Characterization of relations between autumn outflow and survival, recruitment, and habitat quality for delta smelt (*Hypomesus transpacificus*)

Collaborative Adaptive Management Team Work Element 3-1-3

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ABSTRACT

In response to a scope of work outlined by the Collaborative Adaptive Management Team for the Sacramento–San Joaquin River Delta, we propose to estimate survival of delta smelt (*Hypomesus transpacificus*) during autumn, conduct a stock-recruitment analysis, and assess occupancy and habitat quality for delta smelt during autumn. Our proposed work will be the first to account for effects of imperfect detection on inferences about relations between population dynamics of delta smelt and environmental covariates. These covariates, which will include but will not be limited to autumn outflow and the position of salinity thresholds, may be relevant at either the level of the Delta or the level of smaller regions. We will use information criteria, which compare model fit while constraining model complexity, to assess the extent to which the observed data support multiple hypotheses about survival, stock recruitment, and habitat quality.

To estimate survival, we will model the abundance of the species in multiple geographic regions and months, accounting both for survival and for movement among regions. We will model survival and movement as functions of environmental covariates that have been hypothesized to drive the status of the species. We then will statistically fit each model to evaluate the extent to which it explains the variability in the number of delta smelt caught by fall midwater trawl surveys from 1967 through 2014. We will build simulation models to determine how accurately our model can estimate the coefficients relating covariates to survival and movement given different probabilities of detection and sample sizes.

We will compare the model-based abundance in December of a given year with abundance of the spawning population and the mean size of spawners in the spring of the following year, and with larval production in April of the following year. Larval production is estimated by the California Department of Fish and Wildlife from the 20 mm survey, and their indices of annual production currently assume perfect detection. We propose to develop a new index of abundance that accounts for variation in the probability of detection as a function of space, time, and covariates.

We will use multi-season patch occupancy models to examine whether environmental covariates are associated with spatially explicit probabilities of presence. This evaluation will extend previous efforts to define delta smelt habitat and account for the probability of capturing delta

smelt. This novel approach for defining delta smelt habitat has the potential to redefine relations between delta smelt presence and salinity gradients, conductivity, and turbidity that previously were used to define critical habitat. By accounting for imperfect detection, our approach also has the potential to expand understanding of the spatial and temporal patterns in habitat among years. Our proposed models differ substantively from, yet complement, other models of the dynamics of delta smelt that are being developed.

INTRODUCTION

Operations of the Central Valley Project and State Water Project, including outflows during autumn, currently are regulated by two biological opinions. The first biological opinion (USFWS 2008) addressed effects of autumn outflows on delta smelt (*Hypomesus transpacificus*) and its designated critical habitat. The second biological opinion (NMFS 2009) addressed effects of water-project operations on Sacramento River winter-run Chinook salmon and Central Valley spring-run Chinook salmon (*Oncorhynchus tshawytscha*), Central Valley steelhead (*O. mykiss*), the southern distinct population segment of North American green sturgeon (*Acipenser medirostris*), and southern resident killer whales (*Orcinus orca*). The reasonable and prudent alternative (RPA) included in the 2008 biological opinion required that outflow be managed such that average X2 in September and October is 74 km when the preceding water year was classified as wet, and 81 km when the preceding water year was classified as above normal. X2 represents the distance in km upstream from the Golden Gate Bridge where the tidally averaged salinity near the bottom of the water column is 2 practical salinity units (psu) (Jassby et al. 1995). Wet and above-normal years are defined on the basis of estimated unimpaired runoff from the Sacramento, Feather, Yuba, and American Rivers during the current year and the previous year (the Sacramento Basin 40-30-30 index). Additionally, in November of any year in which the preceding water year was classified as wet or above normal, the inflows to the two projects' reservoirs in the Sacramento Basin must be added to reservoir releases to increase outflows up to the 74 or 81 km targets.

The RPA reflects hypotheses that as outflows increase, the low salinity zone (LSZ; generally defined as salinities from 0.5–6 psu or 1–6 psu) moves westward, increases the amount of habitat for delta smelt, and increases the probability of persistence of delta smelt (Feyrer et al. 2007, 2011). An increase in outflows requires either reducing the amount of water exported from the estuary or increasing the amount of water released from reservoirs upstream, which limits the amount of water available for agriculture and other uses. However, the relation between the location of X2 and the presence of delta smelt may be complicated by static, regional environmental attributes. Geographic region alone (13 subdivisions) explained 4.7% of the variability in delta smelt detections by the fall midwater trawl survey (FMWT) (Manly et al. 2015). Region and the interactions between region, turbidity, and salinity explained 19.1% of the variability (Manly et al. 2015).

There is persistent debate about whether the survival and recruitment of delta smelt is a function of the location of the X2 isohaline and the extent to which the location of the X2 isohaline is associated with habitat quality for the species. Scientific evidence is equivocal (e.g., Feyrer et al. 2007, 2011, Mac Nally et al. 2010, Thomson et al. 2010, Maunder and Deriso 2011, Miller et al.

2012). In some cases, questions have been raised about the reliability of analyses that were interpreted as supporting the hypothesis that survival and recruitment of delta smelt is a function of the location of X2 (NRC 2012). But regardless of the analytical method applied, data on distribution and abundance of delta smelt, and on environmental covariates that may be associated with measures of the species' viability, are limited (see *Research Challenges*). For example, there are few data on the distribution and abundance of potential predators of delta smelt, and on the transport mechanisms and distribution of some toxicants (Brooks et al. 2012, Scholz et al. 2012). Furthermore, some of the surveys for delta smelt sample a relatively narrow portion of the full gradient of some environmental attributes that likely are associated with the distribution and abundance of delta smelt, such as salinity (Merz et al. 2011).

Our proposed work responds to the desire of regulators and stakeholders to determine the extent to which hypothesized components of habitat, including salinity in autumn and turbidity in autumn, are related to measures of the viability of delta smelt. The Collaborative Science and Adaptive Management Program (CSAMP) for the Sacramento–San Joaquin River Delta (Delta) expects that our results will be relevant to management of the quantity of water exported from the Delta, the timing of release of water, and other management actions that may contribute to conservation of delta smelt.

Goals and objectives

We aim to achieve three goals that reflect a scope of work outlined by the Collaborative Adaptive Management Team (CAMT). The CAMP is guided by the Collaborative Science Policy Group, which in turn was created by the CSAMP. The first goal is to understand which environmental variables are associated with survival of delta smelt during autumn. The second goal is to evaluate whether abundance of delta smelt in December is related to recruitment of the species as measured in the spring (i.e., the probability that pre-reproductive individuals survive and produce larvae). The third goal is to characterize occupancy and habitat quality for delta smelt during autumn. We will conduct separate analyses to achieve each of these goals.

We propose to use quantitative models that relate environmental covariates to survival, recruitment, and habitat of delta smelt to address these three goals. We will explore both local covariates (i.e., those measured at each sampling station) and global covariates (e.g., system level covariates such as outflow from the Delta). Of particular interest to CAMT is the role of outflow, such as whether high outflow may displace fish from areas of high habitat quality or create areas of high habitat quality. Our selection of covariates for inclusion in each analysis will reflect hypotheses presented in numerous articles, reports and conceptual models therein (e.g., IEP 2015), and collaborative meetings. If desired, we will work with members of the Delta Smelt Scoping Team (DSST) and CAMT to frame their existing hypotheses about attributes of habitat, or the gradient of habitat quality, in ways that are amenable to quantitative evaluation and comparison with other hypotheses (see *Model fitting and comparison of hypotheses*).

Local and global covariates that we include in our analyses may include but will not be limited to outflow, X2, electrical conductivity (a measure of salinity), turbidity (e.g., Secchi depth or suspended sediments), water temperature, surface area or volume of tidal marsh, locations or concentrations of toxicants, abundance or density of prey, and abundance or density of predators,

such as pike minnow (*Ptychocheilus oregonensis*) and striped bass (*Morone saxatilis*). The rationale for hypothesizing that these variables are directly or indirectly associated with survival, recruitment, or presence of delta smelt has been documented in numerous sources (see Mac Nally et al. 2010, Thomson et al. 2010, Brooks et al. 2012, Scholz et al. 2012, IEP 2015). We will not make *a priori* assumptions about values of these variables that are associated with presence of habitat or quality of habitat; doing so would create a lack of independence in the analyses given that one of our implicit aims is to objectively quantify habitat quality.

To understand how the covariates may affect survival, recruitment, and habitat quality, models must also be developed for the process of detecting or catching animals given that they are present. For example, models of abundance must define processes for catching fish (see *Estimating survival of delta smelt during autumn*). Also, multi-season patch-occupancy models treat detection and occupancy as distinct response variables (see *Occupancy and habitat quality for delta smelt during autumn*) and thus must define models for detection. We expect that the probability of capture and probability of detection will vary as a function of environmental conditions and gear selectivity (changes in detection probability as a function of fish size). Covariates of detection probability may include but are not limited to turbidity, water temperature, time of day, date, month, year, tow duration, and tow depth. For example, time of day of sampling is relevant because delta smelt may avoid areas with high light levels. Additionally, if there is an independent source of data on size of delta smelt (i.e., data that were not derived from the FMWT), we will include the size distribution of delta smelt as a detection covariate to account for the fact that size varies among months and among years. If there are no independent data on size, we will use existing assumptions about gear efficiency as a function of the week of capture (K. Newman personal communication).

We have five objectives. First, we aim to model the abundance of delta smelt in four geographic regions and four months, accounting both for survival and for movement among regions. Our second objective is to build simulation models to determine how accurately our model can estimate the coefficients relating covariates to survival and movement given different probabilities of detection and sample sizes. Our third objective, which we will begin to pursue when the project is initiated, is to conduct an expert elicitation of predation covariates. Fourth, we seek to compare the model-based abundance in December of a given year with abundance of the spawning population and the mean size of spawners in the spring of the following year, and with larval production in April of the following year. We propose to develop a new index of larval abundance that accounts for variation in the probability of detection as a function of space, time, and covariates. Our fifth objective is to use multi-season patch occupancy models to examine whether environmental covariates are associated with spatially explicit probabilities of presence. This evaluation will extend previous efforts to define delta smelt habitat and account for the probability of capturing delta smelt.

METHODS

Data

Because our analysis of survival will focus on autumn, we will estimate model parameters on the basis of the dynamics of each annual cohort of delta smelt from August through December. Our estimates of abundance in August will come from the summer townet survey (STN), which samples juveniles. Since 1959, the STN has collected samples of delta smelt from a set of 31 index stations that extend from San Pablo Bay to Rio Vista (Figure 1). Before 2003, the number of summer townet surveys per year ranged from two to five. Since 2003, six surveys have been conducted at approximately two-week intervals from June through August.

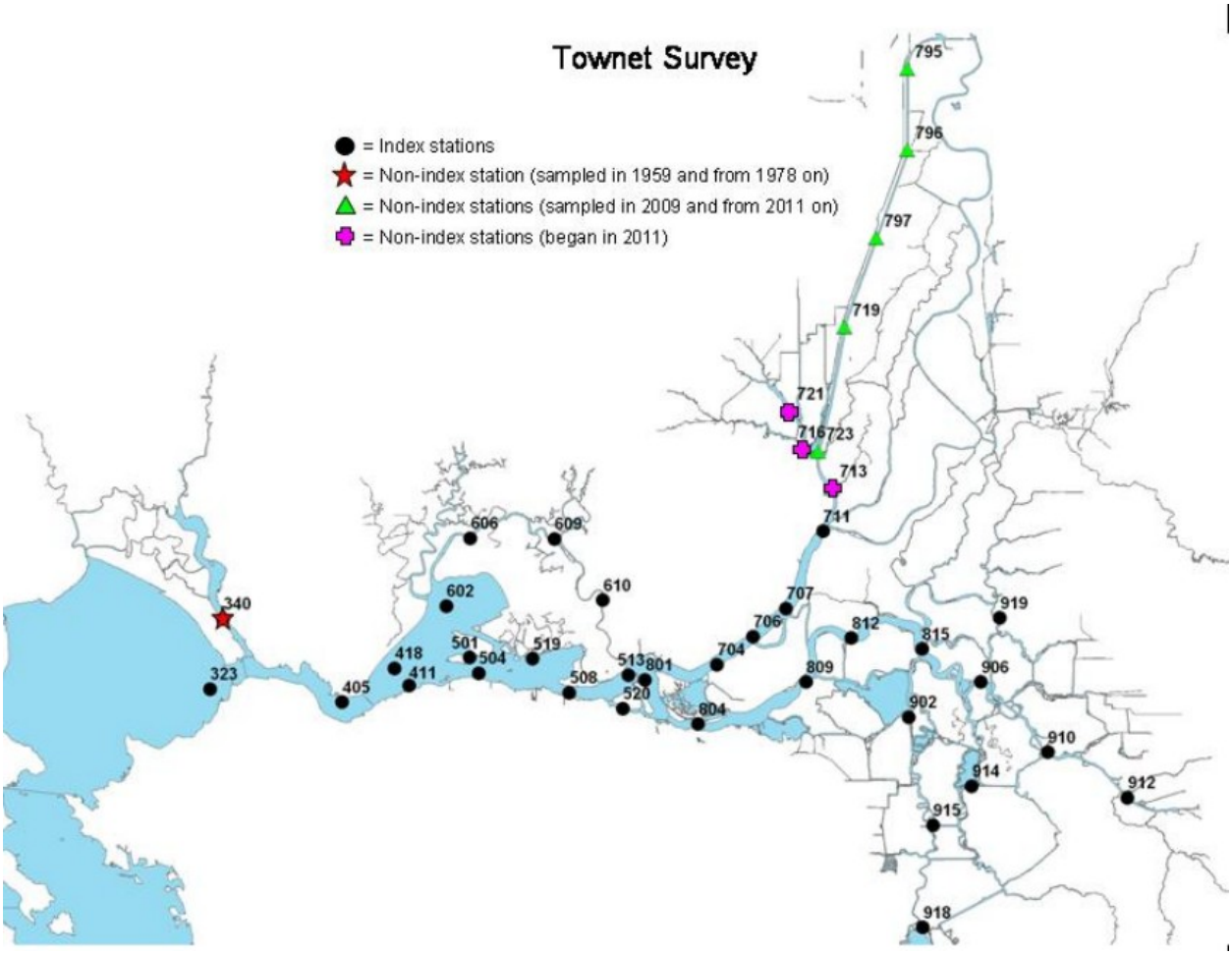

Figure 1. Stations sampled by the Summer Townet Survey. Figure from the California Department of Fish and Wildlife.

We will derive estimates of abundance for September through December from the FMWT, which has operated since 1967 (we will omit years for which data are missing or incomplete). Both age-0 delta smelt (subadults) and age-1 delta smelt (adults) are captured by the FMWT,

although relatively few age-1 fish have been caught in recent years. Beginning in 1990, the number of fish caught was used by the California Department of Fish and Wildlife (formerly California Department of Fish and Game) to estimate the abundance of each cohort. We will use the sum of the number of subadults and the number of adults. The FMWT collects samples from about 122 stations, but a subset of 100 index stations are used to estimate the annual abundance of delta smelt (Figure 2). We will use the catches from these 100 index stations to be consistent with previous analyses of catch data and occurrence (e.g., Feyrer et al. 2011, Manly et al. 2015).

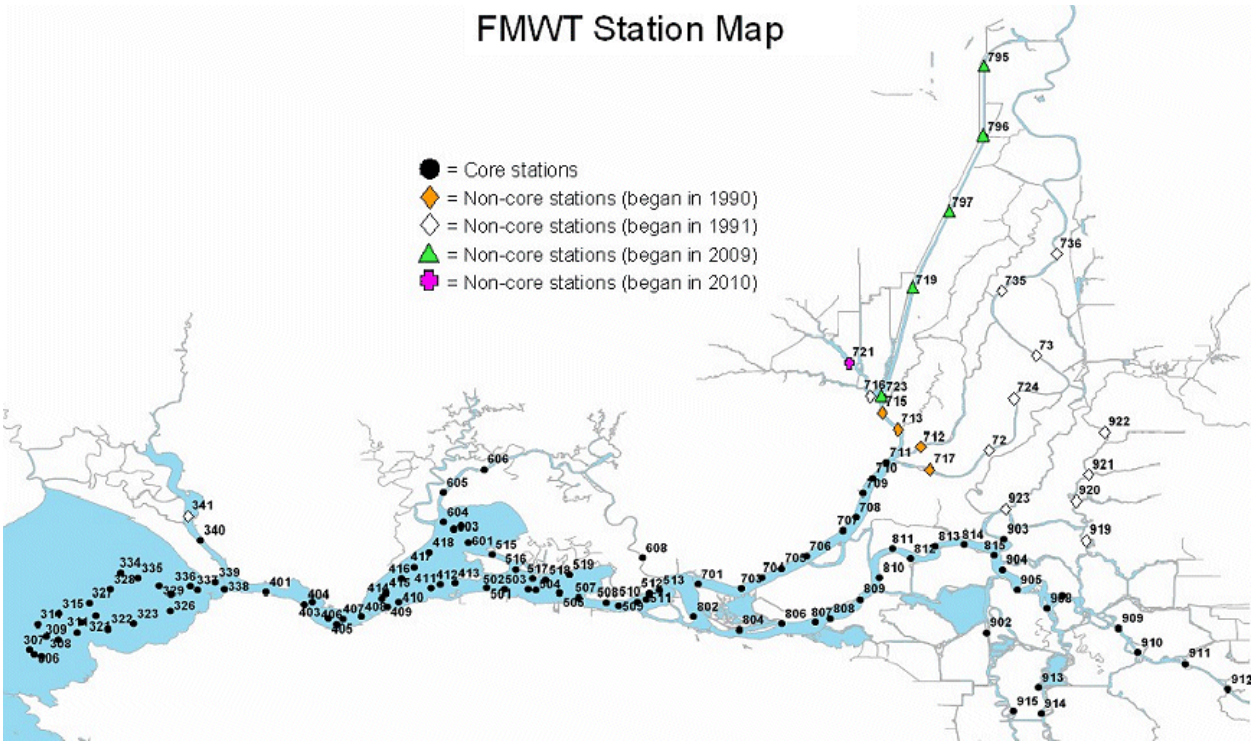

Figure 2. Stations sampled by the fall midwater trawl (FMWT) survey. Figure from the California Department of Fish and Wildlife.

The 20 mm survey, which captures larvae and juveniles, has been conducted since 1995. In the 1990s, surveys typically began in April. More recently, surveys have begun in March and extended through June or July. In most cases, three replicate tows are conducted at each station, and estimates of the station-level density of delta smelt are calculated by the California Department of Fish and Wildlife as a function of the average catch per volume of water sampled. The distribution of larvae and juveniles varies among years.

We will delineate multiple regions (r) within the Delta. Ideally, one would define regions that are known to be biologically meaningful to delta smelt. Current efforts by Newman et al. to construct a life-cycle model for delta smelt divide the Delta into four main regions (far west, west, north, and south), each with subregions (Figure 3). Data likely are not sufficient to delineate more than four regions for models of abundance. For our assessment of habitat quality, we expect to divide the Delta into a greater number of regions among which there is spatial and temporal variability in the presence of delta smelt. For example, each of the four regions

differentiated by Newman could be divided into two regions—far west: (a) Carquinez Strait and Napa River, (b) San Pablo Bay; west: (a) west of Honkers Bay to Carquinez Straight, (b) Honkers Bay and lower Sacramento River; north: (a) Cache Slough and Sacramento Ship Canal, (b) upper Sacramento River; south: (a) San Joaquin River near Stockton, Twitchell, and Prisoners Point, Disappointment Slough, and Mokelumne North and South, (b) Franks Tract, Holland Cut, Mildred Island, Old and Middle River, and Grant Line Canal. As another example, regions could be delineated on the basis of hydrology and geomorphology (e.g., MacWilliams et al. 2015; S. Culberson and S. Hamilton, personal communication)—for instance, east delta, including the Sacramento and San Joaquin Rivers; south delta, south of the San Joaquin River; north delta, north of the Sacramento river; confluence, extending up to Decker Island and Three Mile Slough to the San Joaquin; north Suisun; Montezuma Slough; south Suisun, extending through the Carquinez Strait; Napa River; and San Pablo Bay (S. Hamilton personal communication). If data are insufficient to include all of the latter regions, the regions could be grouped into north Suisun, confluence, north Delta, south Suisun, and all other locations (S. Hamilton personal communication). The habitat-quality model will allow us to construct multiple regional configurations (likely three or four, given the current budget) that reflect alternative hypotheses about what differentiates the regions.

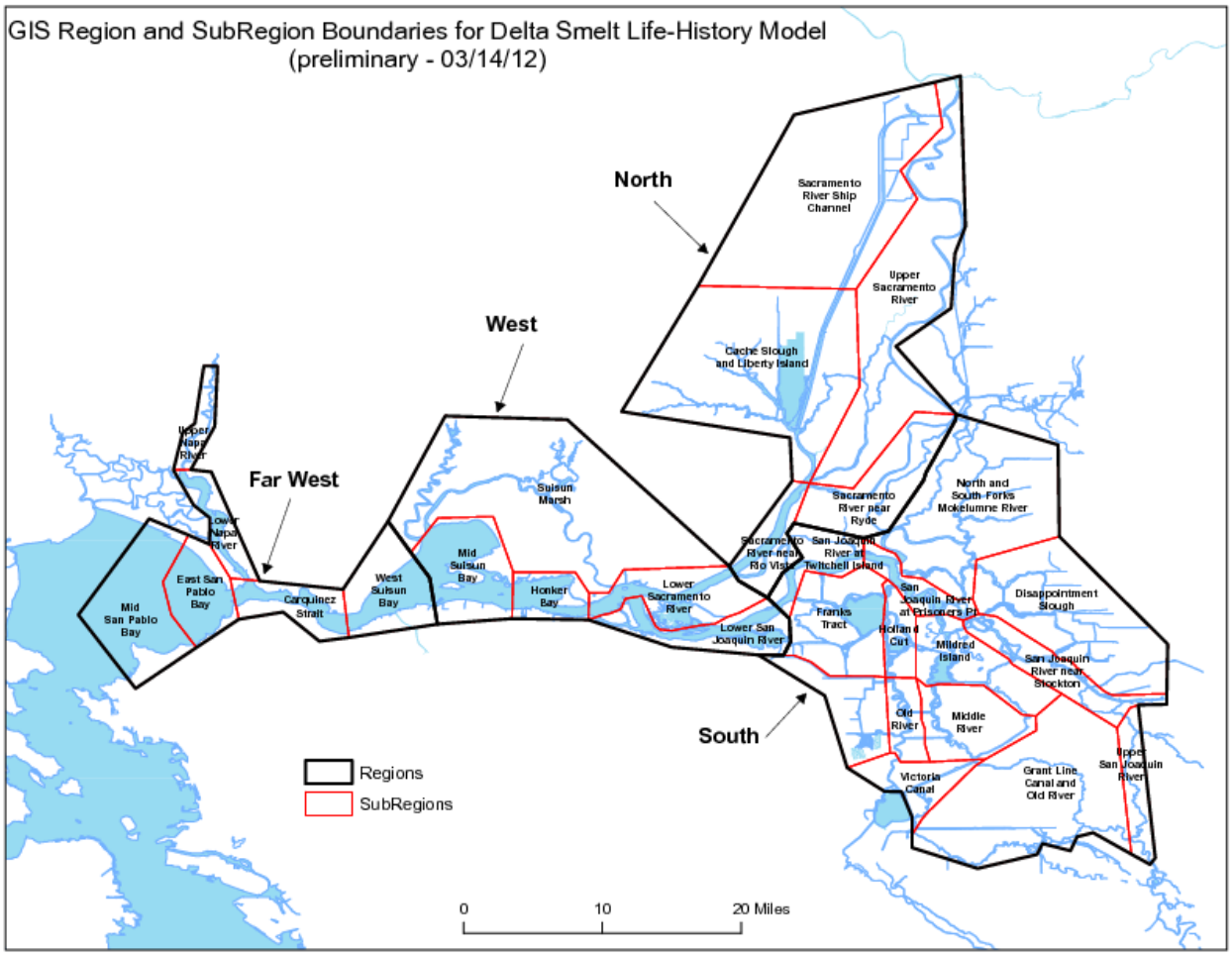

Figure 3. Regions (black) and subregions (red) in the Newman et al. life-cycle model.

If, in the future, each station (*s*) is sampled repeatedly during each month (see *Research Challenges*), then the sampling stations also could be considered as patches.

We will capitalize on existing data and metadata covering the period through 2010 that have been compiled by Ken Newman and his research group. We also may use data that were archived in 2008 with the Knowledge Network for Biocomplexity, an international repository that largely is supported by the U.S. National Science Foundation (knb.ecoinformatics.org). We will work with the appropriate agencies or individuals to update these data sources with field data gathered through 2014. We also will coordinate with a CAMT-associated group that aims to inform selection of covariates for a suite of CSAMP-supported investigations, and with other investigators who are examining potential biases in detection or capture probability of delta smelt (e.g., Ken Newman, Robert Latour). Because data on predators are sparse, yet predation often is hypothesized to affect survival and recruitment of delta smelt, we propose to conduct an expert elicitation to develop one or more predation covariates (see *Expert elicitation of predation covariates*).

We will assess collinearity among covariates before incorporating covariates into any of our models. Assessment of collinearity allows one to understand whether changes in values of multiple covariates are synchronous (strong positive correlation between or among covariates) or asynchronous (strong negative correlation). If covariates are strongly synchronous or asynchronous, they may provide similar signals about biological relations. We will use correlation analyses to assess collinearity among the covariates. Variables typically are considered to be correlated strongly if variance inflation factors are > 10.0 or correlation coefficients are > 0.60 (Neter et al. 1996). If we find strong correlations, then we will use ordination to construct orthogonal projections across the covariate data to capture the collinearity in the covariates. The best-known ordination method is principal components analysis, which transforms correlated variables into a set of linearly uncorrelated variables. Other ordination methods often are more appropriate for ecological data (Pielou 1984), and we will evaluate several alternatives if we find evidence of such collinearity.

Expert elicitation of predation covariates

One way to estimate values of parameters for which empirical data are sparse is to use expert elicitation (e.g., Martin et al. 2012). An expert on a particular topic has knowledge that a typical member of the general public does not have. However, extensive studies in psychology have demonstrated that experts have predictable, manageable cognitive biases (e.g., Tversky and Kahneman 1974, Ericsson 1996) and that judgments of the most knowledgeable individual in a group are consistently less accurate than the mean judgment of a diverse group. Accordingly, it is more reliable to use a structured method to seek information from multiple experts than to use information from one expert.

Expert elicitation encompasses a rigorous set of methods for synthesizing expert knowledge to inform decision-making, and has proven reliable and practical when field data are limited (e.g., Donlan et al. 2010). It is useful for identifying plausible alternative hypotheses, estimating model parameters, and prioritizing collection of data that may have considerable bearing on policy or management decisions (Martin et al. 2012). The information may be elicited as point estimates or

as distributions of parameters (Runge et al. 2011). Our investigative team has experience with this method (e.g., Oedekoven, C., E. Fleishman, P. Hamilton, J.S. Clark, and R.S. Schick. Expert elicitation of seasonal abundance of North Atlantic right whales [*Eubalaena glacialis*] in the mid-Atlantic. Endangered Species Research, in review) and believes it may yield useful information until such time as empirical estimates are available.

We anticipate receiving an exemption from human-subjects review from the University of California, Davis' Institutional Review Board. Nevertheless, we will obtain informed consent from all participants in the elicitation (henceforth, experts). We anticipate engaging about six to 12 experts with knowledge of the ecology and management of delta smelt and their predators and with collectively diverse organizational affiliations, ages, and career stages (Krueger et al. 2012).

The investigative team, with input from the covariates working group, will develop a set of brief, distinct questions (Hoffrage and Gigerenzer 1998) about likely predators on delta smelt. For example, if we aim to elicit information on the abundance of pike minnow within a defined space or time period, we might ask experts to provide a low estimate (minimum value), a high estimate (maximum value), an estimate of the mode, and an estimate of confidence in his or her answers to that question (Speirs-Bridge et al. 2010). Wherever possible, we will elicit numbers as integers rather than as proportions or percentages because people are able to conceptualize numbers better than percentages (Kynn 2008, Kuhnert et al. 2010).

Before asking experts to answer the questions, we will distribute a draft of the questions to the experts. We will convene the experts in person or by conference call to discuss the language in the questions and to ensure that all experts are interpreting each question in the same way (Martin et al. 2012). We will not discuss answers to the questions at this stage, only how the questions were presented. The investigative team then will improve the clarity of the questions, and distribute the revised questions and a description of the revisions to the experts. Experts will be instructed to answer the questions on the basis of their ecological knowledge without consulting anyone else.

We will convene the group of experts for an in-person meeting during which they will discuss the set of answers to each question in turn. In some cases, experts may voluntarily identify their responses. Following the discussion, each expert will have the opportunity to revise his or her answers (analogous to a Delphi process [Delbecq et al. 1975], although we are not seeking consensus). For each question, we then will merge the experts' answers into a single distribution (Iman and Conover 1982, Helbraun 2014). This distribution will be incorporated into our models as data on predation covariates. Because the full elicitation will require several months to complete, we expect that the elicited predation covariates will be incorporated into the second run of the occupancy model.

Estimating survival of delta smelt during autumn

To estimate survival of delta smelt during autumn, we will model the abundance of the species in each of the four major regions (Figure 3) and months. The monthly abundance of animals in a given region may be affected by both survival and movement. Emigration from a given region may occur because the region no longer serves as habitat, because habitat quality in the region

decreases, or because habitat quality in another region increases. Thus, our model structure will allow for movement among regions as a function of habitat quality. Consistent regional differences in densities may suggest whether different regions consistently have high or low relative habitat quality for delta smelt.

Model structure for estimation of abundance

Each cohort of delta smelt is produced from adults that spawn in the spring of a given calendar year, *y*. Because Delta Smelt are essentially an annual species, each calendar year corresponds to a unique cohort. We will follow the transition of each cohort *y* from 1967 to 2014 over the monthly time step *t* that extends from August through December. For clarity, we do not include the subscript *y* in the equations below.

We will assume that the abundance in each region has a Poisson distribution, and model the state process of abundance as

$$\mathbf{N_t} \sim \text{Poisson}(\mathbf{M_{t-1}S_{t-1}N_{t-1}}) \qquad (1)$$

The initial abundance in each region ($\mathbf{N_0}$) reflects the latent-state abundance in August. Subsequent abundances for the months of September through December are described by the state dynamics. Because delta smelt do not reproduce during autumn, we will partition the state equations that describe temporal changes in abundance in each region into two state processes, survival (**S**) and movement (**M**) (Newman et al. 2014). The vector of regional abundances at time *t* for four regions [($\mathbf{N_t} = (N_{1,t}, N_{2,t}, N_{3,t}, N_{4,t})$] is related to the abundances at the previous time step by survival first and by movement second.
In the Poisson distribution, the variance is equal to the mean. However, if the individual events (e.g., detections of an individual fish) are positively correlated, then the variance may exceed the mean. Thus, abundance also can be modeled as a negative binomial random variable, which allows the mean and variance can be different. Overdispersion (high variability relative to the mean) is common in ecological contexts, including in estimation of abundance. The negative binomial has a formal statistical relation with the Poisson distribution. If abundance is modeled hierarchically, then the mean parameter of the Poisson is a random variable. If the gamma distribution is used to define the mean parameter of the Poisson, the mean parameter will have the same functional form as a negative binomial. Accordingly, the negative binomial is equivalent to a mixture of Poisson distributions in which the means of those Poisson distributions are distributed as gamma random variables.

The survival matrix for multiple regions is a square with survival (ϕ) during each time step on the diagonal. For example, if there are four regions, then the survival matrix is

$$\mathbf{S}_t = \begin{bmatrix} \phi_{1,t} & 0 & 0 & 0 \\ 0 & \phi_{2,t} & 0 & 0 \\ 0 & 0 & \phi_{3,t} & 0 \\ 0 & 0 & 0 & \phi_{4,t} \end{bmatrix} \qquad (2)$$

where $\phi r,t$ is the survival rate (e.g., number of fish that survived during a given month) in region r and month t.

The movement matrix also is square. Columns represent the locations of delta smelt during the previous time step (t-1) and rows represent the locations of delta smelt during the current time step (t). The movement matrix is

$$\mathbf{M}_t = \begin{bmatrix} \psi_{1\to1,t} & \psi_{2\to1,t} & \psi_{3\to1,t} & \psi_{4\to1,t} \\ \psi_{1\to2,t} & \psi_{2\to2,t} & \psi_{3\to2,t} & \psi_{4\to2,t} \\ \psi_{1\to3,t} & \psi_{2\to3,t} & \psi_{3\to3,t} & \psi_{4\to3,t} \\ \psi_{1\to4,t} & \psi_{2\to4,t} & \psi_{3\to4,t} & \psi_{4\to4,t} \end{bmatrix} \qquad (3)$$

To illustrate, in the second row, the first cell reflects the probability that an individual present in region 1 during the previous time step moves to region 2 during the current time step. The second cell reflects the probability that an individual present in region 2 during the previous time step remains in region 2. The third cell reflects the probability that an individual present in region 3 during the previous time step moves to region 2 during the current time step, and so forth.

The movement matrix could be modeled in different ways to reflect different hypotheses about movement, such as a hypothesis that delta smelt only can move between adjacent regions. In this case, the probability of movement between non-adjacent regions is 0.

Modeling survival and movement as functions of covariates

We will model survival and movement as functions of covariates. The rate of survival and the rate of movement both fall within the interval (0,1). Furthermore, the values in each column of the movement matrix must sum to 1. To model survival rates for region r and month t $\phi_{r,t}$ we will use the logit() transformation

$$\begin{aligned} &\text{logit}(\phi_{r,t}) = \mathbf{X}_{\mathbf{r,t}}\beta_{r,t} + \varepsilon_{r,t} \\ &\varepsilon_{r,t} \sim N(0,\sigma_M^2) \end{aligned} \qquad (4)$$

as a function of covariates that also vary among regions and among months ($\mathbf{X}_{r,t}$), a vector of associated coefficients $\beta_{r,t}$, which can also vary by region and month, and an error term, $\varepsilon_{r,t}$,that accounts for process error. The error term is distributed as a normal random variable with mean 0 and variance σ_M^2.

We will use a different function to model dynamic rates of movement from region *q* to region *r* during month *t* ($\psi_{i \to j,t}$). Movement may be related to resource selection or to the relative quality of habitat among regions (e.g., Newman et al. 2009, Conn et al. 2015). In this case, the probability of movement from region *i* to region *j* is

$$\psi_{i \to j,\mathrm{t}} = \frac{h_{j,t}\eta_{i,j}}{\sum_{r=1}^{4} h_{r,t}\eta_{r,j}} \qquad (5)$$

where $h_{r,t}$ is the habitat quality in region *r* at time *t*, and $\eta_{i,j}$ is the dispersal probability, which is related to the distance between region *i* and another region *j* (Newman et al. 2009, Conn et al. 2015). We will use a log-linear model to characterize habitat quality as a function of covariates:

$$\log(h_{r,t}) = \mathbf{W}_{\mathbf{r,t}}\kappa_{r,t} \qquad (6)$$

We will calculate the dispersal probability as a function of the Euclidean distance between the centroids of two regions. Use of Euclidean distances reflects an assumption that the probability of dispersal between any two regions decreases as the distance between those regions increases. For example, the probability of dispersal between region *i* and region *j* is

$$\eta_{i,j} = \exp(-D_{i \to j} / \sigma_D^2) \qquad (7)$$

where $D_{i \to j}$ is the Euclidian distance between the centroids of regions *i* and *j* with σ^2_D controlling the effect of distance between regions on the probability of movement (Newman et al. 2009).

Modeling the observation process

In the simplest version of the abundance model, the number of individuals that are observed (detected or captured) is modeled as a binomial random variable (*Bin*) given the true abundance in the region and samples taken during month *t* at a given station *s*, which is in region *r*:

$$Y_{s(r),t} \sim Bin(p_{s(r),t}, N_{r,t}) \qquad (8)$$

where *Y* is the number of individuals observed at station *s(r)* at time *t*. The replicated samples needed to estimate region-level abundances ($N_{r,t}$) will come from FMWT tows at multiple stations within each region *r* during month *t*. The probability of capture at each station ($p_{s(r),t}$) can

vary as a function of covariates:

$$\text{logit}(p_{s(r),t}) = \mathbf{Z}_{s(r),t}\gamma_{r,t} + v_{s(r),t}$$
$$v_{s(r),t} \sim N(0,\sigma_p^2) \qquad (9)$$

where $\mathbf{Z}_{s(r),,t}$ is a matrix of covariates and $\gamma_{r,t}$ is a vector of coefficients describing the relations between covariates measured at the station and the probability of capture, and $v_{s(r),t}$ is a random effect that allows additional error in the probability of capture.

The initial abundances in each region can be estimated either as free parameters in the model or from the number of fish caught by the STN in August. For years in which the STN was conducted, we propose to use the STN catches to estimate abundance prior to the autumn.

$$Y^{STN}_{s(r),r,0} \sim Bin(p_{s(r),r,0}, N_{r,0}) \qquad (10)$$

Because the STN gear is different from the FMWT gear, we will structure the model to estimate relations between the probability of capture and the environmental covariates measured at the time of each STN.

Modeling multiple cohorts with the abundance model

The above equations reflect the dynamics for a single cohort of delta smelt. As explained above, each cohort corresponds to a year. The initial state is the abundance in August, and subsequent movement and survival dynamics describe the changes in abundance from September through December. We propose to model the dynamics of all cohorts from 1967–2014 for which FMWT data are available. To provide replication for estimating the effect of covariates among cohorts, we initially will assume that the functional relations between survival and movement rates and a given covariate do not change over cohorts. We potentially can relax this assumption by incorporating annual random effects in the survival and movement dynamics, and we will explore the ability to estimate such random effects with the data sets.

The abundance model will provide estimates of regional survival rates by month and cohort, $\phi_{y,r,t}$ but there may be interest in estimating a cohort survival rate over the autumn, e.g., ϕ_y. To compute this quantity as a model output, the abundance over all regions in December could be divided by the abundance over all regions in September, as

$$\phi_y = \frac{\sum_{r=1}^{4} N_{r,Dec}}{\sum_{r=1}^{4} N_{r,Sept}}$$

Simulation models for evaluating abundance models

We expect that data limitations may make it difficult to detect underlying relations between environmental covariates, including outflow, and survival and movement given the current field-sampling design. We propose to conduct simulations to determine how accurately our model can estimate the coefficients relating environmental covariates to survival and movement (i.e., relative habitat quality) given different probabilities of detection and sample sizes. The simulations also will provide insight into how sampling biases might be overcome with modifications to the existing sampling design, such as repeated surveys at each station on each sampling date (Polanski et al. 2014).

We illustrate the simulation modeling process with an example of the relation between survival $\phi_{r,t}$ and a global outflow covariate, x_t. This example assumes that survival in each of the four regions $r = 1, \ldots, 4$ has a different relation to outflow.

$$\begin{aligned} &\text{logit}(\phi_{r,t}) = \beta_0 + \beta_r x_t + \varepsilon_{r,t} \\ &\varepsilon_{r,t} \sim N(0, \sigma_M^2) \end{aligned} \qquad (11)$$

with β_0, β_1, β_2, β_3, and β_4, and σ^2_M known. The betas are coefficients that describe the functional relation between survival and outflow in each region.

There are six steps in simulating the data and estimating the coefficients. First, simulate the covariate values (x_t) over the four months (t = September through December). Second, initialize the abundances of delta smelt in each region ($\mathbf{N_0}$) in August. Third, run the model from September through December and sample the cohort during each month: calculate and apply regional survival (Equation 11), use a known movement matrix to move animals among regions, and calculate the number of fish caught at each station given a specified station-level probability of detection and a specified regional abundance. Fourth, repeat these three steps for the next cohort. Fifth, use the covariate values from step 1 and the number of fish caught from step 3 as inputs to the statistical abundance model for each of the $y = 1, \ldots N$ cohorts. Sixth, estimate the coefficients β_0, β_1, β_2, β_3, and β_4 and σ^2_M in the statistical model and compare these coefficients with the known values.

Multiple model configurations and data-generation processes could be tested with similar simulation models. For example, one could simulate a factorial design with two state processes (survival and movement), three levels of heterogeneity in detection probability (homogeneous across stations; heterogeneous across regions but homogeneous at stations within regions; heterogeneous across stations and dependent on a measured, station-level covariate), and three different numbers of cohorts (40, 60, 80).

Accounting for effects of zero inflation and overdispersion on abundance

Distributions other than the Poisson (equation 1), such as the zero-inflated Poisson (useful for count data with a high proportion of zeros), negative binomial (useful for cases in which the

variance is greater than the mean), Poisson log-normal, or zero-inflated negative binomial, could be used to reflect the underlying abundance of delta smelt. If abundance is assumed to have some probability of being drawn from multiple distributions, then another option is to model abundance as a mixture distribution with two or more components. For example, the zero-inflated Poisson and zero-inflated negative binomial models treat abundance as a two-component mixture distribution. In the first distribution, some proportion of the probability mass (or probability density) is at zero. The second distribution is applicable to the non-zero proportion of the probability mass. The second distribution is described by a parameter for the mean (zero-inflated Poisson) or by parameters for the mean and overdispersion (zero-inflated negative binomial).

Overdispersed data also may reflect a mixture distribution in which a certain set of environmental conditions lead to aggregation or regionally high abundance of delta smelt. In other words, it may be reasonable to hypothesize that the underlying distribution of abundance or density of delta smelt has three components: a zero-inflated component for events that lead to the true absence of delta smelt, a component that reflects typical densities of delta smelt, and a component that reflects abundances when conditions lead to aggregation or unusually high abundance.

Annual recruitment of delta smelt

There is no consensus on a single response variable that best represents recruitment. The DSST and CAMT wish to understand whether autumn survival of delta smelt and environmental attributes in autumn are associated with recruitment of delta smelt in spring, but wish to avoid confounding analyses of recruitment with survival of larvae, which could reflect other environmental attributes or environmental attributes in spring (and is outside our scope of work).

We propose to conduct a stock-recruitment analysis. Several metrics derived from the modeled abundance in of delta smelt in December could be used as the stock, such as the estimates of abundance in December and a spatial diversity metric reflecting the distribution of delta smelt in December.

Our discussions with the DSST identified three potential metrics of recruitment. The first is abundance estimates from the spring kodiak trawl. In this case, the underlying state variable is winter abundance (i.e., abundance of potential spawners). The second potential response variable is the length of delta smelt, which also would be derived from fish captured by the spring kodiak trawl. Use of this response variable reflects implicit hypotheses that length is related to body weight, body weight is related to fecundity, and fecundity is related to recruitment. The third potential response variable is abundance as derived from the 20 mm survey. In this case, the underlying state variable is abundance of larvae (i.e., production).

As noted above, density of delta smelt in the 20 mm survey currently is calculated as the average catch per unit effort (CPUE). The accuracy of estimates of recruitment potentially could be improved by using data from replicate tows at each station and N-mixture models (Royle and Dorazio 2008). Three repeated tows would allow for estimation of capture probability, which in turn would improve the accuracy of the estimate of abundance at each station. The current

method assumes that detection probability is 1, thus that the abundance equals the number of fish caught. Given that detection probability is not 1, the number of fish caught almost certainly is a biased estimate of abundance. Spatial and temporal differences in detection probability as a function of environmental conditions could be evaluated as part of the recruitment analysis. Potential covariates for analyses of recruitment include but are not limited to covariates in autumn (e.g., outflow, turbidity, estimated survival), and temperature, prey, and predators during different seasons.

Occupancy and habitat quality for delta smelt during autumn

Previous efforts to identify the environmental conditions that define delta smelt habitat in autumn typically have used catches of delta smelt by the FMWT (Feyrer et al. 2007, 2011; Manley et al. 2015). These analyses implicitly have assumed that the detection probability of delta smelt in the FMWT equals 1.0. But if detection probability is not quantified, true presence (occupancy) and other estimators related to environmental covariates will be biased, and may lead to erroneous inferences about species occurrence or demographic parameters (Gu and Swihart 2004, MacKenzie 2005). In the absence of an explicit model of detection probability, covariates attributed to the quality of delta smelt habitat actually may have been associated with the probability of detection.

Imperfect detection has been recognized as a potential source of bias in models of presence or abundance indexes of delta smelt, but has not previously been addressed quantitatively. We propose to use occupancy models (MacKenzie et al. 2003, 2006) to characterize habitat quality for delta smelt during autumn. Patch occupancy models (e.g., MacKenzie et al. 2003, Royle and Dorazio 2008) are a relatively straightforward and fast way to examine spatially explicit patterns in detection or non-detection. Patch occupancy models address occupancy and detection processes separately. Thus, these models estimate both the true underlying occupancy state (presence or absence) and the probability of detection given animals are present. The probability that the patch is occupied is modeled as a Bernoulli random variable, where 1 indicates presence and 0 indicates absence. Apparent absence may reflect either true absence or failure to detect animals that are present (false absence). The model outputs differentiate clearly between covariates associated with detection and those associated with occupancy.

Patch occupancy models are applicable regardless of a species' abundance, although there is a theoretical link between occupancy and abundance. As a species' abundance increases, its probability of occupancy increases (MacKenzie and Nichols 2004), and abundance and geographic distribution are strongly related to probability of continued occupancy or persistence (Lande 1993, Foley 1994, Harris and Pimm 2008). Still, patch occupancy models may be especially useful when abundance of the species is relatively low. For example, the abundance of delta smelt as measured by the fall midwater trawl has been relatively low since the early 2000s. As a result, abundances of delta smelt estimated on the basis of the FMWT may provide little information beyond whether the species was present. Data on occupancy patterns of a species in a given system, especially over time, allow one to examine the strength of association between diverse environmental attributes and occupancy, or between interactions among those attributes and occupancy. Values of many environmental attributes have considerable spatial and temporal variability, and incorporating such environmental dynamics into occupancy models can allow

inference to which environmental attributes are components of habitat for the species and the relative contributions of those attributes to habitat quality.

Model structure for estimation of patch occupancy

We will describe the occupancy state of the Delta as

$z_{r,t} \sim \text{Bernoulli}\ (\omega_{r,t})$ (10)

where $z_{r,t}$ describes whether a given region (r) is occupied in a given month (t). Occupancy is a state variable with a Bernoulli distribution. The two states are occupied ($z = 1$) or unoccupied ($z = 0$).

Occupancy of a given region ($\omega_{r,t}$) further can be modeled as a function of a matrix of covariates ($\mathbf{X}_{r,t}$):

$$\text{logit}(\omega_{r,t}) = \mathbf{X}_{\mathbf{r,t}}\beta_{r,t} \quad (11)$$

where β is the vector of coefficients. The coefficients may be region-specific or time-specific to reflect alternative hypotheses about environmental variables associated with presence of the species among regions or time periods, which also could be interpreted as hypotheses about environmental variables associated with presence or quality of habitat.

Modeling detection probability

The observation process u addresses the probability of imperfect detection and is conditional on the state variable (occupancy). The probability of detection (d) is modeled as Pr ($u = 1|z = 1$); (1-d) is the probability of false absence. The observation process is modeled as a Bernoulli (Bern) variable at the level of the samples as

$$u_{s(r),t} \sim Bern(z_{r,t} \times d_{s(r),t}) \quad (12)$$

The probability of detection [$d_{s(r),t}$] also can be modeled as a function of covariates via a logit transformation:

$$\text{logit}(d_{s(r),t}) = \mathbf{X}_{\mathbf{s(r),t}}\delta_{s(r),t} \quad (13)$$

where the covariates reflect the conditions at the time of sampling.

Model of patch-level persistence and colonization

Biological processes can be incorporated into occupancy models to analyze regional occupancy dynamics as a function of persistence (i.e., whether individuals are present in a given patch for successive time steps) and colonization. This approach is derived from metapopulation theory, and colonization and extinction dynamics can be modeled to accommodate the spatial arrangement of regions. We will use logistic regression to model the persistence process (ν) and the colonization process (ξ) as functions of covariates. The methods are similar to those we will use to model patch occupancy. The interpretation is slightly different, however, because the covariates are hypothesized to be associated with dynamic processes (i.e., the probability that delta smelt remain in a region given specific environmental conditions). This model may be useful if the environmental attributes of some regions are associated with a high probability of occupancy, but those regions cannot be colonized over the given time step.

The model of patch-level persistence and colonization can be conceptualized as a hybrid between the abundance model, which tracks dynamics of a cohort during autumn, and the occupancy model, which estimates presence at a finer spatial resolution than the abundance model. We will use the patch-level persistence and colonization model to describe the cohort dynamics during autumn and to evaluate the strength of association between environmental covariates and the probability that delta smelt persist in or colonize certain regions during autumn.

We will modify the patch occupancy model to allow Markov transitions among occupancy states in each region. The initial state condition is a function of the initial probability of being colonized:

$$z_{r,0} \sim Bern(\xi_{r,0}) \qquad (14)$$

A region can be colonized if it was unoccupied in the previous month, and the probability of persistence of a population in a given region is $\nu_{r,t}$ if the region was occupied in the previous month.

$$z_{r,t+1} \sim \begin{cases} Bern(\xi_{r,t}) & \text{if } z_{r,t} = 0 \\ Bern(\nu_{r,t}) & \text{if } z_{r,t} = 1 \end{cases} \qquad (15)$$

The observation equation is the same as that for the patch occupancy model:

$$u_{s(r),t} \sim Bern(d_{s(r),t} \times z_{r,t}) \qquad (16)$$

We again will estimate the initial occupancy states by fitting to the STN data for August when those data are available. We will estimate subsequent probabilities of colonization and persistence from the FMWT catches at each station within region *r* from September through December. Similar to the patch occupancy model, multiple regional configurations can be used to evaluate the dynamics of persistence (and its complement, extinction) and colonization over multiple cohorts and multiple annual hydrologic conditions.

Model fitting and comparison of hypotheses

We will use maximum likelihood and Bayesian methods to fit all of the models. We will use the R package unmarked (Chandler et al. 2015) to fit maximum likelihood models for the patch occupancy and patch persistence models. We will use JAGS (Just Another Gibbs Sampler; http://mcmc-jags.sourceforge.net/) for Bayesian estimation in the models. The JAGS package implements Markov Chain Monte Carlo (MCMC) simulations and other samplers to obtain samples from posterior distributions of parameters.

Assessment of alternative hypotheses requires the development of multiple model structures. The evaluation of alternative models depends on the statistical method being applied. For both maximum likelihood and Bayesian estimation, we will use information criteria to penalize complex models with many parameters. We will use the Akaike Information Criterion (AIC) to assess alternative models fit with maximum likelihood (Burnham and Anderson 2004). However, the AIC may have limited value for evaluating out-of-sample predictions (i.e., data that were not used to fit the model), particularly in cases in which the ecological system, and the modeled dynamics of the system, are relatively complex, but sample sizes are small and provide limited information about the underlying processes (Leeb 2008). Instead, alternative models fit with maximum-likelihood methods can be evaluated with cross validation (i.e., partitioning the data used to fit the model into a training set and a validation set) and a mean square error of predicted versus observed values. We will use the Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002) or Widely Applicable Information Criterion (WAIC) (Wantanabe 2010) to assess alternative hypotheses that were addressed with Bayesian estimation. Both the DIC and WAIC are useful for model selection because they provide optimal, asymptotic out-of-sample predictions.

RELATIONS TO ONGOING MODELING EFFORTS

Our proposed models differ in three substantive ways from other models of the dynamics of delta smelt that currently are being developed. First, although the theory of patch occupancy is well established and the models have been applied to diverse taxonomic groups, the models have not previously been applied to address the detection and non-detection of delta smelt. The presence and absence of delta smelt previously was assumed to serve as a surrogate measure of habitat quality and quantity (e.g., Feyrer et al. 2011, Manly et al. 2015), yet the latter analyses did not differentiate between nondetection and absence. Patch occupancy models likely will represent the underlying ecological processes more accurately. Much of the statistical structure for estimating dynamic patch occupancy models has been developed and implemented in the R package unmarked (Chandler et al. 2015), and thus models can be developed and fit relatively quickly. JAGS code also exists for Bayesian estimation of dynamic patch occupancy models (e.g., Kéry and Schaub 2012).

Second, the abundance model we propose to implement focuses on a cohort's trajectory from August through December, whereas Newman et al. are developing a model of the full life cycle of the fish. Accordingly, our model is somewhat simpler than that of Newman et al. For example, our proposed model includes a single movement function for the age-0 and age-1 delta smelt

captured by the FMWT, whereas Newman et al. have a different movement function for each of the life stages. The relatively simple structure of our model allows us to explore hypotheses about environmental covariates associated with survival and movement during autumn more easily than would be the case with the Newman et al. model. Still, both our proposed model and the work by Newman et al. involve fitting models to monthly catches by the FMWT in four regions. Both our investigative team and the Newman et al. team hope that the modest redundancy in model-fitting methods, spatial structure, and exploration of hypotheses related to movement will useful to both groups.

The third distinction between our proposed models and ongoing efforts is that we are proposing to evaluate recruitment as a function of factors that may affect delta smelt during autumn. The estimates of recruitment that currently are being computed (station-level CPUE in the 20 mm survey) do not account for imperfect detection. We propose to improve the estimates of recruitment by using models that estimate abundance on the basis of repeated samples over time (i.e., N-mixture models; Royle and Dorazio 2008). Our estimates of recruitment will allow us to use the dynamic patch occupancy models to compare the spatial distribution of delta smelt in December with the spatial distribution of recruitment the following April. Furthermore, we can compare the spatial distribution of density of delta smelt in December with the spatial distribution of recruitment density in the following April on the basis of our abundance model and the estimates of abundance from the N-mixture models.

All of our proposed models can be modified easily to accommodate updated data (e.g., longer time series), data with higher temporal resolution or greater spatial extent, different covariates that reflect different hypotheses about relations between delta smelt and natural or anthropogenic environmental attributes, and more-accurate estimates of gear efficiency or other aspects of detection probability. If data are sufficient, our models can accommodate different delineations of regions. After we identify covariates that are strongly associated with occupancy or abundance, we can vary values of covariates to conduct sensitivity analyses or to project how delta smelt may respond to environmental change.

Pending research by Rob Latour may inform our estimates of detection probability. Latour is beginning to assess two assumptions about estimates of delta smelt abundance that are based on CPUE: that samples are independent rather than temporally or spatially correlated, and that catch probability has been temporally and spatially constant. Latour will examine these assumptions for both the FMWT and the spring kodiak trawl survey. The results of the first analysis can be used to structure the random effects in detection probability, $v_{s(r),t}$, to reflect temporal or spatial correlation structures. He also will assess whether environmental covariates are associated with catch probability and, in turn, projected CPUE values and probabilities of false absences. The results of the second analysis can be used to suggest covariates of capture probability for inclusion in the abundance model and covariates of detection probability for inclusion in the patch occupancy and patch persistence models.

RESEARCH CHALLENGES

Trade-offs among models of abundance

Overdispersed and mixture distributions

The simplest model of abundance is the Poisson distribution, in which the mean and variance are equal, yet there may be a high probability that no individuals of rare species are present. Thus, a zero-inflation process, such as the zero-inflated Poisson, is needed to describe the abundance of delta smelt. In addition, there are infrequent cases in which a relatively high number of delta smelt are caught, suggesting that the underlying abundance is high. Distributions in which there are many zeros and, infrequently, high numbers are challenging to describe statistically. Nevertheless, we would like our sampling model to reflect both of these aspects of the underlying abundances of delta smelt. The infrequent high catches suggest that the variance is greater than the mean and that overdispersion needs to be incorporated into the sampling distribution. Two statistical distributions, the negative binomial and the zero-inflated negative binomial, can be used to incorporate this additional variability (i.e., the overdispersion in the underlying abundance). We also may consider other methods for evaluating the unusual conditions under which high numbers of delta smelt are observed, such as a multi-component Poisson. There are trade-offs between using a method that accounts for overdispersion (e.g., the negative binomial) and using a more restrictive statistical distribution (e.g., the Poisson) and attempting to model the processes that lead to the overdispersion (e.g., a two-component Poisson distribution).

To illustrate, suppose that detection probability is 1 and 100 tows were conducted, with an average of 15 fish was captured per tow. Under the Poisson distribution, the 95% interval is (8, 23). In addition, suppose that the number of fish detected in two of the tows was 100—i.e., much greater than the average. In this hypothetical example, the catch data cannot be described as a pure Poisson process. If abundance is modeled as a Poisson random variable, then the estimated average number of fish captured will be 17, but the data will appear to be overdispersed relative to the estimated average (a comparison of model degrees of freedom to residual variability will indicate this overdispersion). One option for addressing the apparent overdispersion would be to use a negative binomial model. If a negative binomial model is fit to these catch data, then the overdispersion parameter is estimated to be 5.3 and the 95% interval around the average of 17 is (4, 35). Another option is to fit a two-component Poisson distribution to the catch data. In this case, the model will estimate a first group of catches with a mean of 15 and a second group of catches with a mean of 100, and will estimate the probability that a given catch will be drawn from either group.

We have allowed for heterogeneity in the detection probability among stations through covariate effects and random effects (Equation 13). Both of these processes also could be responsible for zero inflation and overdispersion in the station-level FMWT catches. Thus, one of the research challenges will be evaluating alternative model structures that reflect hypotheses about whether overdispersion is occurring in the state process, in the observation process, or both.

Multi-state approaches

Abundance generally is considered to be an informative state variable for monitoring animal populations. However, estimating abundance with high precision can be expensive and either impractical or not feasible logistically. Occupancy has been proposed as an alternative to abundance, particularly for monitoring across large spatial extents, but occupancy may not be highly sensitive to changes in abundance.

A potential method for reconciling trade-offs between measurements of abundance and occupancy is to use ordered categorical analysis (multistate occupancy models; MacKenzie et al. 2009). These analyses use data on relative abundance to classify the abundance of each location as, for example, none, low, medium, or high. Use of ordered categories allows one to estimate the proportion of locations in each state. If data are collected for multiple time steps (e.g., months or years), then inference can be drawn about trends in the proportion of locations in each state.

Multistate occupancy models may be useful if there is a testing procedure in which the results of the test are not good indicators of the underlying continuous state. In this case, ranking the output of the test (i.e., placing each outcome of the test into one of a number of bins) may reduce the error induced by the testing procedure. A multistate method also could be useful when the relation between catches and abundances has high uncertainty, as may be the case with estimates of the true abundance of delta smelt that are derived from fall midwater trawl catches.

In an ordered categorical analysis, one defines a set of C categories for an ordinal response variable Y (e.g., low, medium, and high), and an associated continuous covariate X. One way of modeling these categories is to imagine a continuous underlying random variable in which each category is a discrete version of the continuous distribution. A latent response variable Z can be defined to represent the underlying continuous variable. The probit model for an ordinal response uses a normal distribution for Z, but any continuous distribution, including a mixture of distributions, could be used for Z. The probability of an observation y_i being in category c is the probability that Z_i lies within the cutoff-off points for the category. The normal or a mixture of normal distributions may be used for Z to model such ordered categorical analysis in a Bayesian framework (Albert and Chib 1993). The output from these models is the probability that the true underlying state lies in a given category.

In our case, the underlying state dynamics include movement and survival for the latent abundance in each region and time $N_{r,t}$,. Thus, we would have a time series of such ordinal observations $Y_{r,t}$ across each annual cohort. Modeling methods for time series of ordered categorical variables that were developed for financial (Chib 1996) and medical (Albert and Chib 2001) applications could be tailored to our objectives. In addition, recent efforts to develop more-general methods for Bayesian nonparametric regression modeling (Papageorgiou et al. 2015, De Yoreo and Kottas. Bayesian nonparametric modeling for multivariate ordinal regression. Available from http://arxiv.org/abs/1408.1027) also could be applicable.

Other models of dependence between abundance and detection

The observation process can be modeled as the relation between probability of detection and abundance. The equations for detection probability can be modified to reflect probability masses at abundance values 1, 2, ..., ∞ rather than modeling all of the mass at 1, which is the case when one is modeling occupancy. Our observation model estimates the probability of detecting $Y_{s(r),t}$ delta smelt in a sample at station s and time t given that there are $N_{r,t}$ individuals available for sampling in the region. The probability of detection at each of the stations at time t is a function of the number available at each station $N_{s(r),t}$:

$$d_{s(r),j(t)} = 1 - (1 - m_{s(r),j(t)})^{N_{s(r),t}}, \qquad (17)$$

where m=(0,1) from repeated samples $j = 1, ..., K_{s(r),t}$ within time period t. The probability of detecting an individual animal is m, and K is the total number of samples taken from all stations in a given region. The station-specific estimate of abundance [$N_{s(r),t}$] could be based on the proportion of volume sampled at the station [$w_{s(r),t}$] relative to the volume of the region (W_r); this is the approach that Newman et al. currently are taking. However, this method is quite challenging because $N_{s(r),t}$ is a latent variable (that is, a variable that is not observed directly). As a result, it is necessary to integrate across all possible levels of $N_{s(r),t}$ (i.e., all possible numbers of individuals available at a station). Integrating across all possible abundances is time-consuming, and these models are likely to become unstable when the data are sparse (Royle and Dorazio 2008).

Alternatively, it is unnecessary to integrate across all values of N if one assumes that the detection probability (d) and the number of individuals available for sampling (N) are functionally independent (Royle and Nichols 2003). The relation then reduces to

$$\Pr(y|d, N) = \Pr(y|d)\Pr(N > 0) + I(y = 0)\Pr(N = 0) \qquad (18)$$

where $I(y = 0)$ reflects that if the true abundance is zero ($N = 0$), then no individuals will be detected (i.e., this methods assumes that false positives are impossible). The probability of occupancy (ψ) in this case is a zero-inflated binomial and is equal to the probability that some number of individuals are available for sampling [$\Pr(N > 0)$] (MacKenzie et al. 2002). Thus, the model that assumes functional independence is equivalent to the model described in equation 10.

Application of this approach is simplified if there is variation in sampling effort, whether in terms of time per fixed area or volume sampled or in terms of fixed effort but variable area or volume. Variation in sampling effort allows one to examine whether detection probability varies as a function of sampling effort. Similarly, variation in values of environmental covariates is necessary to explore whether those covariates are associated with detection probability.

We can estimate the sampled area as the volume sampled at each station in each region, and model the local abundance as a function of volume, although the ability to estimate detection probability depends on the differences in volume sampled. For example, if abundance is assumed to have a Poisson distribution, then the local abundance at a given station in a given region [$s(r)$]

during a given time step (t) would be modeled as

$$N_{s(r),t} \sim Poisson\ (\mu_{r,t} \times w_{s(r),t}/W_r), \qquad (19)$$

where $\mu_{r,t}$ is the mean abundance in a given region (r) during a given time step (t). A similar model for $N_{s(r),t}$ could be developed in which abundance is assumed to have a negative binomial distribution, with an additional parameter estimating the degree of overdispersion relative to the Poisson.

Estimates of detection probability

Replicate samples from each region during each time step are necessary to estimate probabilities of detection and occupancy. It is possible to use spatial replicates (e.g., samples from multiple stations within a region) during a given time step, and we will do so in our models given the constraints of the data. However, violations of the assumptions that accompany use of spatial replicates can bias estimates of abundance (Kendall and White 2009). Use of replicate samples within a given time step at multiple locations has a greater likelihood of avoiding biased parameter estimates than use of spatial replicates. We stress that uncertainty in parameter estimates will be reduced if such samples are taken more frequently. Such sampling designs have been used in pilot projects with the goal of improving the quality of inference on the underlying delta smelt dynamics and probability of detection given delta smelt are present (Polansky et al. 2014). Repeated sampling at stations throughout the range of delta smelt would provide similar improvements in inference across a broader range of environmental gradients as is being developed by Newman et al. in a proposal to monitor entrainment of delta smelt. Our models will allow for incorporation of more-robust data if and when they are collected.

Similarly, there is little information on detection probabilities associated with different sampling methods or gear types. The information base for estimation of detection probability would be increased by conducting simultaneous surveys with multiple gear types, repeating these surveys at a given station within a relatively short window of time, and conducting such surveys at many stations. Repeating samples on the same day at the same station is useful, but it will be even more informative to vary the position of the tow line between successive samples on that day.

TASKS AND DELIVERABLES

We have organized the proposed work into six major tasks: abundance modeling, expert elicitation of predation covariates, recruitment modeling, patch occupancy modeling, modeling of patch-level persistence and colonization, and project management. Some elements of the tasks will occur in synchrony and some sequentially. Project management will cover the full project period.

Estimated timetables assume that our investigative team has been provided with clean, reliable data before initiating a given analysis (as necessary, following collaborative generation of alternative hypotheses). We have not budgeted time or money for quality control or data cleaning. For all tasks except project management, we anticipate presenting initial results to CSAMP groups (e.g., the DSST and CAMT) and, on request, to other audiences, including but not limited to public water agencies or nongovernmental organizations. Our estimated delivery dates account for an iterative process of presentation, discussion, and refinement of deliverables. We anticipate submission of manuscripts on each of the five analytical tasks to peer-reviewed scientific journals. In general, we expect to submit those manuscripts within about two months of the delivery dates indicated below.

Deliverable (assuming start date of 1 September 2015)	**Delivery date**
Outputs of abundance model	February 2016
Elicited data on predators of delta smelt	February 2016
Outputs of recruitment models	April 2016
Outputs of patch occupancy models	June 2016
Outputs of persistence and colonization models	August 2016
Any derived data included in the analyses and standardized metadata; the data and metadata will be deposited in one or archives that are publicly available	winter 2017
Analytical scripts and associated metadata; these will be deposited in one or archives that are publicly available	winter 2017

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