Habitat affinity analysis as a tool to guide environmental restoration for an imperiled estuarine fish: the case of the delta smelt in the Sacramento-San Joaquin Delta

Dennis D. Murphy
Biology Department
University of Nevada
Reno, Nevada 89557

Scott A. Hamilton
Center For California Water Policy and Management
1017 L Street, Suite 474
Sacramento, CA 95814

ABSTRACT

Habitat restoration efforts in the Sacramento-San Joaquin Delta in central California move forward under the state's ambitious Bay Delta Conservation Planning process, despite a paucity of information on the habitat needs of many of the plan's targeted species. The endemic delta smelt, protected as threatened under the federal Endangered Species Act, is a primary focus of those efforts despite key uncertainties regarding many aspects of its relationship with the estuary's physical and biotic resources. Here we carry out habitat affinity analysis for multiple life stages of the delta smelt drawn from time-series data from four trawl surveys, and data on environmental attributes taken from throughout the distribution of the fish. Ranges of conditions acceptable to delta smelt for each of seven environmental attributes were identified. Low turbidity and high water temperatures render a large portion of the estuary seasonally unacceptable to delta smelt. Within areas that experience largely acceptable water quality conditions, patterns of delta smelt occurrences indicate that habitat occurs where deep channels adjoin shallow-water circumstances and extensive patches of emergent vegetation. Habitat suitability indices show that favored environmental circumstances vary with life stages, and delta smelt move as they mature to access suitable areas with environmental attributes in acceptable ranges. Areas that exhibit highest geometrically weighted average HSI values for environmental attributes are displayed on maps, and can be viewed as representing potential priority target areas for habitat restoration efforts. Delta smelt should benefit in priority target areas with channel modification and directed wetlands restoration efforts.

Keywords – delta smelt, habitat, habitat affinity analysis, habitat suitability index.

Introduction

The need for reliable knowledge regarding the habitats of imperiled species frequently outstrips available information (Karieva et al. 1998, Johnson et al. 1999, Reed et al. 2006). A paucity of data and observations can stymie planning even for the flagship species and their habitats that are the focal targets in those conservation efforts. Planning for species with particularly narrow distributions, very limited numbers, and especially cryptic behaviors can be challenged by a lack of observations, and constrained by limited data sets from which species-habitat relationships can be gleaned. Examples abound, from conservation efforts for the few remaining marbled murrelets, sea birds nesting high in old growth and late seral forests along the northern Pacific Coast (Peery 2004, USFWS 1997), to attempts to provide beneficial hydrodynamics for the pallid sturgeon, a species sparsely distributed in the murky depths of the lower Missouri River (Bajer and Wildhaber 2007, USFWS 2013). One federally protected species suffering from an incomplete understanding of its habitat requirements is the narrowly endemic delta smelt from central California's Sacramento-San Joaquin Delta and adjacent areas of the San Francisco estuary. The elusive delta smelt's ecological relationships are obscured under turbid waters, and many of the essential attributes of its habitat are still the subject of surmise, rather than hard data (see Sommer and Meija 2013). Two decades after its listing as a threatened species, it actually has yet to be observed to reproduce in nature (Bennett 2005).

The limited understanding of essential habitat attributes of the diminutive delta smelt has contributed to strident disagreement regarding necessary management actions to protect the species that culminated in litigation pitting the federal and state governments against one another (Consolidated Delta Smelt Cases, 717 F. Supp. 2d 1021 [E.D. Cal. 2010]). The need for an understanding of the ecology of the delta smelt and the resources that support it is immediate, reflecting its role as a focal species in the Bay-Delta Conservation Plan, an ambitious effort to restore and manage the most extensive and environmentally disrupted estuary on the Pacific Coast (BDCP 2013). Plan architects hope to restore and enhance delta smelt habitat in order to bolster the fish's numbers and enhance the likelihood of its persistence, noting that its actual numbers can only be speculated upon (see Bennett 2005, Kimmerer 2008, Newman 2008, Kimmerer et al. 2009), its patterns of dispersal are the subject of ongoing debate (Sommer et al. 2011, Murphy and Hamilton 2013), and the causes of its imperilment appear to be many, but are largely not quantified (see Feyrer et al. 2007, Nobriga et al. 2008, Grimaldo et al. 2009, Winder and Jassby 2010). The current draft Plan calls for the restoration of delta smelt habitat and that of co-occurring species, with commitments of funding of hundreds of millions of dollars over decades. Yet what actions those habitat restoration efforts should entail, where they should be carried out, and how they might be prioritized remains in fair doubt (NRC 2011). It is the purpose of this study to draw inference from publically available survey data on delta smelt and concurrently gathered data on environmental attributes regarding the ecological conditions that contribute to habitat for the fish, and identify areas of the Delta and adjacent estuary that are inappropriate targets for restoration efforts, thereby guiding those conservation activities to locations that offer greater promise for BDCP program success.

A holistic description of delta smelt habitat that can be used to guide actions to manage and recover the fish, direct programmatic monitoring efforts to better assess its numbers and distribution, and provide a basis for evaluating the success of conservation activities and expenditures remains elusive. But, at least some of the basic ecological needs of delta smelt have been inferred from a number of retrospective studies using a combination of time-series survey data taken in trawls that are designed to sample pelagic fishes in the estuary, paired with long-term environmental data on a number of water quality parameters, landscape attributes, and biotic factors near sampling stations (see Bennett 2005 for a then-contemporary summary, and Sommer and Meija 2013)). Much of that same information has been used to inform a number of conceptual models that provide descriptions of pathways by which environmental variables are believed to directly and indirectly contribute to determining delta smelt numbers and distribution (Armor et al. 200x, Baxter et al. 200x, Nobriga and Herbold 2009, Miller et al. 2012). Dozens of ongoing studies are extending efforts to address discordant patterns of variation in the constellation of environmental attributes of the Delta that seem likely to affect the distribution and abundance of delta smelt, but critical uncertainties undoubtedly will freight conservation planning for some time to come.

What is generally agreed upon is that the delta smelt's geographic range is narrow and diminished from its historical extent (Whipple et al. 2012). Delta smelt reside in a more or less continuous distribution, from freshwater circumstances in the north Delta, west across the confluence of the Sacramento and San Joaquin rivers in tidally influenced waters, to the western portions of Suisun Bay and Suisun Marsh. A satellite population is sometimes found further west in the lower Napa River and its estuary. The species' distributional range in the San Francisco estuary is a scant 50 kilometers (see Merz et al. 2012), across which the delta smelt is found in open waters during most of its annual life cycle, and from which the fish appears to disperse seasonally to shoreline situations, where it spawns in and adjacent to freshwater inlets to the estuaries more saline waters (Moyle et al. 1992, Bennett 2005, Murphy and Hamilton 2013).

Several recent multivariate studies offer a lens into inter-year responses of delta smelt to a number of environmental attributes of the Delta, therefore provide some fundamental guidance to conservation planners. Feyrer et al. (2007) considered the roles of salinity, turbidity, and temperature in determining the distribution of delta smelt in a portion of its low-salinity-zone range in the San Francisco estuary, finding that the former two water-quality variables explained about a quarter of variance in the distribution of the fish. Thomson et al. (2010) used change-point analysis to investigate step changes in nearly two-dozen environmental factors, many that contribute to the extent and quality of delta smelt habitat. The authors found that reductions in turbidity and the increases in the volume of water exports in winter months corresponded with declines in delta smelt numbers that have been recorded over the past decade. MacNally et al. (2010) used multivariate autoregressive modeling to evaluate 54 fish-environmental factor relationships, including the factors considered by Thomson et al., and found generally weak relationships, but enhanced signals from food availability and the position of the low-salinity zone in the spring correlated with delta smelt numbers. Maunder and Deriso (2011) used a multistage life-cycle model that varied levels of presumptive density dependence to consider environmental factors acting on delta smelt abundance. The study found a substantive deterministic relationship to be the availability of the fish's food resources, and signals of effects of predator abundance and temperature on different delta smelt life stages. The environmental data in that study were shared in a multivariate regression analysis by Miller et al. (2012), who asserted that their specification of environmental variables was spatially and temporally rectified to better reflect within-Delta patterns of environmental variation. Among habitat attributes, they found food availability to be a major explanatory variable in dictating population responses in delta smelt, with overarching effects from density dependence. The findings from these studies, considered in the context of inferences that can be drawn from the several available conceptual models contribute to identifying a number of essential attributes of delta smelt habitat, and the physical and biotic resource conditions that contribute to determining habitat extent and quality.

To assess the importance of habitat attributes to delta smelt and, at the same time, to offer at least contingent guidance to agency managers charged with constructing, restoring, and rehabilitating delta smelt habitat , we followed the approach of Guay et al (2000), applying habitat affinity analysis in conservation planning. Guay et al. considered the relevance of water depth, substrate composition, and water velocity to the quality of habitat for juvenile Atlantic salmon in a reach of the Sainte-Marguerite River. They divided the water body into "tiles" (geographic segments of the river), which were smaller than, but analogous to sampling stations in the San Francisco estuary, and collected attribute and fish data for areas where fish were observed and not observed. They developed preference curves for discrete interval ranges of each attribute by comparing the percentage utilization of an interval with the percent availability of it. Preference indices ranged from 0 (considered poor habitat) to 1(considered best habitat). Utilizing a multiplicative regression analysis, they developed a weighted habitat suitability index (HSI) enabling them to rank the quality of the habitat at any site based on the attributes at that location. Applying the techniques developed by Guay et al, we develop habitat suitability indices in an effort to parameterize descriptions of the direct and indirect effects and influences of physical and biotic attributes of the estuary on delta smelt. We draw from publically available trawler-based survey data on the distributions and relative abundances of multiple life stages of the delta smelt, and relate those demographic data to data available on physical and biotic attributes of the estuary, including bathymetric data derived from USGS databases, to inferentially identify landscape characteristics that may contribute to delta smelt habitat. We endeavor to inform habitat restoration for delta smelt by following a sequence of steps.

First, drawing on agency-generated conceptual models that articulate hypothesized, inferred, and established relationships between delta smelt and environmental variables, we identify candidate environmental attributes that appear to contribute to the extent and quality of habitat for delta smelt. Second, we use affinity analyses, in which we compare the frequency of delta smelt co-occurrence with the availability of physical and biotic resources and their spatially and temporally varying conditions to infer how environmental attributes determine the distribution of delta smelt at each of its life stages. Third, we utilize the results of the affinity analysis to develop suitability indices for each deterministic attribute separately, and then combine the suitability indices to derive numerical meta-indices of aggregated habitat quality for each life stage using multiple regression analysis. The approach permitted us to identify specific environmental attributes that are relevant to delta smelt when several are considered simultaneously in a comprehensive treatment of its habitat. Having identified important habitat attributes, we are able to determine the environmental factors that are lacking or appear to fall out of the range of acceptable conditions for delta smelt, and where those circumstances occur in support of efforts to inform the selection of locations and prioritization of potential restoration projects.

Carrying out these steps we find it possible to offer substantive guidance to agency managers and technical staff. The results of our analysis offer prescriptions on (at least) two spatial scales. First, delta smelt distribution data mapped on three physical variables indicate that broad geographic portions of the contemporary estuary may not be appropriate targets for mechanical habitat restoration efforts because one or more physical variables, which are not under management control, fall outside ranges acceptable to the fish. Efforts to restore habitat structure and function in those locations appear to be unlikely to result in the local (re)establishment of delta smelt occupancy, or increased delta smelt numbers. Second, in situations not so constrained, the mapped habitat-affinity relationships that we have generated can be used to identify locations that appear to be suitable targets for restoration and assist in identifying the habitat-enhancing actions that might contribute to supporting delta smelt. This application of habitat affinity analysis to provide limited guidance to restoration efforts in the Delta seems apt. In effect, we infer from patterns of presence and absence of delta smelt in the estuary conditions that are favorable for the species and thereby identify locations that may be suitable sites for restoration, because they approximate some of the conditions that are associated with the presence of delta smelt. Arguably more importantly, planners can use the affinity analysis and habitat suitability indices to avoid areas wherein restoration efforts are likely to be unsuccessful.

METHODS

Study system

The San Francisco Estuary is the largest of its kind along the U.S. Pacific Coast (Rosenfield and Baxter 2007). Formed by the confluence of the Sacramento and San Joaquin rivers watersheds, the estuary drains nearly 40% of California's surface area (van Geen and Luoma 1999, Sommer et al. 2007). The estuary is tidally influenced, with fresh river water from the east mixing with saline ocean water from the west. The major water bodies within the estuary include the Sacramento-San Joaquin Delta (Delta), which lies east of the confluence of the Sacramento and San Joaquin rivers, Suisun Bay, Carquinez Strait, and the Napa River, as well as San Pablo and San Francisco bays to the west (Figure 1). The internal estuary is highly altered from its pre-settlement physiognomy, existing now as a network of mostly fortified waterways surrounding a patchwork of subsided islands behind earthen levees. The extensive marshlands that previously dominated the estuary and the floodplains that surrounded it have largely been replaced by cultivated agriculture.

Two native fishes – the Sacramento perch (*Archopilites interruptus*) and thicktail chub (*Gila crassicauda*) – vanished with the post-Gold Rush settlement, conversion, and utilization of the estuary, as extensive tule-dominated wetlands that were dissected by dendritic channels and subject to complex tidal currents were diked and dredged. The estuary now supports a limited assemblage of native fishes; some are resident, some are anadromous transients, and several are endemic, notably the federally protected delta smelt. But the delta smelt and the rest of the native fishes now exist in communities dominated by non-native competitors and predators, supported by a highly altered food web and local shortages of essential habitat-defining environmental features and resources. Against that background, resource managers in the San Francisco estuary are challenged to identify conservation actions that will contribute to sustaining an imperiled native fishery and contribute to the recovery of listed species from inferences of those species ecological relationships and habitat needs.

Candidate habitat attributes

We began by developing a list of candidate environmental attributes that previously had been observed or surmised to potentially contribute to habitat quality for estuarine fish. These include turbidity, salinity, temperature, dissolved oxygen, pH, aquatic vegetation, prey density, water depth, substrate composition, and the extent of adjoining marshlands (see Pardue 1983, Weinstein 1986, Stier and Crance 1985, Brown et al. 2000 for lists). Environmental factors that are suspected to affect delta smelt are only slightly more limited in number (Armor et al. 2005, Baxter et al. 2005, Bennett 2005, and Nobriga and

Herbold 2009 for conceptual models and natural history syntheses). Federal and state agency scientists have hypothesized that three standard water quality factors, salinity, turbidity, and temperature, affect habitat quality (Feyrer et al. 2007, Nobriga et al. 2008). Water temperature has an influence on spawning (Wang 1986, Meng and Matern 2001, Bennett 2005, Feyrer 2004, Grimaldo et al. 2004, Sommer et al. 2004), embryo survival (Moyle 2002, Mager et al. 2004), available habitat during the summer (Nobriga et al. 2008), and adult survival (Swanson et al. 2000). Hieb and Fleming (1999) suggest that delta smelt are found across a near estuary-wide range of salinity conditions. It has been asserted that delta smelt prefer turbid water, perhaps for successful feeding (Baskerville-Bridges et al. 2004, Mager et al. 2004), and because it may reduce susceptibility to predation.

Investigators have described the calanoid copepod prey that support delta smelt (Lott 1998, Nobriga 1998 and 2002). Two multivariate analyses of an array of environment attributes of the Delta identified prey abundance as the primary determinant of population dynamics in delta smelt (Maunder and Deriso 2011, Miller et al. 2012). The fish is often described as frequenting shoals adjacent to deeper channels (Moyle 2002), with an assumption that emergent wetlands contribute to productivity at the base of the food web that supports the delta smelt. Hobbs et al. (2006) linked superior nursery conditions to increased feeding success; and other studies have recognized the potential importance of fish access to wetlands and floodplains (see Lindberg and Marzula 1993, McIvor et al. 1999). Moyle et al. (1992) and Bennett (2005) indicate that spawning occurs near estuary and river shorelines and adjoining sloughs. Substrate composition may be important in determining spawning habitat (Moyle 2002). McGowan (1998, and McGowan and Marchi

1998) found that areas inhabited by the invasive water-weed *Egeria densa* are not typically inhabited by native fish in the estuary, including delta smelt, and that low abundance of delta smelt is generally associated with areas supporting higher concentrations of submerged aquatic vegetation of all types (see also Nobriga et al. 2005, Grimaldo et al. 2009). Lehman et al. (2010a) document low delta smelt abundances in areas subject to episodic blooms by the toxic blue-green alga *Microcystis.*

From the preceding sources and agency-generated conceptual models we organized a list of candidate environmental attributes for consideration in habitat affinity analyses for delta smelt (Table 1).

Data Sources and Treatment

Fish surveys -- A synthetic description of delta smelt habitat must consider suites of environmental attributes and thresholds that act on its individual life stages. Habitat extent and quality, and the geographic location of habitat may vary between life stages; concomitantly, different sites within the estuary may be suitable or unsuitable for the fish at different stages in its life cycle. The California Department of Fish and Wildlife carries out multiple surveys of Delta fishes, returns from which include delta smelt in temporal samples that span its annual life cycle. Surveys include the 20 mm Survey, Summer Tow-net Survey (STN), Fall Midwater Trawl (FMWT), and Spring Kodiak Survey, which sample extensive areas of the Delta and collect delta smelt in meaningful numbers. The methods for these surveys have been documented previously (Moyle et al. 1992, USFWS 2004, Bennett 2005); the varying strengths and weaknesses of several of these surveys as population assessment tools for delta smelt have been discussed in detail by Bennett (2005). We used data from these publicly available fish surveys, delineating life stages as depicted in Table 2, to assess the distribution in local densities of delta smelt. We utilized data from consistently surveyed stations; that is, stations that were surveyed in every year, or in every year but one since 1995, to ensure multiple observations at sites. The time period represented for each life stage reflects the months when that life stage typically predominates among sampled delta smelt. On average, more than 75% of individuals from a given life stage were sampled during the temporal windows presented. Because year-to-year variation exists in the timing of the appearance of each life stage, we considered the period during which 90% of the specific life-stage was sampled. Doing so, we excluded the temporal extremes when habitat attributes and delta smelt presence are less certain due to the very small numbers of individuals sampled. For the FMWT, however, we considered only the months of September and October, rather than the full period of the survey through December; the first two months of the trawl period had been identified by CDFW as the basis for regulatory decisions.

Covariate Specification -- In order to assess the relative influence of local and regional environmental factors that operate to determine delta smelt occurrences, we considered habitat associations at two spatial scales -- site and regional. At the site scale we addressed covariates using data drawn from individual monitoring stations – either as data collected that were taken along with fish samples (temperature, salinity, and turbidity), or as geographic and bathymetric data drawn from geographic areas adjacent to those stations (depth, area of shallows, channel width, distance to wetlands). Additionally, we collected data on substrate composition in March 2010 at stations where water depth was less than seven meters, classifying substrates using delineations in Table 3. At the regional scale we considered factors that operate at broader spatial scales (including water body type, prey availability, and predation pressure). Specification of these attributes is provided in Table 3.

Not unexpectedly, upon investigating data availability, we found insufficient data to support the inclusion of some variables in the affinity analyses. Specifically we were unable to obtain suitable data on dissolved oxygen, pH, contaminants, velocity, predation pressure, aquatic vegetation, or presence of *Microcystis* in a regular spatial and temporal frame. Data on several of these variables do exist, but not in time series or in data sets that cover the geographic range of delta smelt. Plainly, as agency managers take stock of the existing data collection scheme, they should seek to gather data – even at limited spatial or temporal scales – regarding these variables that could affect the quality and quantity of available habitat.

Affinity Analyses

Affinity analysis compares the availability of an environmental resource, or physical characteristic or its condition, with the use of that resource or co-occurrence with that physical characteristic by a target species (Lechowitz 1982, Grost et al. 1990, Monaco et al. 1998, Cardona 2006). When little is known about a species, an affinity analysis can offer insights into the nature of the relationship between an environmental attribute and the target species, depending on whether the species exhibits an affinity with or aversion to the environmental attribute, and whether an affinity, if found, is strong or weak. It does not require the *a priori* specification of a functional ecological relationship; therefore, it does not presuppose the nature of the relationship that may exist. Graphical depictions of the results can assist in identifying threshold phenomena and other non-linear relationships that may be inherent to the fish-factor interaction. In utilizing an affinity analysis approach, care must be taken to consider collinearity between variables, as well as appropriate segmentation of the attribute range in depictions of continuous data.

The environmental attributes that appeared to be pertinent and that met data-adequacy criteria for inclusion in the affinity analysis (from Table 1) were turbidity, salinity, temperature, food availability, channel depth, channel width, water body type, area of shallow water, proximity to wetlands, and substrate during spawning.

In conducting the affinity analyses, we divided the full range of data for each attribute into 6 to 9 segments (or increments). The delineation of the segments reflected the nature of the attribute considered. The segments were generally of equal magnitude through the range of delta smelt occurrences for turbidity and depth. For temperature, the magnitudes of some segments were narrowed to provide more detailed information for the response variable (for example, temperatures during summer that might induce stress). For other attributes, including salinity, turbidity, prey density, channel depth, area of shallows, and distance to wetlands, the delineation of segments reflected a near-exponential increment spacing. Other delineations reflected discrete categories of the attribute (for water body type and substrate).

For each monitoring-program month during which a targeted life stage was abundant (that defined here as exceeding 10% of the annual total of individuals sampled), we used pivot tables (in Microsoft Excel) to enumerate the number of delta smelt individuals and the number of observations in each attribute segment. We then converted each of those to a percentage value for each month, and generated summary statistics across months and years to produce statistics on the average percentage of availability for each attribute segment, the average use of each segment, the average difference between the two, and the standard deviations of each to determine a 90% confidence interval.

We present affinity analyses as graphs for each life stage showing the percentage distribution of delta smelt across a segmented attribute range compared to the availability of the resource. We display the difference between resource availability and its use, along with the 90% confidence interval surrounding the difference. These graphics appear in supplementary material to this paper.

Derivation of Suitability Indices

It has been frequent practice to present the value of an environmental attribute to a species in a habitat suitability index, as demonstrated by its application to more than 50 fish species (http://el.erdc.usace.army.mil/emrrp/emris/emrishelp3/list_of_habitat_suitability_index_hsi_models_pac.htm). Suitability indices are hypothetical models, which are typically developed from a review and synthesis of existing information on the established use of a resource by that species. The relationship is scaled to produce an index of habitat suitability on a scale between 0 (unsuitable habitat) and 1 (optimally suitable habitat) (see Weinstein 1986). Guay et al. (2000) utilized affinity studies to develop suitability indices for juvenile Atlantic salmon, which they referred to as "preference indexes." We largely follow that approach by employing average use-to-availability ratios across months and years for each attribute segment and life stage to assess environmental factor suitability for delta smelt. But Guay and his colleagues utilized the maximum score from the use-to-availability ratio to scale remaining ratios in other segments, while we used the ratio of the use to availability of a habitat attribute or 1, which ever was less, in an attempt to differentiate suitable environmental attribute ranges (that is, those with a suitability index values equaling 1) from ranges less suitable. In so doing, we recognize that expressed preference or aversion by a species to a specific environmental factor and condition is relative – individuals may actually inhabit a location because conditions there are "better" than at alternative locations, not necessarily because the location offers environmental conditions that might be described as optimal, good, or even adequate. Rather than producing peaked functions similar to those presented by Guay et al., our approach produces an attenuated (flatter) response, more representative of the response functions that might be inferred from historical distributions of fish and environmental conditions in the Delta (Pardue 1983, Weinstein 1986, Stier and Crance 1985). To obtain values for the entire range of an attribute with continuous values, we used linear interpolation between the index values at the midpoints of each segment.

Development of numerical indexes for habitat quality

An indication of the overall suitability of prevailing environmental conditions for delta smelt at any geographic location (l) and any point in time (t) may be derived by calculating a Habitat Suitability Index (HSI), which is the geometric mean of suitability indices for multiple individual attributes (S_i) (Brown et al. 2000, Guay et al. 2000), with:

$$HSI_{lt} = \Pi S_{ilt}$$

HSI values can then be aggregated over space and time to enumerate the quality of habit in a region or over time. We believe the multiplicative nature of this model is appropriate and important. A multiplicative, rather than additive model provides that any one attribute, if at a sufficiently bad level will cause the HSI score to be close to zero. For example, a site with water that at lethal temperatures will be uninhabitable, even if there is ample food.

To allow for the possibility that habitat attributes may not be of equal importance in determining habitat quality, we followed the approach of Guay et al. (2000), and specified a functional form utilizing a weighted geometric mean of attributes, offered as:

$$HSI_{lt} = \alpha \Pi S_{ilt}^{\beta i}$$

We calculated the weights, β_i, by regressing the suitability values in log form against the log of the percentage of delta smelt at a given survey station. A value of 0.01 was added to time series that included zero values to allow logarithmic calculation. We chose to use the relative distribution of delta smelt, rather than absolute densities, to correct for inter-annual variation in abundances. We use the results of the multiple regression analysis both to identify significant attributes and to calculate a weighted HSI for each observation.

Spatial Depictions

Having identified environmental variables that appear to influence the distribution of delta smelt, the final element of the study was to identify how frequently environmental attributes occur in ranges that may be less than adequate, and where these circumstances occur, to suggest an appropriate type of restoration activity and location for a next level of management planning consideration.

We calculated the frequency with which attributes were less than adequate (that is, exhibited suitability index values in an aversion range) for salinity, turbidity, temperature, and prey density. We also identified locations where water depth was considered less than adequate (using estuary-wide bathymetric data) or where wetlands could be considered too distant. This enabled us to identify areas for potential channel modification and wetlands restoration. We developed criteria for candidate restoration sites where elevations approximate sea level (to utilize tidal processes without undue earthwork) or areas where other environmental attributes frequently occur in adequate ranges (to increase the likelihood of use by the species). We did not attempt to evaluate any potential sites in Suisun Marsh, because we do not have the detailed understanding of the hydraulic connectivity between tidal marshlands and main channels that is needed for rigorous evaluation.

On terminology

Acknowledging that the *de rigueur* terms used to convey "preferences" by organisms for essential resources, other environmental attributes, and landscape circumstances tend to default to value judgments -- environmental conditions are sometimes described as "optimal," or as near anthropomorphisms, wherein conditions are often referred to as "desirable" -- we have restricted this presentation to a purposefully neutral terminology. We describe delta smelt as showing *strong affinity* or *strong aversion* for environmental attribute conditions where survey returns indicate that the difference between delta smelt occurrences in a range segment and availability of that range segment in the estuary is significantly different from zero at the 90% level of confidence. Environmental conditions in areas to which delta smelt show strong affinity are considered *suitable;* conditions where delta smelt exhibit a strong aversion are *inadequate.* Where delta smelt exhibit weak affinity, areas are referred to as *adequate.*

RESULTS

Affinity Analyses

Delta smelt associations with seven environmental attributes of (or resources in) the estuary for five life stages during six sampling periods are presented as ranges of conditions in Table 4 and as histograms in Supplementary Figures S1-S7. These seven attributes can be inferred to contribute to delta smelt habitat – turbidity, salinity, temperature, food availability, sub-surface depth, extent of shallow water, and distance to large wetlands. Affinity studies for water body type, water body width, and substrate at spawning revealed no notable relationships that appear to inform habitat restoration. Delta smelt life stages are described as expressing affinity for a range of conditions for each environmental attribute, where the attribute or resource use or co-occurrence (the height of the red column in the supplementary histograms) exceeds that of relative attribute or resource availability (the height of the blue column with which it is paired). Delta smelt are averse to circumstances in which that relationship is reversed. Differences between the paired columns are depicted with green dots bracketed by a 90% confidence interval and referenced by the right axis. Life stage-specific affinities and aversions for the suite of environmental attribute conditions can be summed to shape a multi-dimensional description of delta smelt habitat, which can be used to inform habitat restoration efforts targeting delta smelt. A multi-dimensional "habitat space" emerges from pairing distribution data for each delta smelt life stage, with temporally appropriate data on each environmental attribute.

Sub-juvenile delta smelt are sampled while dispersing from shallow spawning areas to the open water areas in which they then feed and grow. Having less-developed swimming abilities, they do not express associations with environmental attributes as closely as they appear to in later life stages. Sub-juveniles do express a strong affinity for moderate turbidity (20-40 cm) (Figure S1a). And, while sub-juveniles are frequently found in near-freshwater conditions typical of spawning areas (Figure S2a), they are tolerant of salinities up to 4000 Ec. Water temperatures are rarely in the ranges that might induce stress in this life stage, but sub-juveniles seem to avoid waters in excess of 22 degrees C (Figure S3a). No consistent pattern of sub-juvenile distribution emerges across the range of bathymetric characteristics in the estuary, although strong affinity exists for water deeper than 7m (Figure S5a), and at least a limited area (5-20 ha) of shallow-water circumstances (Figure S6a). A requirement for channel complexity – essentially deep channels that meander through tidal marshlands – presumably is consistent with conditions that were present in the pre- settlement estuary. No strong affinity is expressed by sub-juveniles for prey density (Figure S4a), perhaps reflecting two factors -- sub-juveniles are a life stage in transit, and there may be a complex interaction between prey and predators that affects copepod densities, which is poorly accounted for in the available data. While a strong affinity by delta smelt for areas supporting greater prey density is not demonstrated, there is an affinity for areas in (close) proximity to wetlands (Figure S7a), which becomes more evident in later life stages.

For *juvenile delta smelt*, a strong affinity exists for turbid water less than 40cm Secchi depth (Figure S1b and S2c). Juveniles demonstrate an affinity for waters with salinity up to 8000 Ec (Figures S2b and S2c). They exhibit a strong aversion to water greater than 22 degrees C and are rarely found in circumstances exceeding 23 degrees C (Figures S3b and S3c). An affinity for water depth more than 7 m (Figure S5b and S5c) and for adjacent shallow areas exceeding 100 ha in extent is apparent (Figures S6b and S6c). The primary area where this suitable condition occurs is in Grizzly Bay; a large area of shallow water into which (presumably) nutrient-rich water from Montezuma Slough empties, providing a food source to a life stage with a not yet fully developed swimming capacity. An affinity for prey densities exceeding 250 individual copepods per m^3 is pronounced in juvenile delta smelt (Figure S4b), as is an affinity for areas within 2 km of wetlands (Figure S7b and S7c). Juveniles appear to express a strong aversion for locations that support high prey densities -- likely an anomaly reflecting the presence of higher prey densities in the south Delta at times when prevailing turbidity or temperature conditions there limit occupancy by delta smelt.

Sub-adult delta smelt appear to be tolerant of a wider range of environmental conditions than earlier stages, likely due to the need for that life stage to cope with variability in several environmental attributes in autumn in the estuary. For example, sub-adults are more tolerant of clear water (Figure S1) and fresh water (Figure S2). They exhibit a weak affinity for salinities up to 8000 Ec, not expressing strong aversion until salinity exceeds 20000 Ec (Figure S2d), twice the salinity level at which aversion is shown by juveniles. Few sub-adults are found in water exceeding 23 degrees C (Figure S3d). Sub-adults show a strong affinity for water 7-9 m in depth (Figure S5d) and for situations where limited shallow water areas (5-20 ha) exist nearby (Figure S6d), reflecting a continuing association with complex bathymetry. A strong affinity for prey density is not exhibited by sub-adult delta smelt until copepod density exceeds 1000 per m^3 (Figure S4d), perhaps reflecting increased food requirements at this life stage. Sub-adults are found close to larger wetland areas, with strong affinities expressed for locations less than 2km from them (Figure S7d).

The *pre-spawning adult delta smelt* that are found predominately in survey samples taken in January and February, are presumably taken while dispersing to spawning areas (Hamilton and Murphy in press). While they exhibit affinities and aversions, few are as strong as displayed by other life stages. An affinity for turbidity is exhibited in the 20-30 cm Secchi-depth range segment (Figure S1e). The affinity range for salinity is 1000 to 8000 Ec (Figure S2e), with an aversion to freshwater (that is, less than 200 Ec). There appears to be no influence of water temperature on the distribution of pre-spawning adults (Figure S3e). Affinity exists for situations adjacent to limited shallow water circumstances (5-20 ha) (Figure S6e). An affinity for depth conditions appears shift to waters 5 to 6 m deep (Figure S5e), perhaps reflecting dispersal to spawning areas in shallower situations. Pre-spawning adults express an affinity for locations with densities of copepods in the range of 250 to 1000 $/m^3$, which is an affinity range lower than observed in previous life stages but locations with copepods at $1000/m^3$ are rare at this time of the year (hence pre-spawning adults exhibit an affinity for the highest prey densities available). An affinity for locations in proximity to wetlands is strong; highest with wetlands in the range of less than 250 meters distant (Figure S7e), suggesting that wetlands may not only be important for food production, but that they also provide some essential conditions for reproduction.

Spawning adults sampled in trawl surveys number the fewest of all life stages. Since the reduction in abundance from pre-spawning to spawning adults is far greater than would be expected due to natural attrition, it is likely that the spawning adults are moving away from the monitoring sites. The few spawners sampled and the truncated duration of the Spring Kodiak Trawl makes it difficult to identify the range of suitable environmental attributes, and, as with other fishes, it might be assumed that spawning areas exhibit attribute conditions that are suitable for the eggs and larvae to come. Spawning adults do express strong affinity for turbid water (20-30 cm Secchi depth), and avoid clear water (greater than 50 cm Secchi depth) (Figure S1f). Interestingly, spawning adults exhibit an aversion to very fresh water (Ec less than 200) (Figure S2f) despite the common description of spawning adults as moving to fresh water to spawn. As with pre-spawning adults, temperature seems to play no apparent role in the distribution of fish at this life stage (Figure S3f); likewise the area of shallow water seems to have no bearing on distribution (Figure S6f), although there is an association with water 5 to 6 meters deep (Figure S5f). Spawning adults avoid areas with little food ($<100/m^3$) (Figure S4f), and express an affinity for waters within 0.25 km and 1 to 2 km of large wetlands (Figure S7f).

Habitat Suitability

Given the purpose of this study -- to identify areas that should benefit from restoration efforts targeting delta smelt and to identify particular management actions at specific sites -- we focus on the areas where physical and biotic conditions are frequently unsuitable, allowing planners to exclude those areas, and in so doing, identify residual areas that may be suitable for physical and biological restoration actions.

Maps illustrating the distribution of categorical environmental variable conditions – turbidity, salinity, temperature, prey density, water depth, extent of shallow water, and distance to large wetlands (Figures 2-13) -- illustrate in a spatially explicit format the extent to which sub-areas of the estuary are inadequate or unsuitable for delta smelt (and see Table 4 for supporting range values).

The habitat suitability index curves for turbidity (Figure S8) depict a generally consistent relationship for all life stages: water with a Secchi depth of 10 to 35 cm represents suitable habitat; that range can be extended up to 55 cm Secchi depth in the fall when the adults begin to move to spawning areas. During June and July, the water in the central and south Delta frequently exhibits Secchi depth greater than 50 cm, making much of that area too clear (not sufficiently turbid) to be suitable for delta smelt (Figure 2). At the same time conditions in the area from Liberty Island, east and up the lower Sacramento River, and west in the lower Napa River rarely experience unsuitable turbidity conditions. In the fall, areas of the estuary with turbidity frequently in a suitable range are reduced in extent (Figure 3), with suitable turbidities frequently being found only in the northern portion of

Suisun Bay, Montezuma Slough, areas around the Sacramento-San Joaquin rivers confluence, and the Sacramento ship channel.

Very fresh water (that is, water less than 200 Ec) is not suitable for any life stage of delta smelt, but delta smelt are found in a wide range of salinities (Figure S9), with the range varying by life stage. Subjuveniles occur in salinity of up to 4,000 Ec; suitable conditions for juveniles includes salinities up to 8,000 Ec, for sub-adults up to 12,000 Ec, and spawning and pre-spawning adults up to 8,000 Ec. Consequently, the estuary can be too fresh in certain places (Figures 4 and 5) and too saline in other places (Figures 6 and 7) to be suitable for delta smelt. Between these limits in the west and east extremes of the estuary, delta smelt persist in diverse circumstances. Suisun Bay and Montezuma Slough rarely experience water conditions that are too fresh in June and July, whereas the lower Sacramento River and lower San Joaquin River, upstream of the confluence with Old River, frequently experience water that may be too fresh for delta smelt (Figure 4). In the fall, only the north Delta above Rio Vista and the east Delta offer conditions that may be too fresh for delta smelt (Figure 5). In June and July, water conditions in the far western portion of Suisun Bay can be too saline, hence not suitable for delta smelt (Figure 6). Salinity levels increase in the fall, but the tolerance of then-older delta smelt to salinity also appears to increase. The net effect is that a portion of western Suisun Bay may be too saline to be suitable for delta smelt (Figure 7).

Delta smelt exist in open water up to 22 degrees C, beyond which suitability decreases quickly (Figure S10). Temperatures greater than 22 degrees C are common in the south Delta during June and July (Figure 8).

Suitability index curves for prey density (Figure S11) do not indicate that sub-juveniles alter their position in the estuary in relation to prey density. As the fish mature, more frequent delta smelt occurrences are associated with higher prey densities. Habitat for juvenile and older life stages appears to require prey densities exceeding 250/m3. Average prey density does not correlate well with the average distribution of delta smelt, suggesting that prey availability and delta smelt occurrences should not be considered on a coincident temporal basis. That noted, there are areas within the Delta that frequently exhibit prey at densities sufficient to provide suitable habitat for delta smelt. Copepod densities in June and July are highest in the south Delta (Figure 9), but these areas frequently have other attributes in ranges that are unsuitable for delta smelt. But areas of the central Delta with frequently higher prey densities exist. Conversely, there are areas within the Delta typically inhabited by delta smelt that are frequently food limited; moreover data suggest that wide areas of the estuary exhibit limitations on food availability in the fall (Figure 10).

The depth requirements for delta smelt occupancy appear to differ during the species' life history and reflect an aversion to both shallow- and deep-water circumstances during much of the species' life cycle. Delta smelt express strong affinities for waters of certain depths, 50% of juveniles and sub-adults are found in water 7 to 9 meters deep from July through November. And yet, in early July, delta smelt show strong aversions for water just a couple of meters shallower; resulting in suitability index curves that are somewhat U-shaped for sub-juveniles and juveniles (Figure S12). Channels in north Suisun Bay and Montezuma Slough include sites with high densities of delta smelt, but also extensive channels with insufficient depth (Figure 11).

The affinity results for areas of shallow water suggest that, for most delta smelt life stages, the presence of at least limited areas of shallow water is an important element of habitat. More than half of delta smelt sampled, from juveniles in the summer through to pre-spawning adults in the winter, are drawn from areas with 5 ha to 20 ha of shallow water within one kilometer of the survey site (Figure S13). While the availability of such circumstances is common in the estuary (Figure 12), some areas could benefit from targeted rehabilitation for that attribute. Such projects may be readily and efficiently combined with wetland restoration efforts to provide significant landscape modification.

The affinity studies identified proximity to large wetlands as an important determinant of delta smelt occupancy of open water circumstances. Suitability index curves (Figure S14) show elevated occupancy by multiple life stages in areas of open water up to 4 km from emergent wetlands. For sub-adults and pre-spawning adults the criterion is 2 km. Although extensive wetlands are widely distributed throughout Suisun Bay, Suisun Marsh, and adjoining waters, they are sparsely distributed and limited in extent throughout most of the rest of the estuary (Figure 13).

Significance of environmental attributes

The maps that depict the frequency with which individual physical and biotic attributes are inadequate indicate that the estuary is both spatially and temporally complex and variable. In an effort to determine those environmental attributes that may be relevant in restoration planning – versus those that may essentially be redundant – in a multivariate context, we first derived suitability index curves (presented in supplementary figures S8-S14) from the results of the affinity analyses (Figures S1-S7). Next, we regressed the suitability index values for the seven habitat attributes against the relative distribution of delta smelt.

When prey density is excluded from the analysis, the results indicate that turbidity, salinity, and average water depth influence the distribution of delta smelt at all life stages (Table 5). Temperature is a significant determinant of distribution for sub-juvenile and juvenile life stages. Distance to wetlands is significant at juvenile and sub-adult life stages. The area of shallow-water circumstances is significant for juveniles in mid summer (based on Summer Tow-net survey data) and for pre-spawning and spawning adults.

When copepod prey density is included in the analysis (Table 6), prey density is significant only for the juvenile life stage during June and July (based on 20mm data), and the pre-spawning life stage. The coefficient for prey density has a negative sign for sub-juveniles and sub-adults, possibly due to collinearity with other variables. Turbidity is significant at all life stages. Salinity is significant at all but the spawning life stage. Average depth, temperature, and distance to larger wetlands (> 100 ha) are significant for sub-juvenile,

juvenile and sub-adult life stages. Area of shallows is significant for juveniles in mid summer (based on Summer Tow-net Survey data) and for pre-spawning adults.

To identify landscape areas that are most likely to host successful restoration programs, we summarize the water quality attributes (turbidity, salinity and temperature) into an average HSI for each station. The HSI was derived from a weighted geometric mean of the suitability index values for the attributes, utilizing the coefficients from Table 5 as the weights. We depicted the average value for each station geographically both for juveniles in the 20 mm Survey (Figure 14) and pre-spawning adults in the Spring Kodiak trawl (Figure 15). These figures indicate that areas in the vicinity of Suisun Marsh, at the confluence of the Sacramento and San Joaquin rivers and in the north Delta have the highest geometrically weighted average HSI values for water-quality environmental attributes, and should be viewed as representing potential priority target areas for habitat restoration efforts.

Restoration Guidance

The results presented in Tables 5 and 6 indicate that modification of channel depth or restoration of emergent wetlands (tidal marsh, freshwater marsh, and riparian strands) could substantively improve the suitability of environmental conditions for delta smelt at locations where other environmental attributes are frequently in suitable ranges. The geographic distribution of areas that are most likely to benefit delta smelt from environmental restoration (habitat improvement) efforts is provided in Figure 15. We suggest that these types of maps (at finer resolution) can assist in establishing priorities for early-term projects where habitat suitability for delta smelt can be enhanced through improvement focused on a select environmental attribute. Examples of potential project sites in priority target areas are presented in Figure 16 (for channel modification and wetlands restoration).

DISCUSSION

Survey returns for multiple life stages of delta smelt were analyzed with time-series data for several environmental factors that contribute to the extent and quality of its habitat in an effort to provide guidance to planned restoration efforts, including those under the ambitious Bay-Delta Conservation Plan. The physical and biotic conditions associated with delta smelt presence are multi-dimensional and the suitability of environmental attribute conditions vary with life stage. Based on analyses using trawl survey data, delta smelt demonstrate an affinity for certain environmental conditions that differ significantly from the frequency with which those conditions occur in the estuary. Delta smelt occupy a continuum of suitable areas of the estuary, and appear to avoid (are averse to) areas of the estuary with environmental attributes in less than adequate ranges. The affinity analyses indicate that different portions of the Delta exhibit diverse conditions for seven environmental variables that contribute to habitat extent and quality for delta smelt. Different sub-regions of the estuary and local areas within those sub-regions vary in their suitability for delta smelt, and do so in discordant patterns.

The results from the analyses in this study facilitate identification of areas of the Delta that experience ranges of environmental conditions that are acceptable and unacceptable to delta smelt. Maps of the distribution of delta smelt in the estuary offer insights into delta smelt habitat requirements, suggesting that environmental (factor) suitability exists on two spatial scales that are salient to planning for habitat restoration. At a broad geographic scale, from many kilometers to the entire Delta, patterns of spatial variation in water-quality factors indicate that large areas of the estuary, especially in south and southeast Delta are frequently unsuitable for delta smelt. At a narrower geographic scale, several kilometers and below, and within Delta areas that experience water-quality conditions that very frequently are suitable for delta smelt, site-specific differences in water-body and channel morphology, and proximity to emergent wetlands, offer a mechanistic explanation for contemporary patterns of delta smelt distribution. Considering both spatial scales in restoration project site selection and prioritization should enhance the prospects for success in establishing or reestablishing delta smelt occupancy in new or formerly occupied areas of the Delta.

Three factors related to water quality -- turbidity, salinity, and temperature -- while alone not competent to characterize the habitat space available to delta smelt, contribute to defining the spaces available for habitat restoration actions targeting delta smelt (see Bennett 2005). Where one or more of these factors frequently fall outside of the range suitable for delta smelt, habitat restoration efforts are likely to fail to provide the full complement of ecological conditions necessary to support delta smelt. In the summer and fall, as delta smelt are feeding and growing in anticipation of spawning, the fish's range in the estuary is located between water that is too saline in the west (west of Suisun Bay) and too fresh in the east (in the lower Sacramento River near and north of Rio Vista, and south across the Cosumnes, Mokelumne, and San Joaquin rivers inputs to the estuary), essentially the entire tidally influenced Delta, along with the lower Napa River (Merz et al. 2012, Murphy and Hamilton 2013). Salinity constrains delta smelt to the Sacramento-San Joaquin Delta and adjacent Suisun Bay and Suisun Marsh, but only to the extent that a portion of western Suisun Bay may not provide suitable salinity conditions in low Delta-outflow circumstances, especially late in very dry years; and, areas that experience purely freshwater circumstances above Sacramento on the Sacramento River appear not to be consistently occupied by delta smelt.

While habitat restoration efforts targeting delta smelt, therefore, largely appear not to be geographically constrained by salinity conditions, inter-seasonal turbidity and temperature regimes serve to differentiate the low-salinity zone of the Delta into areas that are often occupied and can be occupied by delta smelt, and areas that experience conditions adverse to the fish. Southern and eastern portions of the estuary are frequently too clear in the fall and too warm in the summer to provide year-round habitat for delta smelt, even if other physical and biotic conditions are suitable for the fish. The finding that water clarity frequently is too high (turbidity too low) and water temperature too high in certain areas should steer habitat restoration planning and actions to elsewhere in the Delta. In addition, neither turbidity nor temperature can be readily addressed through targeted management actions in the estuary -- for example, reduced turbidity in the San Joaquin River and southeastern estuary in part may be resulting from sediment impoundments behind tributary dams and hardened river channels that are located far from the conservation planning area. Therefore, for purposes of near-term conservation planning, those areas should be at best low-priority sites for delta smelt habitat restoration. Furthermore, anticipated trends in environmental factor conditions may render additional portions of the estuary unsuitable for delta smelt; for example, water temperatures in the estuary can be anticipated to rise, expanding the footprint of conditions that are unsuitable for the fish (see Cloern et al. 2011). Nonetheless, a wide swath of the estuary, from Suisun Bay and Suisun Marsh in the west to Cache Slough and the Sacramento ship channel in the east, appears to consistently experience turbidity and temperature conditions suitable for delta smelt.

The physical and biotic conditions required for delta smelt presence, which collectively serve as a proxy for delta smelt habitat, are multi-dimensional. The findings presented here indicate that habitat restoration efforts for delta smelt must consider, on the one hand, the broad ranges in, and geographic patterns exhibited by, water turbidity, salinity and temperature conditions, which vary by life stage; and, on the other hand, the availability of adequate supplies of its copepod prey, the presence of which at least in part is determined by landscape conditions. The trophic linkages between the production of the phytoplankton that serve as the primary foods for the zooplankton (copepods) that are the primary prey of delta smelt are well established (Kimmerer and Orsi 1996, Nobriga 1998). And, the clear relationships between wetlands and primary productivity in adjacent waters (see Alpine and Cloern 1992) has prompted a generally recognized need for ecosystem rehabilitation at the land-estuary interface to enhance the “production, transport, and transformation of organic matter that constitutes the primary food supply to the base of the food web" (Jassby and Cloern 2000). Although "the production and distribution of phytoplankton can be highly variable within and between nearby habitats of the same type, due to phytoplankton sources, sinks, and transport" (Lucas et al. 2002), the restoration of tidal wetlands has been identified as the primary means for enhancing habitat for delta smelt (BDCP 2013). Combine the findings from the habitat affinity analyses for channel (or embayment) depth, area of adjacent shallow circumstances, and distance to emergent wetlands, and a target condition for site-specific habitat restoration emerges. Delta smelt show an affinity for areas with heterogeneous bathymetry where deep channels are found in proximity to shallower circumstances and emergent wetlands, the latter land-cover type providing for greater primary production and abundance of prey used by delta smelt.

Conservation planners seeking to implement projects that have higher likelihoods of success in producing habitat conditions that are associated with delta smelt presence might view higher-priority projects as those that fall within the existing geographic range of delta smelt and require minimal redirection of resources available for conservation. The copepod prey that supports delta smelt frequently appears to be limiting in early summer in a number of locations in the northern portions of the estuary, and in Napa River and its estuary, especially in autumn months. It is likely that targeted tidal marsh and freshwater marsh restoration (and creation) in northern portions of the estuary would serve to enhance the availability of food, as well as access to spawning areas. More specifically, it appears that restoration of large emergent wetlands in eastern Montezuma Slough, the Sacramento River below Isleton, and the Cache Slough area could improve habitat availability and conditions for delta smelt. Furthermore, it appears that habitat conditions in areas in north Suisun Bay and Montezuma Slough could be improved with channel modifications; and, increasing the availability of areas of shallow water in Grizzly Bay, Suisun Bay, and some stretches of the lower Sacramento River could improve habitat in those areas for young delta smelt.

The results of the affinity analyses presented here appear to have immediate application. The proposal to restore habitat for delta smelt in the BDCP is embedded in a conservation strategy that follows a biological opinion produced by the U.S. Fish and Wildlife Service in 2008, which determined that ongoing water export operations from the estuary by state and federal pumping projects likely jeopardize the continued existence of the delta smelt. While recognizing that a broad array of physical and biotic factors provide essential resources and contribute to habitat for delta smelt, the Service chose to use the location of the low-salinity zone in the estuary as a surrogate measure of the extent and quality of habitat for delta smelt. The BDCP is following the agency lead by employing the extent of the low-salinity zone, which expands during periods of high outflow through the estuary, as proxy for the summed environmental attributes that must co-occur to allow for the presence delta smelt. The plan concludes that increased suitable habitat for delta smelt becomes available when the lower-salinity portions of the Delta's low-salinity zone is particularly expansive, and it measures benefits to delta smelt and program success as a function of a salinity-habitat relationship (BDCP 2013). But, the mapped analyses presented here illustrate potential trade-offs that may be important in restoration planning decisions. For example, water management decisions that contribute to shifting the location of the low-salinity zone in the Delta to the west (downstream, as proscribed under certain "water-year" circumstances in a recent delta smelt biological opinion [USFWS 2008]) may improve habitat conditions in some parts of the estuary, but at the same time render other areas less suitable or unsuitable to delta smelt during portions of the year.

The location and extent of the low-salinity zone in the estuary is a "coarse filter" (see Noon, et al. 2007) for purposes of conservation planning for delta smelt; providing little guidance to site-specific restoration efforts beyond setting wide bounds on the estuary landscape within which directed management actions should occur. As the maps accompanying the affinity analysis clearly indicate, the location of the low-salinity zone is a weak predictor of the presence of delta smelt at the scale that habitat restoration for the species will be carried out. In the zone where delta are currently found, landscape cover and bathymetric factors appear to be the best predictors of the presence of delta smelt and may be the most effective surrogate environmental attributes for, or environmental indicators of, habitat for delta smelt habitat.

The validity of these findings is, of course, related to the reliability of the survey data on delta smelt and the accompanying environmental variables upon which the affinity analysis was based. The longer time-series data sets on delta smelt that were used in this study are derived from trawler-based surveys of fishes taken from the estuary's open waters; few samples in shorter time-series are available from across the bathymetric gradient occupied by delta smelt. Water-quality data were taken concurrently with fish samples, hence are similarly limited. Zooplankton samples are largely collected independently, and suffer from degrees of spatial and temporal discordance with delta smelt samples. Both the fish survey and environmental factor data sets are derived from studies that unfortunately are limited in geographic footprint, missing data from essential geographic locations on the estuary's periphery, where range limits of environmental attributes are commonplace. These shortcomings in the database for the estuary will need to be rectified in any performance measure-based monitoring efforts that are developed to accompany restoration efforts. But, given the ambitions of this study and its accompanying information needs, the extent and resolution of the data might fairly be viewed as adequate. At the same time, the urgency for restoration actions within the estuary to facilitate the recovery of protected native fishes cannot wait for improved monitoring programs -- restoration must proceed utilizing the best currently available data.

The absence of well-resolved environmental variables, beyond the seven used in the habitat affinity analyses carried out here, has implications to restoration planning. Geographic patterns of predation on delta smelt are not known, but the marsh-edge conditions to which delta smelt show a strong affinity host high-densities of non-native fish species, many of them documented to prey on delta smelt (Feyrer 2004, Sommer et al. 2004). Cohen and Carleton (1998) found in the San Francisco estuary up to 97% of the total number of organisms and 99% of the biomass to be alien invasive species, leading Grimaldo et al. (2004) to opine that management efforts should "create or restore wetlands that only flood during winter and spring, the period when native fishes spawn and recruit into the estuary." Clearly restoration actions that might benefit predators over the imperiled delta smelt should be avoided.

Contaminant loading is a lead concern in the conservation of delta smelt and other native fish species in the Delta and adjacent areas of the estuary. Concerning the latter, one contaminant that has been recorded in ecologically relevant concentrations in areas occupied by delta smelt is ammonium. It is released from municipal wastewater treatment facilities, creates imbalances in nitrogen-phosphorus ratios and contributes to increases in chemically reduced nitrogen concentrations that impair primary productivity (Dugdale et al 2007) and is associated with food web disruption, including reduced availability of diatom species that serve as prey for the zooplankton upon which delta smelt depend (Glibert et al 2011). Changes in nutrient ratios and nutrient concentrations, which are correlated with elevated ammonium, create conditions conducive to invasions of rooted aquatic vegetation, toxic blue-green algae, and bi-valve mollusks (Glibert et al 2011), all habitat quality-compromising stressors that are thought to have direct and indirect deleterious effects on delta smelt abundance. Otherwise well-crafted restoration efforts in locations that could be expected to support delta smelt, could well fail or under perform due to local contaminant conditions that could not be considered in this study.

Environmental variables in addition to those addressed in this habitat affinity analysis need to be considered by restoration planners before location-specific actions are taken. But, the approach taken here in assessing estuary conditions for delta smelt uses environmental variables on water quality, food availability, morphological water-body and channel characteristics, and proximity to wetlands to effectively describe the multidimensional space that supports much of the current distribution of multiple delta smelt life stages. Using a diversity of estuary attributes in the affinity analysis allows for a comprehensive characterization of conditions that are acceptable, and conversely appear to be undesirable, to delta smelt. The environmental variables considered here shed light on resource conditions that appear to determine the presence and absence of delta smelt at a range of spatial scales. Guidance that can be gleaned from this study for future environmental restoration efforts targeting delta smelt includes, not just identification of areas of the estuary that should be avoided because they are unlikely to support delta smelt regardless of restoration actions, but also direction toward areas where actions are likely to succeed in enhancing delta smelt productivity, and identification of the restoration and enhancement measures necessary to generate and sustain that productivity. This study can be used as a helpmate in identifying and locating candidate restoration actions; where preferred or highest-priority projects are those that fall within the existing geographic range of delta smelt, require minimal redirection of other resources, and can be implemented where the geographic extent of actions needed is limited – in other words, where more focused restoration efforts targeting fewer environmental attributes (habitat factors) are addressed on landscape areas adjacent to locations that already support delta smelt.

That recommendation married with spatially explicit observations from the affinity analyses and mapped data can form the foundation for a strategic approach to restoration site selection and site-specific management planning. All restoration projects require direct engagement of resources, frequently redirection of resources away from other beneficial applications, which inevitably has both ecological and economic consequences. In that light we believe it would not be prudent to invest in restoration actions in areas that are determined now or projected to be deleteriously impacted in the future by water quality variables that fall out of the range of suitability for delta smelt. The creation of habitat, or the restoration of areas that exhibit attributes within affinity ranges for delta smelt (but are currently unsuitable) inside the contemporary range of the fish, should be those most likely to contribute to enhancing the fish's productivity and recovery.

Literature Cited

Alpine, A.E. and J.E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography 37:946-955.

Armor, C., R. Baxter, W. Bennett, R. Breuer, M. Chotkowski, P. Coulston, D. Denton, B. Herbold, W. Kimmerer, K. Larsen, M. Nobriga, K. Rose, T. Sommer, and M. Stacey. 2005. Interagency Ecological Program Synthesis of 2005 Work to Evaluate the Pelagic Organism Decline (POD) in the Upper San Francisco Estuary. Interagency Ecological Program. Available online at: http://www.science.calwater.ca.gov/pdf/workshops/POD/2005_IEPPOD_synthesis_report_111405.pdf

Bajer, P.G. and M.L. Wildhaber. 2007. Population viability analysis of lower Missouri river shovelnose sturgeon with initial application to the pallid sturgeon. Journal of Applied Ichthyology 23:457-464.

Baskerville-Bridges, B., J. Lindberg, and S.I. Doroshov. 2004. The effect of light intensity, alga concentration, and prey density on the feeding behavior of delta smelt Hypomesus transpacificus larvae. In: Feyrer F., L.R. Brown LR, R.L. Brown, J.J. Orsi, editors. Early Life History of Fishes in the San Francisco Estuary and Watershed. Bethesda (MD): American Fisheries Society Symposium 39: 219-228.

Baxter, R., R. Breuer, L. Brown, M. Chotkowski, F. Feyrer, M. Gingras, B. Herbold, A. Mueller-Solger, M. Nobriga, T. Sommer, and K. Souza. 2008. Pelagic Organism Decline Progress Report: 2007 Synthesis of Results. Available online at: http://www.science.calwater.ca.gov/pdf/workshops/POD/2007_IEPPOD_synthesis_report_031408.pdf

BDCP. 2013. http://baydeltaconservationplan.com/Home.aspx

Bennett, W.A. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. San Francisco Estuary and Watershed Science. Volume 3, Issue 2 (September), Article 1. Available online at: http://repositories.cdlib.org/jmie/sfews/vol3/iss2/art1

Brooks, M.L., E. Fleishman, L.R. Brown, et al. 2012. Life histories, salinity zones, and sublethal contributions of contaminants to pelagic fish declines illustrated with a case study of San Francisco estuary, California, USA. Estuaries and Coasts…

Brown, L.R. 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. Environmental Biology of Fishes 57: 251-269. Available online at: http://www.springerlink.com/content/w17n763hl7337802/

Brown, C.L. and S.N. Luoma 1995. Use of the euryhaline bivalve *Potomocorbula amaurensis* as a biosentinel species to assess trace metal contamination in San Francisco Bay. Marine Ecology Progress. Series 124: 129-142.

Cardona L. 2006. Habitat selection by grey mullets (Osteichthyes: Mugilidae) in Mediterranean estuaries: the role of salinity. Scientia Marina 70:443-455.
Available online at:
http://scientiamarina.revistas.csic.es/index.php/scientiamarina/article/viewArticle/96

CDWR. 2007. California State Water Project 2006 Watershed Sanitary Survey Update, Final Report, June 2007. Chapter 4 on file (Key concerns in the Central valley Watershed and the Delta).

Cloern, J.E., N. Knowles, L.R. Brown, et al. 2011. Projected evolution of California's San Francisco Bay-Delta-River system in a century of climate change. PLoS ONE 6(9): e24465.

Cohen A.N. and J.T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555-558.

Connon, R.E., J. Geist, J. Pfeiff, A.V. Loguinov, L.S. D'Abronzo, H. Wintz, C.D. Vulpe and I. Werner. 2009. Linking mechanistic and behavioral responses to sublethal esfenvalerate exposure in the endangered delta smelt, *Hypomesus transpacificus*. BMC Genomics 19:1-18.

Dugdale, R.C., F.P. Wilkerson, V.E, Hogue, and A. Marchi. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. Estuarine, Coastal and Shelf Science 73: 17-29.

Feyrer F. 2004. Ecological segregation of native and alien larval fish assemblages in the southern Sacramento-San Joaquin Delta. Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society Symposium 39:67-79. Available online at:
http://swrcb2.swrcb.ca.gov/waterrights/water_issues/programs/bay_delta/wq_control_plans/2006wqcp/exhibits/append2/doi/doi-33d.pdf

Feyrer, F., M. Nobriga, and T. Sommer. 2007. Multi-decadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 136:1393-1405.

Glibert, P.M., D, Fullerton, J.M. Burkholder, J.C. Cornwell, and T.M. Kana. 2011. Ecological stoichiometry, biogeochemical cycling, invasive species, and aquatic food webs: San Francisco estuary and comparative systems. Reviews in Fisheries Science 19: 358-417.

Grimaldo, L.F., R.E. Miller, C.M. Peregrin, and Z.P. Hymanson. 2004. Spatial and temporal distribution of ichthyoplankton in three habitat types of the Sacramento-San Joaquin Delta. Pages 81-96 in F. Feyrer, L.R. Brown, R.L. Brown, and J.J. Orsi, editors. Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society, Symposium 39, Bethesda, Maryland. Available online at: http://www.iep.ca.gov/AES/Grimaldo_et_al_2004.pdf

Grimaldo, L.F., T.R. Sommer, N. Van Ark, G. Jones, E. Holland, P.B. Moyle, P. Smith, and B. Herbold. 2009a. Factors affecting fish entrainment into massive water diversions in a freshwater tidal estuary: can fish losses be managed? North American Journal of Fisheries Management. 29:1253-1270. Available online at: http://afsjournals.org/doi/abs/10.1577/M08-062.1

Grimaldo L.F., A.R. Stewart , and W.J. Kimmerer. 2009b. Dietary segregation of pelagic and littoral fish assemblages in a highly modified tidal freshwater estuary. Marine and Coastal Fisheries: Dynamics Management, and Ecosystem Science 1:200–217.

Grost, R.T., W.A. Hubert, and T.A. Wesche. 1990. Redd site selection by brown trout in Douglas Creek, Wyoming. Journal of Freshwater Ecology 5:365-371. Available online at: http://library.wrds.uwyo.edu/wrp/90-22/90-22.pdf

Guay J.C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*) Canadian Journal of Aquatic Sciences 57:2065-2075.

Healey, M.C. 2007. Context memorandum: Delta ecosystem. Available online at: http://deltavision.ca.gov/Context_Memos/Environment/Ecosystem_Iteration1.pdf

Hieb, K. and K. Fleming. 1999. Summary chapter. In: Orsi, J., editor. Report on the 1980-1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. Interagency Ecological Program for the San Francisco Estuary Technical Report 63. 503 p.

Hobbs, J.A., W.A. Bennett, and J.E. Burton. 2006. Assessing nursery habitat quality for native smelts (Osmeridae) in the low-salinity zone of the San Francisco estuary. Journal of Fish Biology 69:907–922.

Jassby and Cloern 2000. Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). Aquatic Conservation:Marine and Freshwater Ecosystems 10:323-352.

Johnson, N.K., F. Swanson, M. Herring and S. Greene. 1999. Bioregional assessments: Science at the crossroads of management and policy. Island Press. Covelo, CA.

Karieva, P. M., S. Andelman, D.F. Doak, et al. 1998. Using science in habitat conservation plans. National Center for Ecological Analysis and Synthesis.

Kimmerer, W.J. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science 6(2): Article 2. Available at http://escholarship.org/uc/item/7v92h6fs

Kimmerer, W.J., E.S. Gross, and M.L. MacWilliams. 2009. Is the response of estuarine nekton to freshwater flow in the San Francisco Estuary explained by variation in habitat volume? Estuaries and Coasts 32:375-389.

Kimmerer, W.J. and J.J. Orsi 1996. Changes in the zooplankton of the San Francisco Bay estuary since introduction of the clam *Potomocorbula amurensis*. In San Francisco Bay: The ecosystem. In: Hollibaugh, J.T. ed., Pacific Division, American Association for the Advancement of Science, San Francisco, CA: 403-424.

Lechowicz, M.J. 1982. The sampling characteristics of electivity indices. Oecologia 52:22-30. Available online at: http://www.springerlink.com/content/q5030586v6647874/

Lehman, P.W., S. The, G.L. Boyer, M. Nobriga, E. Bass, and C. Hogle. 2010a. Initial impacts of *Microcystis* on the aquatic food web in the San Francisco Estuary. Hydrobiologia 637:229-248.

Lehman P.W., S. Mayr, L. Mecum, and C. Enright. 2010b. The freshwater tidal wetland Liberty Island, CA, was both a source and sink of inorganic and organic material to the San Francisco Estuary. Aquatic Ecology 44:359-372.

Lindberg, J.C., and C. Marzuola. 1993. Delta smelt in a newly created, flooded island in the Sacramento–San Joaquin Estuary, Spring 1993. BioSystems Analysis Inc. Prepared for California Department of Water Resources, Sacramento, CA. Available online at: http://www.calwater.ca.gov/Admin_Record/C-044803.pdf

Lott, J. 1998. Feeding habits of juvenile and adult delta smelt from the Sacramento-San Joaquin River Estuary. Interagency Ecological Program Newsletter 11: 14-19.

Lucas, L.V., J.E. Cloern, J.K. Thompson, et al. 2002. Functional variability of habitats within the Sacramento-San Joaquin Delta: Restoration implications. Ecological Applications 12: 1528-1547.

Mac Nally, R., J.R. Thompson, W.J. Kimmerer, F. Feyrer, K.B. Newman, A. Sih, W.A. Bennett, L.R. Brown, E. Fleishman, S.D. Culberson, and G. Castillo. 2010. An analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Ecological Applications 20: 1417-1430.

Mager, R.C., S.I. Doroshov, J.P. Van Eenennaam, and R.L. Brown. 2004. Early Life Stages of Delta Smelt. In Feyrer, F., L.R. Brown, R.L. Brown, and J.J. Orsi editors. Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society Symposium 39:169-180.

Maunder, M.N. and R.B. Deriso. 2011. A state–space multistage life cycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt (*Hyposmesus transpacificus*). Canadian Journal of Fisheries and Aquatic Sciences 68:1285-1306.

McGowan, M.F. 1998. Fishes associated with submerged aquatic vegetation, *Egeria densa*, in the Sacramento-San Joaquin Delta in 1998 as sampled by pop nets. Romberg Tiburon Center, San Francisco State University. Unpublished report prepared for the California Department of Boating and Waterways.

McGowan M.F., and A. Marchi. 1998. Fished collected in submersed aquatic vegetation, *Egeria densa*, in the Delta. Interagency Ecological Program for the Sacramento-San Joaquin Estuary Newsletter 11(1):9-10.

McIvor, C., L.R. Brown, and Z. Hymanson. 1999. Shallow water habitat workshop summary. IEP Newsletter 12(1), [np].

Meng L., and S.A. Matern. 2001. Native and introduced larval fishes of Suisun Marsh, California: the effects of freshwater flow. Transactions of the American Fisheries Society 1309:750-765. Available online at: http://afsjournals.org/doi/abs/10.1577/15488659(2001)130%3C0750:NAILFO%3E2.0.CO%3B2

Merz, J.M., S. Hamilton, P.S. Bergman, and B. Cavallo. 2011. Spatial perspective for delta smelt: a summary of contemporary survey data. California Fish and Game 97: 164-189.

Miller W.J., B.F. Manly, D.D. Murphy, D. Fullerton, and R.R. Ramey. 2012. An investigation of factors affecting the decline of delta smelt (*Hypomesus transpacificus*) in the Sacramento-San Joaquin Estuary. Reviews in Fisheries Science 20:1–19.

Monaco, M.E., S.B. Weisberg, and T.A. Lowery. 1998. Summer habitat affinities of estuarine fish in U.S. mid-Atlantic coastal systems. Fisheries Management and Ecology 5:161-171. Available online at: http://www3.interscience.wiley.com/journal/120829574/abstract?CRETRY=1&SRETRY=0

Moyle, P.B., B. Herbold, D.E. Stevens, and L.W. Miller. 1992. Life history of delta smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67-77. Available online at: http://afsjournals.org/doi/abs/10.1577/15488659(1992)121%3C0067:LHASOD%3E2.3.CO%3B2

Moyle PB. 2002. Inland Fishes of California. University of California Press, Berkeley.
National Research Council. 2011. A review of the use of science and adaptive management in California's Draft Bay-Delta Conservation Plan. National Academies Press. Washington, D.C.

Murphy D.D. and S. A. Hamilton. 2013. Eastward migration or marsh-ward dispersal: understanding seasonal movements by delta smelt. San Francisco Estuary and Watershed Science: in press.

Newman, K.B. 2008. Sample design-based methodology for estimating delta smelt abundance. San Francisco Estuary and Watershed Science 6(3).

Nichols F.H., J.E. Cloern, S.N. Luoma, and D.H. Peterson. 1986. The modification of an estuary. Science 231:567-573. Available online at: http://adsabs.harvard.edu/abs/1986Sci...231..567N

Nobriga, M.L. 1998. Evidence of food limitation in larval delta smelt. Interagency Ecological Program Newsletter 11(1): 20-24.

Nobriga, M.L. 2002. Larval delta smelt composition and feeding incidence: environmental and ontogenetic influences. California Fish and Game 88:149-164.

Nobriga, M.L., F. Feyrer, R. Baxter, and M. Chotkowski. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries 28:776-785. Available online at: http://www.iep.ca.gov/AES/Nobriga_etal_2005.pdf

Nobriga, M.L., and B. Herbold. 2009. The little fish in California's water supply: a literature review and life-history conceptual model for delta smelt *(Hypomesus transpacificus)* for the Delta Regional Ecosystem Restoration and Implementation Plan (DRERIP). Available online at: http://www.dfg.ca.gov/ERP/conceptual_models.asp

Nobriga, M.L., T.R. Sommer, F. Feyrer, and D. Fleming. 2008. Long-term trends in summertime habitat suitability for delta smelt (*Hypomesus transpacificus*). San Francisco Estuary and Watershed Science 6: Issue 1 (February), Article 1. Available on line at: http://repositories.cdlib.org/jmie/sfews/vol6/iss1/art1

Noon, B.R., D.D. Murphy, S.R. Beissinger, M.L. Shaffer, and D. DellaSala. 2003. Conservation palnning for US National Forests: conducting comprehensive biodiversity assessments. BioScience 53: 1217-1220.

Norgaard, R.B., G. Kallis, and M. Kiparsky. 2009. Collectively engaging complex socio-ecological systems: Re-envisioning science, governance, and the California delta. Environmental Science and Policy 12: 644-652.

NRC 2011. A review of the use of science and adaptive management in California's draft Bay Delta Conservation Plan. National Academies Press.

Pardue, G.B. 1983. Habitat suitability index models: alewife and blueback herring. U.S. Fish and Wildlife Service FWS/OBS-82/10.58.

Peery, M.Z., S.R. Bessinger, S.H. Newman, B.H. Becker, E. Burkett and T.D. Williams. 2004. Individual and temporal variation in inland flight behavior of marbled murrelets: implications for population monitoring. Condor 106:344-353.

Reed, M.J., H.R. Akcakaya, M. Burgman, et al. 2006. Critical Habitat. In: The Endangered Species Act at thirty. Scott, J.M., D.D. Goble and F.W. Davis. Island Press, Covelo, CA.

Rosenfield, J.A., and R.D. Baxter. 2007. Population dynamics and distribution patterns of longfin smelt in the San Francisco Estuary. Transactions American Fisheries Society 136:1577- 1592. Available online at: http://afsjournals.org/doi/abs/10.1577/T06-148.1

Sommer T.R., C. Armor, R.D. Baxter, R. Breuer, L.R. Brown, M. Chotkowski, S. Culberson, F. Feyrer, M. Gingras, B. Herbold, W.J. Kimmerer, A. Mueller-Solger, M. Nobriga, and K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. Fisheries 32:270-277.

Sommer, T.R., W.R. Harrell, R. Kurth, F. Feyrer, S.C. Zeug, and G. O'Leary. 2004a. Ecological patterns of early life stages of fishes in a river-floodplain of the San Francisco Estuary. Pages 111-123 in F. Feyrer, L.R. Brown, R.L. Brown, and J.J. Orsi, editors. Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society, Symposium 39, Bethesda, Maryland.

Sommer T.R., W.C. Harrell, A. Mueller-Solger, B. Tom, Kimmerer W.J. 2004b. Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. Aquatic Conservation: Marine and Freshwater Ecosystems 14:247-261. Available online at: http://www.iep.ca.gov/AES/Aquatic%20Conserv%20Manuscript.pdf

Sommer, T., F.H. Meija, M.L. Nobriga, F. Feyrer, L. and Grimaldo. 2011. The spawning migration of delta smelt in the upper San Francisco Estuary. San Francisco Estuary and Watershed Science 9(2).

Sommer T.R. and F. Meija. 2013. A place to call home: A synthesis of delta smelt habitat in the upper San Francisco estuary. San Francisco Estuary and Watershed Science: in press.

Stier, D.J., and J.H. Crance. 1985. Habitat suitability index models and instream flow suitability curves: American shad. U.S. Fish and Wildlife Service Biological Report 82(10.88).

Swanson C., T. Reid, P.S. Young, and J.J. Cech. 2000. Comparative environmental tolerances of threatened delta smelt (*Hypomesus transpacificus*) and introduced wakasagi (*H. nipponensis*) in an altered California estuary. Oecologia 123:384-390.
Available online at: http://www.springerlink.com/content/t1440mrxbhn2cwua/

Thompson, J. 1957. Settlement geography of the Sacramento-San Joaquin Delta, California. Dissertation, Stanford University.

Thomson, J., et al. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. Ecological Applications 20:1431-1448.

URS. 2007. Status and Trends of Delta-Suisun Services. Report prepared for the California Department of Water Resources, May 2007.

U.S. Fish and Wildlife Service. 1997. Recovery plan for the threatened marbled murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California.

U.S. Fish and Wildlife Service. 2004. Five-year review of the delta smelt. August 1, 2003. Federal Register 68(148): 45270-45271.

U.S. Fish and Wildlife Service. 2008. Delta smelt biological opinion on the coordinated operations of the Central Valley Project and State Water Project.

U.S. Fish and Wildlife Service. 2013. Draft revised recovery plan for the Pallid Sturgeon (*Scaphirhynchus albus*).

van Geen, A., and S.N. Luoma. 1999. The impact of human activities on sediments of San Francisco Bay, California: an overview. Marine Chemistry 64: 1–6.

Wang JC. 1986. Fishes of the Sacramento-San Joaquin Estuary and adjacent waters, California: A guide to the early life histories. Interagency Ecological Study Program for the Sacramento–San Joaquin Estuary. Technical Report 9. FS/B10-4ATR 86-9.

Weinstein M.P. 1986. Habitat suitability models: inland silverside. U.S. Fish & Wildlife Service Biological Report 82(10.120).

Whipple, A., R.M. Grossinger, D. Rankin, B. Stanford and R. Askevold. 2012. Sacramento-San Joaquin Delta historical ecology investigation: exploring pattern and process. San Francisco Estuary Institute.

Winder, M. and A.D. Jassby. 2010. Shifts in zooplankton community structure: implications for food web processes in the upper San Francisco Estuary. Estuaries and Coasts…

Table 1. *Candidate habitat attributes that may affect the distribution and abundance of delta smelt.*

Aquatic/hydraulic attributes of delta waters

1. Physical water-quality properties (turbidity, salinity, temperature)
2. Chemical water-quality properties (dissolved oxygen, pH)
3. Presence, concentration, absence of contaminants
4. Flow velocity

Biological attributes of the estuary

1. Prey availability (types and densities of food source items)
2. Predation pressure
3. Areal extent, type, and density of aquatic vegetation
4. Presence of *Microcystis*

Physical attributes of the estuary

1. Type of water body
2. Depth of channel/water body
3. Width of channel/water body
4. Extent of proximate shallow water
5. Substrate structure and composition (grain size, organic content)
6. Distance to wetlands

Table 2. *Delineation of life stages used to examine delta smelt affinity for habitat attributes. Monitoring program data used for each life stage description (either fish length or reproductive stage), and months and years of sampling data used in our study are described. Gonadal stages of male and female delta smelt found in spring Kodiak Trawl database were classified by CA Department of Fish and Game (CDFG) following Mager (1986). Descriptions of reproductive stages are available at http:/www.dfg.ca.govdelt/data/skt/eggstages.asp*

	Sub-juveniles	Juveniles	Juveniles	Sub-adults	Mature Adults: Pre-spawning	Mature Adults: spawning
Monitoring Program	20-mm	20-mm	STN	FMWT	Kodiak	Kodiak
Life Stage Distinction	≥ 15, <30mm	30-55 mm	30-55 mm	> 55 mm	Reproductive stages: females 1-3, males 1-4	Reproductive stages: females 4, males 5
Time Period	May-Jun	Jun-Jul	Jun-Aug	Sep-Oct	Jan-Feb	Mar-Apr
Years of data used in this study	1995-2009	1995-2009	1967-2009	1967-2009	2002-2009	2002-2009

Table 3. *Specification of covariates and sources of data for the affinity analyses.*

Attribute	Method of measurement or category list	Source description or derivation
Turbidity	Secchi depth (cm)	IEP[1] Monitoring Programs
Salinity	Electrical Conductivity (Ec)	IEP[1] Monitoring Programs
Temperature	Degrees Celsius	IEP[1] Monitoring Programs
Water body type	Bay-Shoal Bay Channel River Channel Slough	Station in a bay overlying a shoal Station in a bay overlying a channel >5 m deep Station on the Sacramento, San Joaquin or Mokelumne Rivers upstream from their confluence Station on a predominantly anthropogenic, tidally influenced channel
Depth	Average depth within 1 km of station	http://sfbay.wr.usgs.gov/sediment/sfbay/downloads.html http://sfbay.wr.usgs.gov/sediment/delta/downloads.html
Width	Water body width (meters)	GIS (ArcInfo) calculated water body width (meters) based on water boundaries digitized from aerial imagery perpendicular to flow.
Area of shallow water	Area of water less than 2 meters deep within 1 km of station	http://sfbay.wr.usgs.gov/sediment/sfbay/downloads.html http://sfbay.wr.usgs.gov/sediment/delta/downloads.html
Substrate composition (categories)	Rip-rap Cobble-gravel Sand Mud Organic Algal Rooted Vascular	>3/4 rip-rap, <1/3 vegetated over <3/4 rip-rap, <1/3 vegetated cover, cobble-gravel dominant <3/4 rip-rap, <1/3 vegetated cover, sand dominant <3/4 rip-rap, <1/3 vegetated cover, mud dominant <3/4 rip-rap, <1/3 vegetated cover, organic material dominant >1/3 vegetated cover, algae dominant >1/3 vegetated dominant, rooted vascular dominant
Prey density	Density (#/m^3) of juvenile calenoid copepods for the 20mm survey, or adult calenoid copepods for other surveys, at the nearest	IEP Zooplankton Survey

	zooplankton survey station within 5 km of an IEP station	
Distance to wetlands	Distance in meters to tidal estuarine emergent wetlands greater than 100 ha	http://www.fws.gov/wetlands/Data/DataDownload.html http://www.dfg.ca.gov/biogeodata/gis/veg.asp (California Central Valley Wetlands and Riparian GIS, published 1997, processed from 1992-93 data)

[1] The Interagency Ecological Program is a long-standing multi-institutional consortium of state and federal water resources and wildlife agencies that carry out research and monitoring on the estuary's environmental resources. (see -- http://www.water.ca.gov/iep/)

IEP Monitoring Programs -- 20mm Survey: ftp://ftp.dfg.ca.gov/Delta%20Smelt/
http://www.dfg.ca.gov/delta/projects.asp?ProjectID=20mm

Summer Townet Survey
http://www.dfg.ca.gov/delta/projects.asp?ProjectID=TOWNET

Fall Midwater Trawl
http://www.dfg.ca.gov/delta/projects.asp?ProjectID=FMWT

Spring Kodiak Trawl: ftp://ftp.dfg.ca.gov/Delta%20Smelt/
http://www.dfg.ca.gov/delta/projects.asp?ProjectID=SKT

Zooplankton Study
http://www.dfg.ca.gov/delta/projects.asp?ProjectID=ZOOPLANKTON

Table 4. *Affinity ranges for delta smelt for seven environmental attributes in the estuary. This table is a summary of the affinity analyses presented in Appendix A. A "suitable" range depicts conditions where delta smelt demonstrated relative use of an attribute range that is significantly greater than the relative availability of that range. A "weak affinity" range depicts attribute ranges where relative use exceeds relative availability. An "inadequate" range depicts conditions where relative use is significantly less than relative availability.*

	Affinity	**Spring**	**Spring**	**Summer**	**Fall**	**Winter**	**Winter**
Life-stage		Sub-juvenile	Juveniles	Juveniles	Sub-Adults	Pre-spawning Adults	Spawning Adults
Primary Months		May-Jun	Jun-Jul	Jun-Aug	Sep-Dec	Jan-Feb	Mar-Apr
Program		20mm	20mm	STN	FMWT	Kodiak	Kodiak
Turbidity	Suitable	20-40	20-40	20-40	30-60	20-30	20-30
(Secchi	Weak affinity	10-50	10-40	0-50	0-60	0-40	20-50
depth cm)	Inadequate	>50	>50	>50	60-70,>80	>60	50-60,>70
Salinity	Suitable	200-1000	1000-4000	1000-4000	1000-8000	1000-4000	-
(Ec)	Weak affinity	200-4000	200-8000	1000-8000	200-12000	1000-8000	200-600 1000-8000
	Inadequate	>4000	<200, >16000	<400, >16000	<200, >20000	<200, >8000	<200, >8000
Temper-	Suitable	20-21	20-21	18-22	-	-	-
ature	Weak affinity	18-22	18-21	18-22	16-21	13-15	12-15
(Celcius)	Inadequate	12-18,>22	16-18,>22	>22	-	-	-
Calenoid	Suitable	1000-2500	250-2500	-	>1000	250-1000	-
Copepods	Weak affinity	-	100-2500	1000-2500	>250	100-2500	250-1000
(#/m^3)	Inadequate	-	<1,>2500	<10	-	-	10-100
Depth	Suitable	>7	7-9	<3, 7-9	7-9	5-6	5-6
(meters)	Weak affinity	various	<3	<3,7-9	6-12	4-6	5-6,>9
	Inadequate	2-4	4-7	4-7	<5	<4,6-7	<4,6-7
Area of	Suitable	5-20	>100	>100	5-20	5-20	-
Shallows	Weak affinity	5-20, >200	>100	5-20,>100	5-20	5-20,>200	5-20,>200
(ha)	Inadequate	20-50	<5	<5,20-100	<5,>20	20-100	50-100
Distance	Suitable	1-2, 3-5	1-2, 3-5	1-2, 3-5	0.5-2	0-0.25	-
from Wetlands	Weak affinity	1-2, 3-5	0.25-0.5, 1-2, 3-5	0.25-0.5, 1-2, 3-5	0-2	0-0.25,1-2	< 0-0.25, 1-2
km	Inadequate	>5	>5	>5	>3	>5	>5

Table 5. *Results of multiple regression analysis when distribution of delta smelt (dependent variable) is regressed against the habitat suitability index values of six habitat attributes during various life stages; "negative" indicates the regression coefficient had a negative sign.*

Attribute	Sub-juvenile		Juvenile (20mm)		Juvenile (STN)		Sub-adult		Pre-spawning adult		Spawning adult	
n	2592		2016		2809		9246		686		614	
	Coeff	P-value	Coeff	P-value	Coeff	P-value	Coeff	P-value	Coeff	P-value	Coeff	P-value
Turbidity	0.31	<0.001	0.09	<0.001	0.05	<0.001	0.21	<0.001	0.26	<0.001	0.19	0.001
Salinity	0.17	<0.001	0.22	<0.001	0.47	<0.001	0.37	<0.001	0.81	<0.001	0.29	0.011
Temperature	0.23	<0.001	0.14	<0.001	0.05	0.031	Negative		Negative		0.12	0.774
Depth	0.44	<0.001	0.19	<0.001	0.40	<0.001	0.33	<0.001	0.15	0.041	0.12	0.024
Shallows Area	Negative		Negative		0.18	<0.001	Negative		0.54	<0.001	0.27	0.021
Wetlands Distance	0.02	0.460	0.16	<0.001	0.22	<0.001	0.36	<0.001	0.10	0.139	Negative	

Table 6. *Results of multiple regression analysis when distribution of delta smelt (dependent variable) is regressed against the habitat suitability index values of seven habitat attributes during various life stages; "negative" indicates that the regression coefficient had a negative sign.*

Attribute	Sub-juvenile		Juvenile (20mm)		Juvenile (STN)		Sub-adult		Pre-spawning adult		Spawning adult	
n	2378		1835		2750		5792		424		376	
	Coeff	P-value	Coeff	P-value	Coeff	P-value	Coeff	P-value	Coeff	P-value	Coeff	P-value
Turbidity	0.30	<0.001	0.10	<0.001	0.05	<0.001	0.27	<0.001	0.28	<0.001	0.18	0.012
Salinity	0.19	<0.001	0.20	<0.001	0.44	<0.001	0.40	<0.001	0.53	0.014	0.27	0.141
Temperature	0.25	<0.001	0.15	<0.001	0.06	0.016	0.04	<0.001	0.06	0.694	0.33	0.525
Depth	0.53	<0.001	0.20	<0.001	0.39	<0.001	0.43	<0.001	0.19	0.067	0.11	0.156
Shallows Area	Negative		Negative		0.16	<0.001	Negative		0.82	<0.001	0.21	0.162
Wetlands Distance	0.12	0.009	0.17	<0.001	0.23	<0.001	0.14	<0.001	Negative		Negative	
Prey Density	Negative		0.26	<0.001	0.02	0.061	Negative		0.89	0.002	0.09	0.145

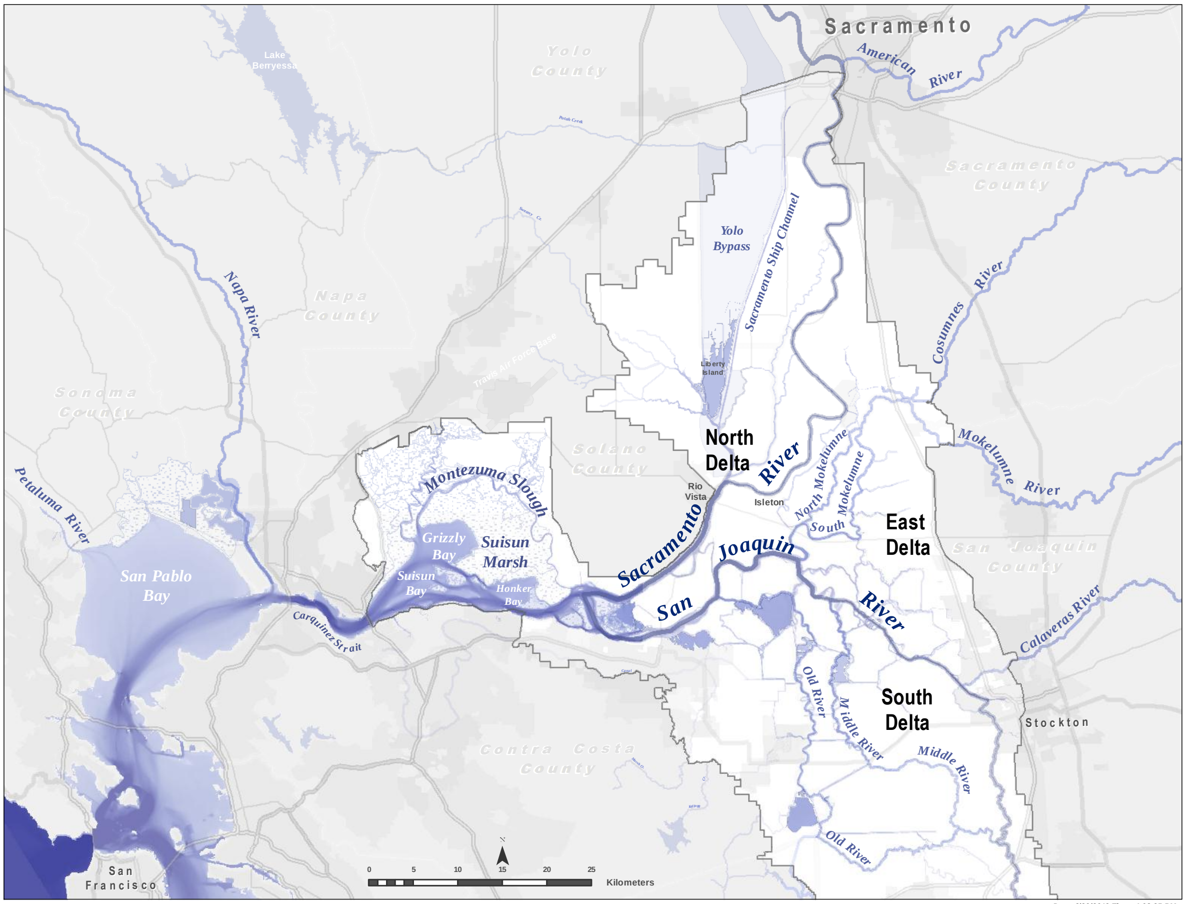

Figure 1. The San Francisco Estuary.

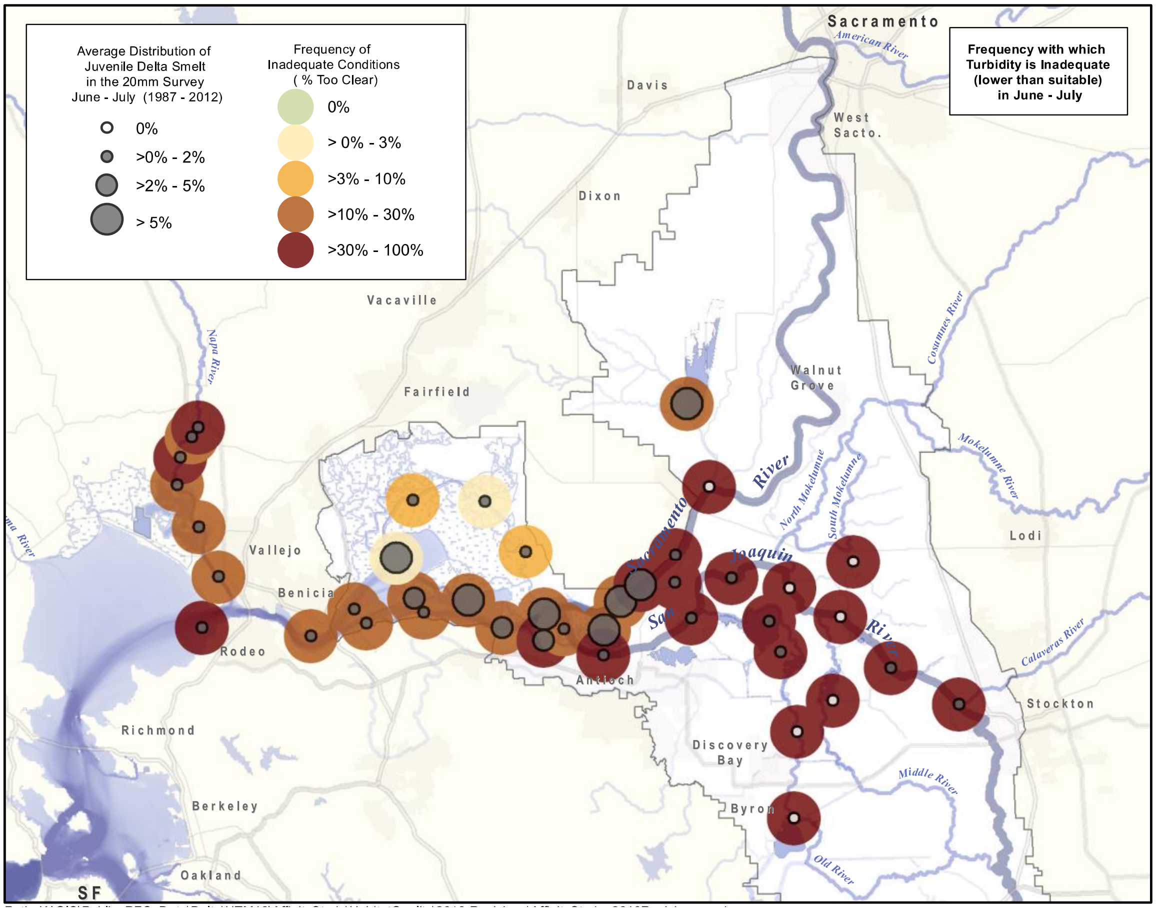

Figure 2. The distribution of juvenile delta smelt from 20mm trawl surveys and the frequency with which turbidity is inadequate (see Table 4). Gray circles indicate the across-years average of the percentage effort-corrected catch of juvenile delta smelt in the 20 mm Survey during June and July at each monitoring station.

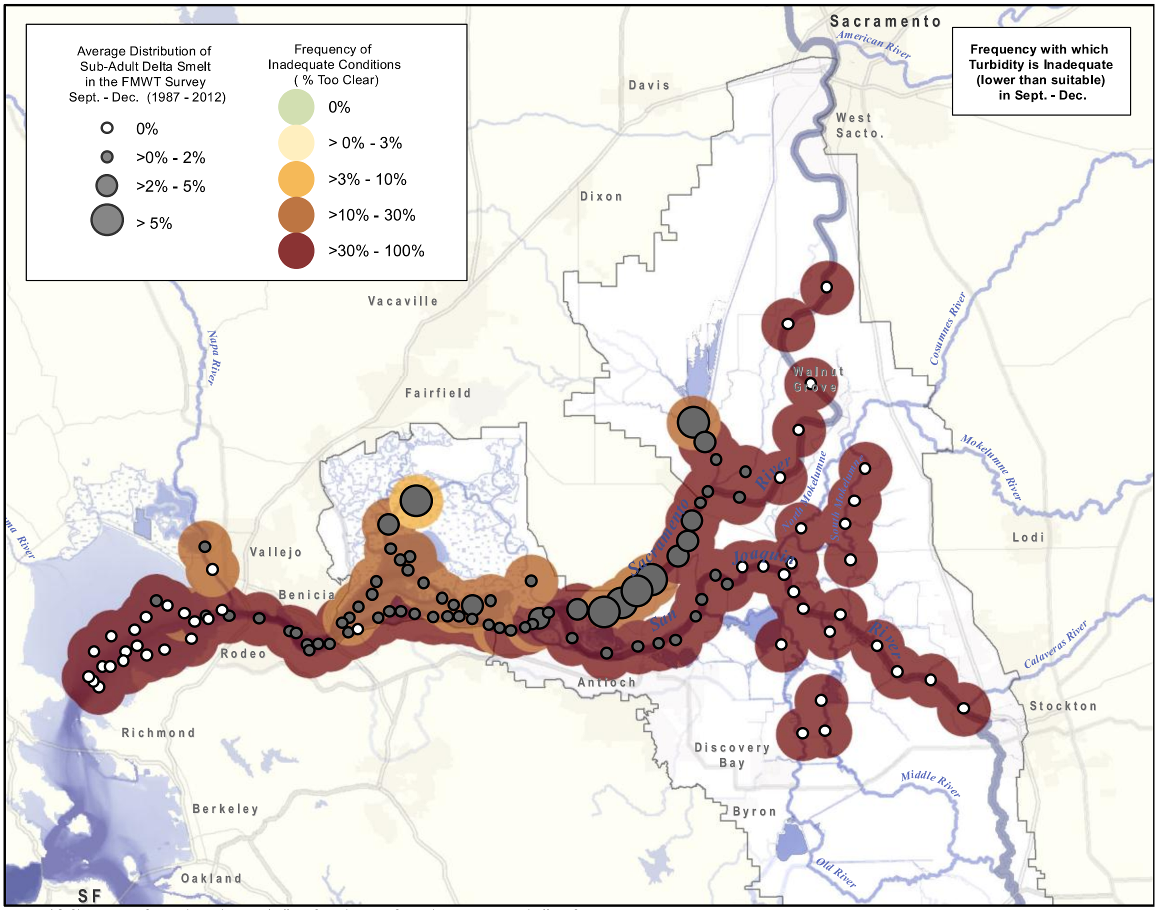

Figure 3. Distribution of sub-adult delta smelt from the Fall Midwater Trawl surveys and the frequency with which turbidity is inadequate (see Table 4). Gray circles indicate the average, across years, of the percentage effort-corrected catch of sub-adult delta smelt in the Fall Midwater Trawl Survey from September through December at each monitoring station.

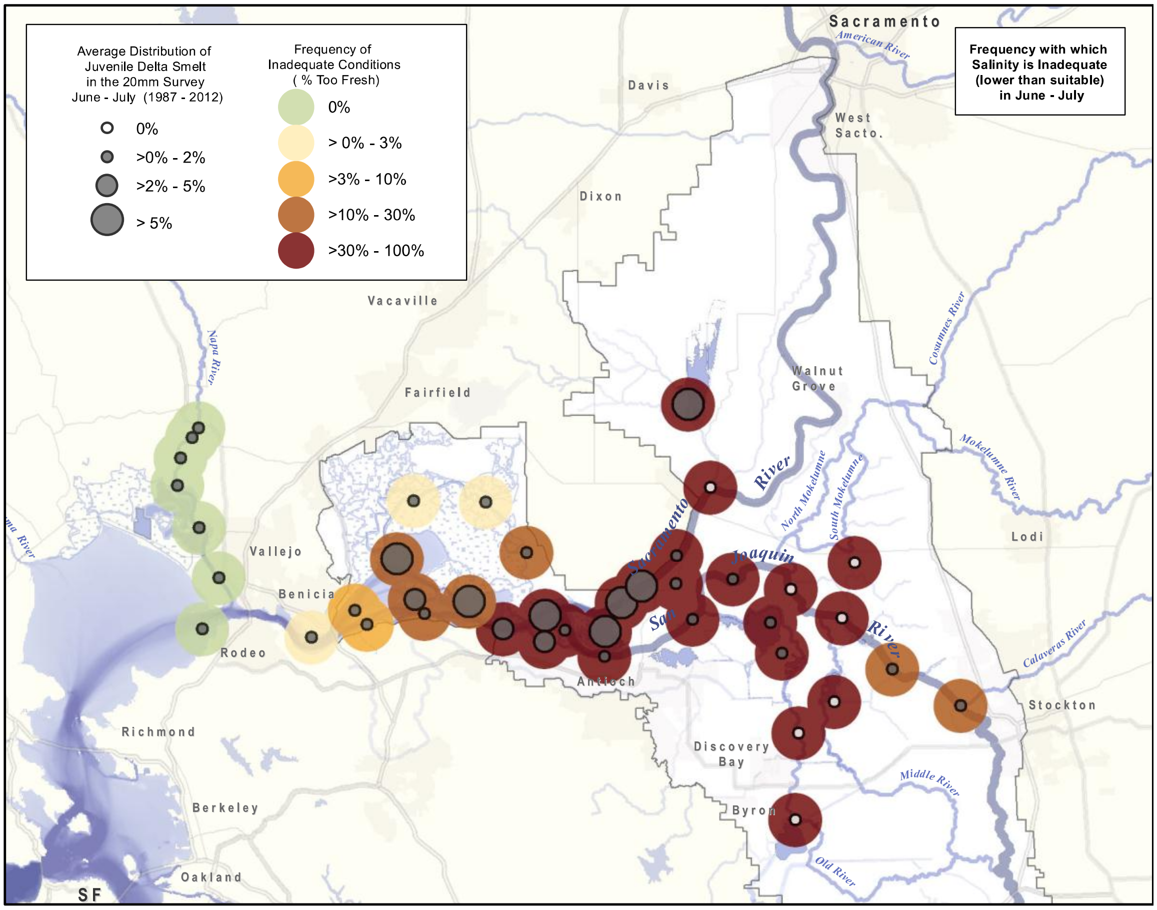

Figure 4. The distribution of delta smelt from 20mm trawl surveys and the frequency with which salinity conditions are inadequate, with salinity levels too low (see Table 4). Gray circles indicate the across-years average of the percentage effort-corrected catch of juvenile delta smelt in the 20 mm Survey during June and July at each monitoring station.

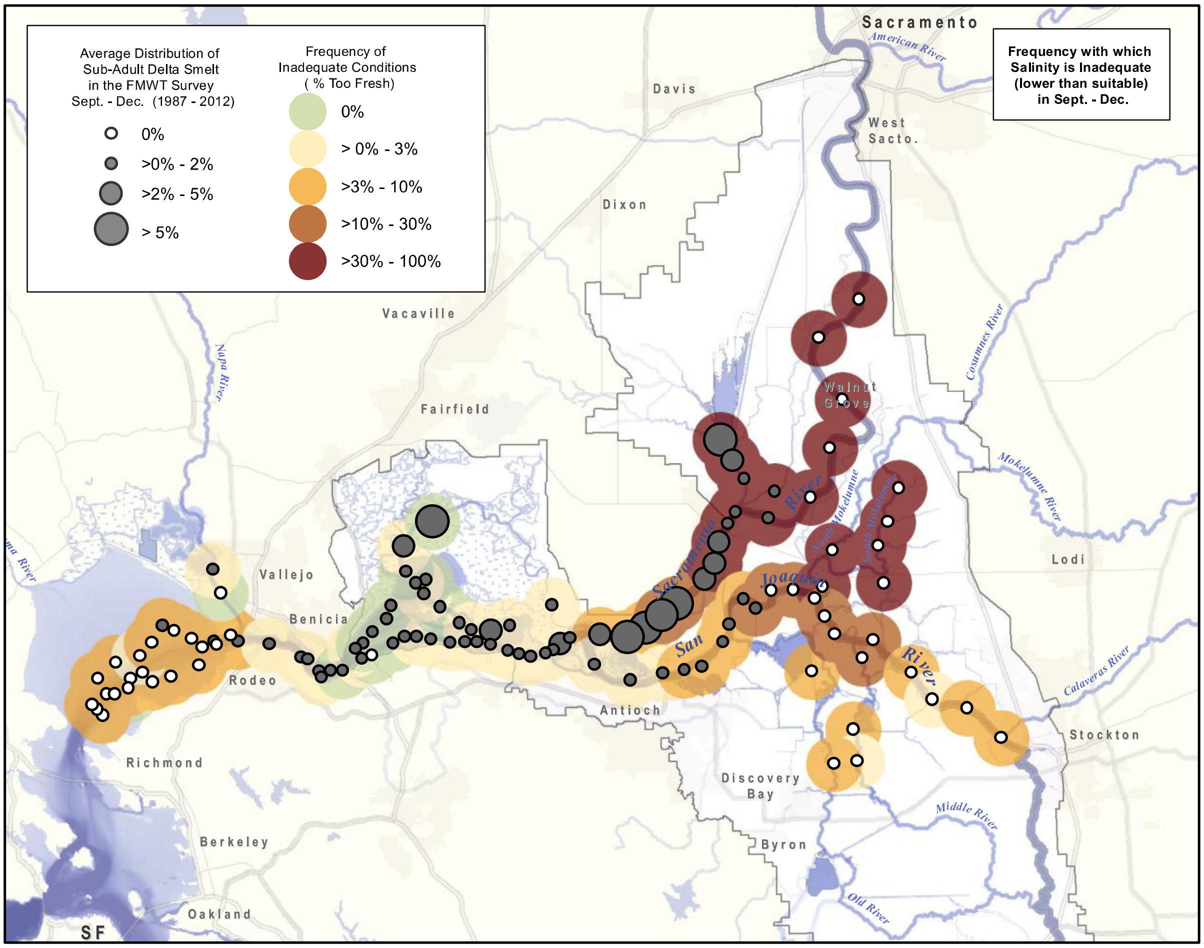

Figure 5. The distribution of delta smelt from the Fall Midwater Trawl survey and the frequency with which salinity is inadequate, with salinity levels too low (see Table 4). Gray circles indicate the across-years average of the percentage of the effort-corrected catch of sub-adult delta smelt in the Fall Midwater Trawl Survey from September through December at each monitoring station.

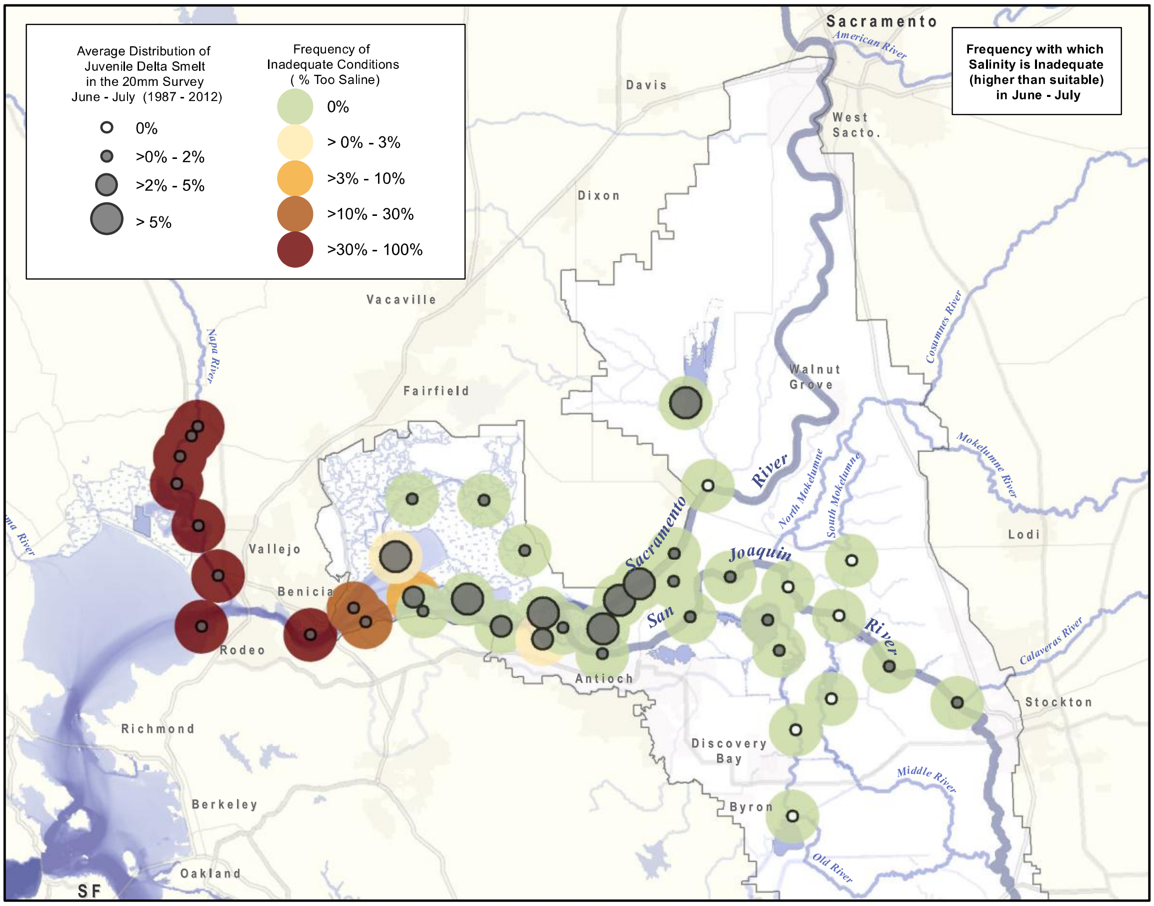

Figure 6. The distribution of delta smelt from the 20mm trawl surveys and the frequency with which salinity is inadequate, with salinity too high (see Table 4). Gray circles indicate the across-years average of the percentage effort-corrected catch of juvenile delta smelt in the 20 mm survey during June and July at each monitoring station.

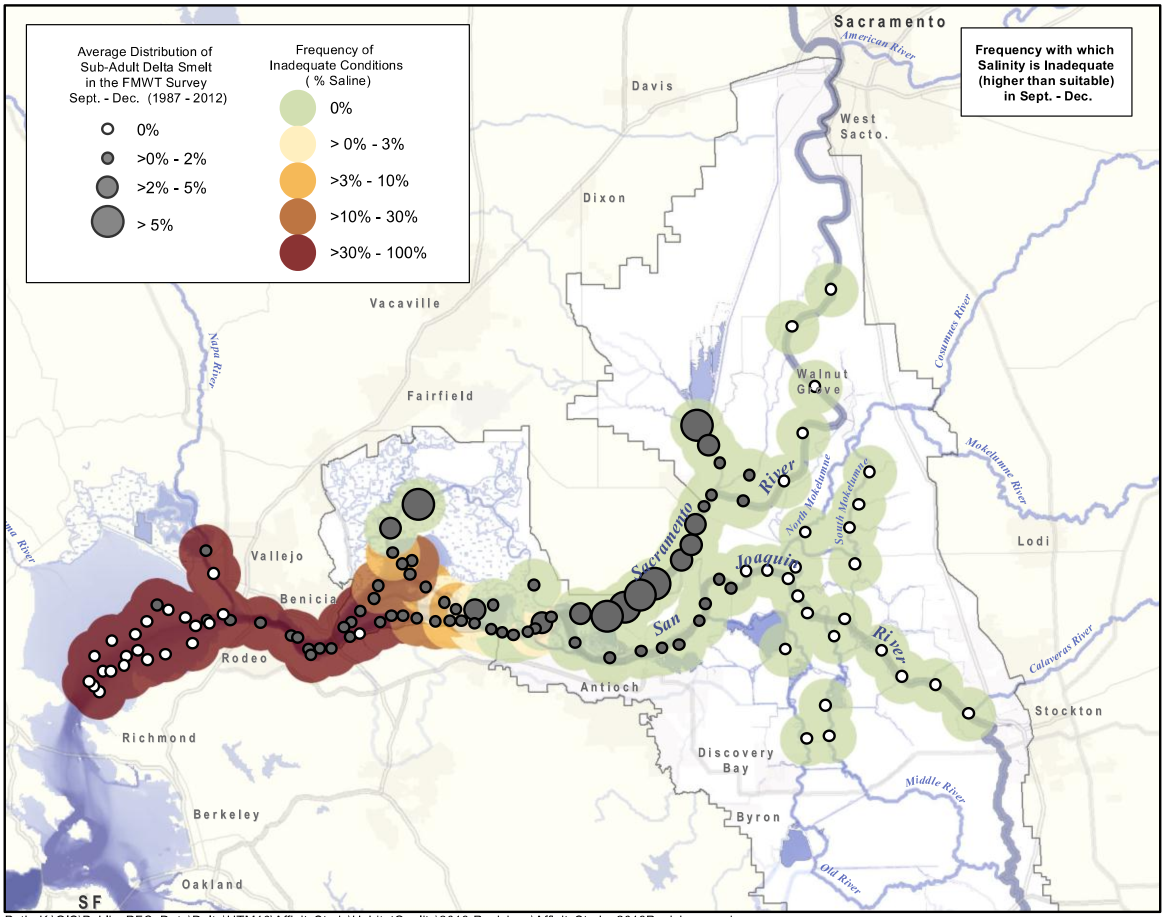

Figure 7. The distribution of delta smelt from the Fall Midwater Trawl survey and the frequency in which salinity is inadequate, with salinity too high (Table 4). Gray circles indicate the across-years average of the percentage effort-corrected catch of sub-adult delta smelt in the Fall Midwater Trawl Survey from September through December at each monitoring station.

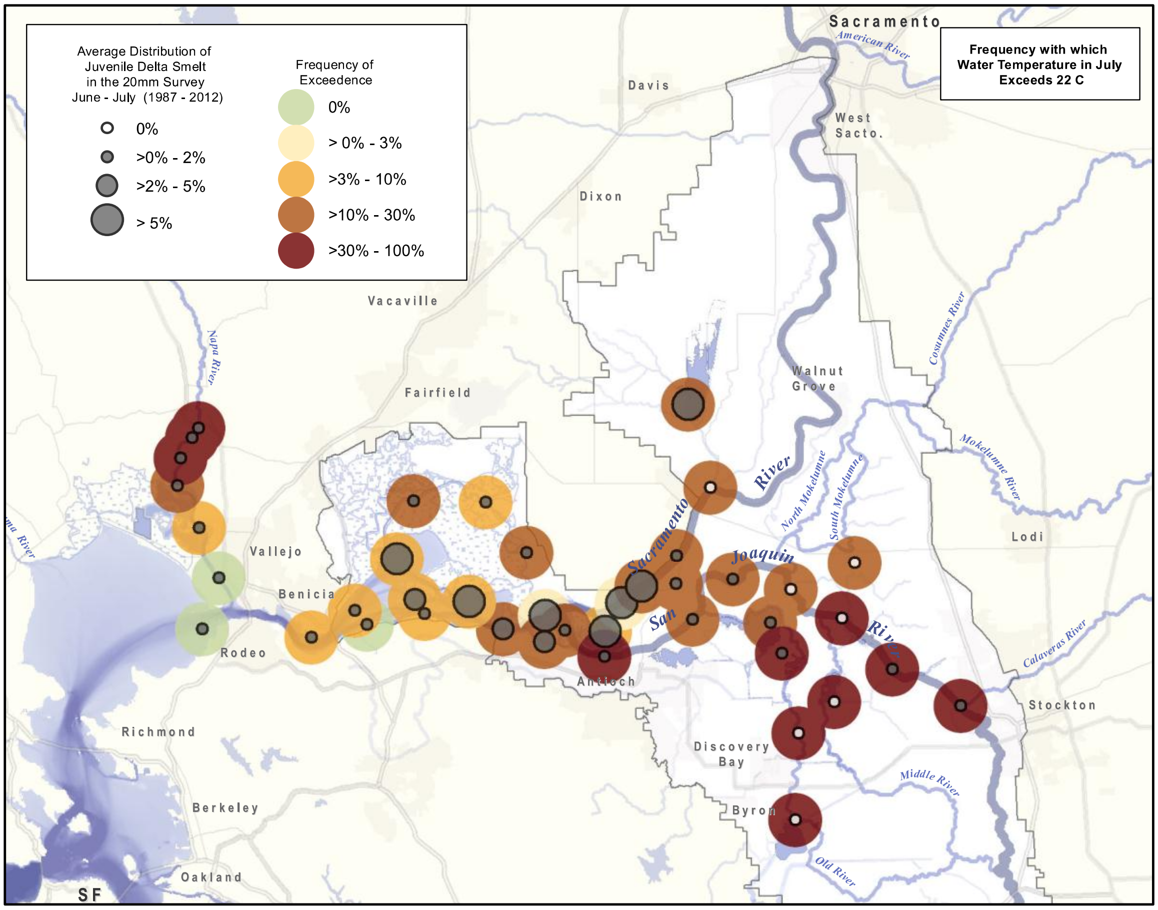

Figure 8. The distribution of delta smelt from the 20mm trawl survey and the frequency with which water temperature in July exceeds the 22-degree C threshold. Gray circles indicate the across-years average of the percentage effort-corrected catch of juvenile delta smelt in the 20 mm survey during June and July at each monitoring station.

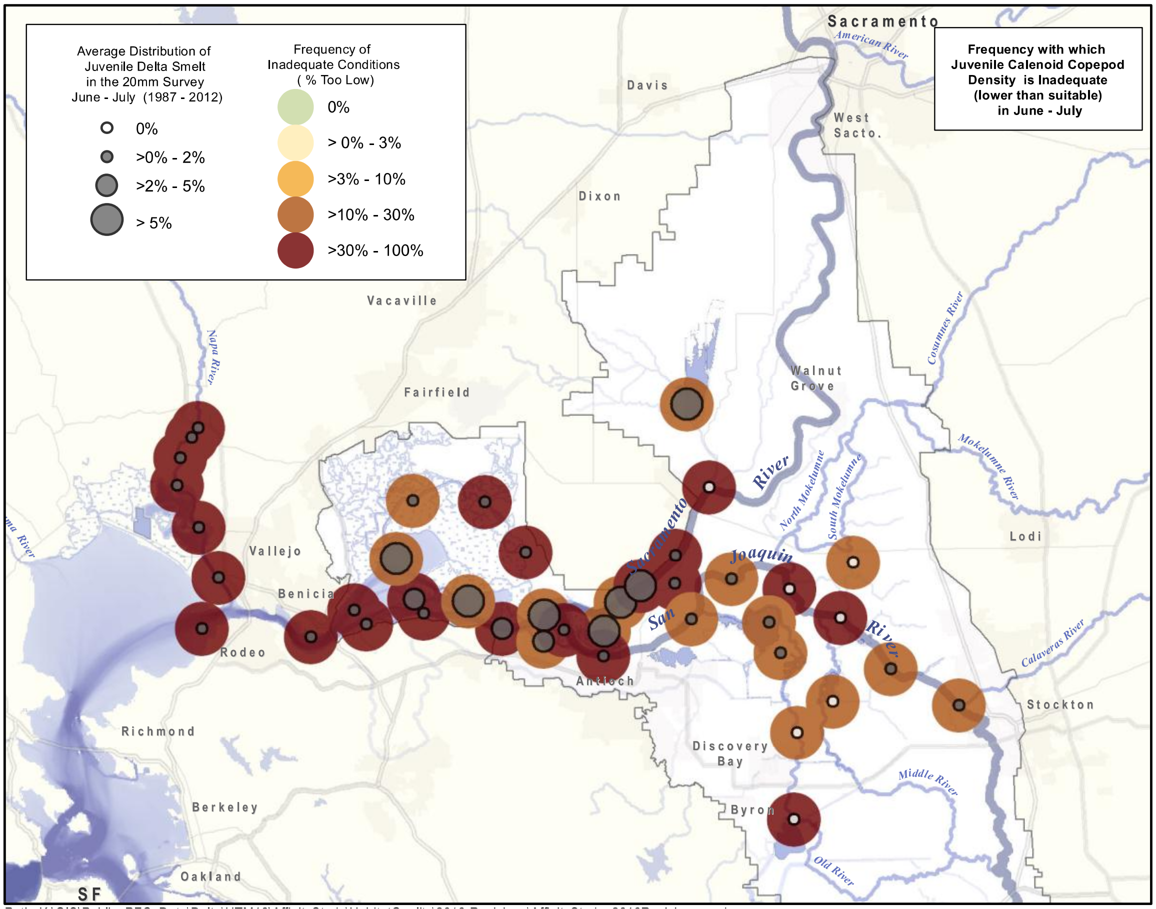

Figure 9. The distribution of delta smelt from the 20mm trawl survey and the frequency with which density of juvenile calanoid copepods is inadequate (Table 4). Gray circles indicate the across-years average of the percentage of the effort-corrected catch of juvenile delta smelt in the 20 mm Survey during June and July at each monitoring station.

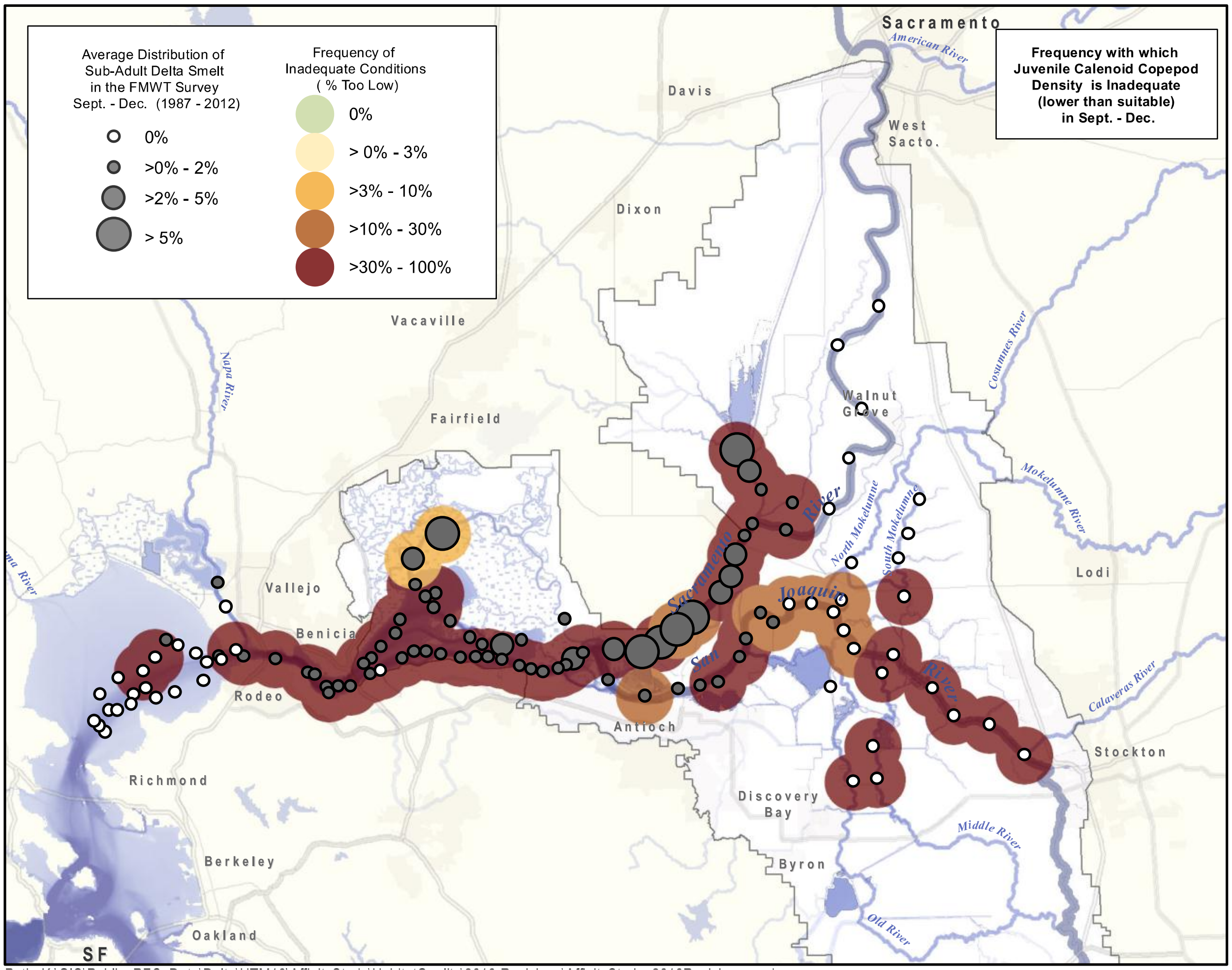

Figure 10. The distribution of delta smelt from the Fall Midwater Trawl survey and the frequency with which density of adult calanoid copepods is inadequate (see Table 4). Gray circles indicate the across-years average of the percentage of the effort-corrected catch of sub-adult delta smelt in the Fall Midwater Trawl Survey from September through December at each monitoring station.

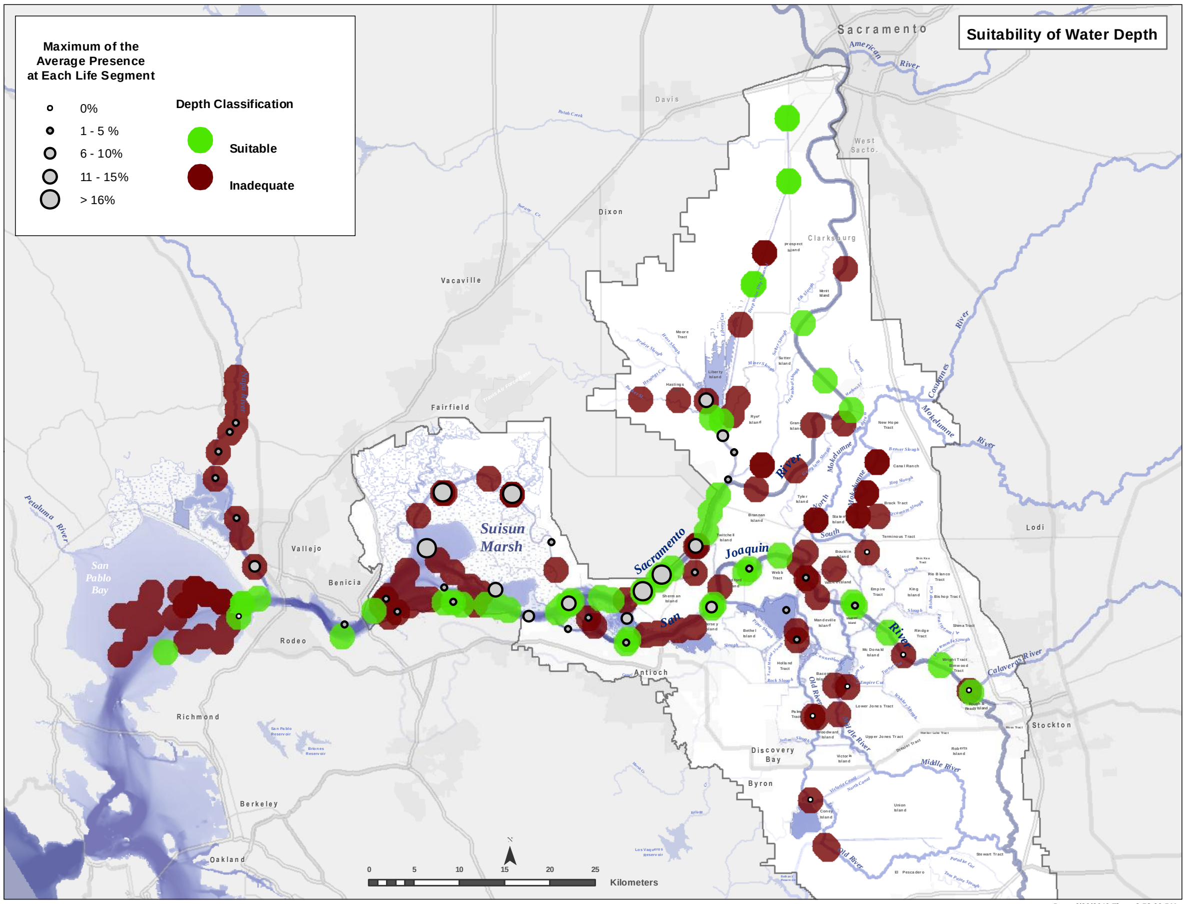

Figure 11. The maximum average presence of each of several life stages of delta smelt (from multiple trawl surveys) and the suitability of proximate water depth. Gray circles indicate the across-years average of the maximum percentage of the effort-corrected catch of delta smelt in any survey at each monitoring station. The colored circles indicate the suitability of average water depth at each station as classified in Table 4.

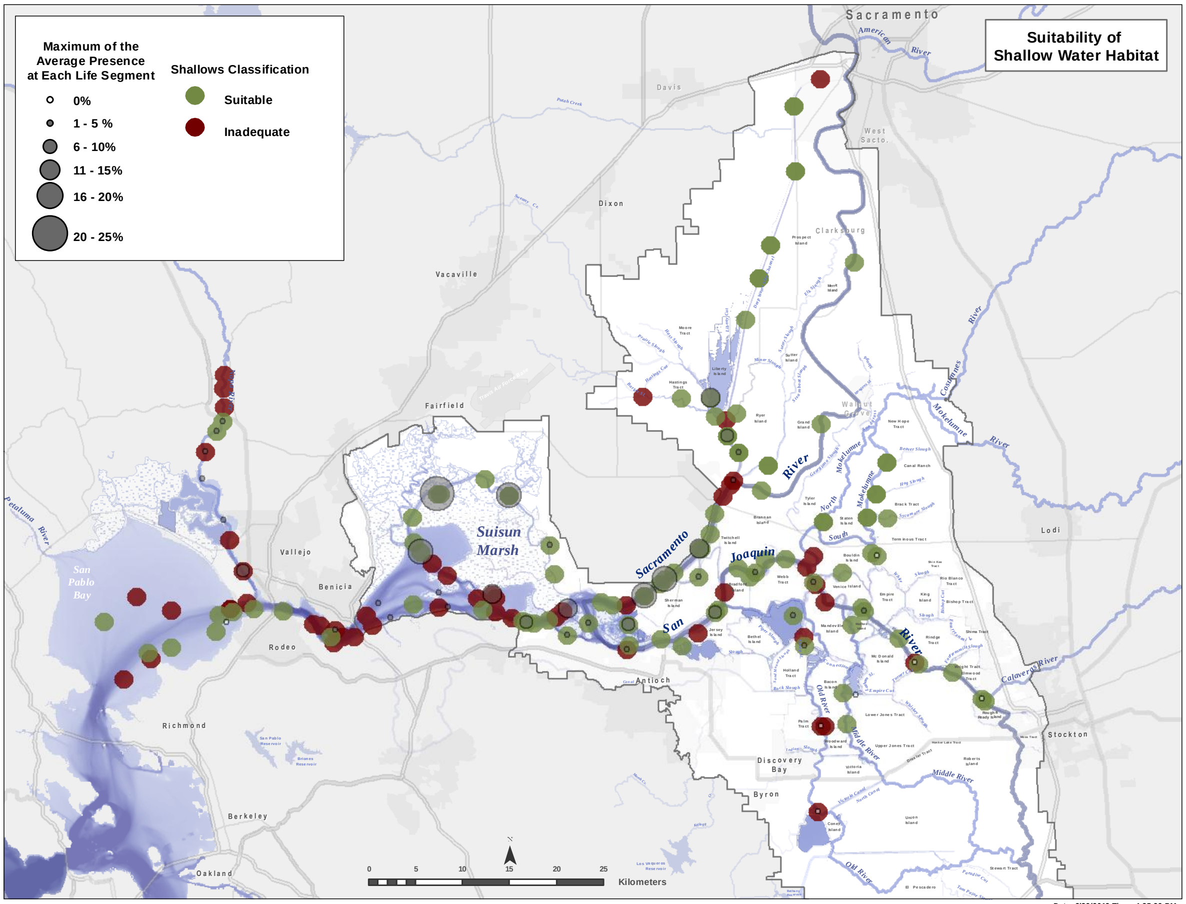

Figure 12. Distribution of the maximum average presence of each life stage of delta smelt, and categorical classification of the availability of shallow water circumstances at and adjacent to survey stations. Gray circles indicate the average, across years, of the maximum percentage effort-corrected catch of delta smelt in any IEP survey at each monitoring station. The colored circles indicate the suitability of the area of shallow water in the vicinity of each station as classified in Table 4.

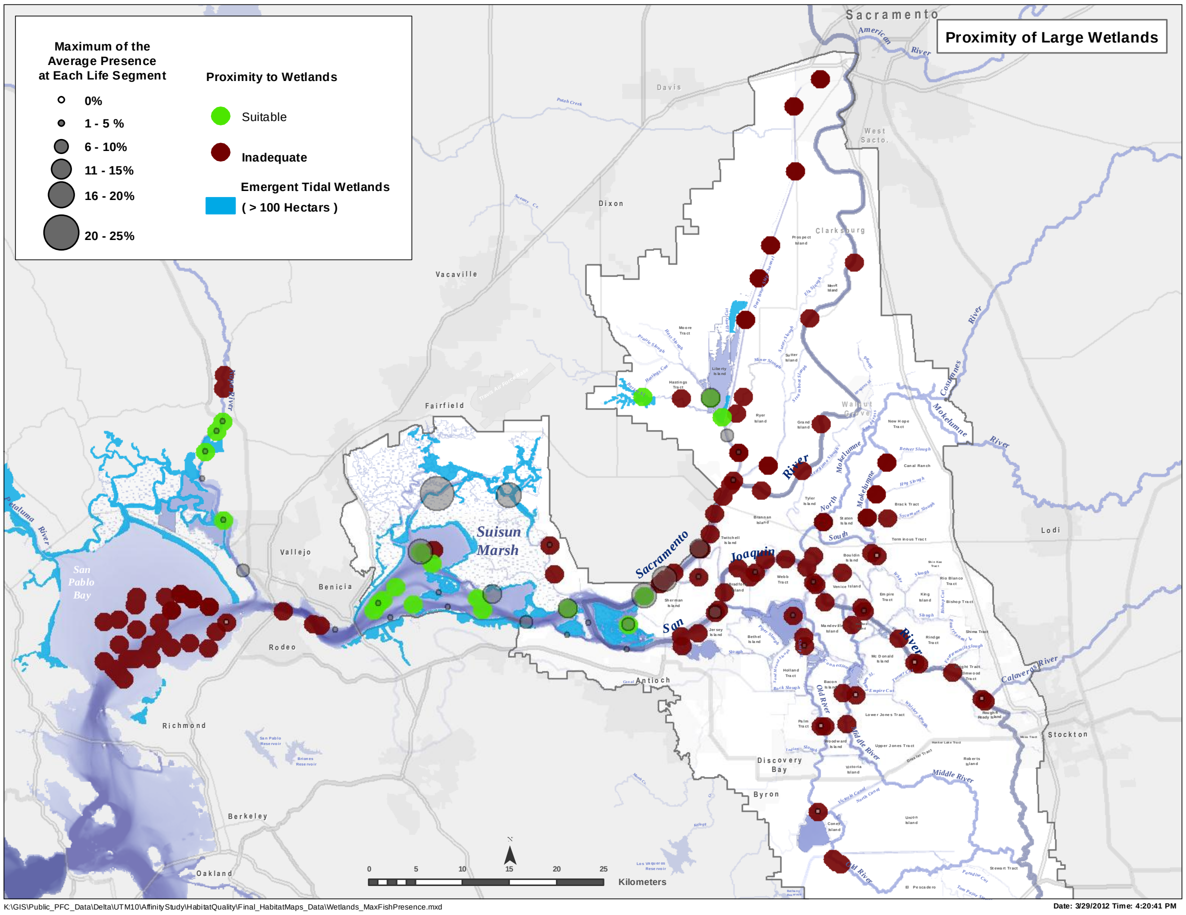

Figure 13. Maximum average presence of multiple delta smelt life stages at trawl survey stations in relation to station distance from wetlands greater than 100 hectares in extent. Gray circles indicate the across-years average of the maximum percentage effort-corrected catch of delta smelt in any IEP survey at each monitoring station. The colored circles indicate the suitability of the proximity of wetlands to each station as classified in Table 4.

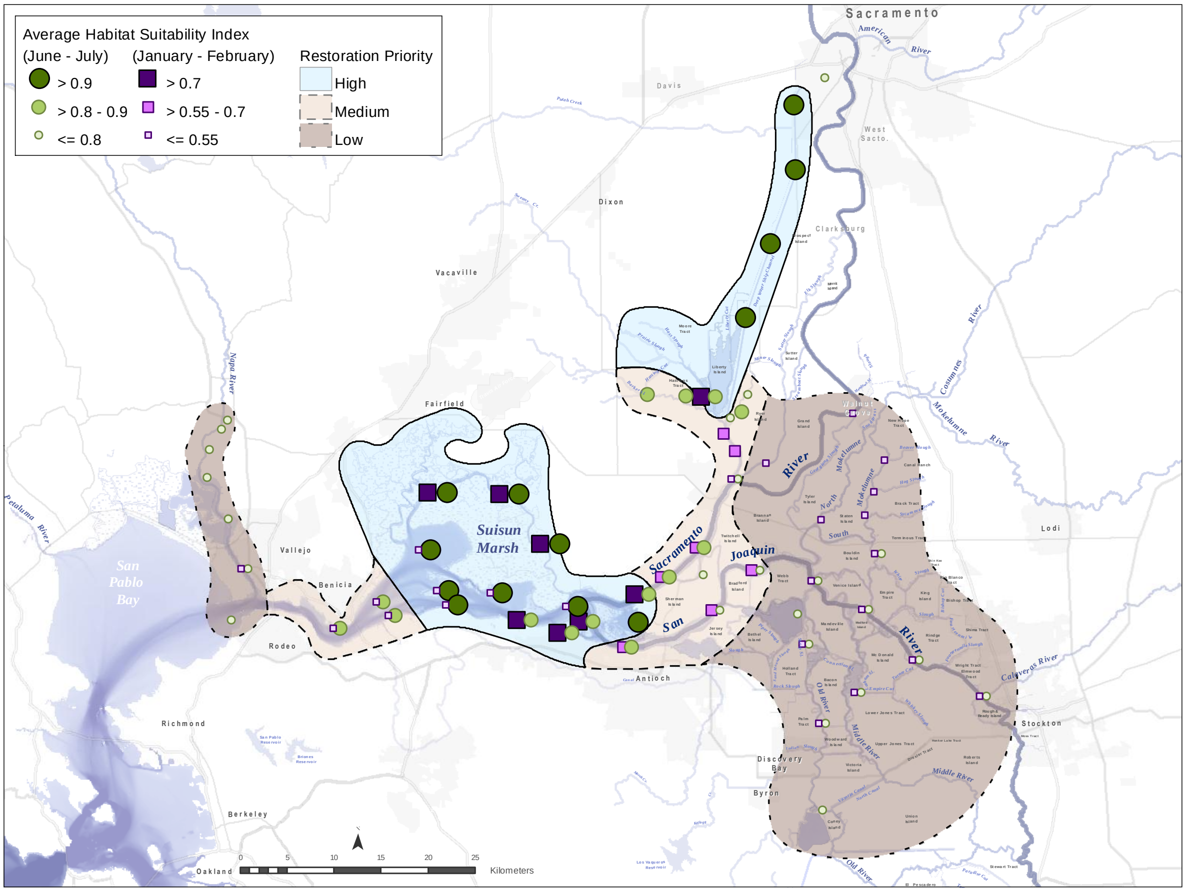

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Figure 14. Aggregated suitability for turbidity, salinity, and temperature at Spring Kodiak Monitoring Stations averaged for January and February and 20 mm Monitoring Stations averaged for June and July. The larger, darker symbols represent those stations with higher average weighted habitat suitability index values derived from these three attributes. Areas designated as high priority for restoration (light blue) contain stations with habitat suitability index values in the upper quartile in either survey. Areas designated as medium priority for restoration (tan) contain stations in the second highest quartile in either survey. Areas designated as low priority (grey) contain stations with habitat suitability index values below the median in both surveys.

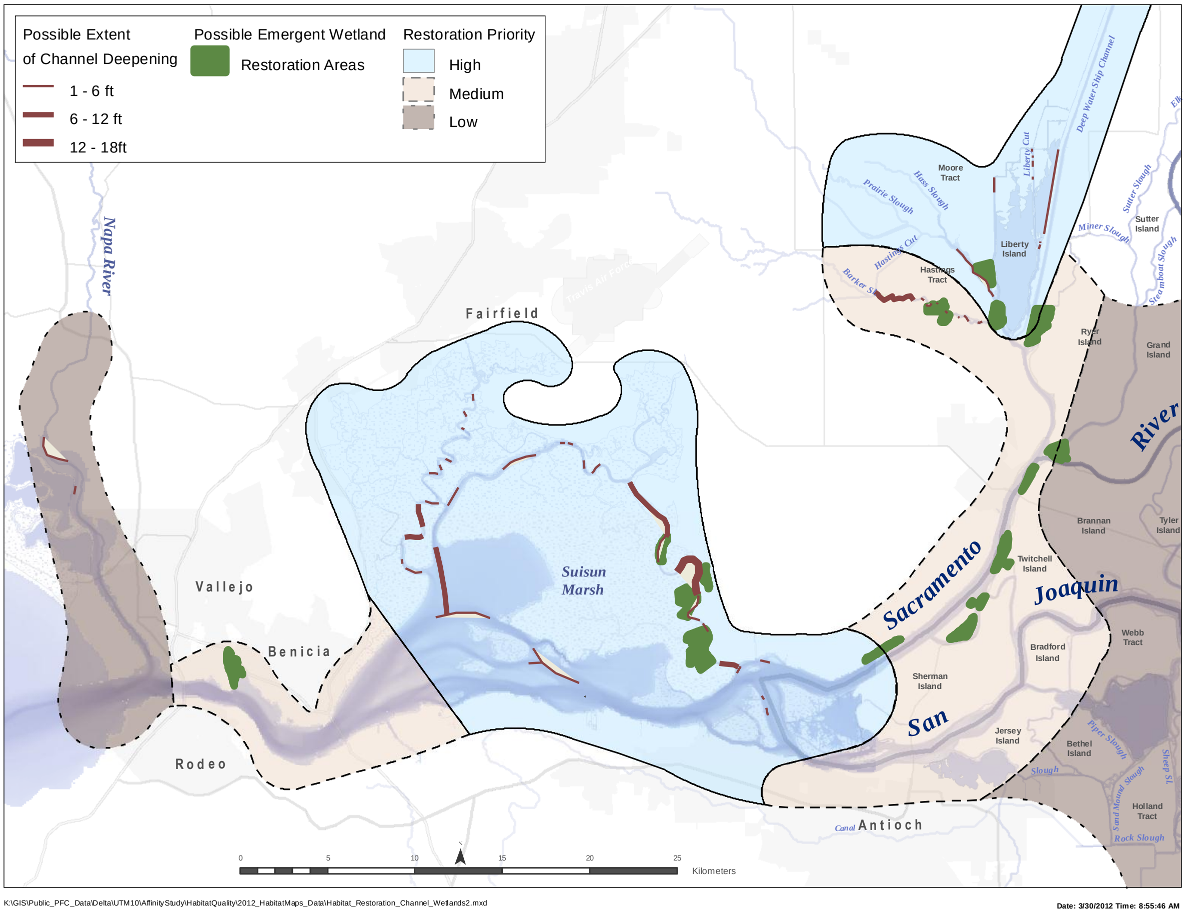

Figure 15. Candidate areas for channel modification and restoration of tidal emergent wetlands. The locations include sites for which environmental variables other than proximity to wetlands are frequently within suitable ranges. Red-tone channel reaches (and other watercourses) are target areas for channel-deepening efforts designed to make local conditions for delta smelt suitable as habitat. The locations for wetlands restoration are sites for which other environmental variables are frequently within suitable ranges, within the current range of delta smelt, close to sea level, and are close to deep-water channel circumstances.

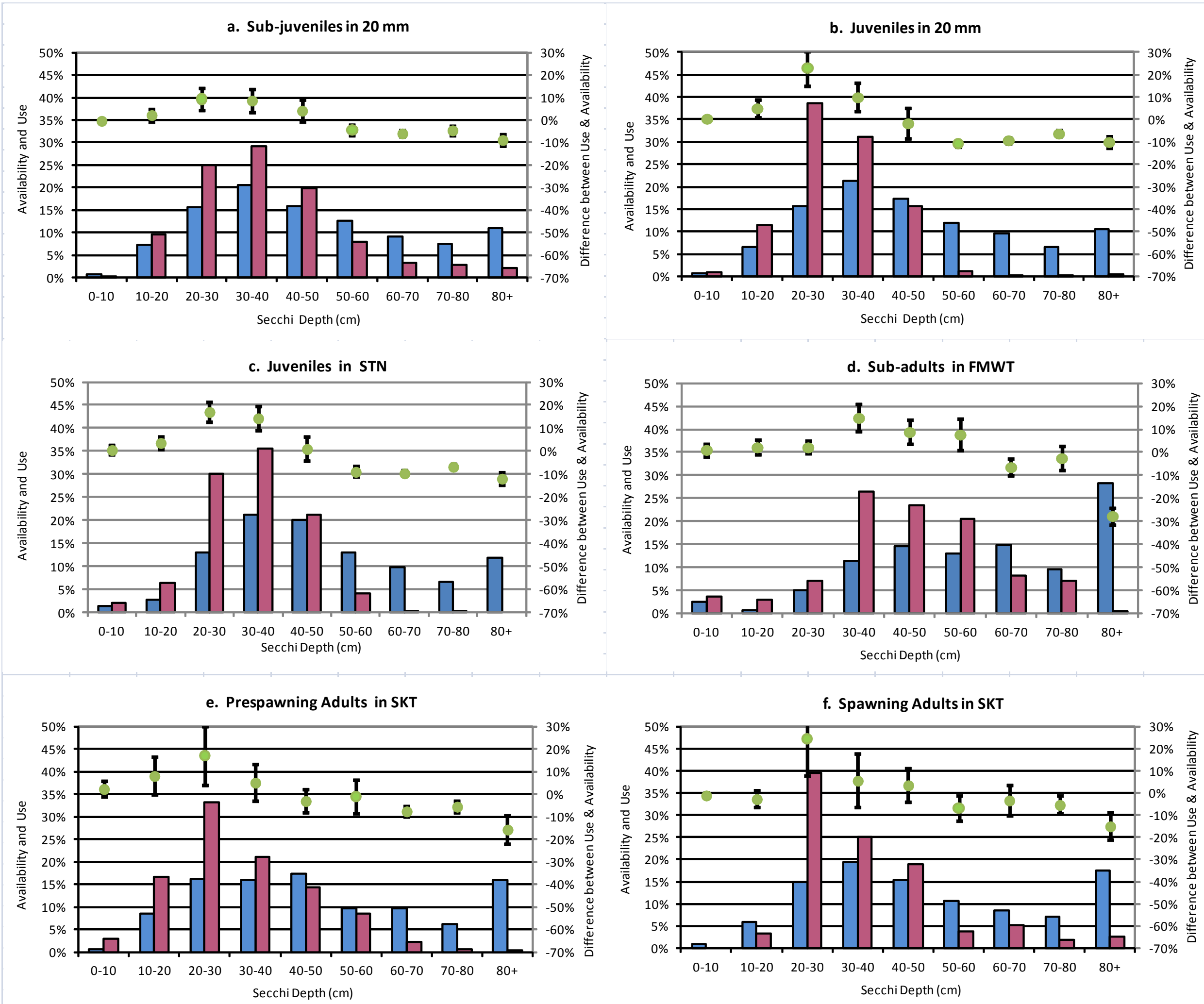

Figure S1. Affinity analysis for water clarity (secchi depth in cm) by life stage. Graphs depict the relative availability of a secchi depth segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

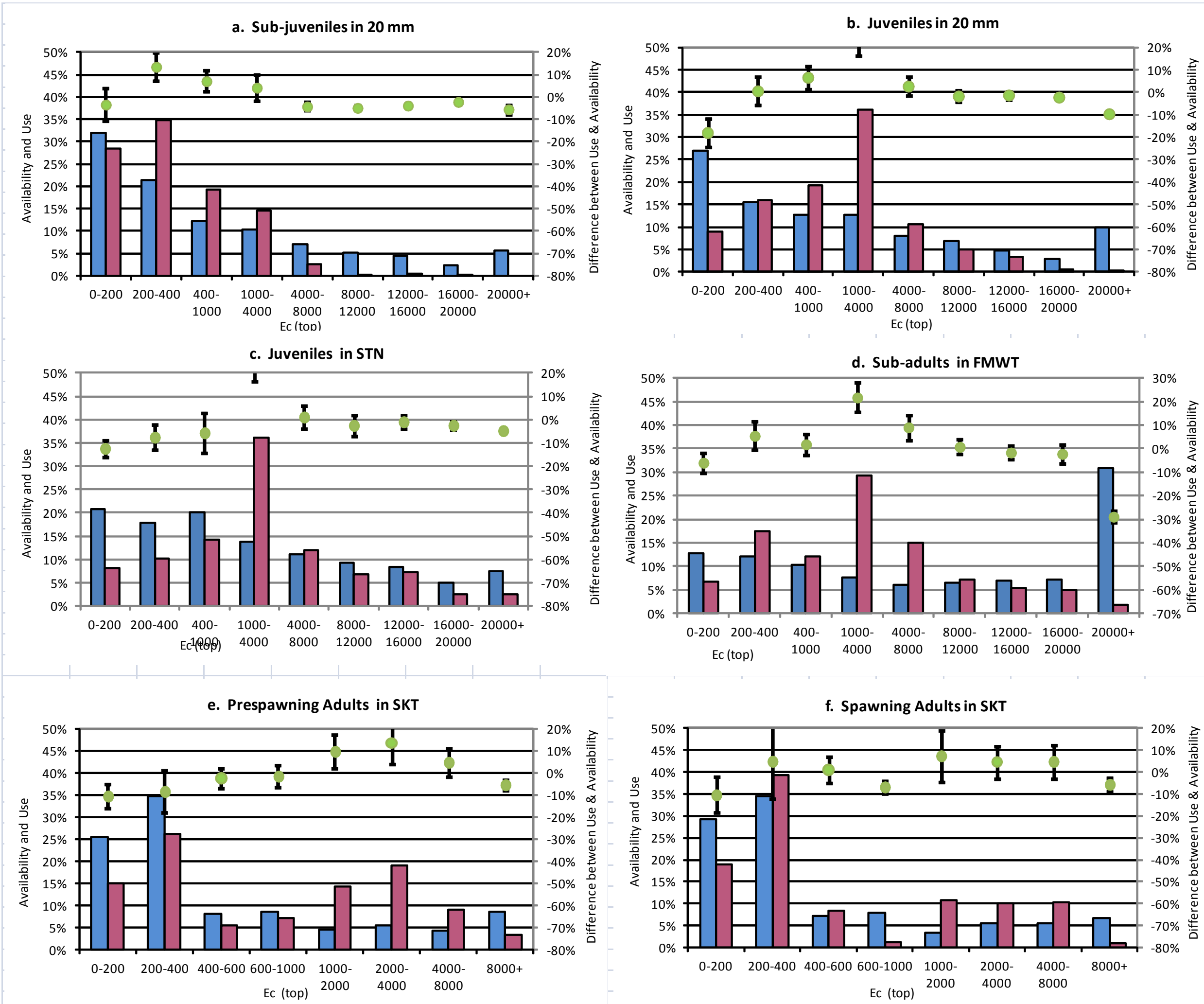

Figure S2. Affinity analysis for salinity (Ec) by life stage. Graphs depict the relative availability of a salinity segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

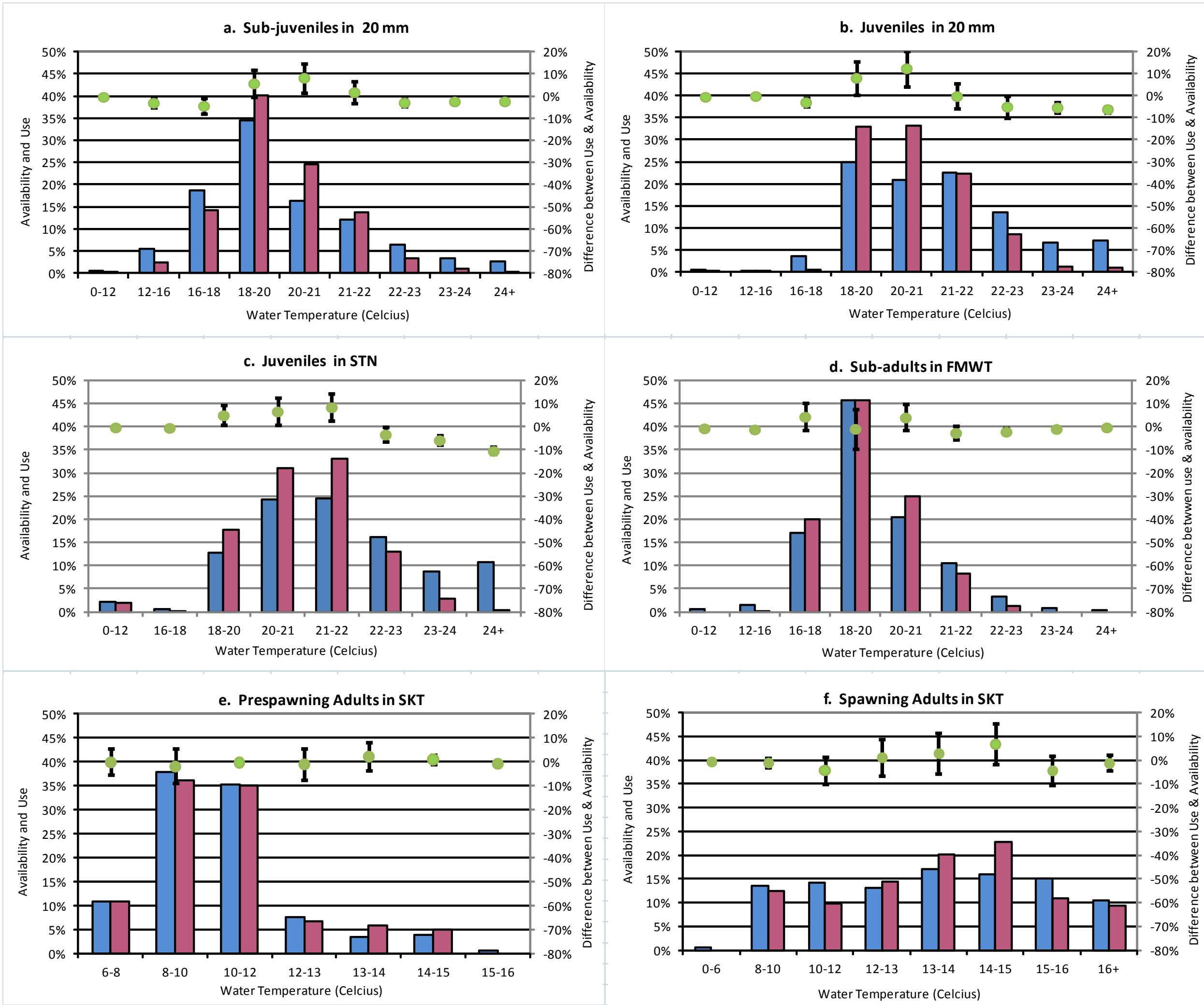

Figure S3. Affinity analysis for water temperature (Celsius) by life stage. Graphs depict the relative availability of a temperature segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

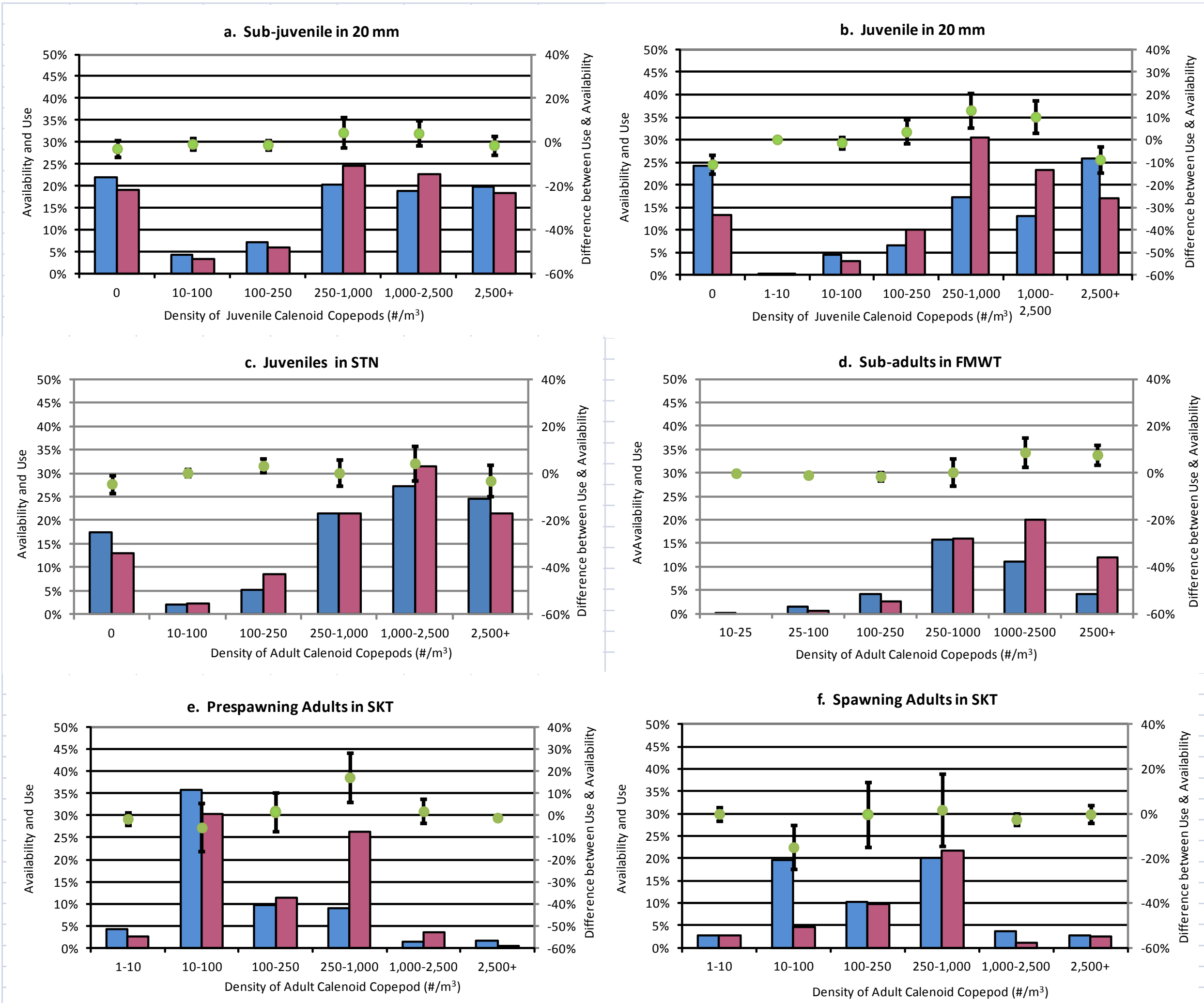

Figure S4. Affinity analysis for density of calenoid copepods by life stage. Graphs depict the relative availability of a calenoid copepod segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

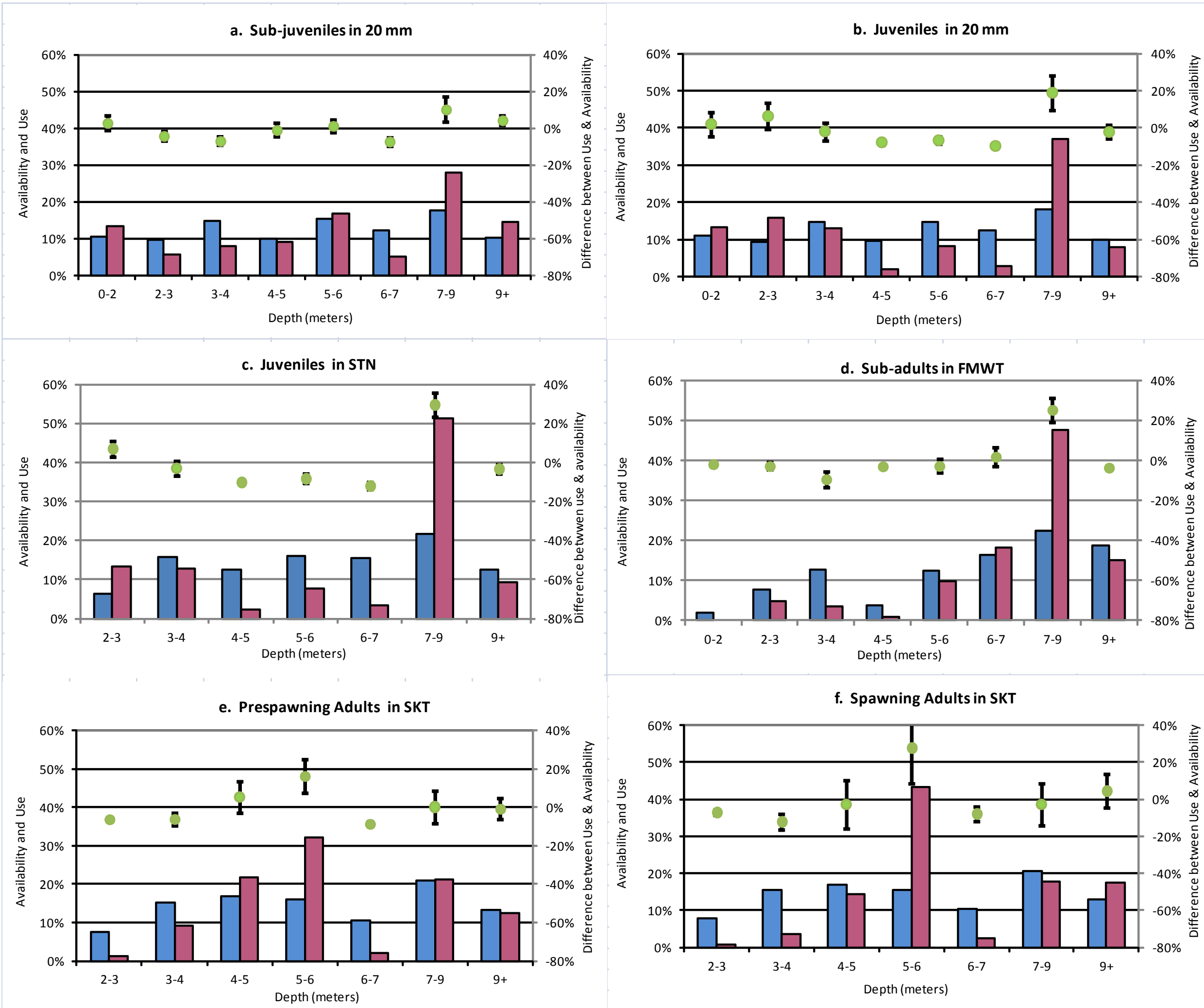

Figure S5. Affinity analysis for water depth (feet) by life stage. Graphs depict the relative availability of a depth segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

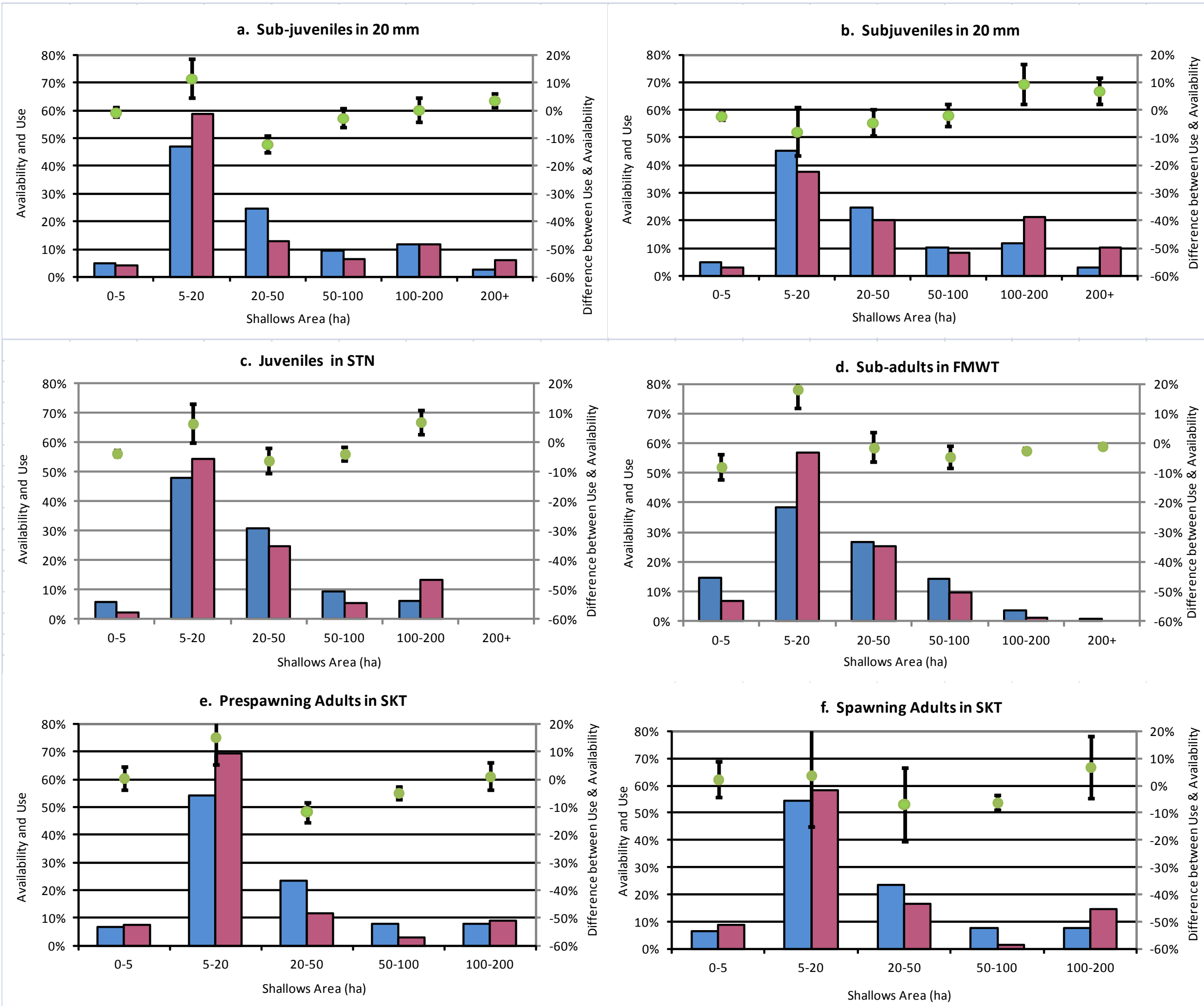

Figure S6. Affinity analysis for area of shallows (water less then 2 meters deep) by life stage. Graphs depict the relative availability of an area-of-shallows segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

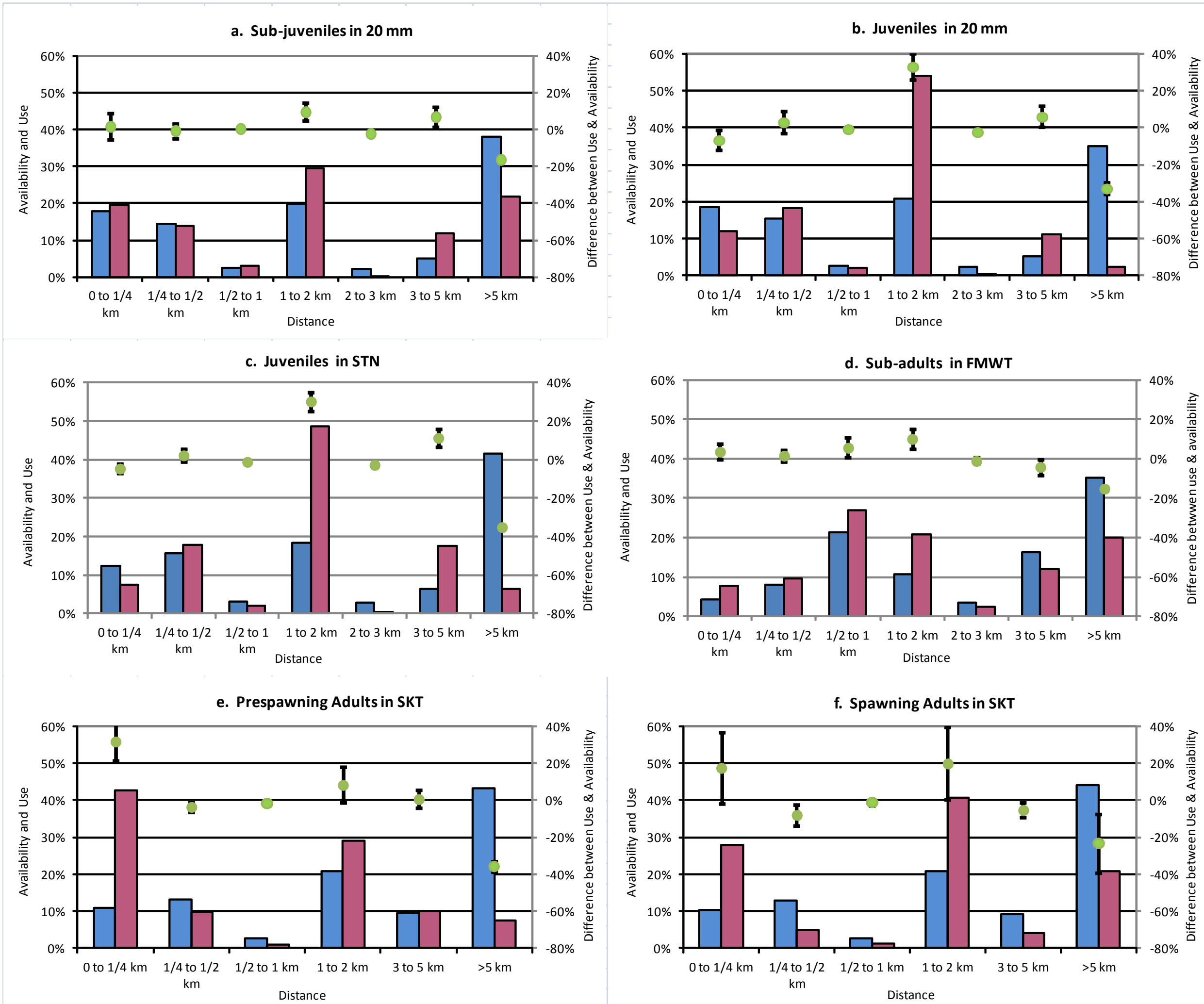

Figure S7. Affinity analysis for distance to large wetlands (wetlands >100ha) by life stage. Graphs depict the relative availability of a distance-to-wetlands segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

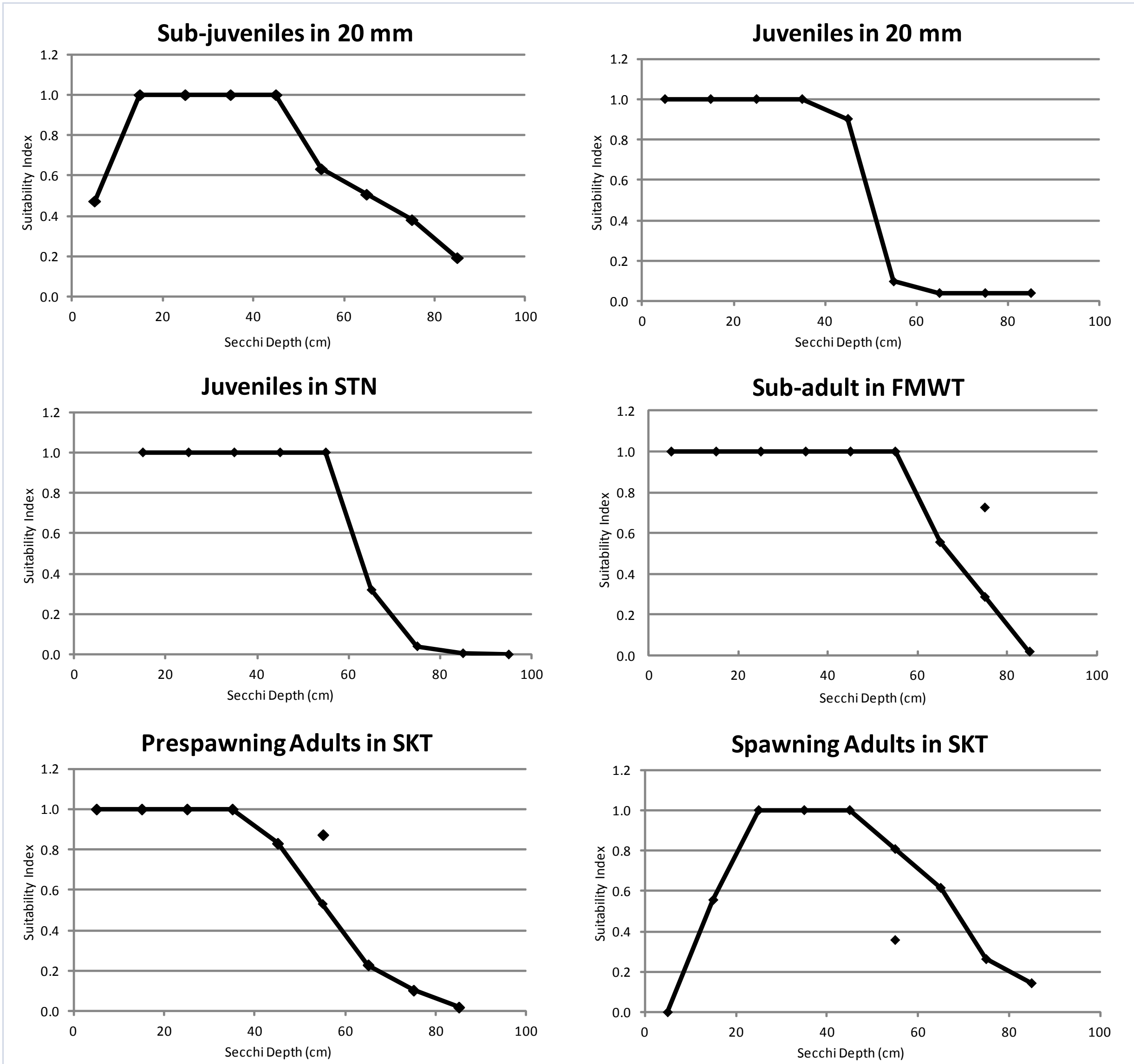

Figure S8. Habitat suitability Index curves for turbidity for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range-segments with a small number of data points.

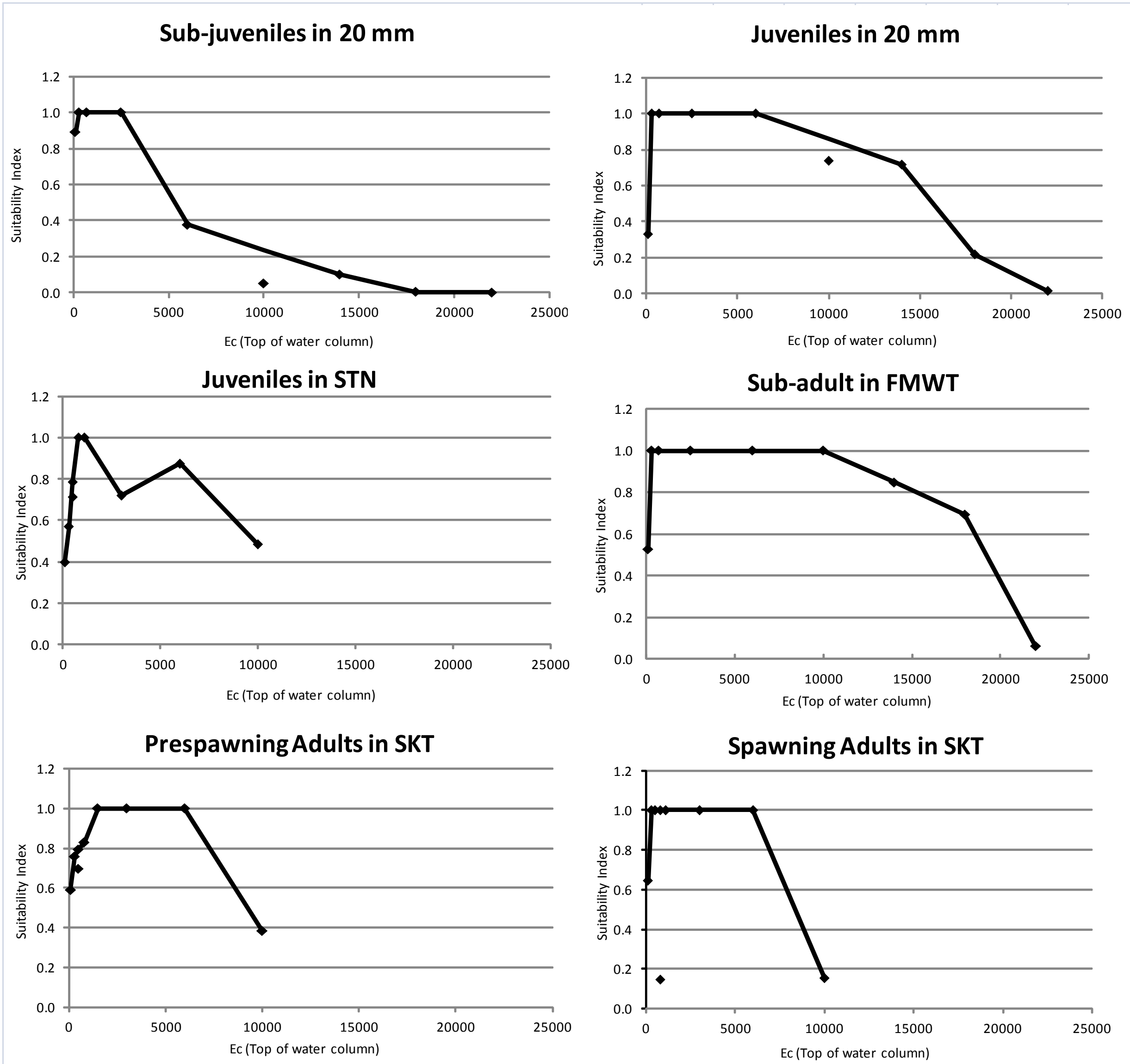

Figure S9. Habitat suitability Index curves for salinity for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.

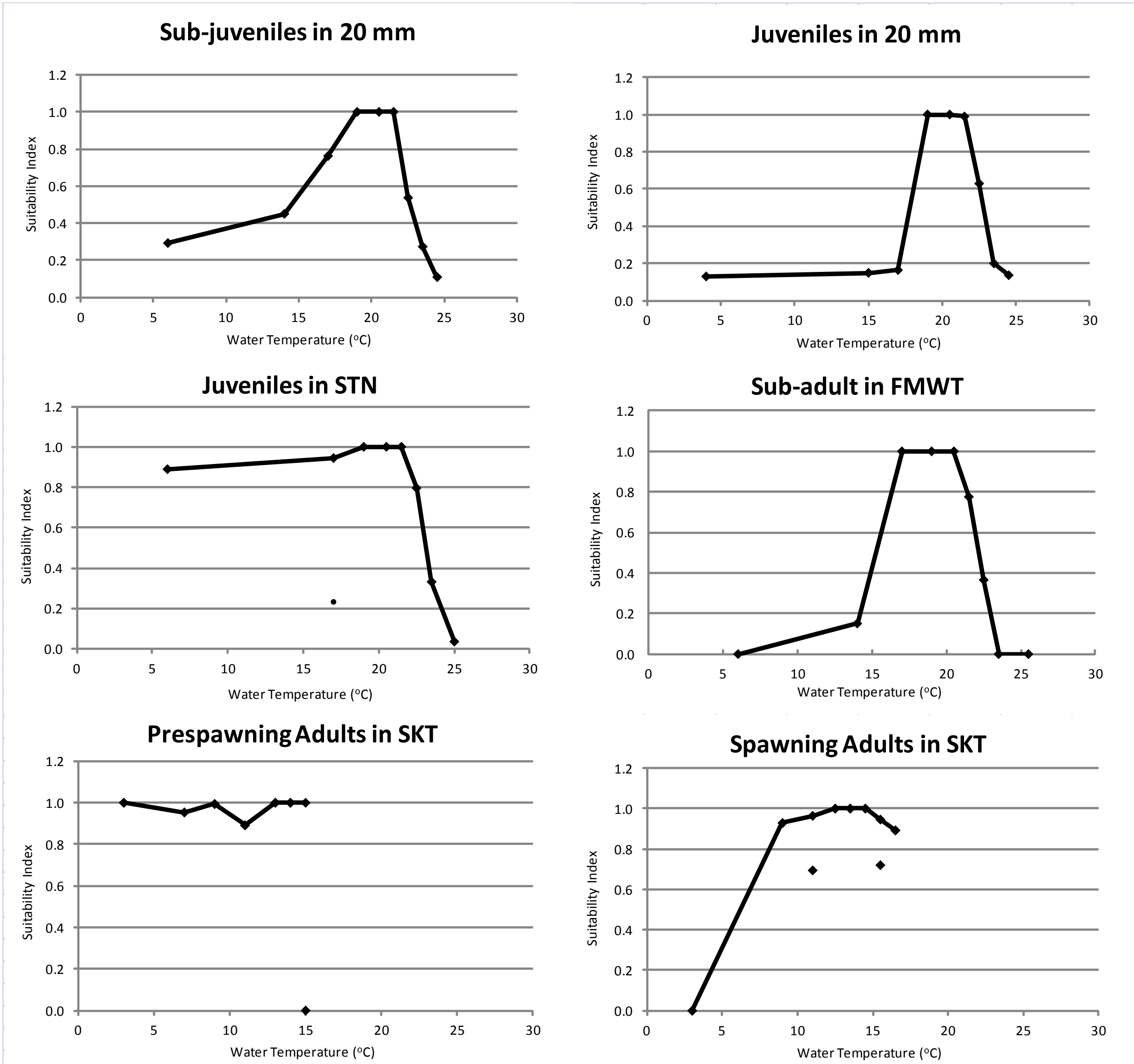

Figure S10. Habitat suitability Index curves for water temperature for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.

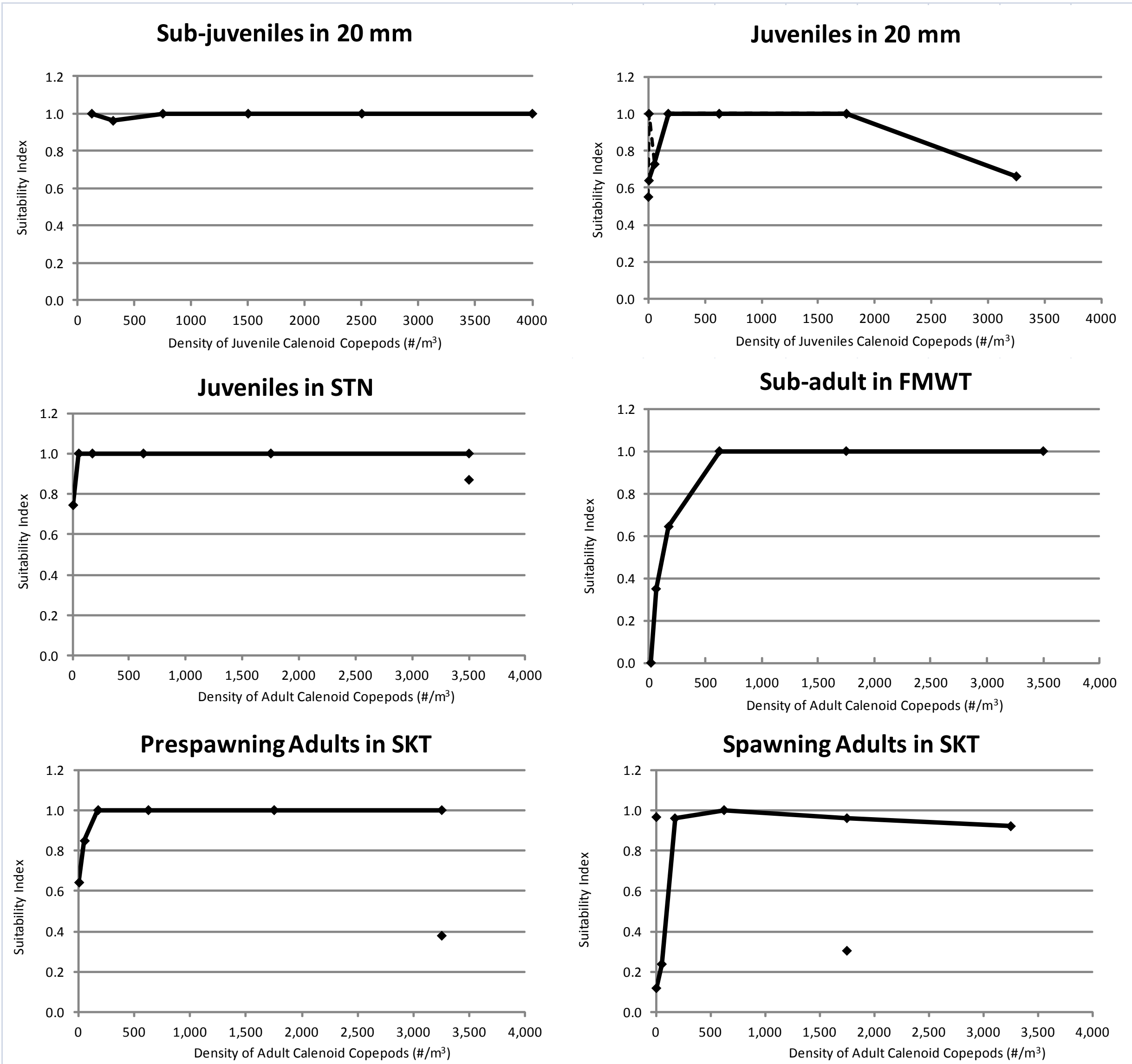

Figure S11. Habitat suitability Index curves for prey density for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.

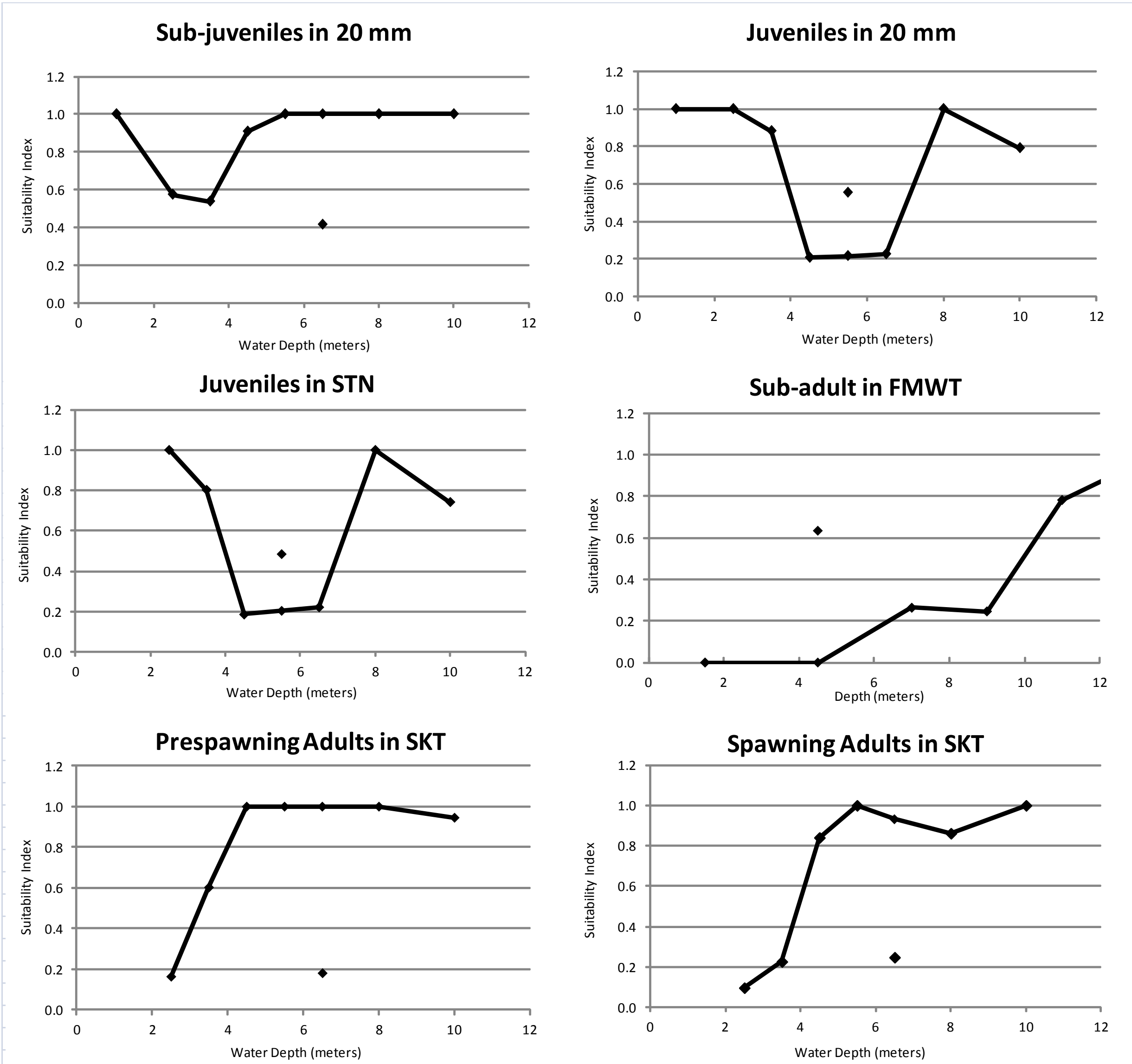

Figure S12. Habitat suitability Index curves for average depth of water for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.

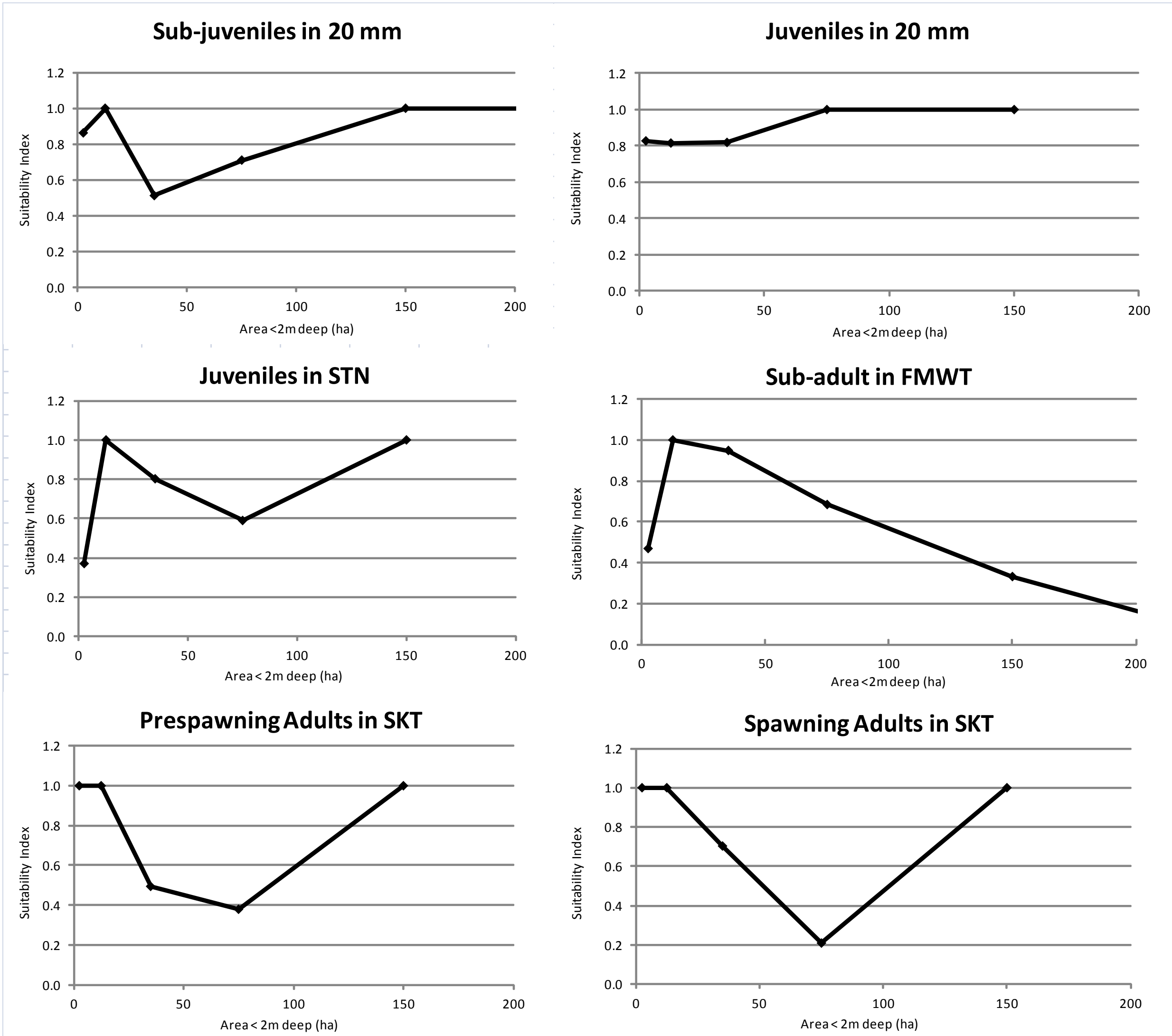

Figure S13. Habitat suitability Index curves for area of shallow (water within 1 km less than 2 meters deep) for various life stages of delta smelt derived from affinity analyses.

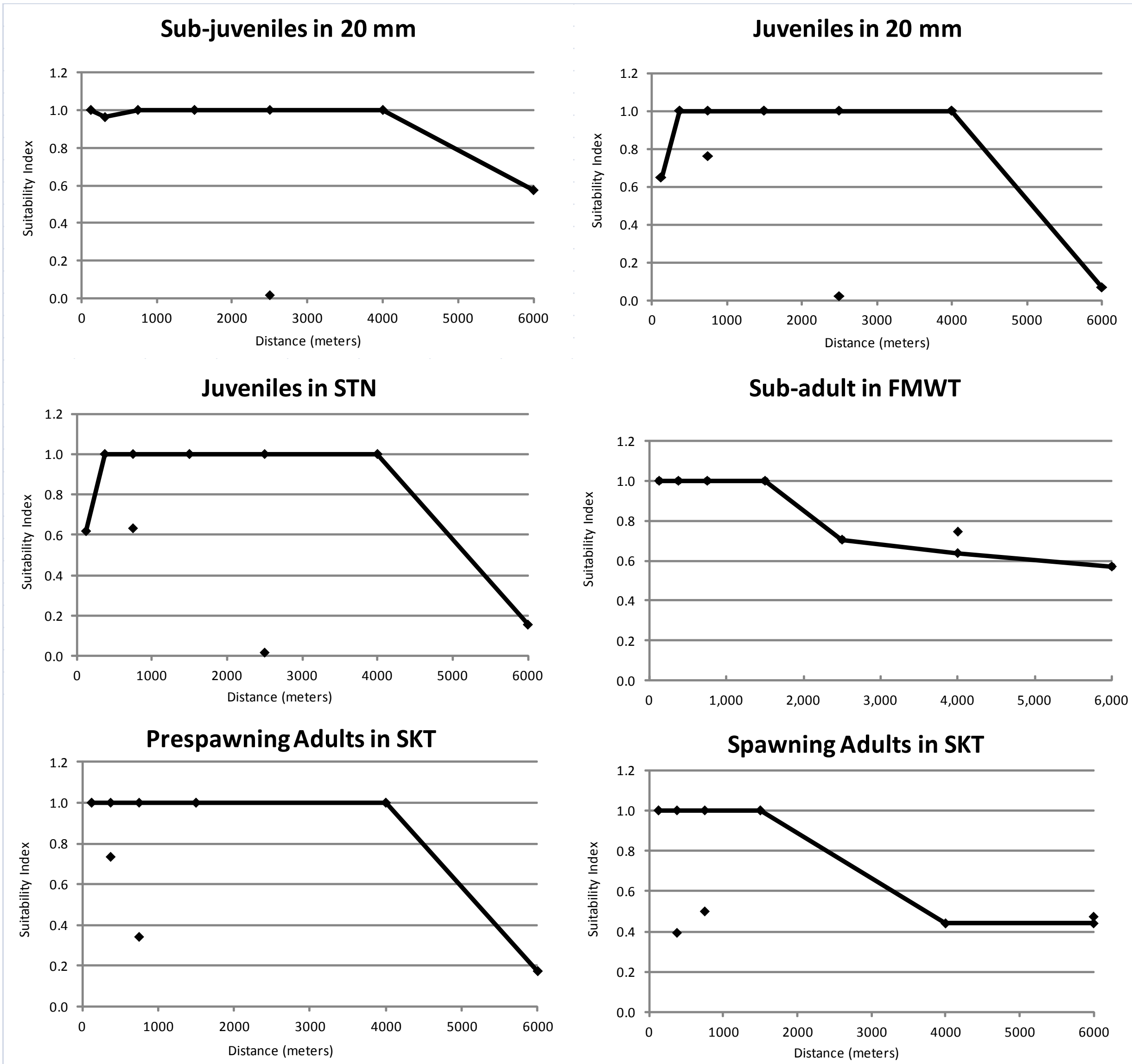

Figure S14. Habitat suitability Index curves for distance to large (>100ha) wetlands for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.