Delta Smelt Life History Model

A Contribution for the CALFED Ecosystem Restoration Program
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Delta smelt (*Hypomesus transpacificus*) are endemic to the northeastern San Francisco Estuary and Delta (Moyle et al. 1992, Moyle 2002, Figure 1). Formerly abundant they are now listed as threatened under the Federal and State Endangered Species Acts (ESA) and thus labeled a "Big R" (at risk) species for priority restoration by the CALFED Bay-Delta Authority. Much of the concern with delta smelt is over ESA restrictions on the numbers of these fish that are lost to freshwater export operations located in the south Delta (Figure 1). These restrictions are highly controversial because they can curtail export pumping and thus have a major influence on how freshwater is allocated to California's agriculture and growing human population.

Delta smelt are one of six species currently recognized in the genus *Hypomesus* that occurs across the Pacific Rim (Saruwatari et al. 1997, Bennett 2005). Delta smelt are small (typically < 80mm total length, TL) translucent fish with a steel-blue lateral stripe and a pleasant cucumber-like aroma (Moyle 2002, Bennett 2005). They most likely evolved from a population of surf smelt (*Hypomesus pretiosus*) isolated from the coastal marine environment as the estuary formed about 8,000 years ago. Although some aspects of their ecology are similar to other smelts and salmonids, delta smelt are not readily classified with other fishes using typical life history characteristics. They are primarily an annual species with rapid growth and high annual mortality during recruitment to the adult stage, but relative to other such species have low fecundity and spawn only once or twice within a protracted spawning period. Moreover, delta smelt hatch as free-swimming larvae and do not have the degree of parental investment provided by the majority of salmonids. Thus under the classification scheme provided by Rose and Winemiller (1992) and McCann and Shuter (1997) they fit somewhere in between an "opportunistic" or "equilibrium" life history strategist.

Delta smelt occur from western San Pablo Bay and the Napa River landward to the tidal freshwater reaches of the Delta (yellow shading, Figure 1). Within this region their distribution is closely tied to the low salinity zone (centered at 2psu salinity, or X2, Kimmerer 2002) and tidal freshwater areas of the Delta. Few delta smelt are caught at salinities over 4psu or in water above 20^{o}C; salinities over 29psu and temperatures above 25.4^{o}C are lethal (Swanson et al. 2000, Bennett 2005). At any given point in time, therefore, geographic position of the population varies widely depending on tidal phase, the amount of freshwater discharge into the estuary, and water temperature. Thus, delta smelt are highly at risk because they are a species with unique and variable life history characteristics whose entire population occurs only within an extremely thin margin of open-water habitat that overlaps with several sources of human water and land development.

Background on the life cycle

The following conceptual model for the delta smelt population (Figure 1) is derived from considerable research and monitoring by resource agency and academic researchers, summarized in the recently-submitted review paper (Bennett 2005). Key features of delta smelt distribution, life cycle, environmental stressors, and uncertainties are outlined in this model (Figure 1) that emphasizes the spatiotemporal extent of the population. ERP habitat restoration actions (solid green dots) and typical spawning regions (open ovals) are shown within the delta smelt habitat (yellow shading). These habitats are linked to a life-cycle diagram showing the temporal sequence of various processes that influence survival at the different life-stages sampled by the IEP monitoring surveys (Figure 1). Processes are shown in rectangular text boxes. Because their effects on delta smelt have been identified only using statistical analyses of monitoring data or with limited field measurements, they are shown as important questions that need further investigation. The relative and combined effects of these processes on the delta smelt population can vary dramatically among years (Bennett and Moyle 1996).

Spawning season: Delta smelt are primarily an annual species with a small number of individuals living two years, and potentially spawning in either one or both years (Figure 1, Bennett 2005). During the fall they gradually begin a diffuse migration landward to the freshwater portions of the Delta, and during years with high freshwater discharge they also locate to Suisun Marsh and the Napa River. Adult delta smelt spawn in freshwater during spring with larval survival optimized when water temperatures lie within about 15-20ºC. One year old females held in captivity have an average of 1,500 eggs, whereas fish surviving two years can have about three times that many (B. Baskerville-Bridges, University of California, Davis, Pers. Communications, Bennett 2005). However, the size-specific fecundity of females in the wild is currently not known. Spawning fish are monitored by the IEP spring Kodiak trawl survey from March to May, and fish are identified to reproductive state. Spawning distribution, inferred from monitoring of fish during the transition from ripe to spawned condition, varies with hydrological conditions. In dry years delta smelt spawn primarily in the North Delta region, while in wet years spawning is more evenly distributed among regions, including the Napa River.

Delta smelt spawn adhesive eggs, but only one egg has been found in the field (K. Fleming, California Department of Fish and Game, Pers. Communications). Therefore, little is known of the spawning habitat other than they probably utilize shallow-water or shoreline areas; their closest relative, surf smelt spawn on sandy beaches along the California coastline during new moon tidal phases (Bennett 2005). Another key uncertainty during the spawning season is the relative contribution of two year old females. These individuals comprise a small percent of adults but have the potential to be highly fecund. Thus, especially during years of poor annual recruitment to the adult stage, successful spawning by two year old females may be a key life history strategy contributing to the persistence of the species (Bennett 2005).

Restoration actions for delta smelt may improve spawning success in different regions by creating shallow-water habitat or by improving water quality. Pesticides that enter the habitat with freshwater run-off from agricultural fields in late winter may impair egg or sperm development in some regions (Thompson 2000, Bennett 2005). Targeting habitat restoration actions for delta smelt will be facilitated once a better understanding of suitable spawning substrate is understood. However, if restored habitats are dominated by exotic fishes such as inland silversides, improvements in spawning could be offset by increased predation on delta smelt larvae (Figure 1, Bennett and Moyle 1996, Grimaldo et al. 2004, Bennett 2005).

Larval and Post-larval Stage: Delta smelt hatch out as yolk-sac larvae and grow and develop on endogenous energy supplies until they begin to feed at about 5mm total length (TL). At about 15-20mm TL delta smelt are considered post-larvae: they have finished developing a functional swim bladder and fin-folds which facilitate larval swimming behaviors. This life stage is monitored by the 20mm survey from April to June. The initial distribution of post-larvae is generally similar to that of adults during the spawning season, but the smelt move seaward so that they are in the Low-Salinity Zone (LSZ) by July. This change in distribution tends to occur as water temperatures exceed 20^{o}C in the Delta.

Historically, delta smelt have been more abundant in northern Suisun Bay, Suisun Marsh, and Delta than elsewhere in the estuary (Radtke 1966, Bennett et al. 2002). Post-larvae and juveniles collected in northern Suisun Bay and lower Sacramento River were 8 times more abundant and were relatively larger than fish in southern Suisun Bay (Aasen 1999, Bennett et al. 2002). While it is currently unknown whether delta smelt prefer the northern reaches of the system or higher abundance reflects enhanced survival, fish collected in that region appear in better body-condition at length, suggesting that feeding success is enhanced there relative to southern Suisun Bay and San Joaquin River (Hobbs et al. 2004).

Delta smelt appear to utilize different swimming behaviors in northern relative to southern Suisun Bay to maintain position in the LSZ. In south Suisun Bay they undergo tidal vertical migrations to near-surface waters on flood tides and at depth on ebb tides, whereas in north Suisun Bay they appear to undergo reverse diurnal migrations to the near-surface during daylight hours and at depth during nighttime (Bennett et al. 2002). This behavior may facilitate horizontal migrations to shoal habitats, thus facilitating retention in the LSZ (Bennett et al. 2002, Hobbs et al. 2004). As in many fishes, survival through this stage is influenced by several factors (Figure 1). Feeding success and exposure to toxic pesticides may be especially important, either directly causing mortality or, more likely, by impairing growth and reducing survival. Rapid growth during early life history is an essential feature of recruitment success in fishes because losses to predation tend to be highest on the smallest fish (Houde 1987, 1989).

Feeding success at first-feeding and later may be particularly poor for delta smelt because the composition of their zooplankton prey has been changed dramatically by the introduction of several exotic species over the last 2-3 decades (Kimmerer et al. 1994, Kimmerer and Orsi 1996, Nobriga 2002). Biomass of calanoid copepods, which are the principal prey of delta smelt (Nobriga 2002), has been lower in spring in and near the LSZ, including the western Delta, since 1987. Total copepod biomass has been supplemented since 1993 by the introduced cyclopoid copepod *Limnoithona tetraspina*, but this copepod is apparently too small to be readily consumed by delta smelt (Lott 1998, Bouley 2004).

Pesticides are known to occur in the regions occupied by larval and post-larval delta smelt (Bennett et al. 1995, Bennett 1996, 2005, Kuivila and Foe 1995, Kuivila and Moon 2004, Thompson et al. 2000). Growth impairments in delta smelt post-larvae due to poor feeding and toxic exposure have been detected during this period (summarized in Bennett 2005). Entrainment in the freshwater export facilities also causes considerable mortality during this period. Currently, however, this mortality is estimated only for fish larger than 20mm, and the extent to which smaller larvae and post-larvae are entrained, or that fish lost represent only those spawned in the south Delta region is a topic of considerable uncertainty.

Restoration actions that improve flow regimes and water quality, or create habitat, may enhance preferred prey species and feeding success, and reduce impairment from exposure to toxic chemicals. The northern reaches of the system (Sacramento River-Suisun Bay and Marsh) consistently appear to be better habitat for delta smelt than those on the southern side (south Suisun Bay, Delta, and San Joaquin River). This difference in habitat quality may be due to the high degree of urbanization on the southern side of Suisun Bay and San Joaquin River relative to the northern side of the system. However, potential benefits of habitat restoration in all areas may be offset by increases in fish entrainment, or differentially favor exotic fishes relative to enhancing feeding success and survival of delta smelt larvae and post-larvae (Grimaldo et al. 2004, Bennett and Moyle 1996, Bennett 2005).

Juvenile stage: The juvenile stage is monitored primarily by the summer tow-net survey from June to August, as well as the September and October surveys of fall mid-water trawl program as the fish recruit to the adult stage. Distribution during this life stage is centered near X2 (2psu salinity) with over 80% of fish sampled in the summer tow net survey coming from salinities less than 3psu (Bennett 2005). Temperature also plays an important role at this stage with fish rarely caught in water above 22oC. As with post-larvae, juveniles tend to be several times more abundant in northern Suisun Bay, Marsh, and lower Sacramento River than in the lower San Joaquin River and south Delta (Figure 1, Bennett et al. 2002).

During the juvenile stage a recruitment bottleneck may occur in late summer in some years. A stock-recruit model suggests that survival during this transition may be density dependent (Bennett 2005). This implies that resources for delta smelt can be limited during this period in some years. In a recent study of delta smelt condition approximately 60% of juveniles examined had growth impairments due to poor feeding success at this life-stage (Bennett 2005). Food abundance, competition, and shrinking habitat volume are typically given as causes of density-dependent survival (Houde 1987, 1989, Cowan et al. 2000, Rose et al. 2001) and a similar relationship exists for juvenile striped bass (Kimmerer et al. 2000), but the factors contributing to this pattern of poor-feeding success in late summer are currently unknown (Bennett 2005).

Pre-Adult stage: Delta smelt pre-adults are monitored by the fall mid-water trawl survey from September to December. During this period juveniles from various cohorts develop into adults by December, then gradually mature during the late-winter months until the spring spawning season.

Key Uncertainties

An overarching uncertainty for the ERP is whether the restoration actions implemented will produce benefits to the delta smelt population. Determining this will require monitoring of fish at the restoration sites and nearby areas that can eventually be linked to the system wide survey programs conducted by the IEP, and then translating that information into parameters for modeling to understand potential consequences for population dynamics. This will not be easy but would be facilitated by a coordinated program that systematically resolves many of the uncertainties outlined below.

Reproduction and Spawning:

- Size-specific fecundity of females in the wild needs to be quantified.
- Spawning microhabitat and suitable substrate(s) need to be identified and its distribution mapped.
- Potential contribution of two year old females to spawning needs to be understood.
- Potential role of toxic chemicals during maturation and spawning is unknown.
- Habitat features that enhance the abundances of exotic species in delta smelt spawning habitat needs to be understood.

Larvae and Post-larvae:

- Relative importance of first-feeding success and exposure to toxic chemicals needs to be estimated.
- Prey preferences for native relative to exotic copepods needs to be understood.
- The magnitude of export losses of larvae and post-larvae < 20mm TL needs to be estimated.
- The interrelationships among natal origin, hydrodynamics, water temperature, fish behavior, and export operations needs to be investigated.
- Habitat features that enhance larval and post-larval feeding success and survival relative to exotic species needs to be understood and estimated for different regions of the delta smelt distribution.
- The efficiency of the sampling-gear used in the 20mm survey needs to be quantified to refine estimates of fish abundance.

Juveniles and Adults:

- The underlying causes of apparent density dependence need to be understood. This will in part require investigation of habitat features that enhance juvenile feeding success and survival relative to exotic species.

- Estimates of abundance need to be refined for juveniles and adults. The design of the tow net survey should be modified (or a companion survey initiated) extending the period of sampling into October using sampling gear and efficiency estimates tailored to juvenile delta smelt. The efficiency of the gear used in the mid-water trawl survey needs to be quantified.

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Delta Smelt Life History Conceptual Model