

Exhibit A: Attachment 1 - Project Narrative
**Understanding the Scale and Mechanisms of Connectivity between
Splittail Populations and the Implications for Management**

2010 Proposal to the Delta Science Program

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1. PROJECT PURPOSE

The purpose of this proposal is to request funding to add three additional research tools, (i) genetics, (ii) physiological performance, and (iii) life cycle modeling, to an existing research effort examining factors affecting splittail (*Pogonichthys macrolepidotus*) life history and population dynamics. Incorporating these elements to the existing research effort will substantially enhance the information gained and contribute to a comprehensive interdisciplinary study that will be immediately relevant to management.

Splittail is listed as a Species of Concern by the State of California and was formerly listed as threatened under the US Endangered Species Act (Sommer et al. 2007a). The US Fish and Wildlife Service recently initiated a status review of splittail to determine whether the species presently requires ESA protection (USFWS 2010). There is an urgent need to better understand splittail population dynamics because it is the only extant member of its genus and is endemic to the San Francisco Estuary system. The San Francisco Estuary and its watershed have been highly modified and, in addition to providing other services, are intensely managed to supply water for 25 million people and the largest (\$27 billion) agricultural industry in the United States (Service 2007; Sommer et al. 2007b). As demonstrated by the on-going high profile issues with the management of other sensitive species in the estuary such as delta smelt and salmonids, a strong scientific foundation is required for balancing the needs of humans and those of the environment for a limited amount of water (Service 2007; Wanger 2007a, b; NRC 2009).

There are limited historical data available on adult splittail (Daniels and Moyle 1983; Moyle 2002; Moyle et al. 2004). The vast majority of existing knowledge about what controls population dynamics is based on early life stages, especially age-0 fish. Historically, splittail abundance has varied in response to delta inflow and the corresponding availability of spawning and nursery habitat (Meng and Moyle 1995; Sommer et al. 1997; Moyle et al. 2004; Feyrer et al. 2006). Wet years typically produce strong year classes of splittail because of increased reproductive effort and improved growth and feeding conditions for juveniles on inundated floodplains (Ribiero 2004; Feyrer et al. 2006; Feyrer et al. 2007a). However, during years encompassing the Pelagic Organism Decline (POD; 2002-2009), splittail abundance indices calculated from the California Department of Fish and Game's Fall Midwater Trawl Survey have been much lower than expected based upon the historical relationship with flow (Figure 1). Abundance measured in other surveys has shown a similar but less pronounced dampened response to flow in recent years (T. Sommer, California Department of Water Resources and R. Baxter, California Department of Fish and Game, Personal Communications). This pattern is striking because it is similar to what has been observed for two POD species, longfin smelt and striped bass (Sommer et al. 2007b; Baxter et al. 2008). The persistently low abundance indices for splittail, a demersal species, may indicate that the POD is just one manifestation of the issues currently plaguing fish populations in the estuary.

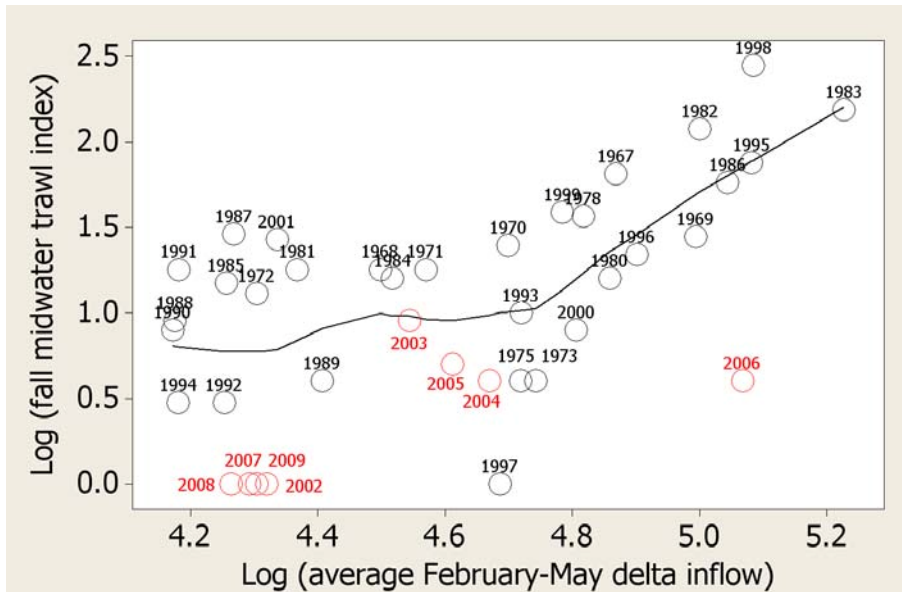


Figure 1. Abundance indices of splittail from the Fall Midwater Trawl plotted against delta inflow. Data points for the POD years (2002-2009) are shown in red. The curve is a lowess smooth.

Previous modeling (Moyle et al. 2004; Foin and Sitts, in preparation), limited to empirical data primarily on age-0 splittail, has suggested that the species is resilient but that abundance is likely to fluctuate wildly in response to floodplain inundation. The model indicates that a long series of dry years is unlikely to result in extinction, even if the population is greatly reduced, as long as conditions not covered in the model do not change. In the model successive wet, and above normal years results in an exploding population, exceeding even what has been observed in the natural system. This result is from an interaction between adult numbers and reproductive potential under a string of favorable years. While the model can be made to simulate population dynamics that mimic the natural situation, actual numbers for mortality and survival rates are lacking. Therefore it is hard to distinguish among various sources of mortality. One of our ultimate goals is to develop a model that more realistically captures the population dynamics of splittail which could then serve as an effective management tool for the species as a whole and for each of the distinct splittail populations independently.

This fall (2010) we are beginning a study funded by the US Bureau of Reclamation that is designed to obtain information on the poorly studied adult life stage of splittail. We seek to test the overarching hypothesis that there is no difference in the estuarine distribution, population dynamics, or life history characteristics between the two genetically distinct splittail populations. To address this hypothesis we have designed a collaborative interdisciplinary study that includes an intensive field effort combined with state-of-the-art laboratory tools that can determine the natal origins, historical habitat use, feeding, and general health of adult splittail. Our field effort is designed to sample adult splittail with gill nets in the estuary during late fall-early winter (October-December) prior to the upstream spawning migration. The sampling will take place over a broad geographic area from the confluence of the Sacramento and San Joaquin Rivers downstream to the Petaluma River and up into the Petaluma and Napa Rivers in order to encompass the full distribution of both splittail populations. We have

coupled this field effort with a laboratory work including otolith ageing, otolith chemistry, muscle stable isotope signatures, diet composition, and health and condition metrics. The study will form the most comprehensive research effort focused on splittail to date.

In the current proposal we seek to leverage additional funds that were not previously available to add genetics, physiological performance, and life cycle modeling components to this study. These three elements will bring a substantial amount of added value to the overall study. The genetic components that we seek to incorporate have been developed for splittail and their utility demonstrated in the peer-reviewed literature (Baerwald and May 2004; Baerwald et al. 2007; Feyrer et al. 2007b; Baerwald et al. 2008). These techniques provide a means to more precisely assign individuals to their respective population than what is possible with otolith chemistry alone (Feyrer et al. 2007b) and to estimate the effective size of the populations. The physiological performance component will re-visit Young and Cech (1996) to determine if the newly discovered Petaluma/Napa population of splittail exhibits different physiological requirements and tolerances than the Central Valley population. The life cycle modeling element will expand upon the model that has already been developed and applied in the peer-reviewed literature (Moyle et al. 2004; Foin and Sitts, in preparation) and will be parameterized with the cumulative information gained by the overall study to evaluate the sensitivity of splittail persistence to demographic variability in population dynamics.

2. BACKGROUND AND CONCEPTUAL MODEL

Many fish species in the San Francisco Estuary are in serious jeopardy. Abundance indices for several high profile pelagic species including delta smelt, longfin smelt, striped bass, and threadfin shad have been at or near record low levels since 2002 (Sommer et al. 2007b). The declines have caught the interest of scientists, resource managers, and the general public, and have lead to an intensive investigation into the potential causes (Service 2007; Sommer et al. 2007b). Studies to date indicate that factors contributing to the declines are multi-faceted with a host of factors affecting the species at different times of the year (Baxter et al. 2008). Despite the intense focus on the pelagic species, other native fishes, including splittail, are also exhibiting declines in recent years (Figure 1).

Life history models result from correlations among organism characteristics that affect their fitness. Winemiller and Rose (1992) developed a triangular model that captures three primary endpoints in life history evolution. The life history strategy endpoints of the Winemiller and Rose (1992) model are characterized as opportunistic (small, short-lived, high reproductive effort), equilibrium (low fecundity, large egg size, parental care), and periodic (long-lived, high fecundity, high recruitment variation). What is currently known about the biological characteristics of splittail through both empirical studies and simulation modeling clearly place the species as a model periodic strategist. For splittail, large body size and long life span (Daniels and Moyle 1983), along with broad environmental tolerances (Young and Cech 1996),

enhance adult survival and permit the storage of energy through high fecundity (Feyrer and Baxter 1998) for successful reproduction when environmental conditions are optimal (Moyle et al. 2004). The expansive inundation of floodplains in wet years produces the highest splittail year classes. Simulation modeling suggests that splittail currently have the capacity to produce offspring in excess of that needed to sustain the population during suitably wet years (Moyle et al. 2004). These characteristics combined with at least some successful reproduction in dry years and extended drought periods are believed to be the primary factors allowing for the persistence of the species (Moyle et al. 2004). However, the simulation model is relatively insensitive to different sources of age-structured mortality because of a lack of empirical data on age-1+ life stages. Thus, confidence in the simulation model can be improved through enriching it with missing data on the population dynamics and life history characteristics of older splittail.

Moyle et al. (2004) developed a generalized conceptual model of the splittail life cycle, which has been supplemented in recent years with empirical data from new studies. According to this model, adult splittail are primarily distributed in brackish and freshwater habitats of the upper San Francisco Estuary. During winter and early spring they migrate upstream to inundated floodplains and river margins for spawning. Gravid adult splittail typically migrate upstream and enter the Yolo Bypass, the primary floodplain of the Sacramento River, starting in January following flow pulses (Harrell and Sommer 2003). Based upon catches from hook and line sampling, Garmin and Baxter (1999) found that peak upstream migration during 1999 occurred in late February-early March. There is some evidence to suggest that large fish tend to migrate upstream before smaller fish (Caywood 1974; Garmin and Baxter 1999). Based upon studies of adults and larvae, spawning is thought to occur on flooded terrestrial vegetation (Caywood 1974; Crain et al. 2004; Sommer et al. 2008). Wet years that provide a large area of floodplain inundation for a suitable time period typically produce the largest year classes of splittail because of improved growth and feeding conditions which improve survival (Jassby et al. 1995; Meng and Moyle 1995; Sommer et al. 1997; Feyrer et al. 2006; Feyrer et al. 2007a). The presence of larvae in Suisun Marsh in very wet years (Meng and Matern 2001) suggests that some spawning may occur downstream or that larvae can be washed downstream at a young age by extreme flow events. In a study within a model floodplain wetland, adult splittail were relatively sedentary after spawning, possibly to recover from the stress of spawning or because their movements were limited to that within a relatively confined study area (Sommer et al. 2008). Larvae and juveniles remain upstream in inundated habitats until they begin to dry and then fish move downstream to tidal freshwater and brackish portions of the estuary during early summer (Feyrer et al. 2005). Peak emigration of age-0 splittail from Yolo Bypass varies temporally among years but typically occurs when fish are 30-40 mm in length, suggesting an ontogenetic influence on downstream emigration (Feyrer et al. 2006). Local floodplain production in Yolo Bypass may be important to, or at least an indicator of, system-wide production because the two measures are correlated (Feyrer et al. 2006). Juveniles will rear in the estuary 1-2 years until they become sexually mature and then initiate their spawning migrations (Daniels and Moyle 1983).

New information has emerged since the Moyle et al. (2004) conceptual model was developed which indicates that there are two genetically distinct splittail populations, one which spawns in the Central Valley and one which spawns in the Petaluma and Napa Rivers (Baerwald et al. 2007). Initial studies of both juvenile (Feyrer et al. 2005; Feyrer et al. 2007a) and adult fish (Baerwald et al. 2008) have suggested that the two populations do not have completely overlapping geographic distributions in the estuary. Thus, it is now apparent that the conceptual model developed by Moyle et al. (2004) is incomplete because it only characterizes the Central Valley population. We propose that the Moyle et al. (2004) conceptual model represents only a single component of a new conceptual model that would incorporate a new component for the life cycle of the Petaluma/Napa population plus a new component for how the two populations interact.

Other than studies on the distribution, habitat use, food habits, and growth of age-0 fish (Feyrer et al. 2005; Feyrer et al. 2007a) and limited information on the distribution of adults (Baerwald et al. 2008), information is lacking on the life history or population dynamics of the Petaluma/Napa population. Given that there is virtually no floodplain habitat and substantially less freshwater habitat in the Petaluma and Napa Rivers than in the Central Valley (Feyrer et al. 2005; Feyrer et al. 2007a), the conceptual model of splittail life history for this population is probably not exactly the same as that depicted by Moyle et al. (2004) for the Central Valley population. Evidence for this comes from Feyrer et al. (2010) showing that splittail from the Petaluma/Napa population utilize higher salinity habitats much earlier in life than the Central Valley population. This is due, in part, to differences in the hydrographs of the Petaluma, Napa, Sacramento, and San Joaquin Rivers (Feyrer et al. 2007a), which likely controls the timing and duration of spawning and rearing in freshwater habitats. Our study seeks to understand the life history and population dynamics of splittail as well as determine if there are differences between the two populations which could have consequences for species management. These data are particularly important and timely given that the USWFS is currently assessing the listing status of splittail.

3. APPROACH AND SCOPE OF WORK

The work outlined in this proposal has three objectives (1) genetically identifying individual splittail observed during the presently-funded study to facilitate population assignments and to estimate the effective size of each population, (2) comparing the physiological tolerances and requirements between splittail populations, and (3) simulation modeling to determine the sensitivity of splittail persistence to demographic variability in population dynamics.

Objective 1: Genetics – This task will be completed by UC Davis staff under the direction of Dr. Melinda Baerwald. The following hypotheses will be addressed: (a) adult splittail of the two populations do not have completely overlapping geographic ranges and (b) effective and census population size estimates for the Petaluma/Napa population are considerably smaller than the Central Valley population.

We previously established the existence of two splittail populations (Baerwald et al. 2007) and our ability to genetically assign individuals back to their population of origin (Baerwald et al.

2008). We now seek to use existing and newly developed genetic markers, in conjunction with telemetry monitoring, to track adult distribution patterns. By identifying the population of origin and conducting genetic mark-recapture for all collected adult splittail, we will greatly increase our knowledge each population's geographic range and migration patterns.

Effective population size (N_e) is an important parameter to estimate for species of conservation concern because of its influence on the rate and magnitude of inbreeding and genetic drift, which can both lower the overall genetic diversity of a population. Determining the N_e for both populations will be extremely useful for the conservation management of the species, particularly since the USFWS is currently reviewing splittail status for ESA protection. We predict that the Petaluma/Napa population has a substantially smaller N_e than the Central Valley population, given the considerably reduced spawning habitat available in the Petaluma and Napa Rivers. N_e estimates will be directly compared to census size (N_c) estimates to gain a better understanding of the predictive power of N_c monitoring for the overall genetic health of the species. Additionally, the ability to genetically identify each individual's sex will allow us to estimate sex ratios, which can have a large influence on effective population size. Moreover, sexual identification will enable us to detect potential life history differences between the sexes for measured parameters (e.g., condition factor, age, physiological tolerances).

Microsatellite Marker Development: Thirteen microsatellite markers are currently available for splittail population genetic analysis. While these markers are capable of accurately assigning individuals to their population of origin, better probabilities of population assignment would benefit from additional markers. The microsatellite enriched library used to discover the original 13 markers (Baerwald and May 2004) will be used to sequence 200 – 300 additional clones. Thirty splittail from each population will be genetically screened to identify polymorphic loci. Additionally, published microsatellites characterized for other cyprinid species will be tested for amplification and polymorphism in splittail. Given our proposed level of genetic screening, we anticipate that the number of splittail microsatellite markers will minimally double and be quite sufficient for identifying population of origin with very high probability.

Individual Assignment to Population of Origin: Genetic assignment of individuals to population of origin for all captured adult splittail will be conducted using GENECLASS2 (Piry et al. 2004) and/or STRUCTURE (Pritchard et al. 2000) and ONCOR (Kalinowski et al. 2008) software programs. Previous individual genetic assignment back to reference populations was achieved with 98% accuracy (Baerwald et al. 2007, Baerwald et al. 2008) so we are confident in our ability to distinguish between the two populations.

Effective and Census Population Size Estimation: After adults are genetically assigned to populations, four single-sample estimators will be used to calculate N_e for both populations: heterozygote excess (Peel et al. 2004), linkage disequilibrium (Waples and Do 2008), Bayesian partial likelihood (Tallmon et al. 2008) and sibship analysis (Wang 2009). Genetic capture mark-recapture (CMR) will allow us to estimate census population size for direct comparison to N_e of each population and track the dispersal of recaptured individuals over time. To ensure that there is sufficient power to distinguish individuals using our microsatellite loci, the probability of observing matching genotypes in random pairs of individuals (probability of identity; PI) and between pairs of siblings (PI_{sibs}) will be calculated using the program GENALEX 6.0 (Peakall and

Smouse 2006). Genotyping error rates will be estimated and individual samples with identical allele calls except at only 1-2 loci will be reamplified for genotype verification. Population census size and confidence intervals will be estimated using programs such as BAYESN (Petit and Valiere 2006) and CAPWIRE (Miller et al. 2005).

Objective 2: Physiological Performance— This task will be completed by UC Davis staff under the direction of Dr. Nann A. Fanguie, assistant professor. The following hypotheses will be addressed: splittail from each population exhibit differences in (a) physiological response to temperature, (b) physiological response to salinity, and (c) ecological swimming performance and metabolism.

Genetic analyses have revealed two clearly distinct populations of splittail, the Petaluma-Napa population and the Central Valley population (Baerwald et al. 2007). What is unknown, however, is whether these genetic differences translate into intraspecific differences in physiological traits that would provide support for local adaptation in splittail populations. The objective of this task is to conduct an evaluation of key physiological performance and tolerance variables in age-1 to 4 splittail sampled from genetically distinct populations in the San Francisco estuary and its tributaries.

Over evolutionary timescales, persistent differences in local environmental conditions may result in adaptive physiological changes among populations (Hochachka and Somero 2002). At a given locality, environmental conditions may also vary on shorter timescales (e.g. daily or seasonally) requiring acclimatory compensation mechanisms. While studies comparing fish species that are widely divergent phylogenetically have revealed major patterns of physiological adaptation, it has also been shown that environmental conditions establish fine scale patterns of physiological adaptation in closely related species or among populations within a species such that their physiology is tailored to their particular environment (reviewed in Schulte 2007). To effectively manage and preserve splittail populations, it is important not only to maintain genetic diversity, but to understand how environmental history has structured population-specific physiological tolerance to reflect natural environmental regimes.

Splittail inhabit a dynamic estuary system with naturally fluctuating abiotic parameters as well as novel environmental challenges associated with anthropogenic impacts such as water export projects and climate change. Splittail are thought to use Suisun Bay, Suisun Marsh, and the Delta as their central foraging grounds with the distribution of both populations in these areas overlapping to some degree (Baerwald et al. 2008). These foraging habitats differ in many environmental features (e.g. temperature, salinity, depth), but it is yet unclear if population-specific patterns of habitat preference and utilization occur. Temperature has been coined as the 'ecological master factor' for fishes (Brett 1971), and fish often show temperature optima in a variety of important physiological functions at or near common habitat temperatures. Fishes show adaptive patterns in thermal tolerance limits such that thermal tolerance thresholds are correlated with habitat temperatures. In splittail, it has been documented that the spawning habitats of these two populations differ notably in salinity with the Petaluma-Napa population rearing in salinities ranging from 0-13ppt whereas the Central valley population in freshwater (Feyrer et al. 2007a; Feyrer et al. 2010). These observations suggest that salinity may be an important selective factor shaping the observed population structure. To date, however, it is

unknown if the correlation between population structure and environmental salinity has adaptive significance.

As an initial step to determine if splittail show evidence of population divergence in physiological traits, we will determine temperature and salinity tolerance and preference as well as measure swimming performance as an ecologically-relevant index of fitness in splittail populations. Among fish populations, intraspecific variation in ecologically-important physiological traits has been demonstrated in response to temperature (e.g., Fangué et al. 2006; Fangué et al. 2009), salinity (e.g., Scott et al. 2004; 2008), and swimming performance (e.g., Fangué et al. 2008). Our data will build on previous work conducted with splittail by Young and Cech (1996) that established some physiological baselines but where population of origin was not taken into account. Understanding whether splittail populations have distinct physiological or life-history traits may reveal critical environmental factor(s) influencing patterns of foraging and spawning in splittail populations.

Methodological approach: In coordination with on-going field sampling efforts in the estuary, age-1 to 4 splittail will be collected from October through December 2011. Fish will be transported to the UC Davis Center for Aquatic Biology and Aquaculture (CABA) and held in outdoor stock tanks at temperature and salinity ranges similar the ambient conditions during field collections until experimental acclimation begins. Because the fish will likely be of mixed genetic origin, each fish will be genotyped (as described above), marked with a unique identifier (NMT, visible elastomer tags) and assigned to either the Central Valley or the Petaluma/Napa population. Groups of four fish of each age class and population of origin will be acclimated to one of four temperatures (5, 10, 15, and 20°C) and 0 ppt for a minimum of 21 days. Each experimental treatment combination will be replicated three times, and the minimum number of fish required to complete the proposed physiological performance measures below is 96 per population and size class. We do not anticipate difficulty in achieving these fish numbers as during year one of this study, fish will be intensively sampled from many locations in the estuary and genetic origin determined. These data will be used to inform our collection location decisions and effort in year two to ensure we have equal representation from each population and size class for our physiological experiments.

Thermal tolerance and preference methodology: Critical thermal maxima (CTMax) will be determined as an index of thermal tolerance. A fish's CTMax is defined as the temperature at which fish lose the ability to escape conditions that will ultimately lead to death. During the CTMax trial, water temperatures are constantly increasing at a rate of 0.3°C/min, which is slow enough to quickly equilibrate with the fish's body temperature, but fast enough to prevent thermal acclimation during the experimental trial. Individual fish are held in plexiglass vessels, and trials continue until a repeatable, ecologically and ethically defensible endpoint is reached. A CTMax represents a lethal endpoint in nature, but will be non-lethal in the laboratory as the fish must recover when returned to acclimation temperatures. Loss of equilibrium (LOE) is the most common endpoint in fish thermal tolerance studies and will be used in these experiments.

Thermal preference will be measured as a behavioral index of physiological optima. In many fish species, there is general agreement between performance optima of physiological

correlates such as feeding, growth, metabolic rates, swimming performance, and reproduction with preferred temperatures (reviewed in Fangué et al. 2009). Preferred temperatures in fishes are quantified in the laboratory using a thermal gradient device. In the Fangué laboratory, we have a custom annular thermal preference device for fishes (Myrick et al. 2004). Fish will be exposed to the thermal gradient and their occupied temperatures recorded. Temperature selection data is bounded by upper and lower avoidance temperatures, and the preferred temperature is calculated as a statistical measure of central tendency (mode) of the temperature distribution reflecting the temperature most often occupied by the fish during the trial.

Salinity tolerance and preference methodology: Salinity tolerance and preference trials will be conducted in much the same way as CTMax trials and following the methodologies described in Young and Cech (1996). Briefly, individual fish will be held at their acclimation temperatures and experimental salinities will be increased at a rate of 3 ppt per hour until LOE is reached as the experimental endpoint. Simple modification of the annular thermal preference device will allow for salinity preference determination.

Metabolic rate determination (MO_2) and ecological swimming performance: Standard respirometry techniques will be used to determine resting and active metabolic rates of splittail for each population, size class, and acclimation temperature group. Critical swimming velocity (U_{crit}) as a measure of swimming performance will also be assessed following the methodology of Fangué et al. (2008). Resting and active metabolic rate measures allow for the calculation of aerobic scope (arithmetic difference between maximum and resting metabolic rate). Aerobic scope determination is emerging as a useful tool to examine the fundamental physiological niches of fishes, particularly in response to abiotic stressors (Farrell 2009). In addition, swimming performance is considered a main character determining survival in many species of fish, and maximal swimming performance may strongly influence fitness.

Objective 3: Modeling – This task will be completed by Dr. Ted Foin, professor emeritus at UC Davis. The following hypotheses will be addressed: (a) the Petaluma/Napa splittail population is dynamically independent of the Central Valley population, (b) the Petaluma/Napa population has a higher probability of extinction than the Central Valley population, and (c) adult mortality and population turnover is higher for the Petaluma/Napa population than for the Central Valley population.

Previous development of splittail simulation models: The original simulation model was based on the conceptual model described above from Moyle et al. (2004). The conceptual model was developed into a life cycle model using STELLA as the model language (Moyle et al. 2004). The schematic flow of this model shows the details of implementation corresponding to the life cycle conceptual model. The splittail population modeled was that of the Central Valley only, with adult splittail having six age classes and juveniles one. Juveniles suffer mortality and survivors mature into the first adult age after one year. Adult splittail have increasing fecundity as they age. Upstream spawning movements are controlled by water flow in the Sacramento and San Joaquin River drainages, which controls the availability of floodplain spawning habitat. Larval survival and downstream migration are greater when floodplains are available. The model time step is one year.

The original model produced results that were largely to be expected, given the structure of the model and the parameters used. The principal finding was that reproduction was so successful in wet years that the population would grow quickly. This conclusion was substantiated by field findings which suggested the same conclusion (Sommer et al. 1997). A second conclusion is that even with an indefinite string of drought years, the population would be expected to decrease, but with enough reproduction to prevent population extinction. In general, this model suggests that splittail are expected to demonstrate great population fluctuation driven by stream flow variability, but that population dynamics insure minimal probability of extinction and a huge capacity for population growth.

A second series of splittail models was constructed to explore the effects of variable stream flow and water diversion within the Central Valley population (Foin and Sitts, in preparation). The main changes to the model involved 1) creating the ability to specify water diversion and the effect of these volumes on juvenile loss and salvage, and 2) separation of the delta into two or three spawning runs (Sacramento, San Joaquin and Cosumnes-Mokelumne) with a single panmictic adult population downstream. The basic life cycle model was used for this model, with necessary changes in spawning runs and downstream flows. The second series produced results consistent with those of the first series. Once again, the reproductive excess characteristic of splittail mitigate juvenile losses from water diversion and other causes so that the dynamics of the Delta population remain unaffected by water operations.

Proposed Model Development: The largest source of uncertainty in the splittail models concerns the dynamics and regulation of adult population size. In the two previous models, adults have fixed mortality and fecundity rates (although fertility is variable), and population regulation (which is required to keep the model from blowing up unrealistically) consists of a simple density-dependent scaling of larval recruitment to the juvenile stage of the life cycle.

The research proposed here will address population size and fecundity directly and should permit some insight into population regulation, although we cannot realistically expect to develop detailed insight into population regulation. The model consists of the same life cycle components as in the earlier versions, with potential connectivity between populations of the Delta and downriver into San Pablo Bay.

The rationale for continuing development of the splittail model (acronym: STALL) is that the other parts of this proposal have the potential to elucidate the dynamics of adult splittail and to provide data needed to differentiate among multiple hypotheses concerning their dynamics. Furthermore, STALL provides one of the only alternatives available to gain a more comprehensive picture of the regional dynamics of splittail. For these reasons, the development of empirical research and the STALL model can be mutually beneficial when pursued together.

Addressing the hypotheses: Baerwald et al. (2007, 2008) have already documented that the Petaluma/Napa and Central Valley populations are both genetically distinct and spatially separated, which suggests that these populations may be dynamically separate. STALL can be used to complete the argument by showing population separation, by comparing versions in which exchange rate of individuals is specified. STALL design was proposed with this objective in

mind. By manipulating both the conditions and rates of exchange, STALL can be used to determine the consequences of specified exchanges on the dynamics of each population. The physiological component can be used to determine how much migration and loss occurs as water year changes from year to year. It is expected that physiological adaptation will prove to be an important part of adult dynamics.

Examining extinction probabilities can only be tested practically using STALL since it requires too long empirically to estimate extinction frequency. This hypothesis can be tested by comparing coupled and uncoupled versions of the STALL model. The control expectation can be estimated by running the Central Valley and Petaluma/Napa models with no coupling. The Central Valley population should never experience extinction (a result seen with previous models), while the Petaluma/Napa populations may experience local extinction and recolonization, given parameters to be estimated from data in this proposal. Running the models with specified coupling, ranging from occasional infusion of Delta juveniles in very wet years to regular exchange of adults should permit estimation of changes in local extinction of the Petaluma/Napa population. A separate analysis of physiological plasticity (using data reported in Young and Cech 1996 and the data on physiological adjustment to aqueous salinity proposed here) should also permit exploration of the influence of the effect rapid changes in the salinity of San Pablo Bay has on the dynamics and local extinction of splittail. Preliminary estimates of adult mortality may be available from the data collected during the field study, but the model is the tool with which to estimate turnover of adults in each population; STALL can be used to estimate population turnover using mortality estimates generated from the empirical data collected in the field.