Chapter 7  Basic Biology and Life History of Delta Smelt and Factors that May Influence Delta Smelt Distribution and Abundance

This chapter provides information on the basic biology, life history, and status of delta smelt, as well as a description of the potential factors that may affect delta smelt and critical habitat in the action area. There has been a long-term decline of delta smelt, with an especially sharp downturn after 1999 as delta smelt other pelagic fish species jointly suffered what has become known as the Pelagic Organism Decline.

The term “Pelagic Organism Decline” (POD) denotes the sudden, overlapping and striking declines of San Francisco Bay-Delta Estuary pelagic fishes since about 2000. The POD species include delta smelt, longfin smelt, threadfin shad, and (young-of-year) striped bass. Recent abundance indices for the POD species have included record lows for delta smelt and young-of-year striped bass, and near-record lows for longfin smelt and threadfin shad. Although abundance improved for each species during the wet 2006, levels for all four species have remained near record lows since 2004.

Factors affecting delta smelt fall into four general categories: (1) prior fish abundance or “stock-recruit effects”, including low-abundance adult effects that may reduce juvenile production; (2) habitat, including physical and chemical variables, disease, and localized toxic algal blooms that affect survival and reproduction; (3) top-down effects, including predation, entrainment, and other processes that cause juvenile and adult mortality; (4) bottom-up effects, including food web interactions that affect growth, reproduction, and, indirectly, survival.

The POD has been the subject of an intensive analytical effort by the Interagency Ecological Program (IEP) since the POD was recognized in 2005. The POD investigation has greatly improved our understanding of the ecology of pelagic fishes in the estuary, especially delta smelt. While the mechanisms responsible for long-term and POD-era declines of the species probably vary by species, it appears very unlikely that they are independent of one another. Rather, the decline appears to be the result of multiple interacting causes, including some that are related to water project operations and others that are not.

**General Biology**

The 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 (Moyle et al. 1992). 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). It typically has an annual life cycle though a small percentage (< 10 percent) of the population can live to and possibly reproduce at age-two (Brown and Kimmerer 2001). On average, ripe females produce about 1,900 eggs, but fecundity can range from about 1,200 to about 2,600 eggs per female (Moyle et al. 1992). Moyle et al. (1992) considered delta smelt fecundity to be “relatively low”, but based on Figure 2a in Winemiller and Rose (1992), delta smelt fecundity is actually fairly high for a
fish its size. Delta smelt move into tidal freshwater habitats to spawn in late winter through spring. Most spawning occurs in the Delta, but some also occurs in Suisun Marsh and the Napa River (DFG unpublished). An optimal spawning temperature “window” of about 12 ºC -18 ºC (59 ºF - 64.4 ºF) has recently been reported (Bridges unpublished; Bennett unpublished). After hatching, larvae are dispersed throughout low salinity habitats, generally moving into Suisun Bay, Montezuma Slough, and the lower Sacramento River below Rio Vista as they mature (Grimaldo et al. 1998; Sweetnam 1999). Delta smelt are zooplanktivorous throughout their lives, feeding mainly on copepods, cladocerans, and amphipods with which they co-occur (Moyle et al. 1992; Lott 1998; Nobriga 2002). In the larger picture of fish life history strategies, delta smelt best fit the “opportunistic strategy” of Winemiller and Rose (1992). Opportunistic fishes are characterized as placing “a premium on early maturation, frequent reproduction over an extended spawning season, rapid larval growth, and rapid population turnover rates”, and “maintain dense populations in marginal habitats (e.g. ecotones, constantly changing habitats) (Winemiller and Rose 1992).”

Legal Status

The delta smelt was listed as threatened under both the Federal Endangered Species Act and the California Endangered Species Act in 1993. The species was recently proposed for re-listing as endangered under the Federal Endangered Species Act.

Distribution, Population Dynamics, and Baseline Conditions

Distribution

Delta smelt spend most of their lives rearing in low salinity habitats of the northern estuary (Moyle et al. 1992; Sweetnam and Stevens 1993). Delta smelt can temporarily tolerate salinities as high as 19 parts per trillion (ppt) (Swanson et al. 2000) and have been collected in the field at salinities as high as 18 ppt (Baxter et al. 1999). However, most delta smelt are collected at much lower salinities- typically in the range of about 0.2 – 5.0 ppt (Sweetnam and Stevens 1993; Feyrer et al. 2007). The geographical position of these low salinity habitats varies principally as a function of freshwater flow into the estuary. Therefore, the delta smelt population’s center of mass has on average been located in the western Delta during years of low freshwater flow and in Suisun Bay during years of high freshwater flow. This relationship between flow and distribution is particularly strong during the larval period (Figure 7-1), but persists throughout the first year of life (Sweetnam and Stevens 1993).
Currently, the approximate spatial position of low salinity habitat in the estuary is indexed by X2, defined as the distance in km from the Golden Gate to the location of 2 psu salinity near the bottom of the water column (Jassby et al. 1995). The longitudinal position of X2 during spring and/or early summer, which varies as a function of freshwater flow into the estuary, has been correlated with abundance or survival indices of numerous estuarine taxa (Jassby et al. 1995) including delta smelt (Kimmerer 2002). Both late larval (Bennett et al. 2002) and juvenile (Aasen 1999) delta smelt are thought to actively maintain positions in low salinity habitats by using swimming behaviors timed to tidal and diel cues.

**Natural History**

**Spawning**

Adult delta smelt spawn during the late winter and spring months, with most spawning occurring during April through mid-May (Moyle 2002). Spawning occurs in sloughs and shallow edge areas in the delta and Sacramento River above Rio Vista, especially, in recent years, in the Cache Slough/ Sacramento Deepwater Ship Channel complex. Spawning has also been historically recorded in Suisun Marsh and the Napa River (Moyle 2002). Most spawning occurs at temperatures between 7—15°C, although it may occur at temperatures up to 22°C (Moyle 2002). Fecundity (59—70 mm SL females) ranges from 1200 to 2600 eggs (Moyle et al. 1992). Most adults do not survive to spawn a second season, but a few (<5%) do (Moyle 2002 and references therein). Large (90—110 mm SL) two-year-old females may contribute disproportionately to the egg supply (Moyle 2002 and references therein).

**Larval Growth and Downstream Transport**

Larval smelt hatch after 9-13 days at 14.8—16.5°C, and feeding begins 4—5 days later (Mager 1996). Early larvae are demersal and are not strongly subject to net water flows until after swim-up and fin development is complete several weeks later. Larvae enter the water column at about
14—18 mm TL and become fully subject to passive transport with water currents (Moyle 2002). At this point, they are very weak swimmers and are moved in the direction of the prevailing net flow of water. Those outside the zone of entrainment surrounding the CVP and SWP export facilities that survive predation and other dangers are transported downstream to the low salinity zone.

**Juvenile Rearing**

As described by Moyle:

In general delta smelt prefer to rear in or just above the region of the estuary where fresh water and brackish water mix and hydrodynamics are complex as a result of the meeting of tidal and riverine currents. This region is typically in Suisun Bay. During the 1987—1992 drought, the smelt were concentrated in deep areas in the lower Sacramento River around Decker Island, where the bottom salinity hovered around 2 ppt much of the year (Herbold 1994), apparently because the salt water-fresh water mixing zone was located in this region. However, smelt may also be common in this region during nondrought years, a finding that suggests they are attracted to favorable hydraulic conditions that allow them to maintain position. (Moyle 2002)

Delta smelt grow rapidly during the summer, especially once they reach 30 mm, a size at which a variety of planktonic prey become available, and reach 40—50 mm FL by early August (Moyle 2002). Juvenile-stage prey include copepods, cladocerans, amphipods, and insect larvae (Moyle 2002). They reach adult size (55—70 mm SL) by early fall (Moyle 2002). At that size, they may also consume larger zooplankton.

**Upstream Migration**

Movement upstream begins in September and October as a “gradual, diffuse migration” toward spawning areas (Moyle 2002). Adult smelt may take several months to reach spawning sites. Recent evidence suggests that more rapid upstream movement is keyed to “first flush” pulses of turbid water through the estuary at the onset of winter rains (Grimaldo et al. in review).

**Population Abundance Trends**

The DFG Fall Midwater Trawl Survey (FMWT) provides the best long-term index of relative abundance of maturing adult delta smelt (Moyle et al. 1992; Sweetnam 1999). It has been conducted each September-December since 1967 (except 1974 and 1979). The DFG Summer Townet Survey (TNS), which has been conducted since 1959 (except 1966-68), provides an index of juvenile delta smelt abundance during June-July. These surveys do not at present support statistically respectable population abundance estimates, though substantial progress has recently been made (Newman, in review; Newman, in prep.). However, they are generally accepted to provide a respectable basis for evaluating interannual trends.

The TNS indices have ranged from a low of 0.3 in 2005 to a high of 62.5 in 1978 (Figure 7-2). The FMWT indices have ranged from a low of 27 in 2005 to 1,653 in 1970 (Figure 7-3). Although peak high and low values have varied in time, the TNS and FMWT indices show similar time series of delta smelt relative abundance (Sweetnam 1999; Figures 7-2 and 7-3).
Figure 7-2 IEP TNS indices 1969-2007.

Figure 7-3 IEP FMWT indices 1969-2007.
From 1969-81, mean delta smelt TNS and FMWT indices were 22.5 and 894 respectively. Both indices suggest the delta smelt population declined abruptly in the early 1980s (Moyle et al. 1992). From 1982-1992, mean delta smelt TNS and FMWT indices dropped to 3.2 and 272 respectively. The population has rebounded somewhat in the mid-1990s (Sweetnam 1999); mean TNS and FMWT indices were 7.1 and 529 during 1993-2002. However, delta smelt numbers have trended precipitously downward since about 1999, as delta smelt and, later, other pelagic fish species jointly suffered what has become known as the Pelagic Organism Decline (Sommer et al. 2007).

The Pelagic Organism Decline
The term “Pelagic Organism Decline” (POD) denotes the sudden, overlapping declines of San Francisco Estuary pelagic fishes since about 2002 (Sommer et al. 2006). The POD species include delta smelt, longfin smelt, threadfin shad, and (age-0) striped bass, which together account for the bulk of the pelagic fish biomass in the upper Estuary. The year 2002 is often reckoned as the start of the POD because of the striking declines of three of the four POD species between 2001 and 2002; however, statistical review of the data (e.g. Manly and Chotkowski 2006) has revealed that for delta smelt, at least, the POD downtrend really began earlier. The POD declines became clearly evident against the high background variability in these species in early 2005, when analysis of the third consecutive year of extremely low numbers in these species made them statistically clear.

Post-2001 abundance indices for the POD species have included record lows for delta smelt and age-0 striped bass, and near-record lows for longfin smelt and threadfin shad. Abundance improved for each species during 2006, have remained relatively poor since 2002 for all four species. Low abundance levels have been especially remarkable in that winter and spring river flows into the estuary have been moderate or very wet (2006) during recent years. Moderate to wet conditions have historically usually been associated with at least modest recruitment of most pelagic fish species. Longfin smelt (discussed at length in a Technical Assistance appendix to this Biological Assessment) is perhaps the best example of this point as the species shows a very strong relationship with delta outflow. 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 2002). 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, which has a historical abundance association with outflow that 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 since the POD (Sommer et al. 2007).

Because of its many management implications, the POD has been the subject of an intensive analytical effort by the Interagency Ecological Program since the POD was recognized in 2005. The POD investigation has greatly improved our understanding of the ecology of pelagic fishes in the Estuary, especially delta smelt. Revisions to this chapter and in the formulation of the delta smelt effects analysis largely reflect changes in our understanding of delta smelt biology that
have emerged from the POD investigation. While mechanisms responsible for POD-era declines of the species probably vary by species, it appears very unlikely that they are independent of one another. Consequently, some of the discussion in the remainder of this chapter involves species other than delta smelt. This chapter borrows heavily from the text of the 2007 POD Synthesis Report (IEP 2008).

**Factors That May Influence the Abundance and Distribution of Delta Smelt**

Numerous factors are hypothesized to have influenced historical population dynamics of delta smelt (Bennett and Moyle 1996). Some of these factors (e.g., climatic influences on the physical environment) are thought to exert strong, consistent influences, while others are thought to exert more subtle influences (e.g., factors affecting growth rates), or to be important only under certain conditions (e.g., entrainment losses). Historically, the evidence brought to bear on most mechanistic hypotheses has been based on statistical correlations of abundance and/or survival with environmental variables (see Sweetnam and Stevens 1993; Brown and Kimmerer 2001). For organization we will use the four categories described in the simple conceptual model presented in the POD 2007 Synthesis Report (POD Team, 2008) and in Sommer et al. (2007). Where the POD Team used the model to describe possible mechanisms by which a combination of long-term and recent changes to the ecosystem could produce the observed pelagic fish declines, we use it simply to organize mechanisms that affect abundance and distribution. The conceptual model is rooted in classical food web and fisheries ecology and contains four major components: (1) prior fish abundance, including low-abundance effects that may reduce juvenile production (e.g. stock-recruit effects); (2) habitat, including physical and chemical variables, disease, and localized toxic algal blooms that affect survival and reproduction; (3) top-down effects, including predation, entrainment, and other processes that cause juvenile and adult mortality; (4) bottom-up effects, including food web interactions that affect growth, reproduction, and, indirectly, survival.

**Prior 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 ‘rebuilt’ itself.

Moyle et al. (1992) and Sweetnam and Stevens (1993) both reported that number of delta smelt spawners (indexed by the FMWT) was a poor predictor of subsequent recruits (indexed by the following year’s TNS). Both linear and nonlinear Beverton-Holt models suggested that only about a quarter of the variance in delta smelt TNS abundance could be explained by the
abundance of the adult spawners. This means that over the range of empirical experience most of the variation in delta smelt abundance is due to other causes.

At present, there is an ongoing scientific debate concerning interpretation of within-year dynamics of delta smelt. Both the TNS and FMWT indices suggest similar long-term abundance trends for delta smelt collected in the summer and fall respectively (Figure 7-2 and Figure 7-3). However, when all of the available data are considered together, a nonlinear Beverton-Holt model describes the relationship between the TNS and FMWT data better than a linear model (Bennett unpublished; reproduced in Figure 7-4).

The standard fisheries interpretation of such a relationship is that it indicates a carrying capacity for the population - in this case during late summer of the first year of life. Phrased another way, this relationship suggests that as the number of juveniles produced increases, so does population mortality. Evidence for this density-dependent mortality was presented in Figure 19 of Brown and Kimmerer’s (2001). In fisheries science, density-dependence is the mechanism allowing stocks to be sustainably fished. A correlation of abundance and mortality means there is “surplus production” that can be harvested without negatively affecting a population’s viability.

The evidence for density-dependent mortality in the delta smelt population has not been universally accepted by delta smelt biologists (Brown and Kimmerer 2001; EET 2007 unpublished). One reason for this skepticism is that it may not be appropriate to pool all years of data. In Figure 7-4, the data points from the pre-decline period (1969-1981) almost all occur outside of the range of the post-decline (1982-2002) data points. Therefore, an alternative explanation of the TNS-MWT relationship is possible - the non-linearity may reflect two different relationships from two time periods with different delta smelt carrying capacities. This latter relationship suggests that summer abundance is not and has never been a statistically

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Figure 7-4 (Beverton-Holt curve was fitted to all data even though time periods are shown separately).

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significant predictor of fall abundance. As stated above, which (if either) of these interpretations is correct remains a subject of debate.

One possible problem with analyses using the TNS index is that it is not considered as robust an abundance index as the FMWT (Miller 2000). However, the TNS indices are correlated with two unpublished versions of a larval abundance index derived from the DFG 20-mm Delta Smelt Survey, which has been conducted each spring-summer since 1995 (Figure 7-5). This provides support for the density-dependent mortality hypothesis because it suggests the Townet Survey reflects the large differences in young-of-year (YOY) delta smelt abundance that underlie the density-dependent mortality hypothesis.

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 7-6). 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 Townet 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 7-7). The strong relationship in summer to fall survival since 2000 (Figure 7-7) suggests that the primary factors affecting juvenile survival recently changed and shifted to earlier in the life cycle, or that the stock has declined to such a low level that prior abundance is now the primary factor controlling abundance. These observations strongly suggest that recent population trends are outside the historical realm of variability and resilience shown by these species, particularly delta smelt.

Scientific debate also continues regarding the meaning of statistically significant autocorrelation in the TNS and FMWT time series. Autocorrelation means that index values within the time series are dependent in part on values that preceded them. Both sets of indices show significant autocorrelation at lag two years, meaning that successive index values are correlated with index values from two years prior. Bennett (unpublished) hypothesized the lag two-year autocorrelation was evidence for a reproductive contribution of age-two spawners, but this interpretation has not thus far been backed by strong empirical evidence. The contribution of age-two spawners to delta smelt population dynamics is currently under investigation (Brown and Kimmerer 2002).
Figure 7-5 Relationships between 20-mm Survey indices and TNS indices, 1995-2002.

Figure 7-6 Water operations impacts to the delta smelt population.
Reclamation and DWR (1994) were concerned about autocorrelation resulting in spurious conclusions about environmental influences on delta smelt population dynamics. Statistically speaking, autocorrelation in a time series or in the residuals from a correlative analysis of the time series and an explanatory variable can complicate interpretation because a variable may happen to covary with, but not actually influence the underlying process resulting in the autocorrelation. Recent statistical analyses have mitigated for this by using residuals from various stock-recruit relationships (Brown and Kimmerer 2001) and by testing regression residuals for significant autocorrelation.

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). A key point is that habitat suitability affects most or all other factors affecting abundance and/or distribution. This is because changes in pelagic habitat, to take an example, affect not only affect delta smelt and other pelagic fishes but also their predators and prey.

Habitat for delta smelt 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, delta smelt habitat is water with suitable values for a variety of physical-chemical properties, especially including salinity, turbidity, and temperature, suitably low levels of contaminants, and suitably high levels
of prey production to support growth. Thus, delta smelt 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, including delta smelt, 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.

Physical Habitat

Changes in delta smelt habitat quality in the San Francisco Estuary can be indexed by changes in X2. The abundance of many local taxa has tended to increase in years when flows into the estuary are high and the 2 psu isohaline is pushed seaward (Jassby et al. 1995), implying that over the range of historical experience the quantity or suitability of estuarine habitat increases when outflows are high.

Currently, X2 (which is controlled by both climate and water operations) is a strong predictor of the delta smelt TNS index but curiously, the slope of the X2-TNS relationship switched sign about the time of the delta smelt decline in the early 1980s (Kimmerer 2002). During 1959-81, TNS indices were highest in years of low freshwater flow. In contrast, during 1982-2000, TNS indices were usually among the lowest recorded during years of low freshwater flow. Throughout 1959-2000, TNS indices have been comparable during years of high freshwater flow. The reason(s) for this change in the relationship of young delta smelt abundance to low spring flow conditions beginning in the early 1980s is unknown.

The number of days during spring that water temperature remained between 15 ºC and 20 ºC (59ºF to 68ºF), with a density-dependence term to correct for the saturating TNS-FMWT relationship (described below), predicts FMWT indices fairly well ($r^2 \approx 0.70$; $p < 0.05$; Bennett unpublished presentation at the 2003 CALFED Science Conference). The spring temperature “window” is thought to influence delta smelt abundance by influencing reproductive success - a longer period of optimal water temperatures during spring increases the number of spawning events and cohorts produced. More cohorts translate into a higher probability for a strong year class. Summer water temperatures have also been shown to be an important predictor of delta smelt occurrence based on multi-decadal analyses of the TNS data (Nobriga et al. 2008). Water temperatures in the Delta and estuary are primarily affected by air temperatures and cannot be controlled by CVP/SWP operations because water storage facilities are too far away from the Delta. Therefore, Delta water operations cannot manage water temperatures to enhance conditions for delta smelt spawning or rearing in a manner analogous to strategies used for salmonid fishes in Delta tributaries.

The number of days during spring that X2 is in Suisun Bay also is weakly positively correlated with the FMWT indices (Brown and Kimmerer 2001). Hypotheses regarding potential mechanisms underlying X2-abundance relationships have been described previously (Moyle et al. 1992; Jassby et al. 1995; Bennett and Moyle 1996; Kimmerer 2002). However, it is probable that X2 position covaries with the number of days spawning temperatures remain optimal during spring, so both of these correlations may reflect the same phenomenon.
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 (Feyrer et al. 2007). The long-term environmental quality declines for delta smelt are defined by a lowered probability of occurrence in samples based on changes in specific conductance and Secchi depth. Notably, delta smelt environmental quality declined recently coinciding with the POD (Figure 7-8). The greatest changes in environmental quality occurred in Suisun Bay and the San Joaquin River upstream of Three Mile Slough and southern Delta (Figure 7-9). 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 FMWT survey. 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 other organisms.

The importance of Secchi depth (a measure of water clarity or, conversely, turbidity) in the longterm 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 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.

**Regional Changes in Habitat**

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 percent 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 Townet Survey) at the scale of the entire estuary (Nobriga et al. 2008).
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.
Figure 7-8  Annual values (± 2 standard errors) of environmental quality (EQ) for (a) delta smelt, (b) threadfin shad, (c) striped bass in San Francisco Estuary, based on data from the Fall Midwater Trawl (from Feyrer et al. 2007).

NOTE: EQ is the probability of capturing the species in a sample based on values of specific conductance and Secchi depth for delta smelt and striped bass and based on values of water temperature and specific conductance for threadfin shad.
Figure 7-9  Spatial distribution of long-term trends in annual EQ for (a) delta smelt, (b) threadfin shad, (c) striped bass in San Francisco Estuary shown for the region bordered downstream at Carquinez Strait.
NOTE: Color shading represents the coefficient for the year term for individual linear regressions of EQ versus year for each station. Lighter shading represents a more negative slope. Open circles and filled circles represent stations with non-significant (P > 0.05) or significant regressions (P < 0.05), respectively (from Feyrer et al. 2007).

Contaminants and Disease
In addition to habitat changes from salinity, turbidity and invasive aquatic vegetation such as E. densa, 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.

Although a number of contaminant issues were first investigated during the POD years, 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 and unpublished; 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.

The POD investigators initiated several studies beginning in 2005 to address the possible role of contaminants and disease in the declines of Delta fish and other aquatic species. Their 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 Hyalella 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 than in wetter previous years. 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 were 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 within the Delta 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.

POD investigators 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). Delta smelt and longfin smelt are generally not present in this region of the Delta during summer (Nobriga et al. 2008; Rosenfield and Baxter 2007) so *M. aeruginosa* toxicity is not likely a factor in their recent decline. However, 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 in other years.

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 percent) 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.).

**Effects of Habitat Change on the Food Web**

Much of the previous discussion about how physical conditions and water quality affect delta smelt and other 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 2008). 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 (exported from the Delta) as a result of CVP/SWP and local agricultural 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 Nieuwenhuyse 2006). Recent particle tracking modeling results for the Delta show that residence times in the southern Delta are highly variable, depending on Delta inflow, CVP/SWP exports, and particle release location (Kimmerer and Nobriga, 2008). Very high inflow leads to short residence time. The longest residence times occur in the San Joaquin River near Stockton under conditions of low Delta inflow and low CVP/SWP export rates.

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: exotic species invasions, and salinity (Peterson et al. in prep). Specifically, the invasion of the overbite clam *Corbula 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 7-10). These changes in the benthic assemblage can have major effects on food availability to pelagic organisms, including delta smelt.
Climate Change

There are several reasons we expect future climate change might have negative long-term influences on pelagic habitat suitability for the POD fishes, including delta smelt. 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 farther upstream into the Delta 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 may have a strong influence on POD fish distributions, and there have been long-term regional increases in temperature (Jassby 2008). Summer water temperatures throughout the upper estuary are fairly high for delta smelt. Mean July water temperatures in the upper estuary are typically 21-24C (Nobriga et al. in press) and the lethal temperature limit for delta smelt is reported to be 25C (Swanson et al. 2000), though entrainment of juvenile delta smelt in spring 2007 continued until central Delta temperatures approached 28C. Thus, if climate change were to result in summer temperatures in the Delta substantially exceeding current levels, the geographical extent of suitable habitat for delta smelt during those months could be reduced in some years.
Top-Down Effects

The two most prominent top-down influences on delta smelt and other pelagic fishes are entrainment into various water diversions and predation by piscivorous fishes. Major water diversions in the delta include the SWP and CVP export facilities, power plants, and agricultural diversions. The CVP and SWP water export operations include upstream reservoirs, the DCC, the SMSCG, the North Bay Aqueduct facilities (NBA), the Contra Costa Canal facilities (CCC), CCF, the Banks Pumping Plant/Skinner Fish Facilities (hereafter SWP), the South Delta Temporary Barriers (SDTB) and the Jones Pumping Plant/Fish Collection Facilities (hereafter CVP). The description and operation of these facilities was covered in the “Project Description” section of this Biological Assessment and will not be repeated here.

Water export operations occur primarily at SWP and CVP, with far smaller amounts of water diverted at NBA and CCC. Because of their size, and because of evidence implicating water
project operations as contributing causes of the POD, the discussion of them below borrows heavily from the POD analysis.

As described in Chapter 2, the NBA diversions have fish screens designed to FWS criteria for delta smelt protection. In addition, a delta smelt monitoring program occurs each spring in the sloughs near NBA. Until 2005, larval delta smelt sampling was conducted in the vicinity of the NBA. It was discontinued with the consent of FWS because of very low larval smelt occurrence. Because the FWS deems these NBA measures to be adequately protective of delta smelt, the NBA will not be considered further.

Water is also temporarily diverted by two power plants located in the western Delta at Antioch and Pittsburgh. Nonconsumptive water use may reach 3200 cfs during full operation of both plants, 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 during such operations can be very high. In recent years these plants have not been operated frequently, and several generating units are now retired. Use of the plants appears to be restricted to supplying power only during periods of extreme demand. They are discussed in more detail below.

**Entrainment**

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 inhabiting the delta (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 upstream, 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 CCF and the waterways leading to the diversion facilities, larvae less than 20 mm FL not efficiently collected by the fish screens, and losses of fish larger than 20 mm FL that because of other inefficiencies are not guided into the salvage tanks 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 delta smelt and other POD species (Grimaldo et al. in review). Increased winter entrainment of delta smelt, longfin smelt and threadfin shad represents a loss of pre-spawning adults and all their potential progeny (Sommer et al. 2007). 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, mostly attributable to the SWP (Figure 7-11). 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 7-12). 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, 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 7-13, L. Grimaldo, in review). The general pattern is that POD species salvage is low when Old and Middle river flows 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 relationship between exports and delta smelt fall abundance. Similarly, Kimmerer et al. (2001) estimated that entrainment losses of young striped bass were sometimes very high (up to 99 percent), but they did not find evidence that entrainment losses were a major driver of long-term striped bass population dynamics.
Figure 7-11 Deviations from average exports (cubic feet per second) in January, February, and March exports from 1984 to 2004 (IEP 2005; Simi et al., U.S. Geological Survey, unpublished data).
These results do not mean, however, that direct export effects can be dismissed as a contributing cause of the POD. There are two aspects of entrainment that explicitly were not addressed by Manly and Chotkowski (2006) and are not well understood: (1) the possibility that selective entrainment among a heterogeneous population of prespawning adults could produce consequences that do not become manifest until the following year (discussed in the next paragraph), and (2) larval entrainment. Very little is known about historical larval entrainment 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 Interagency Ecological Program (IEP) monitoring programs to estimate entrainment of delta smelt. These approaches suggest that larval delta smelt entrainment losses could exceed 50 percent of the population under some low flow and high export conditions depending on spawning distribution. Although not necessarily a realistic operational scenario, the effect of larval entrainment could be significant. Because there are few reliable larval entrainment data, it is not possible to directly address the question of how important these losses were historically.

Figure 7-12  Proportion of Delta inflow coming from the San Joaquin River and the Sacramento River, including Yolo Bypass from 1984 to 2004 (IEP 2005; Simi et al., U.S. Geological Survey, unpublished data).
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 7-14), 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 (or same-water year) predictors. This hypothesis is presently being evaluated by Bennett’s laboratory using otolith methods.
Figure 7-13  Relationship of mean combined salvage of delta smelt, longfin smelt, and striped bass at the State Water Project (SWP) and Central Valley Project (CVP) to combined Old and Middle rivers (OMR) flow (cubic feet per second).

Figure 7-14 Delta outflow (m3/s) averaged over water years (top) and export flow (m3/s) averaged over seasons (bottom).

NOTE: Water years begin on 1 October of the previous calendar year. Seasons are in 3-month increments starting in October. Export flows are the sum of diversions to the Federal Central Valley Project and State Water Project pumping plants. The outflow and export data are from DWR (http://iep.water.ca.gov/dayflow) (from Sommer et al. 2007).

The CVP and SWP export operations are most likely to impact adult delta smelt during their upstream spawning migration between December and April. A significant negative correlation between November-February delta smelt salvage and the residuals from a FMWT index at year one vs. FMWT index at year two stock-recruit relationship is evidence for an influence of adult entrainment on delta smelt population dynamics (Brown and Kimmerer 2001). Delta smelt
spawn over a wide area (much of the delta and some areas downstream). In some years a fairly large proportion of the population seems to spawn in or be rapidly transported to the central and southern delta. Presumably, entrainment vulnerability is higher during those years. Unfortunately, it is not currently known what cues decisions about where to spawn.

The CVP and SWP water operations are not thought to have any impact on delta smelt eggs because they remain attached to substrates. Shortly after hatching, larvae are vulnerable to entrainment at all points of diversion, but, as mentioned earlier, are not counted in SWP or CVP fish salvage operations. Juvenile delta smelt also are vulnerable to entrainment and are counted in salvage operations once they reach 20-25 mm in length. Most juvenile salvage occurs from April-July with a peak in May-June (Nobriga et al. 2001).

Salvage of delta smelt population has historically been greatest in drier years when a high proportion of YOY rear in the delta (Moyle et al. 1992; Reclamation and DWR 1994; Sommer et al. 1997; and Figure 7-6). In recent years however, salvage also has been high in moderately wet conditions (Nobriga et al. 2000; 2001; Grimaldo et al., in prep.; springs of 1996, 1999, and 2000) even though a large fraction of the population was downstream of the Sacramento-San Joaquin River confluence. Nobriga et al. (2000; 2001) attributed recent high wet year salvage to a change in operations for the VAMP that began in 1996. The VAMP provides a San Joaquin River pulse flow from mid-April to mid-May each year that probably improves rearing conditions for delta smelt larvae and also slows the entrainment of fish rearing in the delta. The high salvage events may have resulted from smelt that historically would have been entrained as larvae and therefore not counted at the fish salvage facilities growing to a salvageable size before being entrained.

However, a more recent analysis summarized in Figure 7-6 provides an alternative explanation. delta smelt salvage in 1996, 1999, and 2000 was not outside of the expected historical range when three factors are taken into account, (1) delta smelt distribution as indexed by X2 position, (2) delta smelt abundance as indexed by the TNS, and (3) the amount of water exported. Therefore, it is uncertain that operations changes for VAMP have influenced delta smelt salvage dynamics as strongly as suggested by Nobriga et al. (2000). Nonetheless, it is likely that actual entrainment has decreased since the initiation of the VAMP because of the improved transport flows it provides. In addition, “assets” from CALFED’s Environmental Water Account (EWA) are often used during this time of year to further reduce delta smelt entrainment. Although the population level benefits of these actions are unknown, they appear to have been successful at keeping delta smelt salvage under the limits set by FWS (1993) (Brown and Kimmerer 2002).

Another possible effect on delta smelt entrainment is the South Delta Temporary Barriers (SDTB). The SDTB are put in place during spring and removed again each fall (see Chapter 2 - “Project Description” of this Biological Assessment for more detail). Computer simulations have shown that placement of the barriers changes south delta hydrodynamics, increasing central delta flows toward the export facilities (DWR 2000). When delta smelt occur in areas influenced by the barriers, entrainment losses might increase.

**Predation Effects**

Predator-prey dynamics in the San Francisco Estuary are poorly understood, but are currently receiving considerable research attention by the IEP as part of the POD investigation. Studies during the early 1960s found delta smelt were an occasional prey fish for striped bass, black crappie and white catfish (Turner and Kelley 1966). This, coupled with the substantial decline in striped bass abundance has been taken as evidence that delta smelt are not very vulnerable to
predation (Sweetnam and Stevens 1993). In recent years, it has become clear that the prey choices of piscivorous fishes switch as the relative abundances of species in the prey field change (Buckel et al. 1999). Even in the 1960s, delta smelt was rare relative to the dominant prey fishes of striped bass (age-zero striped bass and threadfin shad) (Turner and Kelley 1966). Therefore, there should have been no expectation that delta smelt would be commonly found in stomach contents samples. Because delta smelt are still rare relative to currently common prey fishes, the same holds true today (Nobriga et al. 2003). Because of the limitations of using stomach samples, IEP researchers are attempting to model potential impacts of striped bass on delta smelt using bioenergetics and individual-based approaches.

Bennett and Moyle (1996) proposed that inland silverside may be impacting delta smelt through predation (on delta smelt eggs and/or larvae) and competition (for copepod prey). This hypothesis is supported by recent statistical analyses showing negative correlations between inland silverside abundance and delta smelt TNS indices, and two indices of egg and/or larval survival (Brown and Kimmerer 2001). The hypothesis also is consistent with the analysis by Kimmerer (2002) showing a change in the sign of the delta smelt X2-TNS relationship (described above) because inland silversides began to increase in abundance about the same time the relationship changed sign (Brown and Kimmerer 2001). It should be noted however that since the early 1980s, there also have been increases in other potential larval fish predators such as coded wire tagged Chinook salmon smolts released in the Delta for survival experiments (Brandes and McLain 2001) and centrarchid fishes (Nobriga and Chotkowski 2000). In addition, striped bass appear to have switched to piscivorous feeding habits at smaller sizes than they historically did following severe declines in the abundance of mysid shrimp (Feyrer et al. in press). We suspect that CWT salmon and centrarchid abundance, as well as the striped bass diet switch have covaried with the increase in inland silverside abundance and the declines in phytoplankton and zooplankton abundance mentioned above.

One hypothesis arising from the POD investigation holds that predation effects on delta smelt and other POD species 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 7-6 with Figure 7-15 and DFG unpublished data). Adult striped bass abundance increased in the latter 1990s (Figure 7-16) 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). While largemouth bass are not pelagic, their presence at the boundary between the littoral and pelagic zones makes it probable that they do opportunistically consume pelagic fishes. Analyses of fish salvage data show this increase occurred somewhat abruptly in the early 1990s and has been sustained since (Figure 7-17). 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 percent 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 America 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.

Agricultural Diversions

There are 2,209 agricultural diversions in the Delta and an additional 366 diversions in Suisun Marsh used for enhancement of waterfowl habitat (Herren and Kawasaki 2001). The vast majority of these diversions do not have fish screens to protect fish from entrainment. It has been recognized for many years that delta smelt are entrained in these diversions (Hallock and Van Woert 1959; Pickard et al. 1982). In the early 1980s delta smelt were the most abundant fish entrained in the Roaring River diversion in Suisun Marsh (Pickard et al. 1982), so it is possible the waterfowl diversions are detrimental. However, delta smelt may not be especially vulnerable to Delta agricultural diversions for several reasons. First, adult delta smelt move into the Delta to spawn during winter-early spring when agricultural diversion operations are at a minimum. Second, larval delta smelt occur transiently in most of the Delta. Third, Nobriga et al. (2002; in press) examined delta smelt entrainment at an agricultural diversion in Horseshoe Bend during July 2000 and 2001, when much of the YOY population was rearing within one tidal excursion of the diversion. Delta smelt entrainment was low compared to density estimates from the DFG 20 mm Delta Smelt Survey. Low entrainment was attributed to (1) offshore distribution of delta smelt, and (2) the extremely small hydrodynamic influence of the diversion relative to the channel it was in. Because Delta agricultural diversions are typically close to shore and probably take small amounts of water relative to what is in the channels they draw water from, delta smelt vulnerability may be low despite their modest swimming ability and their poor performance near
simulated fish screens in laboratory settings (Swanson et al. 1998; 2002). It should be noted however that DWR screened five agricultural diversions around Sherman Island, an area consistently used by delta smelt of all life stages.

**Antioch and Pittsburgh Power Plants**

Mirant, an independent power company, operates two power generation facilities within the range of delta smelt: Contra Costa Power Plant and Pittsburg Power Plant. Contra Costa Power Plant is about six miles east of the confluence of the Sacramento and San Joaquin rivers. Pittsburg Power Plant is on the south shore of Suisun Bay, in the town of Pittsburg. Each power plant has seven generating units that rely on diverted water for condenser cooling. Cooling water is diverted at a rate as high as about 1,500 cfs for the Contra Costa plant and 1,600 cfs for the Pittsburg plant, forming a thermal plume as it is discharged back into the estuary. Pumping rates are often significantly lower under normal operation. Potential impacts of the power plants fall into two categories - direct and indirect. Previous data on direct and indirect impacts of the power plants were summarized by Reclamation and DWR (1994). However, robust data analyses of population level effects of power plant operation on delta smelt and other fishes have not been performed. Briefly, the direct impact of the power plants comes from the removal of fish during diversion operations. Indirect effects stem from water temperature increases when the cooling water is returned to the estuary. Intakes at all units at both power plants employ a screening system to remove debris, but the screens allow entrainment of fish smaller than about 38 mm and impingement of larger fish.

In recent years, the plants have been operated only on a standby basis when regional power consumption is not high. However, although they may not be routinely operated, the plants are most likely to be called into use during the summer, at a time when delta smelt are potentially close to the intake and discharge points, and thus vulnerable to entrainment and other adverse effects.
Figure 7-15  Abundance of age-1 and age-2+ striped bass in midwater trawls in A) San Francisco Bay based on the California Department of Fish and Game Bay study (Bay Study) and B) in the Delta from the Fall Midwater Trawl.
Figure 7-16  Peterson population estimates of the abundance of adult (3+) striped bass < 460 mm total length from 1969 to 2004. 

*NOTE:* Error bars represent 95% confidence intervals (DFG, unpublished data). Confidence intervals are not shown previous to 1987. Striped bass were only tagged during even years from 1994 to 2002, so no estimates are available for odd years during that period.

Figure 7-17  Annual salvage density (fish per acre foot) of largemouth bass at the CVP and SWP combined from 1979 to 2005 (DFG, unpublished data).
Bottom-Up Effects

The quality and availability of food may have important effects on the abundance and distribution of delta smelt. Historical food quality and availability have varied substantially, largely because of the history of exotic species introduction into the Estuary. In this section, information developed by the IEP and others on the delta smelt and its trophic support is presented. Because a large part of this discussion has evolved only in the last few years as a result of the POD investigation, this account borrows heavily from the POD work (Baxter et al. 2008).

Interconnected Recent Changes in Plankton and Benthos

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 production and abundance. Compared to other estuaries, pelagic primary productivity in the upper San Francisco estuary is poor and a low fish yield is expected (Figure 7-18). 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 is filter-feeding 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 the overbite clam 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 overbite clam invasion changed this formerly dynamic clam assemblage because the overbite clam, which is tolerant of a wide range of salinity, is now 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 Delta and 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 Nieuwenhuyse (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 Delta.

Figure 7-18  Mean value and range in primary production in Suisun Bay and the Delta in the 1970s and 1990s plotted on the relationship of fishery yield to primary production from other estuaries around the world (modified from Nixon 1988, using data provided by Alan Jassby, U.C. Davis and James Cloern, U.S. Geological Survey).
Starting in the late 1980s, a series of major changes was observed in the estuarine food web that negatively influenced pelagic fish (including delta smelt) 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 overbite clam 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 overbite clam 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 declines of delta smelt and other pelagic fishes, phytoplankton may nevertheless play a role 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 7-19; 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 the overbite clam, contaminant exposures, and entrainment of source populations in the Delta (Durand et al. in prep., Mueller-Solger et al. 2006). For example, overbite clam 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 7-20, 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.

Figure 7-20 Biomass of copepods in summer delta smelt habitat as defined by salinity and turbidity.

Fish Co-Occurrence with Food

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, particularly delta smelt, 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 7-21). 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 7-20).

Figure 7-21  Summer to fall survival index of delta smelt in relation to zooplankton biomass in the low salinity zone (0.15 – 2.09 psu) of the estuary.
NOTE: The survival index is the log ratio of the Fall Midwater Trawl index to the Summer Townet Survey index. The line is the geometric mean regression for log(10) -transformed data, \( y = 2.48x – 0.36 \). The correlation coefficient for the log-transformed data is 0.58 with a 95% confidence interval of \( (0.26, 0.78) \) (Kimmerer, in press).
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 DFG, unpublished; Figure 7-22). 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.

![Figure 7-22 Prey volume in guts of delta smelt collected during summer 2005 and 2006. Note: Sample size appears in parentheses (Steve Slater, California Department of Fish and Game, unpublished data).](image)

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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 declines. 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, including delta smelt.

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 *Microcystis 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 *Eurytemora affinis* and *Pseudodiaptomus forbesi*, Mueller-Solger et al (2006) found evidence for “trophic upgrading” of essential fatty acids by *Eurytemora* and *Pseudodiaptomus*, 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 *Pseudodiaptomus* population in Suisun Bay. It is possible that the increase in *Pseudodiaptomus* 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 *Pseudodiaptomus* 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 affects 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.