a distinct population segment of the species.

Striped bass is native to the Atlantic Coast of North America. It was introduced to California in 1879. Striped bass is a large (> 1 m), long-lived (> 10 years) species. Striped bass is widespread in the San Francisco Estuary watershed as juveniles and adults. The species can be found in the larger river systems downstream of impassable dams and in the coastal ocean. Striped bass is a generalist predator. Larval and juvenile striped bass feed primarily on invertebrates. Larval and small post-larval bass feed mainly on copepods. As the fish grow they consume larger invertebrates and fishes. Striped bass is an anadromous mass spawner. Females spawn at 4-6 years of age and can spawn every year depending on environmental conditions. In the Sacramento River spawning occurs in the upper parts of the tidal portion of the river and lower portions of the riverine portion of the river. A small proportion of spawning occurs in the San Joaquin River within the Delta. Embryos and larvae drift into the Delta and larval striped bass are associated with X2. As the juveniles grow, they disperse throughout the Delta and San Francisco Bay. Although an introduced species, striped bass supports a popular and economically important recreational fishery.

Threadfin shad was introduced to California in 1954 to provide forage for predatory fish in reservoirs. It was planted in the San Francisco Estuary watershed in 1959. Adult threadfin shad

are typically less than 100 mm total length and primarily inhabit freshwater, where they omnivorously filter-feed on phytoplankton, zooplankton, and detritus. They can also selectively sight-feed on individual organisms, primarily zooplankton. Most threadfin shad spawn as 1-year olds in their second summer of life, although some may spawn at the end of their first year. Spawning occurs from April to August, but most occurs in June and July. Larval and juvenile threadfin shad are mainly found in the freshwater portions of the Delta. Threadfin shad is the most abundant pelagic fish in the upper estuary and is exceptionally important as prey for piscivorous species.

The apparently simultaneous declines of these four species of fish were surprising because of the differences in their life histories and differences in how each species utilizes Delta habitats. These differences suggested one or more Delta-wide factors to be important in the declines. The following description of the Pelagic Organism Decline is taken directly from Sommer et al. (2007):

“The Interagency Ecological Program (IEP), a consortium of nine state and federal agencies, has been monitoring fish populations in the San Francisco Estuary (Figure 1) for decades, and has developed one of the longest and most comprehensive data records on estuarine fishes in the world. One of the most widely-used IEP databases is fish catch from the Fall Midwater Trawl Survey, which has been regularly conducted by DFG since 1967 (Stevens and Miller 1983; Sommer et al. 1997). This survey samples the pelagic fish assemblage in the upper estuary, the tidal freshwater and brackish portion of the system from the delta to San Pablo Bay. The most abundant resident pelagic fishes captured are two native species, delta smelt (*Hypomesus transpacificus*) and longfin smelt (*Spirinchus thaleichthys*), and two introduced species, striped bass (*Morone saxatilis*) and threadfin shad (*Dorosoma petenense*). The San Francisco Estuary is physically very dynamic, so it is not surprising that annual abundance of all of these populations is extremely variable (Figure 2), and that much of this variability is associated with hydrology (Figure 3). Historically, the lowest abundance levels for the pelagic fishes typically have occurred in dry years, such as a six-year drought during 1987-1992. Consistent with this observation, several of these species show strong statistical associations with flow during their early life stages (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002a).

We [IEP biologists] became concerned when Fall Midwater Trawl abundance indices for these four pelagic fishes began to decline around 2000 and deteriorated over the next several years (Figure 2). Abundance indices for 2002-2005 included record lows for delta smelt and age-0 striped bass, and near-record lows for longfin smelt and threadfin shad. By 2004, these declines became widely recognized and discussed as a serious issue, and collectively became known as the Pelagic Organism Decline (POD). Longfin smelt and age-0 striped bass showed some recovery in 2006 but delta smelt and threadfin shad remained at low levels. The abundance of delta smelt is of particular concern because it is listed as a threatened species under both federal and state endangered species legislation.

The extreme variability in the data makes it difficult to say whether these indices are truly at unprecedented low levels. Mean catch per trawl with 95% confidence intervals developed using resampling methods indicate that the recent indices are indeed quite low, and for some

species the lowest on record (Figure 2). Abundance improved somewhat for each species during 2006, but the levels remain relatively poor as compared to long-term trends. Moreover, these low abundance levels are remarkable in that winter and spring river flows into the estuary were moderate or very wet (2006) during the recent years (Figure 3), conditions that typically result in at least modest recruitment of most of the pelagic fishes. Longfin smelt is perhaps the best example of this point as the species shows a very strong relationship with delta outflow (Figure 4). The introduction of the overbite clam (*Corbula amurensis*) in 1986 and associated changes in the food web reduced the magnitude of the response of longfin smelt without altering its slope (Kimmerer 2002b). Specifically, the grazing effects from *Corbula* are thought to have resulted in a substantial decline in phytoplankton and calanoid copepods, the primary prey of early life stages of pelagic fishes. As a consequence, comparable levels of flow did not generate the expected levels of fish biomass (as indexed by abundance) after 1986. During the POD years, the abundance indices for longfin smelt deviated substantially from both the pre- and post-*Corbula* relationships with outflow. The situation is similar for young-of-the-year striped bass, whose historical association with outflow was also altered by *Corbula*, whereas the recent abundance indices were well below expected levels based on outflow. Hence, it appears that the response of these pelagic fishes to environmental conditions has fundamentally changed.”

The recognition of the POD as an important management issue resulted in IEP undertaking a new program of data analysis and research. The early steps in this program were also summarized by Sommer et al. (2007):

“In response to the POD, the IEP formed a work team in 2005 to evaluate the potential causes of the decline (IEP 2005, 2006). The team organized an interdisciplinary, multi-agency effort including staff from DFG, California Department of Water Resources, Central Valley Regional Water Quality Control Board, U.S. Bureau of Reclamation, U.S. Environmental Protection Agency, U.S. Geological Survey, California Bay Delta Authority, San Francisco State University, and the University of California at Davis. A suite of 47 studies was selected based on the ability of each project to evaluate the likely mechanisms for the POD, and the feasibility of each project in terms of methods, staffing, costs, timing, and data availability. In addition to funding for regular IEP monitoring, the program’s budget was augmented by \$2.4 million in 2005, and \$3.7 million for 2006 and 2007 to fund the recommended research.”

Initial Conceptual Model Development

Based on the initial observation that fish abundance indices declined abruptly around 2000, the POD Management Team developed an initial conceptual model (IEP 2005). Specifically, we proposed three general factors that may have been acting individually or in concert to lower productivity of pelagic fish populations: 1) toxins; 2) exotic species; and 3) water projects.

After the completion of the first set of studies in late 2005, alternative models were developed based on the results available at that time. Matrix models were created for the four target fish species (delta smelt, longfin smelt, threadfin shad and juvenile striped bass) to summarize the

potential role of various stressors in the recent decline. The matrices depicted the consensus of professional judgment of the POD Management Team regarding the extent to which each stressor was likely to have affected each species-life stage during recent years. The level of information used to support the consensus was also ranked. The nine stressors evaluated were: 1) Mismatch of larvae and food; 2) reduced habitat space; 3) adverse water movement/transport; 4) entrainment; 5) toxic effects on fish; 6) toxic effects on fish food items; 7) harmful *Microcystis aeruginosa* blooms; 8) *C. amurensis* effects on food availability; and 9) disease and parasites.

These earlier conceptual models provided a useful way to (1) summarize our understanding of factors that may have contributed to the POD and (2) design the initial suite of research studies; however, they proved to have several shortcomings. First, they did not adequately reflect spatial and temporal variation in the nine stressors evaluated. Second, new data showed several assumptions to be incorrect. Finally, the initial models were relatively cumbersome.

2007 Conceptual Models

The 2007 models represent an improvement over the earlier efforts, but it is important to recognize that they still have numerous limitations. Many of the results and inferences are preliminary at this writing and have not yet been peer-reviewed, so the new models should be considered preliminary, like the previous models. Moreover, the models may have been influenced by potential biases in the sampling programs. Several changes in the size and distribution of the target species have the potential to change our perception of trends in abundances and distributions. This, in turn, would affect our conceptual models. Throughout this discussion we use indices of abundance such as the Fall Midwater Trawl and Summer Townet surveys or catch-per-unit-effort as estimates of abundance. The relationship between these indices of abundance and the actual population size of any species is not known.

Finally, it is important to recognize that the recent decline in pelagic fish species is superimposed over long-term declines for several of these species and their long-term relationships with other environmental factors. Change-point analyses (Manly and Chotkowski 2006, Manly and Chotkowski, unpublished data) suggest that distinctly different statistical models might be appropriate for different time periods. As described below, a clear line divides the POD era from the years preceding it for some species. There also appear to be multiple periods within the historical record preceding the POD and the periods are not always the same across species. The conceptual models developed here explicitly focus on mechanisms that might have contributed to the decline of pelagic fishes during the POD era. However, the historical antecedents to the POD are a crucial part of the story.

Note that these conceptual models are not intended to exclude other explanations for the observed changes in fish abundance, nor are they designed to set priorities for resource management. Instead, they are intended as examples of how the different stressors may be linked. Moreover, no single model component can explain the declines of all four species. The models will be developed and refined as additional data become available. In the meantime, we believe the new models provide a useful basis for organization of the POD study and the initial synthesis of the results.

Basic Conceptual Model

We have developed an intentionally simple basic conceptual model to describe possible mechanisms by which a combination of long-term and recent changes in the ecosystem could produce the observed pelagic fish declines (Figure 5). This conceptual model is rooted in classical food web and fisheries ecology and contains four major components: (1) prior fish abundance, which posits that continued low abundance of adults leads to reduced juvenile production (i.e., stock-recruit effects); (2) habitat, which posits that estuarine water quality variables, disease, and toxic algal blooms in the estuary affect survival and reproduction; (3) top-down effects, which posits that predation and water project entrainment affect mortality rates; and (4) bottom-up effects, which posits that food web interactions affect survival and reproduction. For each model component, our working hypotheses are: (1) the component was responsible for an adverse change at the time of the POD; and (2) this change resulted in a population-level effect. The model components are described in detail in the following sections. The basic conceptual model generally does not evaluate the relative importance of the model components. Often the data are not sufficient to make such judgments. Also it is likely that the relative importance of various components changes with specific environmental conditions (e.g. river flow) within and among years. Finally, the relative importance of factors will differ among the four species. We begin to address this final point in the individual species models presented later in the report.

Previous Abundance

The relationship between numbers of spawning fish and the numbers of young subsequently recruiting to the adult population is known as a stock-recruit relationship. Stock-recruit 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). Different forms of stock-recruit relationships are possible, including density-independent, density-dependent, and density-vague types. The latter refers to situations where there is not a statistically demonstrable stock-recruit relationship observable in available data. In any form of a stock-recruit model, there is a point at which low adult stock will result in low juvenile abundance and subsequent low recruitment to future adult stocks even under favorable environmental conditions while the stock 'rebuilds' itself. There is evidence for a density-dependent stock-recruit relationship in San Francisco Estuary striped bass (Kimmerer et al. 2000). However, the adult striped bass stock is currently not particularly low (Figure 6), so stock size is not likely a mechanism contributing to recent very low age-0 striped bass abundance. In other words, there appears to be enough adults in the system for the population to recover.

There is a significant stock-recruit relationship for threadfin shad (Feyrer and Sommer, unpublished data). Fall abundance of pre-adults is a significant predictor of young-of-year abundance the following summer (Figure 7). Similar relationships have been proposed for longfin smelt (Tina Swanson, The Bay Institute, unpublished data). However, current populations of longfin smelt and threadfin shad are similar to low populations observed in previous years (Figure 2). Threadfin shad rebounded fully from previous abundance lows in the 1970s and 1980s. Longfin smelt populations rebounded somewhat in the 1990s following

previous lows during the 1987-1992 drought. Note that recovery of these species is only expected if the factors affecting recruitment have not changed substantially. If the factors affecting survival from egg to adult have changed substantially since the beginning of the POD, then recovery might not occur even though recovery from low abundance occurred in the past. The changes in the statistical relationships between outflow and population abundance indices for longfin smelt and striped bass (Figure 4) are evidence that changes in the drivers of recruitment have occurred. These changes are discussed in more detail in subsequent sections.

From a stock-recruit perspective, the present low abundance of delta smelt is of particular concern. The current population is an order of magnitude smaller than at any time previously in the record (Figure 2). The delta smelt stock-recruit relationship appears to be density vague over the entire period that data is available (Bennett 2005), meaning there is no clear relationship between the adult spawning population and the number of adult recruits expected in the following year, as measured by the Fall Midwater Trawl. There was also a historically weak statistical association between summer abundance (as measured by the Summer Towntnet Survey) and abundance a few months later during the Fall Midwater Trawl Survey, suggesting that delta smelt year-class strength was often set during late summer. However, Feyrer et al. (2007) found that the abundance of pre-adult delta smelt during fall was a statistically significant predictor of juvenile delta smelt abundance the following summer, for the time period 1987-2005. Similarly, delta smelt summer abundance is a statistically significant predictor of fall abundance. These relationships are particularly strong for the period 2000-2006 (Figure 8). The strong relationship in summer to fall survival since 2000 (Figure 8) suggests that the primary factors affecting juvenile survival recently changed and shifted to earlier in the life cycle. These observations strongly suggest that recent population trends are outside the historical realm of variability and resilience shown by these species, particularly delta smelt. Thus, recovery is likely to require changes in the stressors that have produced the current low levels of abundance and perhaps stressors that have since become more important.

Given the unprecedented low abundance of delta smelt since 2000 (Figure 8), 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 spirals to extinction. For delta smelt, possible mechanisms for Allee effects include mechanisms directly related to reproduction and genetic fitness such as difficulty finding mates, genetic drift, and inbreeding. Other mechanisms related to survival such as increased vulnerability to predation are also possible and will be briefly discussed in the “top-down” model component section. The interactive effects of multiple Allee effects have not been well explored in ecology and may have important implications for species conservation (Berec et al. 2006).

Habitat

Aquatic habitats are the suites of physical, chemical, and biological factors that species occupy (Hayes et al. 1996). The maintenance of appropriate habitat quality is essential to the long-term health of aquatic resources (Rose 2000; Peterson 2003). For the habitat component of the model,

a key point is that habitat suitability affects all other components of the model (Figure 5). Hence, changes in habitat not only affect pelagic fishes, but also their predators and prey. Although not a focus of this report, we expect that the habitats of the POD species are especially vulnerable to future climate change. Thus, any findings regarding habitat must be considered in light of expected changes in climate and changes in water management operations anticipated in response to climate change.

Pelagic Fish Habitat: Habitat for pelagic fishes is open water, largely away from shorelines and vegetated inshore areas except perhaps during spawning. This includes large embayments such as Suisun Bay and the deeper areas of many of the larger channels in the Delta. More specifically, pelagic fish habitat is water with suitable values for a variety of physical-chemical properties, including salinity, turbidity, and temperature, suitably low levels of contaminants, and suitably high levels of prey production to support growth. Thus, pelagic fish habitat suitability in the estuary can be strongly influenced by variation in freshwater flow (Jassby et al. 1995; Bennett and Moyle 1996; Kimmerer 2004). Several of the POD fishes use a variety of tidally-assisted swimming behaviors to maintain themselves within open-water areas where water quality and food resources are favorable (Bennett et al. 2002). The four POD fishes also distribute themselves at different values of salinity within the estuarine salinity gradient (Dege and Brown 2004), so at any point in time, salinity is a major factor affecting their geographic distributions. As mentioned earlier, pelagic habitat quality in the San Francisco Estuary can be characterized by changes in X2. The abundance of numerous taxa increases in years when flows into the estuary are high and the 2 psu isohaline is pushed seaward (Jassby et al. 1995), implying that the quantity or suitability of estuarine habitat increases when outflows are high.

Based on a 36-year record of concurrent midwater trawl and water quality sampling, there has been a long-term decline in fall habitat environmental quality for delta smelt and striped bass, but not for threadfin shad (Feyrer et al. 2007). The long-term environmental quality declines for delta smelt and striped bass are defined by a lowered probability of occurrence in samples based on changes in specific conductance and Secchi depth. Notably, delta smelt and striped bass environmental quality declined recently coinciding with the POD (Figure 9). The greatest changes in environmental quality occurred in Suisun Bay and the San Joaquin River upstream of Three Mile Slough and southern Delta (Figure 10). There is evidence that these habitat changes have had population-level consequences for delta smelt. The inclusion of specific conductance and Secchi depth in the delta smelt stock-recruit relationship described above improved the fit of the model, suggesting adult numbers and their habitat conditions exert important influences on recruitment.

The importance of salinity in this study was not surprising, given the relationships of population abundance indices with X2 for many species. Fall salinity has been relatively high during the POD years, with X2 positioned further upstream, despite moderate to high outflow conditions during the previous winter and spring of most years. Recent increases in fall salinity could be due to a variety of anthropogenic factors although the relative importance of different changes have not yet been fully assessed. *Initial results from 2007 POD studies have identified increased duration in the closure of the Delta Cross Channel, operations of salinity gates in Suisun Marsh, and changes in export/inflow ratios (i.e. Delta exports/reservoir releases) as contributing factors.*

There appeared to be a curious anomaly in the salinity distribution of delta smelt collected during the September 2007 survey of the Fall Midwater Trawl. All seven delta smelt collected during this survey were captured at statistically significant higher salinities than what would be expected based upon the relationship generated by Feyrer et al. (2007). There could be any number of reasons why this occurred, including the substantial Microcystis bloom which occurred further downstream than normal and may have affected the distribution of biological organisms.

The importance of Secchi depth (a measure of water clarity or, conversely, turbidity) in the long-term changes in pelagic fish environmental quality (Feyrer et al. 2007) was more surprising. Unlike salinity, interannual variation in water clarity in the Delta is not primarily a function of flow variation (Jassby et al. 2002). The primary hypotheses to explain the increasing water clarity are (1) reduced sediment supply due to dams in the watershed (Wright and Schoellhamer 2004), (2) sediment washout from very high inflows during the 1982-1983 El Nino (Jassby et al. 2005), and (3) biological filtering by submerged aquatic vegetation (Brown and Michniuk 2007; Dave Schoellhamer, USGS, unpublished data). In lakes, high densities of *Egeria densa* and similar plants can mechanically filter suspended sediments from the water column (Scheffer 1999). Vegetation has also been shown to facilitate sedimentation in marshes and estuaries (Yang 1998; Braskerud 2001; Pasternack and Brush 2001; Leonard et al. 2002). The mechanisms causing the negative associations between water clarity and delta smelt and striped bass occurrence are unknown, but based on research in other systems (e.g. Gregory and Levings 1998), Nobriga et al. (2005) hypothesized that higher water clarity increased predation risk for delta smelt, young striped bass, and other fishes typically associated with turbid water.

Initial results from a POD-funded study indicate that E. densa, an introduced species, is continuing to spread by expansion of existing patches and invasion of new areas (Erin Hestir et al., UC Davis, unpublished data). Areal coverage of E. densa increased more than 10% per year from 2004 to 2006. Light penetration and water velocity are the factors likely controlling its distribution in the Delta and salinity likely limits its penetration into the estuary (Hauenstein and Ramirez 1986). In clear water, E. densa can grow to depths of 6 m (Anderson and Hoshovsky 2000). If Delta clearing continues, it seems likely that E. densa will spread into progressively deeper water.

Trends in environmental quality for delta smelt differ during the summer period. Specific conductance, Secchi depth, and water temperature all significantly predict delta smelt occurrence in summer, suggesting they all interact to affect delta smelt distribution (Nobriga et al. in press). However, none of the water quality variables were correlated with delta smelt abundance (as indexed by the Summer Towntnet Survey) at the scale of the entire estuary (Nobriga et al. in press). Based on these habitat variables, Nobriga et al. (in press) identified three distinct geographic regions that had similar long-term trends in the probability of delta smelt occurrence. The primary habitat region was centered on the confluence of the Sacramento and San Joaquin rivers near Sherman Island; delta smelt relative abundance was typically highest in the confluence region throughout the study period. There were two marginal habitat regions, one centered on Suisun Bay where specific conductance was highest and delta smelt relative abundance varied with specific conductance. The third region was centered on the San Joaquin River and the southern Delta. The San Joaquin River region had the warmest water temperatures

and the highest water clarity. Water clarity increased strongly in this region during 1970-2004. In the San Joaquin River region, delta smelt relative abundance was correlated with water clarity; catches declined rapidly to zero from 1970-1978 and remained consistently near zero thereafter. These results support the hypothesis that basic water quality parameters are predictors of summer delta smelt relative abundance, but only at regional spatial scales. These regional differences are likely due to variability in habitat rather than differences in delta smelt responses. Water management operations are targeted on keeping the lower Sacramento and San Joaquin rivers fresh for water exports so the range in salinity is probably smaller than the range in turbidity. In the Suisun Bay region, there is a wider range of salinities relative to the other regions, so a response to that variable is possible.

Contaminants and Disease: In addition to habitat changes from salinity, turbidity and invasive aquatic vegetation such as *E. densa*, and contaminants can change ecosystem functions and productivity through numerous pathways. The trends in contaminant loadings and their ecosystem effects are not well understood. We are currently evaluating direct and indirect toxic effects on the POD fishes of both man-made contaminants and natural toxins associated with blooms of *M. aeruginosa* (a cyanobacterium or blue-green alga). The main indirect contaminant effect we are investigating is inhibition of prey production.

Concern over contaminants in the Delta is not new. There are long standing concerns related to mercury and selenium in the watershed, Delta, and Bay (Linville et al. 2002; Davis et al. 2003). Phytoplankton growth rate may occasionally be inhibited by high concentrations of herbicides (Edmunds et al. 1999). New evidence indicates that phytoplankton growth rate may at times be inhibited by ammonium concentrations in and upstream of Suisun Bay (Wilkerson et al. 2006, Dugdale et al. 2007, Dugdale et al unpublished). Toxicity to invertebrates has been noted in water and sediments from the Delta and associated watersheds (e.g., Kuivila and Foe 1995; Giddings 2000; Werner et al. 2000; Weston et al. 2004). Undiluted drainwater from agricultural drains in the San Joaquin River watershed can be acutely toxic (quickly lethal) to fish and have chronic effects on growth (Saiki et al. 1992). Evidence for mortality of young striped bass due to discharge of agricultural drainage water containing rice herbicides into the Sacramento River (Bailey et al. 1994) led to new regulations for discharge of these waters. Bioassays using caged fish have revealed DNA strand breakage associated with runoff events in the watershed and Delta (Whitehead et al. 2004). 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, but concentrations of individual pesticides were low and much less than would be expected to cause acute mortality. However, the effects of exposure to the complex mixtures of pesticides actually present are unknown.

We initiated several studies to address the possible role of contaminants and disease in the POD. Our primary study consists of twice-monthly monitoring of ambient water toxicity at fifteen sites in the Delta and Suisun Bay. In 2005 and 2006, standard bioassays using the amphipod *Hyaella azteca* had low (<5%) frequency of occurrence of toxicity (Werner et al. unpublished data). However, preliminary results from 2007, a dry year, suggest the incidence of toxic events was higher this year. Parallel testing with the addition of piperonyl butoxide, an enzyme inhibitor, indicated that both organophosphate and pyrethroid pesticides may have contributed to the

observed 2007 toxicity. Most of the tests that have been positive for *H. azteca* toxicity have come from water samples from the lower Sacramento River. Pyrethroids are of particular interest because use of these insecticides has increased (Ameg et al. 2005, Oros and Werner 2005) as use of some organophosphate insecticides has declined. Toxicity of sediment-bound pyrethroids to macroinvertebrates has also been observed in watersheds upstream of the Delta (Weston et al. 2004, 2005).

Larval delta smelt bioassays were conducted simultaneously with a subset of the invertebrate bioassays. The water samples for these tests were collected from six sites during May-August of 2006 and 2007. Results from 2006 indicate that delta smelt is highly sensitive to high levels of ammonia, low turbidity, and low salinity. There is some preliminary indication that reduced survival under low salinity conditions may be due to disease organisms (Werner, unpublished data). No significant mortality of larval delta smelt was found in the 2006 bioassays (Werner 2006), but there were two instances of significant mortality in June and July of 2007 (Werner, unpublished). In both cases, the water samples were collected from sites along the Sacramento River and had relatively low turbidity and salinity and moderate levels of ammonia. It is also important to note that no significant *H. azteca* mortality was seen in these water samples. While the *H. azteca* tests are very useful for detecting biologically relevant levels of water column toxicity, interpretation of the *H. azteca* test results with respect to fish should proceed with great caution. The relevance of the bioassay results to field conditions remains to be determined.

We have also monitored blooms of the toxic cyanobacterium *Microcystis aeruginosa*. Large blooms of *M. aeruginosa* were first noted in the Delta in 1999 (Lehman et al. 2005). Further studies (Lehman et al. in prep.) suggest that microcystins, the toxic chemicals associated with the algae, probably do not reach concentrations directly toxic to fishes, but during blooms, the microcystin concentrations may be high enough to impair invertebrates, which could influence prey availability for fishes. The *M. aeruginosa* blooms peak in the freshwaters of the central Delta during the summer at warm temperatures (20-25°C; Lehman et al. in prep). Longfin smelt and delta smelt are generally not present in this region of the Delta during summer (Nobriga et al. in press; Rosenfield and Baxter 2007) so *M. aeruginosa* toxicity is not likely a factor in their recent decline. However, large striped bass (Moyle 2002) and all life stages of threadfin shad occur widely in the central and south Delta during summer, and thus may be at higher risk. Moreover, in the low flow conditions of 2007, blooms of this cyanobacterium spread far downstream to the west Delta and beyond during summer (Lehman, unpublished data), so toxicity may have been a much broader issue than previously.

The POD investigations into potential contaminant effects also include the use of biomarkers that have been used previously to evaluate toxic effects on POD fishes (Bennett et al. 1995; Bennett 2005). The results to date have been mixed. Histopathological and viral evaluation of young longfin smelt collected in 2006 indicated no histological abnormalities associated with toxic exposure or disease (Foott et al. 2006). There was also no evidence of viral infections or high parasite loads. Similarly, young threadfin shad showed no histological evidence of contaminant effects or of viral infections (Foott et al. 2006). Parasites were noted in threadfin shad gills at a high frequency but the infections were not considered severe. Thus, both longfin smelt and threadfin shad were considered healthy in 2006. Adult delta smelt collected from the Delta during winter 2005 also were considered healthy, showing little histopathological evidence for

starvation or disease (Teh et al. unpublished). However, there was some evidence of low frequency endocrine disruption. In 2005, 9 of 144 (6%) of adult delta smelt males were intersex, having immature oocytes in their testes (Teh et al. unpublished).

In contrast, preliminary histopathological analyses have found evidence of significant disease in other species and for POD species collected from other areas of the estuary. Massive intestinal infections with an unidentified myxosporean were found in yellowfin goby *Acanthogobius flavimanus* collected from Suisun Marsh (Baxa et al. in prep.). Severe viral infection was found in inland silverside *Menidia beryllina* and juvenile delta smelt collected from Suisun Bay during summer 2005 (Baxa et al. in prep.). Lastly, preliminary evidence suggests that contaminants and disease may impair striped bass. Ostrach et al. (in prep.) found high occurrence and severity of parasitic infections, inflammatory conditions, and muscle degeneration in young striped bass collected in 2005; levels were lower in 2006. Several biomarkers of contaminant exposure including P450 activity (i.e., detoxification enzymes in liver), acetylcholinesterase activity (i.e., enzyme activity in brain), and vitellogenin induction (i.e., presence of egg yolk protein in blood of males) were also reported from striped bass collected in 2006 (Ostrach et al. in prep.). Further, striped bass may be especially vulnerable to contaminant effects because the long lived females can sequester contaminants bioaccumulated over several years in egg yolk, resulting in contaminant effects in developing embryos and larvae.

Habitat for Other Aquatic Organisms: Much of the previous discussion about how physical conditions and water quality affect pelagic fishes is also relevant to other aquatic organisms including plankton and the benthos. It is important to keep in mind that river flows influence estuarine salinity gradients and water residence times. The residence time of water affects both habitat suitability for benthos and the transport of pelagic plankton. High tributary flow leads to lower residence time of water in the Delta (days), which generally results in lower plankton biomass (Kimmerer 2004), but also lower cumulative entrainment effects in the Delta (Kimmerer and Nobriga in press). In contrast, higher residence times (a month or more), which result from low tributary flows, may result in higher plankton biomass. This can increase food availability for planktivorous fishes; however, much of this production may be lost to water diversions under low flow conditions. Under extreme low flow conditions, long water residence times may also promote high biological oxygen demand when abundant phytoplankton die and decompose (Lehman et al. 2004; Jassby and Van Nieuwenhuysse 2006). Recent particle tracking modeling results for the Delta show that residence times in the southern Delta are highly variable depending on Delta inflow, exports, and particle release location (Kimmerer and Nobriga, in press). Very high inflow leads to short residence time. The longest residence times occur in the San Joaquin River near Stockton under conditions of low inflow and low export flow.

Salinity variation can have a major effect on the benthos, which occupy relatively “fixed” geographical positions along the gradient of the estuary. While the distributions of the benthos can undergo seasonal and annual shifts, benthic organisms cannot adjust their locations as quickly as the more mobile pelagic community. Analyses of long-term benthic data for four regions of the upper San Francisco estuary indicate that two major factors control community composition: species invasions, and salinity (Peterson et al. in prep.). Specifically, the invasion of the clam *C. amurensis* in the late 1980s resulted in a fundamental shift in the benthic community; however, the center of distribution of *C. amurensis* and other benthic species varies

with flow and the resulting salinity regime. So at any particular location in the estuary, the benthic community can change substantially from year to year as a result of environmental variation and species invasions (Figure 11). As will be discussed below, these changes in the benthos can have major effects on food availability to pelagic organisms.

Climate Change Effects on Habitat: There are several reasons we expect climate change will have negative long-term influences on pelagic habitat suitability for the POD fishes. First, there has been a trend toward more Sierra Nevada precipitation falling as rain earlier in the year (Roos 1987, 1991; Knowles and Cayan 2002, 2004). This increases the likelihood of winter floods and may have other effects on the hydrographs of Central Valley rivers and Delta salinity. Altered hydrographs interfere with pelagic fish reproduction, which is usually tied to historical runoff patterns (Moyle 2002). Second, sea level is rising (IPPC 2001). Sea level rise will increase salinity intrusion unless sufficient freshwater resources are available to repel the seawater. This will shift fish distributions upstream and possibly further reduce habitat area for some species. Third, climate change models project warmer temperatures in central California (Dettinger 2005). As stated above, water temperatures do not currently have a strong influence on POD fish distributions. However, summer water temperatures throughout the upper estuary are fairly high for delta smelt. Mean July water temperatures in the upper estuary are typically 21-24°C (Nobriga et al. in press) and the lethal temperature limit for delta smelt is about 25°C (Swanson et al. 2000). Thus, if climate change resulted in summer temperatures in the upper estuary exceeding 25°C, delta smelt would have little chance of maintaining viable populations.

Top-Down

This model component proposes that the most recent fish declines can be envisioned as the result of the interactive, top-down influence of two kinds of “predators”, piscivorous fishes and water diversions. Note that predation is a common mechanism by which weakened fish are ultimately killed. Thus, increased predation can be a manifestation of other changes in the ecosystem like decreased habitat suitability, starvation, and disease. However, in the top-down section of our conceptual model, we are referring to elevated predation on healthy individuals. Thus, the top-down effects are predicated on the hypothesis that consumption or removal of healthy fish biomass by piscivores (principally striped bass and largemouth bass *Micropterus salmoides*) and water diversions (SWP/CVP exports; power plant diversions) increased around 2000. This could have occurred if one or more of the following happened: water diversions and exports increased during periods the POD fishes were vulnerable to them; piscivorous fishes became more abundant relative to the POD fishes; pelagic fish distribution shifted to locations with higher predation risk (e.g. habitat changes); or the POD fishes became more vulnerable to predation as a consequence of their extremely low population size (i.e., predation could contribute to the Allee effect hypothesized in the “previous abundance” section) or increases in water clarity.

Predation-driven Allee effects can arise from diminished anti-predator behavior or increased predator swamping of individuals in smaller prey groups (Berec et al., 2006). They are most likely to occur with generalist predators in situations where predation is a major source of mortality, and predation refuges are limited (Gascoigne et al. 2004). In this situation individuals of depleted populations continue to be consumed even though they are at low density. More specialized predators often switch between abundant prey and consequently reduce consumption

of rare prey species. As will be described below, the combination of a widely distributed pelagic piscivore (striped bass), an efficient littoral piscivore (largemouth bass), cumulative entrainment losses of multiple life stages, and decreased habitat suitability (Figure 9) suggest the conditions listed by Gascoigne et al. (2004) could apply in the Delta.

Predation Effects: This hypothesis suggests that predation effects have increased in all water year types as a result of increased populations of pelagic and inshore piscivores. In the pelagic habitat, age-1 and age-2 striped bass appear to have declined more slowly than age-0 striped bass (compare Figure 2 with Figure 12, CDFG, unpublished data). Adult striped bass abundance increased in the latter 1990s (Figure 6) so high striped bass predation pressure on smaller pelagic fishes in recent years is probable. Further, largemouth bass abundance has increased in the Delta over the past few decades (Brown and Michniuk 2007). Analyses of fish salvage data show this increase occurred somewhat abruptly in the early 1990s and has been sustained since (Figure 13). The increase in salvage of largemouth bass occurred during the time period when *E. densa*, an introduced aquatic macrophyte was expanding its range in the Delta (Brown and Michniuk 2007). The habitat provided by beds of *E. densa* provide good habitat for largemouth bass and other species of centrarchids. Thus, the increased abundance of this introduced predator was likely caused by an increase in an introduced plant, which provided favorable habitat. The areal coverage of *E. densa* in the Delta continued to expand by more than 10% per year from 2004 to 2006, by infesting a greater portion of channels and invasion of new habitat (E. Hestir et al., U.C. Davis, unpublished data). This suggests that populations of largemouth bass and other species using submerged aquatic vegetation will continue to increase. Although none of the IEP surveys adequately tracks largemouth bass population trends, the Delta has become the top sport fishing destination in North American for largemouth bass, which illustrates the recent success of this species. Each year, lucrative fishing tournaments are held in the Delta to take advantage of the large number of trophy-sized bass in the region. Largemouth bass have a much more limited distribution in the estuary than striped bass, but a higher per capita impact on small fishes (Nobriga and Feyrer 2007). Increases in largemouth bass may have had a particularly important effect on threadfin shad and striped bass, whose earlier life stages occur in littoral habitat (Grimaldo et al. 2004; Nobriga and Feyrer 2007).

A change in predation pressure may, in part, be an effect of interactions between biotic and abiotic conditions. Natural, co-evolved piscivore-prey systems typically have an abiotic production phase and a biotic reduction phase each year (e.g., Rodriguez and Lewis 1994). Changing the magnitudes and durations of these cycles greatly alters their outcomes (e.g., Meffe 1984). Generally, the relative stability of the physical environment affects the length of time each phase dominates and thus, the importance of each. Biotic interactions like predation will have stronger community-structuring influence in physically stable systems (e.g., lakes). Historically in the estuary, the period of winter-spring high flow was the abiotic production phase, when most species reproduced. The biotic reduction phase probably encompassed the low-flow periods in summer-fall. Multi-year wet cycles probably increased (and still do) the overall 'abiotic-ness' of the estuary, allowing populations to increase. Drought cycles likely increased the estuary's 'biotic-ness' (e.g., Livingston et al. 1997), with low reproductive output and increased effect of predation on population abundance. Our managed system has reduced flow variation much of the time and in some locations more than others. This has probably affected the magnitudes and durations of abiotic and biotic phases (e.g., Nobriga et al. 2005). In

other words, reduced flow variability in the estuary may have exacerbated predation effects. However, there is no clear evidence that such changes have been abrupt enough to account for the POD.

Entrainment: Major water diversions in the delta include the SWP and CVP export facilities, power plants, and agricultural diversions. Of these, the patterns of agricultural diversions are the least likely to have changed during the pelagic fish decline. A detailed study of one of these diversions found evidence that their effects on delta smelt are small (Nobriga et al. 2004). As a consequence, our discussion focuses on the power plant and export diversions.

The two power plants of concern are located in the western Delta at Antioch and Pittsburgh. Nonconsumptive water use by the power plants may reach 3200 cfs, which might be enough to create a substantial entrainment risk for fishes residing in the vicinity (Matica and Sommer, in prep.). Studies in the late 1970s indicated that losses of pelagic fishes can be very high. The recent effects of the diversions are unknown; however, the distribution of some pelagic fishes including young striped bass and delta smelt is centered near these diversions. There may also be some risk to fishes created by thermal pollution or residual chlorine from antifouling activities. The magnitude of these risks is unknown. However, operators of these facilities report that the power plants were run relatively infrequently during the POD years, so these power plants seem unlikely as a primary cause of the POD.

Because large volumes of water are drawn from the estuary, water exports and inadvertent fish entrainment at the SWP and CVP export facilities are among the best-studied top-down effects in the San Francisco Estuary (Sommer et al. 2007). The export facilities are known to entrain most species of fish in the upper Estuary (Brown et al. 1996), and are of particular concern in dry years, when the distributions of young striped bass, delta smelt, and longfin smelt shift closer to the diversions (Stevens et al. 1985; Sommer et al. 1997). As an indication of the magnitude of the effects, approximately 110 million fish were salvaged at the SWP screens and returned to the Delta over a 15-year period (Brown et al. 1996). However, this number greatly underestimates the actual number of fish entrained. It does not include losses at the CVP. Even for the SWP alone, it does not account for mortality of fish in Clifton Court Forebay and the waterways leading to the diversion facilities, larvae < 20 mm FL are not collected by fish screens, and losses of fish > 20 mm FL are inefficiently removed by the louver system.

One piece of evidence that export diversions played a role in the POD is the substantial increases in winter CVP and SWP salvage that occurred contemporaneously with recent declines in each of the four primary fishes (Figure 14). Increased winter entrainment of delta smelt, longfin smelt and threadfin shad represents a loss of pre-spawning adults and all their potential progeny. Similar increases in the salvage of littoral species including centrarchids and inland silverside were observed during the same period (Figure 15). The littoral species are less influenced by flow changes than the POD fishes. However, as mentioned earlier for largemouth bass, the increases in salvage for centrarchids may be at least partially a result of the range expansion of *E. densa*, which provides favored habitat. This hypothesis is supported by the observation that the greatest increases in centrarchid salvage occurred at the CVP. The intake of the CVP is located in an area with significant areas of *E. densa* nearby. Nonetheless, the increase in entrainment of both groups of fishes suggests a large change in the hydrodynamic influence of the export

diversions during recent winters. Note that winter salvage levels subsequently decreased to very low levels for all POD species during the winters of 2005-2006 and 2006-2007, possibly due to the very low numbers of fish that appear to remain in the estuary.

In trying to evaluate the mechanism(s) for increased winter-time salvage, POD studies by USGS made three key observations (IEP 2005). First, there was an increase in exports during winter as compared to previous years (Figure 16). Second, the proportion of tributary inflows shifted. Specifically, San Joaquin River inflow decreased as a fraction of total inflow around 2000, while Sacramento River increased (Figure 17). Finally, there was an increase in the duration of the operation of barriers placed into south Delta channels during some months. These changes may have contributed to a shift in Delta hydrodynamics that increased fish entrainment.

These observations led to a hypothesis that the hydrodynamic change could be indexed using net flows through Old and Middle rivers (Figure 1B), which integrate changes in inflow, exports, and barrier operations (Arthur et al. 1996; Monsen et al. 2007). Net or residual flow refers to the calculated flow when the effects of the tide are mathematically removed. An initial analysis revealed that there was a significant inverse relationship between net Old and Middle rivers flow and winter salvage of delta smelt at the SWP and CVP (P. Smith, unpublished). These analyses were subsequently updated and extended to other pelagic fishes (Figure 18, L. Grimaldo, in preparation). The general pattern is that POD species salvage is low when Old and Middle rivers flow are positive.

The hydrologic and statistical analyses suggest a reasonable mechanism by which winter entrainment increased during the POD years; however, the direct population-level effects of increased entrainment are less clear. As part of the POD investigation, Manly and Chotkowski (IEP 2005; Manly and Chotkowski 2006) used log-linear modeling to evaluate environmental factors that may have affected long-term trends in the Fall Midwater Trawl abundance index of delta smelt. They found that monthly or semi-monthly measures of exports or Old and Middle rivers flow had a statistically significant effect on delta smelt abundance; however, individually they explained a small portion (no more than a few percent) of the variability in the fall abundance index of delta smelt across the entire survey area and time period. Hence, there are other factors that dominate the long-term trends of delta smelt fall abundance. Similarly, Kimmerer et al. (2001) estimated that entrainment losses of young striped bass were sometimes very high (up to 99%), but they did not find evidence that entrainment losses were a major driver of long-term striped bass population dynamics.

These results do not mean, however, that direct export effects can be dismissed as contributing causes of the POD. There are two aspects of entrainment that were not addressed by Manly and Chotkowski (2006) and are not well understood: (1) the cumulative effects of entrainment of multiple life stages, and (2) larval entrainment. Larval entrainment is unknown because larvae are not sampled effectively at the fish screening facilities. To address this shortcoming, Kimmerer and Nobriga (in press) coupled a particle tracking modeling with survey results to estimate larval entrainment. Kimmerer (in press) used data from several IEP monitoring programs to estimate entrainment of delta smelt. These approaches suggest that larval delta smelt entrainment losses could exceed 50% of the population under low flow and high export

conditions. Because there are few reliable larval entrainment data, it is not possible to directly address the question of how important these losses were historically.

Moreover, export effects may be subtle and operate at specific times or in specific years to disproportionately affect only one life stage of delta smelt. For example, it has been proposed that losses of larger females and their larvae may have a disproportionate effect on the delta smelt population (B. Bennett, unpublished data). Bennett (unpublished data) proposes that larger females spawn earlier in the season and produce more eggs, which are of better quality, and survivability, as has been noted for Atlantic cod and other commercially harvested species (Marteinsdottir and Steinarsson 1998; Swain et al. 2007). As a consequence, winter and early spring exports, which have continually increased as described above (Figure 3), could have an important effect on reproductive success of early spawning female delta smelt. Bennett hypothesizes that the observed reduction in the mean size of adult delta smelt in the early 1990s (Sweetnam 1999) is a result of selective losses of earlier spawning adults and their larvae, thereby selecting for later spawned offspring (that have less time to reach maturity). Under this hypothesis, the most important result of the loss of early spawning females would manifest itself in the year following the loss, and would therefore not necessarily be detected by analyses relating fall abundance indices to same-year predictors. This hypothesis is presently being evaluated by Bennett's laboratory using otolith methods.

Bottom-Up

In the "bottom up" portion of the conceptual model, we propose that changes in the quality and availability of food have had important consequences for pelagic fishes. Here, we describe the evidence that there have been long-term and recent changes in food web function.

Food Availability: Estuaries are commonly characterized as highly-productive nursery areas for a suite of organisms. Nixon (1988) noted that there actually is a broad continuum of primary productivity levels in different estuaries, which in turn affects fish yield. Compared to other estuaries, pelagic primary productivity in the upper San Francisco estuary is poor and a low fish yield is expected (Figure 19). Moreover, there has been a significant long-term decline in phytoplankton biomass (chlorophyll *a*) and primary productivity to very low levels in the Suisun Bay region and the lower Delta (Jassby et al 2002). Hence, low and declining primary productivity in the estuary is likely a principal cause for the long-term pattern of relatively low and declining biomass of pelagic fishes.

A major reason for the long-term phytoplankton reduction in the upper estuary was benthic grazing by the overbite clam (*Corbula amurensis*), 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 *C. amurensis*' invasion, there were periods of relatively low clam biomass in the upper estuary because the Asiatic freshwater clam (*Corbicula fluminea*) colonized Suisun Bay during high flow periods and the native marine clam *Mya arenaria* (also known as *Macoma balthica*) 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. The *C. amurensis* invasion changed this formerly dynamic clam assemblage because *C. amurensis*, which is

Deleted: *Corbicula*

tolerant of a wide range of salinity, is always the dominant clam species in the brackish water regions of the estuary and its grazing influence extends into the Delta (Kimmerer and Orsi 1996; Jassby et al. 2002) beyond the clam's typical range, presumably due to tidal dispersion of phytoplankton-depleted water.

According to recent research, shifts in nutrient concentrations may also contribute to the phytoplankton reduction as well as to changes in algal species composition in the San Francisco Estuary. While phytoplankton production in the San Francisco Estuary is generally considered light limited and nutrient concentrations exceed production limiting levels, nutrients may affect production during times when light conditions are more favorable and also affect species composition. 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. Ammonium concentrations in the Delta and Suisun Bay have significantly increased over the last few decades due to increased loading from sewage treatment plants (Jassby, in press, Mueller-Solger, in prep.). Van Nieuwenhuysse (2007), on the other hand, found that a rapid reduction in wastewater total phosphorus loads in the mid-1990s coincided with a similarly rapid drop in phytoplankton biomass at three stations in the upper estuary.

Starting in the late 1980s, a series of major changes were observed in the estuarine food web that negatively influenced pelagic fish production. Major step-declines were observed in the abundance of phytoplankton (Alpine and Cloern 1992) and the copepod *Eurytemora affinis* due to grazing by the clam (Kimmerer et al. 1994). Northern anchovy abandoned the estuary's low-salinity zone coincident with the *C. amurensis* invasion, presumably because the sharp decline in planktonic food items made occupation of low-salinity waters unprofitable for this marine fish (Kimmerer 2006). There was also a major step-decline in mysid shrimp in 1987-1988, presumably due to competition with the clam for phytoplankton (Orsi and Mecum 1996). The mysid shrimp had been an extremely important food item for larger fishes like longfin smelt and juvenile striped bass; its decline resulted in substantial changes in the diet composition of these and other fishes (Feyrer et al. 2003). As described above, the population responses of longfin smelt and juvenile striped bass to winter-spring outflows changed after the *C. amurensis* invasion. Longfin smelt relative abundance was lower per unit outflow post-clam (Kimmerer 2002b). Young 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).

Several recent studies have shown that pelagic consumer production is limited by low phytoplankton productivity in the San Francisco Estuary (Sobczak et al. 2002, 2004; Mueller-Solger et al. 2002). However, in contrast to the substantial long-term declines in phytoplankton biomass and productivity (Jassby et al. 2002), phytoplankton trends for the most recent decade (1996-2005) are actually positive in the Delta and neutral in Suisun Bay (Jassby, in press). While this does not support the hypothesis that changes in phytoplankton quantity are responsible for the recent POD, phytoplankton may nevertheless play a role in the recent POD via changes in species composition, as will be discussed in the food quality section below.

A notable finding for the POD is that *Pseudodiaptomus forbesi*, a calanoid copepod that has replaced *Eurytemora affinis* as the most common delta smelt prey during summer, continued to decline in the Suisun Marsh and confluence regions from 1995 to 2004, while its numbers increased in the southern Delta (Figure 20; Kimmerer et al. in prep., Mueller-Solger et al. in prep.). Although substantial uncertainties about mechanisms remain, this trend may be related to increasing recruitment failure and mortality in Suisun Bay and the western Delta due to competition and predation by *C. amurensis*, contaminant exposures, and entrainment of source populations in the Delta (Durand et al. in prep., Mueller-Solger et al. 2006). For example, *C. amurensis* abundance and distribution in the Suisun Bay and the western Delta during 2001-2004 was greater than during the 1995-1999 wet period, but similar to abundance indices and distribution patterns during the 1987-1992 drought (IEP 2005, Peterson et al. in prep.). Further, in the two most recent years (2005 and especially 2006), *P. forbesi* has started to rebound substantially in the western Delta (Figure 21, Mueller-Solger et al. in prep., Jassby et al. in prep.).

There is also interest in a more recent invader, the cyclopoid copepod *Limnoithona tetraspina*, which significantly increased in the Suisun Bay region beginning in the mid-1990s. It is now the most abundant copepod species in the low-salinity zone (Bouley and Kimmerer 2006). 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). Experimental studies addressing this issue are ongoing (Sullivan et al., unpublished). *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. Its suitability as food for pelagic fish species remains unclear, but is also being investigated (Sullivan et al., unpublished).

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, residual 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. Similarly, during 2003 and 2004 striped bass condition factor decreased in a seaward direction from the Delta through Suisun Bay.

Thus far, there is little evidence that the unusually poor growth rates, health, and condition of fishes from Suisun Bay and western Delta are due directly to the effects of toxic contaminants or other adverse chemical or physical habitat conditions. Therefore, our working hypothesis is that the poor fish growth and condition in the upper estuary are due to food limitation. Note, however that contaminant episodes may be contributing to poor phytoplankton growth (Dugdale et al. 2007) and invertebrate mortality (Werner unpublished data), which could exacerbate food limitation. If fishes are food limited in Suisun Bay and west Delta during larval and/or juvenile development, then we would expect greater cumulative predation mortality, higher disease incidence, and consequently low abundance indices at later times.

Food Co-occurrence: The above patterns in fish food have generally been described at rather broad scales. Recently, interest has focused on determining patterns of co-occurrence of fish

predators and their zooplankton prey. The assumption is that predators should co-occur with their prey. This idea was first explored by Nobriga (2002) who showed that delta smelt larvae with food in their guts typically co-occurred with higher calanoid copepod densities than larvae with empty guts. Recently, Kimmerer (in press), Miller and Mongan (unpublished data), and Mueller-Solger (unpublished data) used similar approaches to look at potential co-occurrence of delta smelt and their prey and its effects on survival. Kimmerer (in press) showed that there was a positive relationship between delta smelt survival from summer to fall and zooplankton biomass in the low-salinity region of the estuary (Figure 22). Miller and Mongan (unpublished data) have concluded that April and July co-occurrence is a strong predictor of juvenile delta smelt survival. Mueller-Solger (unpublished data) defined delta smelt habitat based on the environmental quality results of Nobriga et al. (in press) and prey spectrum more broadly (as all copepods) compared to Miller and Mongan (unpublished data) and found no long-term decline in the total biomass of copepods potentially available for consumption by delta smelt in midsummer, although species composition has changed considerably (Figure 21).

There are two shortcomings of co-occurrence analyses like those described above. First, it is difficult to characterize fish prey suitability. For instance, *E. affinis* and *P. forbesi* are generally believed to be preferred prey items for delta smelt (Nobriga 2002; Miller and Mongan unpublished). However, diet data show that delta smelt will actually feed on a wide variety of prey (Lott 1998; S. Slater, California Department of Fish and Game, unpublished; Figure 23). Thus, the question of prey co-occurrence involves questions of prey catchability (e.g., Meng and Orsi 1991) and profitability (energy per item consumed and nutritional quality of individual prey items). For example, *L. tetraspina* has a large biomass in the system but individual *L. tetraspina* are smaller and possibly more evasive than the larger calanoid copepods. The energy needed by an individual delta smelt to harvest a similar biomass of *L. tetraspina* compared to the energy needed to harvest a larger species could be very different, as suggested by optimal foraging theory (e.g., Stephens and Krebs 1986). Another major limitation of co-occurrence analyses is that IEP sampling programs sample fish and zooplankton at larger spatial and temporal scales than those at which predator-prey interactions occur. Both fish and copepods are likely to be patchy and the long tows required to collect sufficient numbers of organisms for counting would homogenize such patch structure. Moreover, it is unlikely that the (monthly or even twice monthly) “snapshot” of fish and prey co-occurrence in specific locations or even small regions provided by the IEP surveys is representative of feeding conditions actually experienced by fish on an hourly or daily basis.

The weight of evidence strongly supports bottom-up food limitation as a factor influencing long-term fish trends in the upper estuary. However, the bottom-up hypothesis is unlikely as a single mechanism for the recent pelagic organism decline. Specifically, it is unclear why there has been a substantial recent decline in some Suisun Bay and western Delta calanoid copepod species, but not in phytoplankton chlorophyll *a* concentration. Also, calanoid copepod densities (especially *P. forbesi*) rebounded substantially in 2006 (Mueller-Solger, unpublished data) while the POD fish abundance indices (especially for delta smelt) remained low. Second, recent *C. amurensis* levels are not unprecedented; they are similar to those found during the 1987-92 drought years, so it is unclear if and why benthic grazing would have a greater effect on the Suisun Bay food web during the POD years than during the earlier drought years. Finally, it is possible that the hypothesis that the San Francisco Estuary is driven by phytoplankton

production rather than through detrital pathways (Sobczak et al. 2002, 2004; Mueller-Solger et al. 2002) may have been accepted too strictly. Many zooplankton are omnivorous and can consume microbes utilizing dissolved and particulate organic carbon. This has recently been demonstrated for several zooplankton species in the San Francisco Estuary (Gifford et al. 2007 and references therein). Thus, shifts in availability of phytoplankton and microbial food resources for zooplankton might favor different species. It is possible that a better understanding of shifts in phytoplankton and zooplankton community composition and perhaps related changes in the microbial food web in the Suisun Bay region could explain these apparent inconsistencies.

Food Quality: Studies on food quality have been relatively limited in the San Francisco Estuary, with even less information on long-term trends. However, food quality may be another limiting factor for pelagic zooplankton and their fish predators.

At the base of the pelagic food web, food quality for consumers is determined by the relative contributions of different phytoplankton and microbial species and detritus to the overall organic particle pool available to primary consumers. For example, diatoms and cryptophytes are thought to be of good food quality for zooplankton, while the nutritional value of cyanobacteria such as *M. aeruginosa* can be very low (Brett and Müller-Navarra 1997), particularly for toxic varieties (Rohrlack et al. 2005). Lehman (1996, 2000) showed shifts in phytoplankton species composition in the San Francisco Estuary from diatom dominated to more flagellate dominated communities. Mueller-Solger et al. (2006) found that in recent years, diatoms were most abundant in the southern San Joaquin River region of the Delta, and Lehman (2007) found greater diatom and green algal contributions upstream and greater flagellate biomass downstream along the San Joaquin River. To date, the *M. aeruginosa* blooms have occurred most intensively in the central Delta, thus POD species that utilize the central Delta such as threadfin shad, striped bass, and the poorly monitored centrarchid populations (largemouth bass and sunfish) would be most likely to suffer any direct adverse effects of these blooms.

In 2007, the M. aeruginosa bloom year was the worst on record in the Delta (P. Lehman, in prep.). The highest cell densities were observed near Antioch, i.e. considerably west of the previous center of distribution, and may thus have affected invertebrates and fishes in the confluence and Suisun Bay regions of the upper estuary.

In general, phytoplankton carbon rather than the much more abundant detrital carbon are thought to fuel the food web in the San Francisco Estuary (Mueller-Solger et al. 2002; Sobczak et al. 2002, 2004); however, that does not mean the detrital pathways are not significant because many zooplankton are omnivorous and capable of utilizing both pathways. For example, Rollwagen-Bollens and Penry (2003) observed that while heterotrophic ciliates and flagellates were the dominant prey of *Acartia* spp. in the bays of the San Francisco Estuary, diatoms and autotrophic ciliates and flagellates also formed an important part of their diet during phytoplankton blooms. Calanoid copepod and cladoceran growth and egg production may often be limited by low levels of phytoplankton biomass. This appears to be true even for omnivorous calanoids such as *Acartia* spp. Kimmerer et al (2005) found a significant relationship between *Acartia* spp. egg production and chlorophyll *a* concentration in the San Francisco Estuary, suggesting that *Acartia* spp. likely also derived a large part of carbon and energy from phytoplankton. Bouley and Kimmerer (2006), on the other hand, reported that egg production rates of the cyclopoid copepod

L. tetraspina were unrelated to chlorophyll *a* concentrations in the low salinity region of the San Francisco Estuary. *L. tetraspina* digestion rates were highest for ciliates, perhaps suggesting a greater importance of the detrital carbon pathway for this species.

In a study focusing on the nutrition and food quality of the calanoid copepods *E. affinis* and *P. forbesi*, Mueller-Solger et al (2006) found evidence for “trophic upgrading” of essential fatty acids by *E. affinis* and *P. forbesi*, confirming their importance as high-quality food for fish. They also found that *E. affinis* gained the greatest nutritional benefits from varied food sources present in small tidal sloughs in Suisun Marsh. *P. forbesi*, on the other hand, thrived on riverine phytoplankton in the southern Delta, especially diatoms. Diatoms are likely also an important food source for other calanoid copepod species. The relative decrease in diatom contributions to the phytoplankton community in the central Delta and Suisun Bay (Lehman 1996, 2000) is thus a concern and may help explain the declines in *P. forbesi* and other calanoid copepods in these areas.

Mueller-Solger et al. (2006) concluded that areas rich in high-quality phytoplankton and other nutritious food sources such as the southern Delta and small tidal marsh sloughs may be critical “source areas” for important fish prey organisms such as *P. forbesi* and *E. affinis*. This is consistent with results by Durand et al. (unpublished data) who showed that transport from upstream was essential for maintaining the *P. forbesi* population in Suisun Bay. It is possible that the increase in *P. forbesi* densities in the western Delta in 2006 could be related to greater San Joaquin River flows during this wet year, which may have reduced entrainment of *P. forbesi* source populations in the Delta.

As noted in earlier sections, the dichotomy between phytoplankton and detrital/microbial energy pathways supporting zooplankton has probably been applied more stringently than is appropriate. Both are likely important, with the balance between them in specific areas of the estuary likely having effects on the success of particular zooplankton species. Additional research into the detrital pathway might be useful in understanding the factors controlling zooplankton populations, which are critical food resources for pelagic fishes.

Species Models

The basic conceptual model provides a useful context for the major factors likely affecting the POD species. However, it has limited value for helping management identify actions or guide research studies because it does not show how the major stressors differ for each species, and how they differ in relative importance during different life history stages or seasons. These shortcomings have been partially addressed by developing individual models for each of the four POD fish species. The degree of detail for each model varies substantially based on the available data, so the degree of confidence in each is not consistent. Nonetheless, we believe that these new models are an effective way to show how the different stressors interact in space and time on each species, which in turn can help identify research and management priorities. Like the basic conceptual model, the species models will continue to evolve as more information becomes available.

Each of the four species models represent a “filtered” version of the basic conceptual model retaining only the factors that at present seem most relevant to the individual species and life stages. The goal of these models is to provide the most reasonable “stories” for each of the four POD fish species based on all research results through late 2007.

For “filtering,” we relied on a *weight of evidence* approach similar to Burkhardt-Holm and Scheurer (2007) who used it to evaluate the results from a large number of laboratory and field studies to identify the most reasonable mechanisms for observed fish declines throughout Switzerland. In our case, we used this type of approach to identify the most plausible linkages between stressors and fish life stages that were most consistent with all available POD laboratory results, long-term monitoring data, correlations, models, and our understanding of how the estuary functions. Here, we present the outcome of this approach. We do not describe all steps of the process itself or reiterate the description of all factors and results already covered in the general conceptual model sections in each of the four species model. In these models, we also generally deemphasize individual study results, including all simple correlations between fish abundance and individual stressors. As with the general conceptual model, we expect substantial changes to these models as new information is collected, particularly with respect to contaminants, and some stressors that are deemphasized in the current species models may play a more prominent role in future versions of these models.

Each model consists of four panels, each representing a portion of the species’ life history (Figures 24-27). The arrows show progression through the life cycle in a clockwise direction. The seasons for each species generally correspond to the traditional definitions of summer (June – August), fall (September – November), winter (December – February), and spring (March – May); however, the exact timing of life history events varies somewhat from year to year, depending on environmental conditions. Within each panel, one or more major stressors are listed, along with the proposed mechanism by which they may affect the fish population. Detailed descriptions of each of the models are provided below.

Delta Smelt

We hypothesize that the long-term patterns in delta smelt abundance indices were strongly influenced by adult abundance, habitat conditions and food availability (Figure 24). Feyrer et al. (2007) found that there was a significant stock-recruit relationship (i.e., adults affect juvenile production) since 1987; this relationship was improved by including fall habitat conditions (salinity, turbidity), indicating that habitat also affects abundance. Food availability also appears to be important to this planktivorous fish as Kimmerer (in review) noted a statistically significant relationship between juvenile smelt survival and zooplankton biomass over the long term (Figure 22). The decline in the mean size of adult delta smelt following the introduction of the clam *C. amurensis* (Sweetnam 1999; Bennett 2005), which caused declines in key zooplankton prey, is also consistent with food web effects.

Statistical analyses of the long-term delta smelt trends (Manly and Chotkowski 2006) confirm that there has been a rapid decline of delta smelt since 2000. We propose that changes in water project operations and adult abundance are contributing causes of this recent decline. Increased water project exports during winter resulted in higher losses of adult smelt, particularly early

spawning fish (and their offspring) that may be proportionally more important to the population. By contrast, reduced exports during spring may have increased survival of later-spawned larvae. Reduced spring exports from the Delta have been the result of the Vernalis Adaptive Management Plan (VAMP), a program designed to benefit outmigrating juvenile Chinook salmon. VAMP has been operating since 2000. Finally, we propose that the population is now at such low levels that recovery is unlikely in a single year but will require several years of successful reproduction and recruitment.

It is unclear whether the population has dropped below critical levels where Allee effects inhibit recovery. However, the fact that delta smelt show an especially strong recent stock recruitment relationship with a declining temporal trend (Figure 8) suggests that record low abundance levels are now a major factor that limits population resiliency. *Our concern was reinforced by the 2007 Fall Midwater Trawl Survey delta smelt abundance index of 28, the second lowest on record just behind that of 2005 (<http://www.delta.dfg.ca.gov/data/mwt>).* The evidence for these long-term and recent abundance patterns is described in detail below for each season.

Summer: Summer is the season that usually has the highest primary and secondary productivity in a temperate zone estuary. Given their annual life cycle, summer represents the primary growing season for delta smelt. However, the availability of prey species is strongly affected by grazing pressure from the benthos (*C. amurensis*) and possibly entrainment of *P. forbesi*, resulting in fewer high quality calanoid copepods (Kimmerer 2002), the most common prey of juvenile delta smelt (Lott 1998). Moreover, in the decade including the early POD years, there has been a further decline in the abundance of calanoid copepods in Suisun Bay and the west Delta (Kimmerer et al., in prep, Mueller-Solger et al., in prep.), part of the core summer habitat of delta smelt (Nobriga et al., in press). At the same time, these calanoid copepods are being replaced by the small cyclopoid copepod *L. tetraspina* which is presumed to be a less suitable prey species (Bouley and Kimmerer 2006).

The long-term reduction in preferred prey availability has likely resulted in slower growth rates of delta smelt, detectable as a reduction in the mean size of delta smelt in autumn since the early 1990s (Sweetnam 1999; Bennett 2005). We propose that over the long term, reduced summer growth rates have reduced the survival of juvenile delta smelt, perhaps from predation, as smaller fish remain more vulnerable for longer periods (Bennett et al. 1995; Houde 1987). As evidence that changes in prey availability have had survival consequences for this fish species, Kimmerer (in review) found a statistically significant relationship between summer to fall delta smelt survival and zooplankton biomass in the low salinity zone from 1972 to 2005 (Figure 22).

Recent preliminary analyses suggest that total zooplankton biomass may not have changed substantially within the core summer habitat of delta smelt, at least when all species including *L. tetraspina* are included (Figure 21; Mueller-Solger, unpublished data). In 2006, zooplankton biomass, including the biomass of the important food organism *P. forbesi*, even increased substantially in the delta smelt summer habitat, but this was not followed by a recovery of delta smelt. Moreover, summer-to-fall survival since 2000 does not appear to be substantially different from survival for all other years since 1972 and actually somewhat higher than in 1972-1980 when delta smelt abundance indices were much higher than they are now (Mueller-Solger, unpublished data). Finally, summer and fall delta smelt abundance indices have been closely

related to each other during the POD years (Figure 8). However, while the fall abundance indices since 2000 have spanned almost the full range of delta smelt abundance indices during the previous three decades, the summer abundance indices have remained in the lower portion of the pre-POD summer abundance range.

These results suggest that impaired recruitment, growth, and survival before the summer period may be more important during the POD years than growth and survival from summer to fall. It is possible that summer food limitation was a more important stressor when population densities were higher and that the decline in summer food availability has contributed more to the long-term decline in delta smelt abundance than to its dramatic deterioration in the POD years (Mueller-Solger, unpublished data).

Summer habitat may be more restricted than in the past. Nobriga et al. (in press) noted a complete absence of delta smelt in the southern Delta that coincided with increased water clarity. However, these changes are unlikely to be important in the POD because delta smelt have not extensively utilized the southern and central Delta since the late 1970s.

Entrainment effects are not thought to be important during summer because the majority of the delta smelt population is north and west of the zone affected strongly by water exports and delta smelt salvage is generally very near zero from July-November (IEP unpublished data). When the toxic blue-green alga *M. aeruginosa* blooms during summer, it occurs primarily upstream of delta smelt, so it is unlikely to be a major factor for the delta smelt's recent decline. *This may have changed in 2007, when M. aeruginosa blooms extended into eastern Suisun Bay, well into the historical rearing habitat of delta smelt.* Other water quality variables such as contaminants could be important, but are yet to be identified as seasonal stressors for this species.

In summary, there is evidence of bottom-up and habitat suitability effects on delta smelt during the summer over the long-term, but the evidence suggests that since 2000, delta smelt population dynamics have been largely driven by factors occurring in seasons other than summer. Near zero salvage suggests SWP/CVP entrainment effects are minimal during this period. Nonetheless, better habitat and food conditions during the summer might improve survival as well as individual fitness of maturing delta smelt and should not be ignored.

Fall: Fall represents the time period when the delta smelt year class matures to adulthood. Hence, fall stressors have a direct effect on the delta smelt spawning population. The evidence to date indicates that habitat is a significant issue for delta smelt in fall (Feyrer et al. 2007). Delta smelt is strongly associated with low salinities and high turbidities, which can be used to index the "environmental quality" of habitat for the species. Feyrer et al. (2007) report that fall environmental quality has shown a long-term decline. There is statistical evidence that these changes have population-level effects (Feyrer et al. 2007). A multiple linear regression of fall environmental quality in combination with adult abundance provided statistically significant predictions of juvenile production the following year. Hence, both habitat and stock-recruit factors are important issues during fall. *Note, however, that the response of delta smelt to salinity was substantially different in 2007, when midwater trawl surveys showed that most of the delta smelt were holding at unexpectedly high salinities (e.g. 8 ppt). The cause of this shift has*

*not yet been determined, but may be related to deteriorating habitat conditions such as more extensive toxic *M. aeruginosa* blooms during late summer.*

Reduction of habitat area as defined by environmental quality likely interacts with bottom-up and top-down effects. Restricting fish to a small area with inadequate food supply would likely maintain or even magnify the bottom up and top down effects already occurring during the summer, although these factors are poorly-understood during fall. Greater mortality due to predation, small adult size by the end of the fall, and the low fecundity of smaller fish likely all contribute to the adult abundance effect observed by Feyrer et al. (2007).

Direct entrainment is not a major stressor during the fall. Delta smelt is rarely salvaged at the CVP and SWP until late December. However, habitat (i.e. salinity) affects the location of delta smelt in fall, which may contribute to their subsequent vulnerability to entrainment in winter.

In summary, both bottom-up effects and habitat restriction appear to be important during the fall. Slow growth because of food limitation combined with habitat restriction may also have resulted in higher mortality due to predation. Poor growth in the summer and fall likely contribute to reduced size and fecundity of maturing fish.

Winter: Winter represents the main period of adult delta smelt migration and spawning. We hypothesize that entrainment of adults and larvae (top-down effects) are particularly important to the delta smelt population during this critical season. The increase in salvage of adult delta smelt during winter since 2000 suggests that entrainment levels were higher during the POD years (Figure 14; IEP 2005; Grimaldo et al. in prep). Although there does not appear to be a strong statistical relationship in the long term between exports (or fish salvage) and subsequent delta smelt abundance (Manly and Chotkowski, unpublished data), these losses may still be important to the population in the short term. For example, Bill Bennett has hypothesized that losses of larger females may have a disproportionate effect on the delta smelt population. Specifically, losses of more fecund, early spawning large females and their offspring could have a large influence on the subsequent development of cohorts. Winter exports may also have an effect on the number of adults which survive a second year, a possible important factor affecting delta smelt population resilience (Bennett 2005). Note that export effects may not be large during very wet years, because exports by the water projects are relatively small compared to delta inflow and outflow.

There is presently no evidence of habitat constriction or food limitation during this period; however, no studies have addressed these questions. Contaminant effects are possible during flow pulses, but there is no major evidence yet that these events cause toxicity to delta smelt.

Spring: Bennett (unpublished data) proposes that reduced spring exports resulting from VAMP has selectively enhanced the survival of spring-spawned delta smelt larvae. Initial otolith studies by Bennett's lab suggest that these spring-spawned fish dominate subsequent recruitment to adult life stages; by contrast, delta smelt spawned prior to the VAMP have been poorly-represented in the adult stock in recent years. He further proposes that the differential fate of winter and spring cohorts may affect sizes of delta smelt in fall because the spring cohorts have a shorter growing season.

Because of natural variability and recent X2 standards, there is no long-term trend in spring salinity (Jassby et al. 1995; Kimmerer 2002a). This suggests there was unlikely to have been a recent change in spring habitat availability or suitability. However, other habitat effects including contaminants or disease could play a role during spring.

Striped bass

The San Francisco Estuary striped bass population has been monitored and researched for many decades so some of the factors that have influenced its long-term abundance index trend are fairly well-understood (Figure 25). The age-0 striped bass abundance index has declined steadily since the latter 1960s (Figure 2), but adult abundance indices have not (Figure 6), in part due to active management actions (Kolhorst 1999). The long-term decline in juvenile abundance was originally attributed largely to entrainment in the SWP and CVP water diversions (Stevens et al. 1985). However, recent research suggests that there was a step-decline around 1977 due to adult mortality and subsequently reduced egg supply (Kimmerer et al. 2000; 2001). There was another step-change around 1987 coinciding with the *Corbula* invasion that decoupled age-0 production from spring flow (Sommer et al. 2007). Young striped bass have a strong predator-prey association with mysid shrimp (Stevens 1966; Feyrer et al. 2003). The carrying capacity for age-0 through age-3 striped bass has shown a long-term decline that is correlated with declining mysid densities (Kimmerer et al. 2000). Thus, it is likely that the much lower abundance of mysids in the post-*Corbula* period has strongly negatively affected juvenile striped bass production. The adult striped bass population increased in the 1990s. This was likely due to a combination of successive wet years in the mid to late 1990s that improved survival and planting of millions of juvenile striped bass into the estuary through 2000 (Kolhorst 1999). Restored populations of striped bass on the east coast have resulted in large reductions in populations of their prey and in high incidence of disease in striped bass (Hartman 2003; Uphoff 2003)

Why the age-0 striped bass abundance index has continued to plummet to record lows during the POD years, including 2007 when the Fall Midwater Trawl age-0 index was the third lowest on record (<http://www.delta.dfg.ca.gov/data/mwt>), despite an increase in adult abundance index and by extension, egg supply, is unknown. Striped bass appear to show more signs of contaminant-related health problems than the other POD species (details below), but we do not know whether this reflects a long-term chronic problem or a recent change. The abiotic habitat suitability for young striped bass has declined during fall like it has for delta smelt (Feyrer et al. 2007) and the entrainment of age-1 striped bass jumped up during the early POD years also (Figure 14). Thus, it is possible that direct (entrainment) and indirect (habitat suitability) effects of water diversions have exacerbated the longer-term stresses of reduced prey availability and contaminant effects.

Spring: In spring, striped bass migrate into the Sacramento and San Joaquin rivers where they broadcast spawn in currents that will suspend eggs and larvae in the water column for the roughly 2 weeks of development needed before larvae can maintain their position in the water column (Moyle 2002). In both rivers, migrating adults and suspended eggs and larvae are subject to discharges carrying toxic contaminants including agricultural return water carrying pesticides and other contaminants (Saiki et al. 1992; Bennett et al. 1995) and municipal discharges carrying a variety of contaminants including potentially estrogenic compounds. Adult

striped bass are top predators and known to bioaccumulate toxins such as mercury. Springtime contaminant effects influence egg and larval survival via two pathways: 1) maternally accumulated contaminant(s) passed on to eggs and larvae, negatively affecting viability and development; 2) direct mortality effects of contaminants in the environment on larvae. Maternal transfer of contaminant was assessed by analyzing larvae taken from 2006 and 2007 spawnings of both domestic striped bass (controls) and river caught striped bass. Initial biochemical assays of 2006 larvae failed, but morphometric measures comparing hatchery and river caught larvae showed that although river larvae were significantly longer than hatchery larvae at day 1, they possessed significantly less body volume and grew significantly slower in length and body volume over the next four days. River larvae also exhibited abnormal eye development (Ostrach et al. 2007). Negative growth at day 5 and abnormal eye development presumably result in high mortality, though it's not clear if the causal factors for these differences abruptly increased after 2000. Analyses of maternal chemical body burdens are not complete and only length information from the 1999 will be available for comparison with 2006-7 samples. Striped bass eggs and larvae are likely exposed to the same suite of contaminants as delta smelt (Kuivila and Moon 2004), possibly in higher concentrations because striped bass spawn closer to river discharge source locations. Striped bass larvae captured in the Sacramento River have exhibited liver lesions sufficient to cause mortality (Bennett et al. 1995).

Striped bass consume primarily copepods and cladocerans at first feeding (Heubach et al. 1963; Foss and Miller 2004), and prey density has been positively correlated with larval growth rate (Heubach et al. 1963, Foss and Miller 2004), which is believed to be inversely related to mortality. Although a long-term reduction in calanoid copepods has occurred (Orsi and Mecum 1986, Kimmerer et al. 1994, Orsi and Mecum 1996), we have not found evidence of a recent decline in spring coincident with the striped bass decline and cladoceran abundance increased steadily during spring of the POD years (Hennessy and Hieb 2007). However, broad seasonal indices of abundance may mask important short-term patterns. For example, early first feeding larvae probably rely on *E. affinis*, whereas those hatching later will encounter primarily *P. forbesi*. During the transition period, it is possible that finding sufficient numbers of either species might be problematic. This aspect remains to be examined.

River flows and south delta exports historically explained much of the variation in striped bass year class strength, though the strongest relationships occurred during the summer (Stevens et al. 1985). Survival from egg to 38 mm larvae in early summer appeared unchanged through the mid-1990s (Kimmerer et al. 2000).

Rapid loss of large fecund females from the spawning stock could reduce total fecundity, and in turn cause a decline in juvenile recruitment (Stevens et al. 1985; Kimmerer et al. 2000). Such a decline occurred between 1976 and 1977 (Stevens et al. 1985; Kimmerer et al. 2000). Bennett and Howard (1997, 1999) hypothesized that a decline in striped bass fecundity since the 1970s resulted from warming ocean conditions leading to an improved coastal feeding environment, which in turn resulted in increased fishing mortality along the coast and increased straying to other river systems. This scenario fits data from the late 1970s through late 1990s, but ocean conditions shifted to a cool regime in 1999 and though the adult population size decreased after 2000 it remained at or above early 1990s levels (Figure 11); a sharp decrease in age of adult spawners could result in a sharp decline in fecundity.

Summer: Summer is a generally a period of rapid growth for striped bass, but food resources may not be uniformly adequate throughout their range to support this growth. In particular, copepod numbers have been reduced recently in the western Delta and Suisun Bay (Kimmerer et al. in prep, Mueller-Solger et al. in prep.). However, striped bass grow rapidly, even in the relatively low copepod densities found in the upper San Francisco Estuary (Foss and Miller 2004). Success from first feeding to 25 mm may have influenced recruitment since 2000, but there was no suggestion of a bottle neck during this period in the past (Kimmerer et al. 2000). By 25 mm in length, age-0 bass exploit larger mysid and amphipod prey, appearing to seek out mysids (Feyrer et al. 2003; Bryant and Arnold 2007). The dominant upper estuary mysid, the introduced *Acanthomysis bowmani*, has suffered a slow decline in summer from 2000 to 2006 (Hennessy and Hieb 2007). Even though declining, *A. bowmani* densities remain higher than those of the late 1990s, thus are unlikely to have influenced the striped bass decline since 2000. Long-term diet and growth have not changed substantially since 2000. Diet data from a long-term study culminating in 2002, revealed that the percentage of age-0 striped bass stomachs with food did not decline in the last two years, nor did the mean ration size, except perhaps in 2002 for fish <25 mm (Bryant and Arnold 2007). Examination of apparent growth patterns (growth determined from length-frequency data) for striped bass did not reveal a decline subsequent to 2000 (IEP 2006). However, when fish condition was compared regionally, striped bass collected from western Suisun Bay weighed significantly less at the same length compared to those collected in regions farther east (IEP 2006).

No long-term studies exist of disease or parasites in young striped bass of the San Francisco Estuary. The incidence and intensity of tapeworm larvae (plerocercoid) was examined in fish collected from 1986-1993 (Arnold and Yue 1997). In this study up to 79% of the larval and juvenile striped bass examined annually contained encapsulated plerocercoids (cestodes) in mesenteries and stomachs, but little immune response was detected. Recent sampling revealed no viral effects in summer 2006. There was a high incidence and intensity of flagellated/ciliated gill and mouth parasites in 2005 but less so in 2006. High vitellogenin levels in young juvenile fish collected from Suisun Slough and elevated levels in fish from Honker Bay indicated contact with estrogenic compounds (Ostrach et al. 2005, Ostrach et al. 2007).

The use of pyrethroid pesticides doubled in the early 2000s as compared to the early 1990s and the main period of application, July through October (Oros and Werner 2005), corresponds to the striped bass growing period.

Striped bass summer distribution appeared to shift after the invasion of the overbite clam in 1987, and that shift along with increases in shoreline predators may have caused a decline. The San Francisco Bay Study deploys two nets at each sampling location: an otter trawl, towed on the bottom, and a midwater trawl towed obliquely through the water column. The proportion of total age-0 caught in the midwater trawl has been highly variable, but with a downward trend and lower peaks over time (Figure 28). Similarly, the proportion of age-0 striped bass caught by the otter trawl at shoal stations compared to deeper stations increased and remained consistently high after 1987, and became less variable after the late 1990s (Figure 28). This suggests that age-0 striped bass spent less time in the water column and moved to relatively shallow water as a group

sooner in the year after the clam arrived. Current analyses cannot discriminate whether these trends became more extreme in the 2000s.

Fall: Fall has historically posed a feeding problem for striped bass, but it is not clear if their feeding environment substantially changed after 2000. Seasonal and decadal declines in mysid (a highly selected diet item) density lead to a broadened feeding niche and an early initiation of piscivory among age-0 striped bass in fall (Stevens 1966; Feyrer et al. 2003). Fall mysid numbers in the upper estuary declined steadily after 2000 with the exception of 2005, but have not reached levels comparable to the early 1990s when *N. mercedis* first became almost undetectable in fall and before the introduction of *A. bowmani* in about 1994 (Hennessy and Hieb 2007). Reduced food availability has been linked to observed declines in carrying capacity (Kimmerer et al. 2000).

Age-0 striped bass environmental quality can be effectively described by Secchi depth and specific conductance (Feyrer et al. 2007). Long-term trends indicate a decline in environmental quality from the late 1960s to present. Fall environmental quality in the 2000s declined from levels in the 1990s, and most of the remaining high quality habitat exists in the lower Sacramento River upstream of the confluence (Feyrer et al. 2007). If the age-0 striped bass population is also shifting toward the Delta and to a smaller habitat area there could be increased intra-specific competition, and predation might increase locally with increased densities and the overlap with additional piscivores (Nobriga and Feyrer 2007). In addition, the upstream shift may increase vulnerability to entrainment at the south delta water export pumps.

Winter: We hypothesize a potential survival roadblock in winter where only the largest and healthiest individuals survive. This derives in part from analyses by Kimmerer et al. (2000) who found little relationship between two indices of age-0 abundance and the number of bass entering the fishery at age 3. In winter, young striped bass revert back to feeding on invertebrate prey (Stevens 1966) and in addition to mysids and amphipods they likely prey upon the recently introduced decapod shrimp, *Exopalaemon modestus*, as they do later in spring (Nobriga and Feyrer 2007). The increased numbers of *E. modestus* (Hieb 2007) likely improved food resources for winter striped bass.

Similar to other species, young striped bass have suffered increased winter entrainment as evidenced by salvage since 2000 (Figure 14; IEP 2005, Grimaldo et al. in prep). However this effect occurs after young-of-the-year trends are assessed. Losses indexed by winter salvage from the early 2000s would only begin to be reflected in adult numbers in 2003 and beyond. Current adult striped bass estimates (DFG unpublished, Figure 11) do not provide the necessary information on age 3 or age 4 abundances to evaluate this effect.

Longfin smelt

Longfin smelt abundance indices (year class strength) remain positively related to freshwater outflow during its winter-spring spawning and early rearing periods (Jassby et al. 1995; Kimmerer 2002; Sommer et al. 2007; Stevens and Miller 1983). The historical relationship changed subsequent to the introduction of the overbite clam in 1987—the slope of the relation remained the same after the introduction, but the abundance index declined significantly

(Kimmerer 2002). The mechanism for the first change in the relationship is believed to be reduced prey availability due to clam grazing (Kimmerer 2002). There appears to have been an additional shift in the relationship during the POD years, when increased outflow did not result in the expected degree of increased abundance (Sommer et al. 2007). *After a large, outflow-related abundance index increase in 2006, the 2007 Fall Midwater Trawl index (I3) declined to a record low (<http://www.delta.dfg.ca.gov/data/mwt>). Some decline was expected due to low winter-spring outflows, but the 2007 index falls well below even the post-clam outflow abundance relationship (Figure 4).* The mechanism for this lack of response to outflow is not known. Also, preliminary analyses support a stock-recruit relationship between adults approaching their second birthday and age-0 fall recruits (Baxter, unpublished); a significant stage-recruit relationship (fall age-0 to fall age-1 abundance), also exists, but survival declined after 1994 (Rosenfield and Baxter 2007) presumably due to continued food limitation. Longfin smelt typically spawn at the end of their second year of life (Baxter 1999; Moyle 2002).

Winter: Upstream migration of mature adults and most spawning occurs in winter (Figure 26), with spawning probably confined to freshwater portions of the estuary (Moyle 2002; Rosenfield and Baxter 2007). The geographic and water column distributions of adults and larvae in winter lead us to hypothesize that entrainment is an important stressor to the population during this season, particularly during low outflow years. Increased salvage of adult longfin smelt since 2000 suggests that entrainment levels were higher during POD years (Figure 14; IEP 2005; Grimaldo et al. in prep). High adult salvage typically precedes high juvenile salvage, but high juvenile salvage (spring-summer) has occurred in the absence of high adult salvage (Grimaldo et al. in prep). Due to their predominant surface orientation (Bennett et al. 2002), entrainment of longfin smelt larvae is presumed high, though undocumented, because larvae are not identified in salvage until ≥ 20 mm. Additional support for negative effects of entrainment on longfin smelt derives from analogy to delta smelt. Initial delta smelt otolith studies by Bennett et al. (unpublished data) suggest that winter-spawned fish have recently contributed poorly to the adult population compared to spring-spawned fish, which benefit from spring export reductions in recent years. The earlier spawning longfin smelt may be losing higher numbers of larvae to recently higher winter exports.

Adult and juvenile longfin smelt occupy the entire range of salinities and temperatures available during this period, though ripe adults are believed to seek freshwater for spawning (Moyle 2002; Rosenfield and Baxter 2007). Larvae are rare at salinities > 18 ppt and salinities between 0.1 and 18 ppt have been hypothesized to represent nursery habitat (Hieb and Baxter 1993). The downstream transport and distribution of larvae within the estuary varies positively with outflow (Baxter 1999; Dege and Brown 2004). Specifically, larvae disperse farther downstream when X2 is farther downstream and young juveniles remain in the same regions even as X2 recedes upstream. Turbidity remains an unexamined factor in the early life history of longfin smelt. Increased turbidity, associated with outflow events, may provide a competitive advantage to longfin smelt larvae. Recent histology revealed that longfin smelt larvae and juveniles possess a large, well developed olfactory system, which probably is used for food acquisition (Scott Foott, pers. comm. 2006).

Contaminant effects are possible during flow pulses, but only limited evidence of recent winter-time water toxicity has been found (Werner et al. 2006; Werner et al. 2007). Nonetheless,

surface oriented early-stage larvae would be particularly vulnerable to pulse-flow transported contaminants. We have not examined larvae from winter collections for contaminant effects.

Food availability for larvae has not been fully evaluated during this period. Limited diet analysis reveals that longfin smelt feed on early life stages of calanoid copepods in general and *E. affinis* in particular (Slater, in prep.). Trends in winter abundance indices of calanoid copepods do not show declines during the POD years (Hennessy pers. comm. 2007). Age-1 and age-2 longfin smelt most likely concentrate feeding on mysids when and where available, and rely on copepods and to some extent amphipods otherwise (Feyrer et al. 2003). We have not completed processing samples to evaluate diet and feeding success of older longfin smelt.

Spring: Like delta smelt, longfin smelt hatched in spring probably benefited from reductions in spring exports since 2000 associated with VAMP (see delta smelt spring). Low winter-spring outflows in 2001-2002 left many young longfin smelt in the Delta vulnerable to entrainment, but higher flow in subsequent years transported most to Suisun Bay and farther downstream.

Longfin smelt apparently take advantage of seasonally increasing copepod numbers in spring (Slater, in prep.). Spring densities of *E. affinis* have not suffered the recent declines like those of summer (Hennessy and Hieb 2007) and appear to be supporting similar pre- and post-2000 longfin smelt apparent growth rates (Baxter et al. 2006). No evidence of food limitation was found in young longfin smelt collected from San Pablo Bay or Napa River in spring 2006 (Foott et al. 2006).

Summer: By mid-summer entrainment is no longer a major stressor of longfin smelt, because like delta smelt, most of the population is downstream of the zone affected by water exports. More highly mobile age-0 longfin smelt disperse farther downstream than larvae and their distribution further diverges from other POD fishes, now ranging primarily from eastern Suisun Bay to marine waters of central San Francisco Bay (Baxter 1999). By summer age-1 longfin smelt have left the Delta beginning a migration toward central San Francisco Bay that concludes in fall (Baxter 1999).

As longfin smelt grow through summer their diet broadens to include amphipods and mysids, but copepods continue to dominate: *Acartia sp.* and *P. forbesii* in San Pablo and western Suisun bays, and *P. forbesii* and *Sinocalanus sp.* in eastern Suisun Bay and the western Delta (Slater, unpublished). In summer, *C. amurensis* grazing has reduced calanoid copepod availability, affecting age-0 longfin smelt survival to fall (Kimmerer 2002b). During the POD years there has been further decline of calanoid copepods in Suisun Bay and the west Delta (Kimmerer et al., in prep, Mueller-Solger et al., in prep.), which represent a sizable portion of the longfin smelt distribution. Regionally diminishing food resources may also be responsible for reduced fall recruitment 2003-2005 (Sommer et al. 2007) and for reduced post drought survival of longfin smelt from their first through second falls (Rosenfield and Baxter 2007). Feeding conditions may improve during high outflow years. Age-0 longfin smelt collected from San Pablo and Suisun Bays in summer 2006 exhibited 13% (n=107) incidence of hepatocyte vacuoles that contained either fat or glycogen reserves, uncommon for rapidly growing fishes (Foott et al. 2006) and longfin smelt abundance increased substantially during fall 2006, though only to the low range of their recent outflow abundance relationship (Sommer et al. 2007).

No direct link has been made between contaminants and longfin smelt. In 2006, invertebrate toxicity was detected from water samples taken within the range of longfin smelt, in particular eastern San Pablo Bay (Werner et al. 2007), yet histopathological examination of longfin smelt from the same region before and after the water collection did not reveal evidence of contact with a toxic substance (Foott et al. 2006)

Fall : Age-0 longfin smelt seek deep water and may be geographically limited by the combination of high water temperatures and high salinities. This combination limits their range in south San Francisco Bay and the shallows of San Pablo Bay (Rosenfield and Baxter 2007). Upper Estuary stressors (e.g., entrainment effects) probably have little effect on age-1 fish during fall, because they appear to emigrate to central San Francisco Bay and some leave the Estuary (Rosenfield and Baxter 2007). Observational data suggests high delta water temperatures may also limit their distribution in early fall, but age-0 longfin smelt reoccupy the Delta as water temperatures drop in late fall (Baxter 1999). Prior to reoccupation, age-0 fish reside outside the influence of the export pumps. Within Delta stressors (e.g., entrainment effects) probably have little effect on age-1 fish during fall, because they follow a movement pattern similar to age-0 (Baxter 1999, Rosenfield and Baxter 2007). By late fall, age-1 longfin smelt begin to mature and their movement into the Delta represents the start of their spawning migration (Baxter 1999; Rosenfield and Baxter 2007)

Threadfin shad

Unlike the other species, virtually nothing was known about the life history of threadfin shad in the Delta prior to the POD investigation. Thus, available data were compiled and analyzed to provide information on the life history and population dynamics of threadfin shad. The model description below (Figure 27) is based upon this work, which is not yet published but is being prepared for two manuscripts. Due to this limited amount of information available for threadfin shad, the conceptual model relies more heavily on correlational analyses than those of the other species. The model will be expanded and take into account other factors as more information is developed.

In contrast to the other fishes, there has not been a consistent long-term decline in threadfin shad abundance indices. The threadfin shad abundance index in the Fall Midwater Trawl Survey declined sharply in 2002 after near record high abundance indices in 2000 and 2001 and only exhibited a slight recovery starting in 2005 that continued into 2007 (<http://www.delta.dfg.ca.gov/data/mwt>). Based on the initial analyses conducted to date, there is stock-recruit relationship in that juvenile abundance largely determines fall recruitment. Food supply (abundance of cladocerans) also appears to be a significant factor affecting larval survival. The limited data from the POD years suggests that there has been a recent change in survival between summer and fall. During this period, we hypothesize that habitat changes may be relevant to the recent low abundance index. Of particular concern is the proliferation of the toxic algae *M. aeruginosa*, which bloomed in the core summer habitat of threadfin shad during each of the POD years. Supporting evidence for this interpretation is provided below based on seasons.

Summer:

Prior fish abundance appears to be important because there is a significant stock-recruit relationship for threadfin shad (Feyrer and Sommer, unpublished data). A major concern with threadfin shad is that recent (2002-2005) survival of fish from the summer to the fall appears to be poor. This recent decline in summer-fall survival has been producing low adult stocks, which may be hindering recovery to higher abundances.

Long-term trends in abiotic habitat during summer have not been examined. However, there is evidence to suggest that it has not directly been a limiting factor. First, habitat conditions during fall exhibit no long-term trend (Feyrer et al. 2007). Second, abiotic habitat variables do not increase the amount of variability explained by the summer to fall survival relationship.

Indirectly, habitat conditions may affect the abundance or survival of young threadfin shad by controlling the density of suitable prey organisms. The abundance of young threadfin shad in the 20mm Survey is significantly associated with the abundance of cladocerans, the abundance of which is explained by environmental conditions, including temperature, chlorophyll *a*, specific conductance and flow (Feyrer and Sommer, unpublished data). Although there are no diet data in the Delta for young threadfin shad of this size, information from the literature indicates cladocerans are important prey items and interactions between food densities and water temperature affect growth and survival (Betsill and Van Den Avyle 1997)

Unlike the other fish species, the primary distribution of threadfin shad overlaps that of *M. aeruginosa*. Since 2002, high densities of *M. aeruginosa* during summer might inhibit feeding of young threadfin shad, limit their survival to fall and reduce the fraction able to grow sufficiently to reproduce in their first summer. High densities of *M. aeruginosa* could also affect the abundance of cladoceran prey.

Threadfin shad is a major component of piscivorous fish diets (Stevens 1966; Nobriga and Feyrer 2007). However, there is insufficient data to determine if predation mortality significantly affects the abundance of threadfin shad during summer. Threadfin shad is also the most common fish collected at the export facilities (Brown et al. 1996). However, there is no clear evidence to date for an important effect of water project diversions as summer to fall survival is not related to the volume of water exported.

Fall:

Prior to 2002, the abundance of age-0 threadfin shad in fall was, at least in part, a function of age-0 abundance in summer (Feyrer and Sommer, unpublished data). However, that relationship deteriorated substantially starting in 2002, suggesting that new unidentified sources of mortality have completely overwhelmed the effect of prior fish abundance during the POD years.

Abiotic habitat variables, namely salinity and water temperature, are important predictors of the occurrence probability of threadfin shad (Feyrer et al. 2007). There is no evidence of a long-term trend in habitat conditions indexed by these variables upstream of the confluence of the

Sacramento and San Joaquin rivers (Feyrer et al. 2007). Similarly, there is no evidence that these factors affect the population because they did not affect the summer to fall survival relationship.

Threadfin shad is a major component of piscivorous fish diets (Stevens 1966; Nobriga and Feyrer 2007). Striped bass move into the Delta from downstream bays and the ocean in large numbers during the fall. This large influx of predators undoubtedly increases predation pressure on threadfin shad. To the extent that the adult striped bass population estimates index predation pressure, there is no evidence that predation affects threadfin shad population dynamics (Feyrer and Sommer, unpublished data). Including striped bass population estimates as a variable in the stock-recruit or the summer to fall survival relationship did not improve the fit of the models. Further analyses may provide greater insight into the dynamics of predation effects on threadfin shad.

There is no direct correlational evidence that food densities affect threadfin shad abundance. However, the apparent growth rate (growth estimated from length frequency analysis) of age-0 fish during fall exhibited a negative trend with abundance, suggesting the population is subject to density-dependent control of vital rates at certain times (Feyrer and Sommer, unpublished data). Food limitation is a possible explanation for the suggested density-dependence.

Winter:

The abundance of threadfin shad is not measured during winter, thus it is not possible to determine if it is affected by abundance during a previous time period. Without some measure of seasonal survival, it is difficult to assess the potential importance of stressors.

Long-term trends in habitat conditions (salinity and temperature) during winter are presumed to be generally similar to the fall, which would suggest no major impacts on the population. However, water temperatures lower than approximately 9° Celsius are known to cause mortality of threadfin shad. The limited winter water temperature data available indicate that water temperatures occasionally reached this level in some locations in some years. However, the data are insufficient to include in statistical models to evaluate an effect on the population.

The top-down effects of predation are presumed to be similar to the fall; however, there is insufficient data to determine if predation mortality significantly affects the abundance of threadfin shad during winter. There has been a recent increase in the salvage of threadfin shad during winter, especially in relation to the abundance index measured by the Fall Midwater Trawl (Figure 14,). However, as described above, there is no direct correlational evidence that this has a population-level effect.

Spring:

The significant stock-recruit relationship suggests that prior fish abundance is important to abundance in spring (Feyrer and Sommer, unpublished data). Long-term trends in habitat during spring have not been examined. However, young threadfin shad habitat associations during spring (20-mm Survey) are similar to those of older fish during fall (Fall Midwater Trawl).

As already mentioned for other seasons, indirect evidence suggests that the availability of food resources may have an effect on the survival and abundance of young threadfin shad (Feyrer and Sommer, unpublished data). Work is in progress to determine if threadfin shad vital rates are similarly affected by cladoceran abundance.

Predation or entrainment mortality is likely an important factor of threadfin shad population dynamics in spring as in other seasons; however, there is no correlational evidence to indicate predation is an important cause of the POD.

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