Eastward migration or marsh-ward dispersal: understanding seasonal movements by delta smelt

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ABSTRACT

Differing and confounding understandings of the seasonal movements of the delta smelt in the San Francisco estuary persist nearly two decades after its listing as threatened under the federal and state Endangered Species Acts. The U.S. Fish and Wildlife Service and Bureau of Reclamation have characterized the delta smelt as a species that migrates extensive distances from Suisun Bay and the confluence of the Sacramento and San Joaquin rivers in the fall and winter, eastward and upstream to the central and east Delta to spawn, with the next generation returning to downstream rearing areas in the following spring. This description of inter-seasonal movements by delta smelt stands in contrast to findings drawn from previous studies, which describe movements by pre-spawner delta smelt from open waters in bays and channels to adjacent marshlands and freshwater inlets. In an effort to resolve this disagreement over the movements of delta smelt, we use publically available data on its distribution drawn from trawl surveys to generate maps from which we infer seasonal patterns of dispersal. In the fall, prior to spawning, delta smelt are most abundant in Suisun Bay, the Sacramento and San Joaquin rivers confluence, the lower Sacramento River, and the Cache Slough complex. By March and April, the period of peak detection of spawning adults, relative densities in Suisun Bay and the rivers confluence have diminished in favor of higher concentrations of delta smelt in Montezuma Slough and the Cache Slough complex. A relatively small percentage of fish are observed in areas of the Sacramento River above Cache Slough. We conclude that inter-seasonal dispersal of delta smelt is more circumscribed than has been previously reported. This conclusion has profound implications for efforts to conserve delta smelt. Our findings support a conservation strategy for delta smelt that focuses on habitat restoration and management efforts for tidal marsh and other wetlands in north Delta shoreline areas directly adjacent to open waters that have been documented to support higher concentrations of the fish.

Keywords: delta smelt, distribution, dispersal, spawning migration, inter-seasonal movement.

Introduction

From assessments of gene flow to projections of metapopulation dynamics, virtually every essential aspect of conservation planning calls for an understanding of patterns of movement by targeted at-risk species. And, while a rough appreciation of dispersal exists for most protected species, the once-abundant delta smelt (*Hypomesus transpacificus*), which is endemic to central California's San Francisco estuary, is a species for which an absence of data on dispersal has fed controversy over appropriate conservation actions that are needed to recover the species and restore its habitats, and allocation of the resources required for its protection. Because the fish is small, nearly transparent, and preternaturally fragile, the movements of delta smelt have proven exceptionally difficult to track in the turbid waters of the estuary. So elusive is the fish throughout its annual life cycle, it actually has not been observed spawning in nature (Moyle 2002, Bennett 2005); and, while its distributional range has recently been resolved to the extent practicable using available surveys (Merz et al. 2011), its dispersal patterns within that range remain in doubt (but see Bennett 2005). Data from a series of trawl surveys in the San Francisco estuary suggest that different delta smelt life stages use different areas of the estuary's water bodies and channels; however, since delta smelt are not directly observed in those habitats and cannot readily be marked or tagged, the details of delta smelt movements have been the subjects of surmise (Sommer et al. 2011).

Two decades after the delta smelt received protection as a threatened species under the federal Endangered Species Act, uncertainties persist regarding distribution and dispersal across the estuary during its short, annual life cycle. But, while individual survey samples that capture delta smelt offer limited direct information regarding dispersal by the species, when the multiple trawler-based surveys in the San Francisco estuary that record the fish throughout its annual life cycle are viewed in sequence, evidence of its continuously shifting overall distribution becomes apparent. And, although the movements of individual delta smelt remain obscure, geographic patterns of its presence and absence, and its temporally and spatially shifting densities, can be gleaned from trawl surveys and used to infer inter-seasonal patterns in its movements.

Despite publically available long-term data sets on the distribution of the species, two dramatically differing perspectives have emerged in the literature and in federal planning documents and presentations regarding the movements of adult delta smelt prior to spawning. One perspective is provided by Bennett (2005), who noted that in "the fall, delta smelt gradually begin a diffuse migration landward to the freshwater portion of the Delta, and during wetter years to the channels and sloughs in Suisun Marsh and the lower Napa River." Bennett's description is consistent with that articulated by Moyle (2002 and Moyle et al. 1992), reflecting previous observations from focused surveys reported by Radtke (1966), Wang (1986, 1991), and Wang and Brown (1993). The narrative depiction that can be drawn from those studies is that of dispersal in multiple directions by pre-spawner delta smelt, from the bays, embayments, and channels of the estuary's low-salinity zone, to adjacent marshlands and freshwater inlets that support spawning, with juvenile fish from the next generation distributing themselves into adjacent open waters where they feed and grow for several months, then repeat the cycle of dispersal toward marshland and freshwater spawning locations.

The other perspective on delta smelt movement describes a uniform, upstream migration of delta smelt from open waters in western portions of the Delta's low-salinity zone toward its eastern freshwater limits. Department of the Interior agencies have described large-scale, seasonal, directional movement by delta smelt in a pair of maps; the first (Figure 1a) was presented by the U.S. Fish and Wildlife Service in a presentation to the National Research Council's Committee on Sustainable Water and Environmental Management in the California Bay-Delta (USFWS 2010). It illustrates a seasonally bimodal distribution of delta smelt in which the fish feeds and matures in the western Delta from the early spring to the late autumn and early winter, at which time pre-spawning adults migrate en masse east to a distinct eastern distribution for spawning. The next generation returns to previously occupied west estuary waters to repeat the cycle. The second map (Figure 1b) was offered in a draft document describing an adaptive management plan that was required to accompany the prescribed management actions in Service's biological opinion (USBR 2012). It shows an eastward shift in the distribution of delta smelt, but from a broader mid-year footprint in the western portion of the Delta toward a partially overlapping, more-eastern distribution just prior to spawning, followed by a return to the more western distribution by the next generation. Both maps were accompanied by discussions that described those seasonal shifts in distribution as migration events by spawning delta smelt. Combined these two maps can be viewed as a conceptual model of the distribution and migration of delta smelt, the validity of which can be assessed using data from multiple trawler-based surveys in the estuary.

Here we use state agency-generated survey data to produce maps of the distribution of delta smelt across seasons and to obtain an understanding of where delta smelt are most commonly found during each of their several recognizable life stages, both in an effort to determine which, if either, perspective on delta smelt dispersal is consistent with available data. By comparing the locations of season- and life-stage specific occurrence polygons, which include 95% of delta smelt sampled from five readily available fish surveys, we draw parsimonious inferences concerning inter-seasonal movements by the fish. We contrast our findings with those presented in a recent assessment of the spawning migration of delta smelt in the upper San Francisco estuary by Sommer et al. (2011).

We consider the relevance of information on delta smelt distribution and dispersal to the multiple conservation planning efforts in the Delta. Resource managers at the Department of the Interior have utilized and are utilizing the first perspective to inform their ongoing conservation planning efforts targeting the delta smelt (USFWS 2008, USBR 2012, BDCP 2013). Comprehensive planning includes recovery actions that directly target delta smelt, restoration efforts that seek to restore essential components of its diminished habitats, and management of Delta through flows, which have been controversially identified as a proximate cause in the decline of the listed species. Implications of the two dispersal perspectives for the types, locations, and prioritization of species recovery actions and habitat restoration activities are profound. The more localized, marsh-ward spawning dispersal phenomenon indicates the need for focused conservation actions in sub-regional context. In contrast, the long-distance, migration phenomenon would expose delta smelt to distinct suites of environmental stressors at either end of a either end of its putative migratory path, and a gauntlet of impacts during long distance movement from one geographic limit of its west-to-east range to the other, all of which presumably need address to realize species recovery.

We attempt to discern the validity of the federal agencies' conceptual model by addressing three de facto hypotheses that are implicit in the geographic details of their maps:

(1) Directional migration by delta smelt occurs in the late autumn and early winter from western and central portions of the estuary to areas in the eastern estuary that support spawning.
(2) In migrating seasonally to areas of the eastern Delta, delta smelt effectively vacate Suisun Bay and Suisun Marsh and do not spawn there.
(3) After spawning occurs, sub-juvenile delta smelt that make up the next generation are predominantly distributed across the central Delta.

We rely on agency-generated, life-stage-specific survey data on delta smelt to test these hypotheses and to draw inferences regarding the spatial distribution of delta smelt and likely patterns of its dispersal. We also consider how the loosely applied nomenclature of dispersal and the generous application of the term "migration" to the many manifestations of animal movement have combined to contribute to a confused narrative regarding the seasonal movements of delta smelt.

Methods

Data Sources and Treatment

Since it is not possible to track delta smelt directly, inferences regarding its inter-seasonal movements require an assessment of the distribution of the fish at each of its life stages. The California Department of Fish and Game carries out multiple surveys of fishes in the San Francisco estuary, returns from which include delta smelt in temporal samples that span the fish's life cycle. Surveys include the 20 mm Survey, Summer Tow-net Survey (STN), Fall Midwater Trawl (FMWT), and Spring Kodiak Survey, which sample extensive, partially overlapping areas of the estuary (within the area in Figure 2). Additionally, USFWS conducts Beach Seine surveys in widely separated areas in the Delta. The methods for those surveys have been documented previously (see 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). Each monitoring program survey effort is conducted during a different seasonal (time) period, with a different sampling frequency (monthly or bi-weekly), and at a varying number of stations (30-113 stations). By employing different gear and tools during different time periods, each survey effort serves to sample delta smelt of different sizes and during different life stages. It is important to note that the first four of the aforementioned ongoing surveys largely (but not exclusively) sample fishes from the open waters of the estuary, including its bays and channel midlines. Accordingly, throughout its range, delta smelt move outside of the survey stations to spawn, making available survey returns less than optimal for addressing delta smelt movements to access the shallow areas and freshwater inlets that all observers agree host spawning by the species.

Drawing from discussions of the life history of delta smelt by Moyle (2002) and Bennett (2005), we differentiated five separate delta smelt life stages -- larvae, sub-juveniles, juveniles, sub-adults, and mature adults (Table 1). We chose a 15-mm body length to differentiate between larvae and sub-juveniles, because at 16-18 mm delta smelt exhibit more developed fin structure and their swim bladders are filled, making them more mobile within the water column (Moyle 2002). We used 30-mm as the length threshold between sub-juveniles and juveniles, because this size is associated with a change in observed feeding regime (Moyle 2002). We chose 55-mm as the length that differentiates between juveniles and sub-adults/mature adults, because delta smelt growth demonstrably slows between 55 and 70 mm, presumably because most of their available energy is channeled toward gonadal development (Erkkila et al. 1950, Radtke 1966). Because the state of maturation of individual delta smelt is reported in the Spring Kodiak Trawl, we used reproductive stage to (further) subdivide mature adults into pre-spawners and spawners. Delta smelt in reproductive stages 1 to 3 for females, and stages 1 to 4 for males, were classified as pre-spawning adults; reproductive stage 4 in females and stage 5 in males were classified as spawning adults (J. Adib-Samii, CDFG, pers. comm.).

Although survey data are available for juvenile and adult delta smelt from the FMWT survey back to 1967, here we present survey results from 1987 onward in our comparisons of life-stage distributions, concordant with the introduction to the estuary of the Asian clam (*Potamocorbula amurensis*), which is believed to be responsible for major changes in the delta food web (Alpine and Cloern 1992, Greene et al. 2011, Nichols et al 1990, Winder and Jassby 2011). The 20-mm (tow-net) survey was first conducted in 1995, and was intended to provide data on larval, sub-juvenile, and juvenile delta smelt. Data from the Spring Kodiak trawl are available from 2002. We have not used data accrued from various supplemental sampling efforts that have recorded delta smelt, because such surveys were conducted for special purposes and were not necessarily consistent with programmatic protocols (R. Baxter, CDFG, pers. comm.). To avoid introducing anomalies that might be caused by the addition of new stations to established survey frames, when using data from any of the monitoring programs we only included sampling stations that were sampled consistently (that is, stations that were sampled in at least 90% of the years).

Distribution by Life Stage

We calculated the average CPUE of delta smelt for each life stage and station for all years by dividing the summed catches C of delta smelt for each life stage l, station s, and time period p in year y by the volume of water in cubic meters V that was sampled for each region and year, then multiplying by 10,000 to determine the catch per 10,000 m^3 for each life stage, region, and year:

[1] $$\text{CPUE}_{lspy} = \Sigma C_{lspy}/\Sigma V_{spy} \bullet 10000.$$

Then, the percentage of delta smelt observed at each station in each sampling period was calculated by dividing the result from equation [1] by the total across all stations for each pertinent period in each year (see Table 1). Finally, the average annual percentage of delta smelt for each life stage observed at each station was calculated as a simple average over all years.

While recognizing that the gear employed to sample the estuary's fishes varies in terms of catch efficiency, and that catch efficiency varies both between monitoring programs and within samples of each monitoring program (depending on a variety of factors, including the size of individual delta smelt), we did not attempt to adjust the results reported here for catch efficiency. As a result, we draw no conclusions regarding the census number of delta smelt, which can vary substantially in returns from different monitoring programs, and discordantly between life stages from within a individual monitoring program.

Our treatment of delta smelt catch data was limited to the observed distribution, rather than informed by population estimates. The latter would have required estimates of the volumes of the targeted bodies of water and reliance on the assumption that samples are representative of the density of fish throughout the water bodies. The validity of such an assumption may be questionable in a variety of circumstances, particularly when using Beach Seine data, since the demarcation between "beach habitat" and "open-water habitat" is inherently arbitrary.

To depict spatially the distribution of each life stage across all years sampled, we identified the fewest stations that accounted for 90% of the sampled fish, showing these as dark circles around the relevant station, and the next 9% as light circles (for example, Figure 3a). Stations that accounted for less than 0.2% of the observed distribution were considered *de minimis* and not depicted. The extent of the range of each survey is shown as a solid surrounding line. Areas without shading within the surrounding line support very few delta smelt.

To test the first hypothesis -- that there is a unidirectional movement by delta smelt toward eastern spawning areas in the Delta -- we looked for a net increase in the percentage of fish east of the rivers' confluence (east of stations 703 and 804), from the sub-adult life stage in September and October to the pre-spawning life stage in the subsequent January to May. For this hypothesis (and the second), we considered data from pre-spawning adults rather than spawning adults, having observed that the number of spawning adults sampled was far fewer (80% less) than the number of pre-spawning adults; spawning adults presumably move out of deeper, open waters where the monitoring stations are largely located. We tested the difference between the numbers of delta smelt in the two geographic areas using a one-tailed t-test, since the federal agencies presume the movement is unidirectional to the east.

To test the second hypothesis -- that delta smelt vacate the Suisun bay and marsh complex to spawn in eastern portions of the Delta -- we tested whether the percentage of pre-spawning adults in the area of the rivers confluence and further west (as identified above) were significantly different from zero. We used a one-tailed test since the percentage could not be negative.

To test the third hypothesis -- that sub-juvenile delta smelt are distributed predominantly across the central Delta in the spring -- we compared the percentage of sub-juveniles in the central delta with the percentage of sub-juveniles in all other areas. For this comparison we defined the central Delta to include stations 704 to 711, and 809 to 915. We focused on sub-juveniles, rather than juveniles, because according to the third hypothesis juvenile fish should be progressively moving to the lower Sacramento River and northern Suisun Bay areas. Length measurements of young delta smelt used data from the 20 mm survey to delineate sub-juveniles (see Table 1), and a one-tailed t-test was used to see if the percentage of sub-juvenile delta smelt in the central Delta was significantly greater than 50%.

Percentage data representing delta smelt distributions were arcsin$\sqrt{x}$ transformed prior to analyses (Zar 2010). Transformed values were checked for normality with a one-sample Kolmogorov-Smirnov test. A non-parametric Wilcoxson signed-rank test was used for data addressing the second hypothesis, since the data were not transformed to normality. A test for independence of data across years showed no first- or second-order temporal correlation in any of the data series. All t-tests (or non-parametric equivalents) were run as paired tests to account for year effects.

Based on the mapped distribution of delta smelt by life-stage and the results of the statistical analyses described above, we generated two synthetic maps, consistent with publically available survey data, which can be used to represent the locations of delta smelt at two key life stages -- 1) juveniles in early summer, as they initiate a protracted period of feeding, growth, and maturation prior to dispersal to spawning areas, and 2) mature adults at or immediately prior to spawning, which reflects the maximum extent of the dispersal that they experience associated with movement to spawning areas.

Results

Distribution of delta smelt by life stage

The distributions of multiple delta smelt life stages are provided in Figures 3a through 3f. During summer months the majority of delta smelt feed, grow, and mature in four adjacent geographic locations -- in Suisun Bay and Suisun Marsh (Montezuma Slough), at the confluence of the Sacramento and San Joaquin rivers, and in the lower Sacramento River (Figure 3a). Data from the Summer Tow-net surveys show that nearly 90% of the delta smelt sampled in summer are found in that circumscribed area (Table 2). Delta smelt are essentially absent from the east and south delta during this period. While it should be noted that prior to 2011 surveys in the summertime did not extend up the Sacramento River to habitat in the Cache Slough complex of river channels in the north, nor into the Napa River and its estuary west of the Delta, data from recent surveys strongly suggest that delta smelt are likely residents in those areas in the summer (Sommer et al. 2011).

Delta smelt continue to occupy the same general locations into the autumn, with more than 80% of the sampled fish resident in the same four areas of the estuary through November, and exhibit a substantial presence in the Cache Slough area (Figure 3b). Survey data do, however, suggest some shifts in areas occupied, with increases in the percentages of total delta smelt captured in north Suisun Bay and Montezuma Slough (Table 2). Based on returns from the Spring Kodiak Trawl from January through May, it appears that a trend toward increased delta smelt numbers in areas beyond the four summer population foci continues, and expands through the winter and into the spring, with occurrences and numbers beyond the mid-year core areas in all compass directions. In the winter and spring, Delta smelt extend to the northwest into the Napa River, are more frequent north in Suisun Marsh, are found to the northeast further up into the lower Sacramento River, are frequent in the Cache Slough area, and can be found in small numbers in the eastern Delta, including the lower San Joaquin River (Figure 3c).

Approximately 80% of pre-spawning adults are sampled from just three areas -- Montezuma Slough, the lower Sacramento River, and the Cache Slough complex (Table 2). Spawning adults in the Spring Kodiak trawl are generally observed in the same locations as their pre-spawning predecessors, although there is 80% fewer spawners than pre-spawners observed in the Spring Kodiak Trawl, providing evidence that some of the fish have moved away from open-water survey sites. Data from the Beach Seine suggests adults are found beyond the boundaries of the Spring Kodiak Trawl, with observations of delta smelt well up the Sacramento River. The differences between these two surveys suggests that the mid-channel Spring Kodiak Trawl under-samples spawning adults.

Data derived from Beach Seine surveys suggest that a northerly dispersal of spawning delta smelt adults is more frequent than dispersal in east or southeast directions (Figure 3d), with just incidental observations along the San Joaquin River. The sub-juveniles produced by these spawning adults are dispersed widely throughout the delta (Figure 3e), frequently to the limit of the range of monitoring, suggesting the reasonable possibility that more individuals exist beyond the geographic range depicted here. However, by summer (June and July), juveniles appear to have retreated to and are concentrated in areas where they will remain for the following six months: north and south Suisun Bay, the rivers confluence, and the lower Sacramento River, particularly around Decker Island, and notably, with an apparent demographic unit residing in the Cache Slough complex.

The lack of a consistent and comprehensive spatial overlap in the five fish surveys leaves several select points of delta smelt distribution and dispersal unresolved by available data. Strong inference can be used, however, to interpret from those information gaps. Regarding delta smelt occupancy of the Cache Slough area at the upper northeastern end of the range of the species -- on average 12% of the sub-adults in September and October were sampled there. Since these months precede dispersion of adults for spawning, and since Cache Slough was not routinely surveyed in the historical Summer Tow-net Survey, it might be reasonably concluded that a year-round population exists in near-freshwater circumstances in the Cache Slough area (Sommer et al. 2009, Sommer et al. 2011). The question of year-round occupancy of the Napa River is uncertain, because neither the Summer Tow-net survey nor the Fall Midwater Trawl survey samples upper reaches of the Napa River. Data from the 20mm survey indicate that spawning occurs well up the Napa River, but the lack of data from other surveys prevents a conclusion being drawn regarding a year-round delta smelt presence there.

When considering the six maps together, it is evident that a wide-ranging population, or a collection of (likely) interacting demographic units, of delta smelt can be found year-round in several areas of the Delta -- north Suisun Bay, the rivers confluence, the lower Sacramento River (around Decker Island), and in and adjacent to Cache Slough. The data used to generate those maps allow the first hypothesis -- that delta smelt move in an easterly direction from Suisun Bay at onset of spawning -- to be addressed. The percentages sub-adult delta smelt in the early fall (September and October) and pre-spawning adults that are located east of the rivers confluence are reported in Table 3. Rather than supporting the hypothesis that the relative abundance of delta smelt east of the rivers confluence increases with fish maturing to spawning condition, the percentage of the surveyed population there actually decreases; with an average of 24% fewer delta smelt being detected in surveys east of the confluence later in their life cycle (with the west-east difference significant at the 95% level).

The second hypothesis -- that delta smelt vacate Suisun Bay and the rivers confluence prior to spawning, was addressed by testing whether the percentage of pre-spawning delta smelt that reside at the rivers confluence or to the west, was not significantly different from zero. The presence of pre-spawning delta smelt at the rivers confluence and west of it averages 67%, which is significantly different from zero at the 95% level (Table 4). The hypothesis that delta smelt vacate the western portion of the estuary for purposes of spawning can be rejected.

The third hypothesis -- that subjuvenile delta smelt are found predominantly in the central Delta -- was also rejected. Data from the 20 mm trawl survey from 1995 to 2009 show that, on average, 39% of sub-juveniles were found in the central Delta, with the remaining 61% found in other locations (Table 5). Moreover, even the finding of 39% of subjuvenile delta smelt presence in the central Delta might be viewed as misleading. Stations 704, 705, 706, and 707 are located in the lower Sacramento River, from Decker Island downstream to the confluence (see locations in Figure 2). As observed on the series of Figure 3 maps, delta smelt are typically located in this area year round; therefore, much of their presence in the central Delta is not likely to be the result of seasonal dispersal. Also, this area is on the very northwest edge of the Delta, and is not usually considered part of the central delta. Removing these four stations from the central-Delta station grouping used in Table 5 reduces the average observed presence in the actual central Delta from 39% to just 12%.

Collectively, the rejection of the three hypotheses lends strong support to the perspective that spawning movement is multi-directional likely toward local freshwater inputs, rather than supporting the conceptual model describing a unidirectional eastward migration phenomenon advocated by the federal agencies.

A pair of synthetic maps depicts inter-seasonal dispersal by delta smelt (Figures 4a and 4b). Juvenile delta smelt are found in late spring 1) in the Napa River estuary, 2) from the western portion of Grizzly Bay through Suisun Bay to the Sacramento-San Joaquin rivers confluence, including Montezuma Slough and likely other larger channels in and about Suisun Marsh, 3) in areas along the lower Sacramento River extending up to and beyond the complex of small embayments and channels around Cache Slough and Liberty Island, and 4) perhaps further north upstream in the Sacramento Ship-channel. Delta smelt adults, just before and into the period of spawning, exhibit a distribution at moderate and greater densities 1) from the area around Suisun Bay and adjacent Montezuma Slough, 2) east up the lower Sacramento River into the area of Cache Slough and Liberty Island, and in lesser densities 3) in the San Joaquin River and its more northern tributaries, 4) in Montezuma Slough in Suisun Marsh, and 5) in the lower Napa River and its estuary. An east-west distributional disjunction between younger and older delta smelt in the Delta is not apparent; lesser shifts in the distribution of delta smelt within its geographic range between life stages are apparent.

Discussion

Five trawler-based fish surveys sample extensive, partially overlapping portions of the Sacramento-San Joaquin rivers delta and adjacent areas of the San Francisco estuary. The known distributional range of delta smelt has been largely informed by those surveys (Merz et al. 2012). Delta smelt range from the just east of the Carquinez Strait, through Grizzly and Suisun bays and adjacent Suisun Marsh, up-delta past the confluence of the Sacramento and San Joaquin rivers on the lower

Sacramento River, in the Cache Slough and Liberty Island complex of waterways, and in the Sacramento Ship Channel. Use of the Sacramento River north of Walnut Grove by delta smelt has been established from Beach Seine surveys. Occasional individuals can be found in eastern, southeastern, and southern portions of the Delta in the winter and spring; and very young juvenile delta smelt may be rather widely distributed across the Delta before settling into a largely northern and western Delta distributional range. Delta smelt have also been observed in a disjunct presence in lower reaches of the Napa River.

The pertinent issue addressed here is the distribution of delta smelt adults prior to spawning and their movement to locations at which spawning apparently occurs. Two alternative perspectives have been offered regarding movement by delta smelt from "rearing" areas to spawning locations. One describes a uniform, upstream migration by delta smelt from rearing areas in the west Delta to freshwater circumstances in the east. The other describes a diffuse dispersal from embayments and channels across the northern Delta, marshward to adjacent shoals and shorelines, where upland freshwater from winter and spring storms is delivered into delta waters. The two perspectives have bearing on the understanding of what constitutes habitat for delta smelt, its spatial extent, and temporal patterns of habitat occupancy, as well as determining the conservation actions that might benefit delta smelt, prioritization of those actions, and the identity of locations at which management actions might yield greatest benefits to delta smelt.

We found no evidence from data generated by seasonal surveys that delta smelt undertake unidirectional movement in late autumn and early winter toward eastern spawning areas in the Delta. Rather, spatial data are consistent with delta smelt dispersal from bay, embayment, and channel areas occupied by pre-spawner delta smelt toward freshwater inlets in nearby shores and marshes, with only a relatively small fraction of delta smelt exhibiting moving east to freshwater, including up and into the Sacramento or San Joaquin rivers. Mapped survey data indicate that most of the delta smelt in Suisun Bay head north to Montezuma Slough and Suisun Marsh to spawn. Fish in the Cache Slough complex of channels and wetlands stay in that general area. And delta smelt in the lower Sacramento River likely disperse in numerous directions -- up the Sacramento River, east toward the San Joaquin River, and west into Montezuma Slough. On average, more than 50% of pre-spawning adult delta smelt sampled are found in Montezuma Slough, more than 17% in the lower Sacramento River, and at least 12% in Cache Slough (Table 2). Given the spatial and temporal patterns of delta smelt in survey samples, it is likely that many pre-spawning delta smelt move inshore and out of the range of institutional monitoring surveys; but, survey data indicate that most adults that are ready to spawn remain in these same three general geographic areas. The data presented here contradict the depiction of delta smelt vacating the Grizzly and Suisun bay areas and the adjacent Suisun Marsh complex of wetlands to spawn in eastern portions of the Delta. In addition, survey returns appear to counter the assertion that sub-juvenile delta smelt are more frequent across the central Delta in the spring, rather than in northern portions of the estuary. Nearly two-thirds of young juvenile fish come from survey stations from Decker Island downstream to the Sacramento-San Joaquin rivers confluence. This finding is consistent with earlier observations of the distribution of young fish; citing Radtke (1966) and Wang (1986), two decades ago Moyle et al, (1992) reported "spawning apparently occurs along the edges of the rivers and adjoining sloughs in the western delta."

In sum, distribution maps generated from multiple, seasonal trawl surveys that regularly capture delta smelt, do not show the sort of annual, large-scale, population-wide migration event by delta smelt as has been described by the U.S. Fish and Wildlife Service and Bureau of Reclamation. The most parsimonious conclusion that can be drawn from surveys that sample delta smelt before, during, and after the winter-early spring spawning period is that the fish move from open-water circumstances to adjacent shoals and shoreline areas, which exhibit the physical attributes, especially freshwater inputs and appropriate substrates, that are necessary to support successful spawning.

Sommer et al. (2011) also recently investigated the annual dispersal patterns of delta smelt. That study invokes the centroid of the distribution of delta smelt (essentially the average position of delta smelt in temporal samples from a subset of Fall Midwater Trawl stations), suggesting that the "population" centroid moves slightly east in the very late autumn in relation to the location of the dynamic low-salinity zone in the estuary. The findings presented here clearly indicate that the centroid of the distribution of delta smelt is an inappropriate parameter for assessing the direction of the fish's inter-seasonal movement. The west to northeast orientation of Delta channels that are occupied by delta smelt perforce can provide for an eastward component to fish spawning movements that are substantively inshore, north (or south) toward freshwater inputs. Moreover, the presence of multiple demographic foci obviates the utility of defining a single delta smelt centroid, the geographic shifting of which can only misrepresent actual site-specific movement patterns. But, perhaps most importantly, the slight eastward shifts in the centroid of the distribution of delta smelt described by Sommer et al. do not support the assertion that delta smelt migrate en mass to the freshwater edge of the Delta's low-salinity zone – even a substantial shift in the distributional centroid of delta smelt with the onset of spawning would leave a large fraction of the fish far from the freshwater limits at the Delta's eastern boundary.

Absent evidence of eastward, "upstream" migration by delta smelt, Sommer et al. (2011) turn to previous studies for support, asserting "…details of its upstream migration have remained elusive (Swanson et al. 1998). Delta smelt are known to inhabit the oligohaline to freshwater portion of the estuary for much of the year until late winter and early spring, when they migrate upstream to spawn. After hatching, their young subsequently migrate downstream in spring towards the brackish portion of the estuary (Dege and Brown 2004)." This description of an "upstream" migration phenomenon is consistent with the large-scale, cross-Delta movement patterns depicted on the agency maps. But neither of the studies cited provide support for the assertion made. Swanson et al. (1998) studied delta smelt swimming performance, and while "winter migration" of delta smelt is mentioned, the authors offer no evidence of the extent of dispersal by the fish, nor would it be expected from a study of physiological phenomena. In reference to the existence of delta smelt migration, Swanson et al. cite Moyle et al. (1992). And, while Moyle et al. (1992) do refer to a “spawning migration” in their Figure 1, no data are provided in support. As for the Dege and Brown (2004) citation, it draws on sequential trawl survey returns to address seasonal shifts in the mean location of delta smelt specifically with respect to the position of the low-salinity zone in the Delta. But it does not offer data that addresses the issue of a spawning migration per se, noting “spawning occurs in freshwater with the larvae gradually moving downstream to the brackish water (1–7 parts per thousand) habitat of juveniles and adults.” There is little else in the study that gives an indication of the direction or magnitude of a spawning migration. Thus, the studies cited by Sommer et al (2011), and studies cited in those studies, do not offer any documentation of eastward, upstream migration by delta smelt.

Use of the term “migration” to characterize seasonal, spawning-related movements in delta smelt certainly has contributed to a confounded dispersal narrative. The federal resource agency maps describe movement phenomena that meet the vernacular use of the term migration, with lots of fish moving extensive distances across the Delta. And, Sommer et al. (2011) used the term in asserting that a long-distance west-to-east dispersal phenomenon exists. But, Moyle (2002) and Bennett (2005) also referred to migration in describing delta smelt moving from open waters to adjacent shorelines – a not quite commonplace use of the term. Migration evokes a picture of long distance unidirectional movement to most observers, but in strict technical usage it is not the distance, rather the intent or purpose of the act of dispersing, that differentiates migration from other dispersal events (Dingle and Alistair Drake 2007, Lack 1968, Ramenofsky and Wingfield 2007). Wilcove (2006) in considering migration as a phenomenon worthy of conservation attention notes that animals “are often on the move, and not all of their wanderings fall into the category of migration.” Wilcove differentiates migratory movements from “daily searches for food and shelter” or “the dispersal movements of offspring, as they establish their own territories.” Notwithstanding the distances involved, he considers “seasonal back and forth journeys between two sites,” including those “spread out between generations” as meeting the definition of migration. Hence, while the term migration conjures up for many a picture of songbird flights from boreal forests to far-distant tropical winter refuges, it is not technically incorrect to invoke the term migration to describe the delta smelt’s far less ambitious dispersal from open waters to adjacent shorelines. That considered, we have used the term dispersal to reflect the not-coherent seasonal movement of the fish between rearing and spawning areas, and to differentiate such movements from the long-distance, unidirectional movements that are associated with certain other fish and wildlife species (including the several salmon runs with which delta smelt seasonally co-occur).

The findings presented here regarding seasonal dispersal have implications to the understanding of delta smelt ecology and behavior. Federal agency maps (in Figure 1) suggest that delta smelt exist as an open, undifferentiated population in the Sacramento-San Joaquin Delta (with a possibly disjunct demographic unit in the Napa River estuary). An annual, east-west migration of delta smelt would serve to provide contact among and mixing of individuals into a single (truly) panmictic population. But, the presence of four or more geographically discontinuous delta smelt spawning foci in the Delta, and, absent mass directional movements, a different demographic picture is indicated. Substantial demographic mixing is certain in such a scenario, but at least within each generation, exchange of individuals from areas of the western Delta (Suisun Bay and marshes) and eastern Delta (Cache Slough and neighboring areas) is likely to be limited; while allowing for the stepping-stone exchange necessary to genetically tie the demographic units of delta smelt east of the Carquinez Strait (see Fisch et al. 2011).

In light of the spatial and temporal patterns of delta smelt distribution presented here, characterization of delta smelt habitat. Extensive portions of the areas depicted on the agency maps as being seasonally occupied, hence providing habitat for delta smelt, appear to support a very small fraction of the overall numbers of the species, and then only for limited periods of the year (see Figure 4 in Merz et al. 2011). According to survey data, much of the area in the large eastern polygon on the two agency maps is infrequently occupied and currently may not provide habitat for delta smelt at all. At the same time, some areas of the west Delta, which have explicitly been considered to have limited or intermittent habitat quality (see Armor et al. 2006), appear to host delta smelt that are preparing to spawn, and those areas and adjacent channels appear to be more consistently occupied by delta smelt that previously described.

These and other distributional insights that can be gleaned from the distribution maps presented here are worthy of consideration by conservation planners and resource managers. The distribution of delta smelt during each of the life stages serves to define the suite of environmental stressors that may affect them. That a substantial portion of the estuary's delta smelt spawners are found in Suisun Marsh, but a small fraction of the youngest delta smelt are subsequently there, suggests a need for close examination of environmental stressors in that area. An ambitious effort to restore tidal marshes and wetlands in the Delta, which are believed to contribute to producing the prey that feed delta smelt, has targeted candidate locations for habitat restoration efforts (BDCP 2013). Available distribution data and the dispersal phenomena that can be inferred from them strongly suggest that marshland restoration efforts would be best directed and prioritized to areas within and between the foci of occurrences of delta smelt in the north Delta. The lack of evidence that delta smelt make an extensive easterly migration to spawn should inform the selection of locations (and prioritization) for restoration targets, with recognition that efforts to construct or rehabilitate habitats for delta smelt should be designed to support local demographic units, not seasonal migrants. Furthermore, a spatially explicit interpretation of inter-seasonal movement in delta smelt has implications in assessing the effects of contaminants, including ammonium loading into the Delta system, on delta smelt. Data and models suggest that ammonium discharges contribute to altered nutrient ratios, with effects on the composition and abundances of phytoplankton that support the zooplankton prey base that delta smelt depend, perhaps leading to disruption of the food web and local declines in fish numbers (Glibert 2010, Glibert et al. 2011). The maps presented may indicate that certain subareas of the Delta that are unoccupied or occupied at low densities or intermittently by delta smelt may suffer from chronic poor nutrient and prey conditions, therefore, may constitute lower-quality habitat. Restoration efforts in such areas that do not address contaminant inputs to the system may be unlikely to deliver the intended benefits to delta smelt.

The maps presented here indirectly address Sommer et al.'s (2011) concern regarding the effects that entrainment of delta smelt at water export facilities in the south Delta may have on the species' status and trends, and indicate that conclusions regarding population-level effects of entrainment at export pumps may warrant reevaluation (see Grimaldo et al. 2009). While salvage samples at export pumps demonstrate that delta smelt are at least intermittently entrained, the assertion that mortality from entrainment is frequently large or is sporadically so (see Kimmerer 2008, Miller 2011, Kimmerer 2012), therefore consequential to the status and trends of delta smelt, is not so clear (and, consider Castillo et al. 2012). While relatively wide dispersal of larvae and very young juvenile delta smelt away from natal spawning areas is suggested from available distribution data, hence some proportion of the very youngest delta smelt may be lost at the pumps, the contention that large numbers of "upstream"-migrating delta smelt pass perilously close to the export facilities or are drawn to them during annual, long-distance spawn movements seems not to be supported by available survey data. .

Using available survey data, we have presented a picture of the distribution and dispersal of delta smelt prior to spawning that is complex. A diffuse collection of delta smelt population foci exist in and adjacent to the northern Delta's open waters, individuals from which undertake diffuse landward movements to spawn. The diffuse movements suggested by the seasonal distribution maps presented here are consistent with the long-understood concept that has delta smelt maturing in the estuary's brackish waters and spawning in freshwater circumstances. The maps offer no support for a unidirectional, easterly spawning migration by delta smelt from open waters in the west of the Delta to fresher waters to the east. The alternative conceptual model of delta smelt spawning movements described here, and supported by earlier studies and inferences, indicates a need to re-evaluate the relative importance of the environmental stressors that are acting to reduce the numbers of delta smelt and appropriate recovery measures that should be taken in efforts to conserve it.

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Table 1. *Delineation of life stages used to examine spatial dispersion of delta smelt. 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 California 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

Life stage	Monitoring Program	Life Stage Distinction	Time Period	Years of data used in this study
Sub-juveniles	20-mm	≥ 15, <30mm	Apr-Aug	1995-2012
Juveniles	20-mm	30-55 mm	May-Aug	1995-2012
Juveniles	STN	30-55 mm	Jun-Aug	1987-2011
Sub-adults	FMWT	> 55 mm	Sep-Oct, Nov, Dec	1987-2012
Mature Adults: Pre-spawning	Kodiak	Reproductive stages: females 1-3, males 1-4	Jan-May	2002-2012
Mature Adults: spawning	Kodiak	Reproductive stages: females 4, males 5	Jan-May	2002-2012
Mature Adults: spawning	Beach Seine		Mar-Apr	1987-2009

Table 2. *Average distribution of delta smelt observed in IEP monitoring surveys by location.*

Life-stage	Sub-juvenile	Juvenile	Juvnile	Sub-adult	Sub-adult	Sub-adult	Prespawn Adult	Spawning Adult	Adult	Spawning Adult	Prespawn & Spawn
Period	All	All	Jun-Aug	Sep-Oct	Nov	Dec	Jan-May	Jan-May	Mar-Apr		
Survey	20mm	20mm	STN	FMWT	FMWT	FMWT	Kodiak	Kodiak	Beach Seine	Combined	
San Pablo Bay											
323	0.0%	0.0%	0.0%	0.1%	0.0%	0.1%					
Napa River											
340	1.3%	0.5%	0.9%	0.0%	0.0%	0.0%	2.0%	4.3%		2.7%	2.7%
342	0.5%	0.7%									
343	1.2%	0.7%									
344	1.0%	0.7%									
345	2.3%	1.3%									
346	3.4%	1.6%									
Subtotal	9.7%	5.5%	0.9%	0.0%	0.0%	0.0%	2.0%	4.3%		2.7%	2.7%
Carquinez Straight											
405	0.2%	1.9%	1.9%	1.6%	0.0%	0.1%	0.2%	0.0%		0.0%	0.0%
411	1.5%	1.8%	0.7%	0.8%	0.4%	0.3%	0.4%	0.1%		0.1%	0.1%
418	0.3%	1.1%	2.4%	2.2%	2.2%	0.5%	0.3%	0.4%		0.2%	0.2%
Subtotal	1.9%	4.9%	5.0%	4.7%	2.6%	0.9%	0.9%	0.5%		0.3%	0.3%
South Suisun Bay											
501	0.7%	2.9%	3.3%	1.5%	1.5%	6.8%	1.8%	0.3%		0.2%	0.2%
504	2.5%	1.0%	1.6%	2.0%	0.3%	0.6%	0.6%	0.2%		0.1%	0.1%
508	1.9%	3.6%	5.4%	6.9%	2.8%	2.4%	1.1%	0.6%		0.4%	0.4%
Subtotal	5.1%	7.5%	10.3%	10.4%	4.6%	9.8%	3.5%	1.2%		0.7%	0.7%
Montezuma Slough											
606	3.6%	1.5%	0.8%	2.9%	7.6%	15.7%	21.7%	14.9%		9.4%	9.4%
609	5.2%	1.7%	1.4%				26.6%	10.6%		6.7%	6.7%
610	3.8%	1.5%	1.0%	0.2%	0.2%	1.5%	2.1%	1.4%		0.9%	0.9%
Subtotal	12.5%	4.7%	3.2%	3.1%	7.8%	17.3%	50.4%	26.9%		17.0%	17.0%
North Suisun Bay (including Grizzly & Honker Bays)											
513	3.6%	6.2%	9.0%	9.1%	8.8%	4.6%	1.2%	1.9%		1.2%	1.2%
602	3.6%	16.2%	15.5%	4.1%	1.2%	4.1%	1.4%	0.5%		0.3%	0.3%
519	1.8%	7.0%	8.9%	2.9%	7.3%	16.0%	4.9%	2.5%		1.6%	1.6%
Subtotal	9.0%	29.4%	33.4%	16.1%	17.3%	24.7%	7.5%	5.0%		3.1%	3.1%
Confluence											
520	3.8%	2.3%	1.7%								0.0%
703	7.1%	7.3%		10.3%	8.4%	6.5%			1.5%	0.6%	0.6%
801	2.8%	1.7%	2.2%	1.3%	0.4%	0.2%	0.8%	0.3%		0.2%	0.2%
804	3.4%	0.9%	1.4%	0.5%	0.5%	0.1%	0.9%	0.2%	0.0%	0.1%	0.1%
Subtotal	17.1%	12.2%	5.3%	12.1%	9.3%	6.7%	1.7%	0.6%	1.5%	0.9%	0.9%
Lower Sacramento River (Decker Is)											
704	9.8%	16.5%	19.0%	15.2%	16.3%	9.7%	8.1%	8.0%		5.0%	5.0%
705	1.9%	0.5%									0.0%
706	11.4%	9.7%	15.4%	17.8%	18.6%	13.8%	6.5%	2.3%		1.5%	1.5%
707	3.8%	1.5%	5.3%	6.1%	13.3%	7.0%	2.7%	9.2%	27.2%	16.5%	16.5%
Subtotal	26.8%	28.0%	39.7%	39.1%	48.2%	30.5%	17.3%	19.5%	27.2%	23.0%	23.0%

Table 2. continued.

Life-stage	Sub-juvenile	Juvenile	Juvnile	Sub-adult	Sub-adult	Sub-adult	Prespawn Adult	Spawning Adult	Adult	Spawning Adult
Period	All	All	Jun-Aug	Sep-Oct	Nov	Dec	Jan-May	Jan-May	Mar-Apr	
Survey	20mm	20mm	STN	FMWT	FMWT	FMWT	Kodiak	Kodiak	Beach Seine	Combined
Cache Slough Complex										
711	0.1%	0.0%	0.0%	5.2%	1.4%	3.4%	0.2%	3.5%	10.6%	6.3%
712							0.0%	0.5%		0.3%
713							1.0%	4.5%		2.9%
715							4.0%	9.5%		6.0%
716	5.5%	6.5%		7.3%	5.2%	2.7%	7.2%	18.1%	5.7%	13.7%
719										
798										
Subtotal	5.6%	6.5%	0.0%	12.4%	6.6%	6.1%	12.3%	36.1%	16.3%	29.2%
Upper Sacramento										
717									5.5%	2.2%
724									2.2%	0.9%
735									4.8%	1.9%
736									11.6%	4.5%
749									19.0%	7.5%
Subtotal							0.0%	0.0%	43.1%	16.9%
Lower San Joaquin River										
802				1.6%	2.0%	1.4%				0.0%
809	5.4%	0.7%	1.8%	0.2%	1.0%	1.8%	2.8%	2.9%	0.0%	1.8%
812	1.8%	0.1%	0.1%	0.1%	0.6%	0.4%	0.6%	1.5%		1.0%
815	1.9%	0.0%	0.2%	0.0%	0.0%	0.0%	0.3%	1.0%		0.6%
Subtotal	9.1%	0.8%	2.1%	1.9%	3.6%	3.7%	3.7%	5.5%	0.0%	3.4%
South Delta										
901	0.8%	0.1%								
902	0.7%	0.1%		0.0%	0.0%	0.0%	0.2%	0.3%	0.0%	0.2%
914	0.3%	0.0%		0.0%	0.0%	0.0%			0.0%	0.0%
915	0.2%	0.0%		0.0%	0.0%	0.0%			0.0%	0.0%
918	0.2%	0.0%		0.0%	0.0%	0.0%				
Subtotal	2.2%	0.1%	0.0%	0.0%	0.0%	0.0%	0.2%	0.3%	0.0%	0.2%
East Delta										
906	0.5%	0.0%		0.0%	0.0%	0.0%			0.1%	0.0%
910	0.1%	0.1%		0.0%	0.0%	0.0%			0.1%	0.0%
912	0.0%	0.1%		0.0%	0.0%	0.0%			0.0%	0.0%
919	0.2%	0.1%		0.0%	0.0%	0.0%			0.2%	0.1%
920										
921										
922									2.5%	1.0%
923									4.2%	1.6%
Subtotal	0.9%	0.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	7.0%	2.8%
Total	100%	100%	100%	100%	100%	100%	99%	100%	95%	100%

Table 3. *Percentage of delta smelt sub-adults located east of the confluence in September and October in the FMWT compared with the percentage of pre-spawning adults in the subsequent Spring Kodiak Trawl.*

Cohort Year	Percentage east of confluence during Sep-Oct in FMWT	Percentage East of confluence during subsequent Jan-May in Kodiak Trawl	Change
2001	90.9%	18.1%	-72.8%
2002	52.7%	61.4%	8.7%
2003	83.3%	17.2%	-66.1%
2004	93.3%	28.2%	-65.1%
2005	76.0%	18.4%	-57.6%
2006	40.9%	26.2%	-14.7%
2007	23.8%	75.3%	15.5%
2008	73.3%	57.6%	-15.7%
2009	62.5%	2.0%	-60.5%
2010	34.1%	27.6%	-6.5%
2011	4.7%	35.8%	31.1%
Average	57.8%	33.4%	-24.4%
Std Dev.	29.1%	22.2%	43.1%

Table 4 -- *Percentage of delta smelt pre-spawning adults located at the confluence and west of it in the Spring Kodiak Trawl.*

Year	Pre-spawning Adults Jan-May
2002	81.9%
2003	38.6%
2004	82.8%
2005	71.8%
2006	81.6%
2007	73.8%
2008	24.7%
2009	42.4%
2010	98.0%
2011	72.4%
2012	64.2%
Average	66.6%
Std Dev	22.2%

Table 5. *Percentage of delta smelt sub-juveniles located in the central Delta, using data from the 20mm survey and life stage delineations from Table 1.*

Year	*Central Delta 704-711, 809-915*
1995	*2.3%*
1996	*8.8%*
1997	*69.4%*
1998	*1.2%*
1999	*29.1%*
2000	*33.8%*
2001	*85.4%*
2002	*70.3%*
2003	*34.7%*
2004	*69.4%*
2005	*6.9%*
2006	*1.4%*
2007	*77.2%*
2008	*80.0%*
2009	*59.7%*
2010	*33.5%*
2011	*1.0%*
2012	*31.9%*
Average	*38.7%*

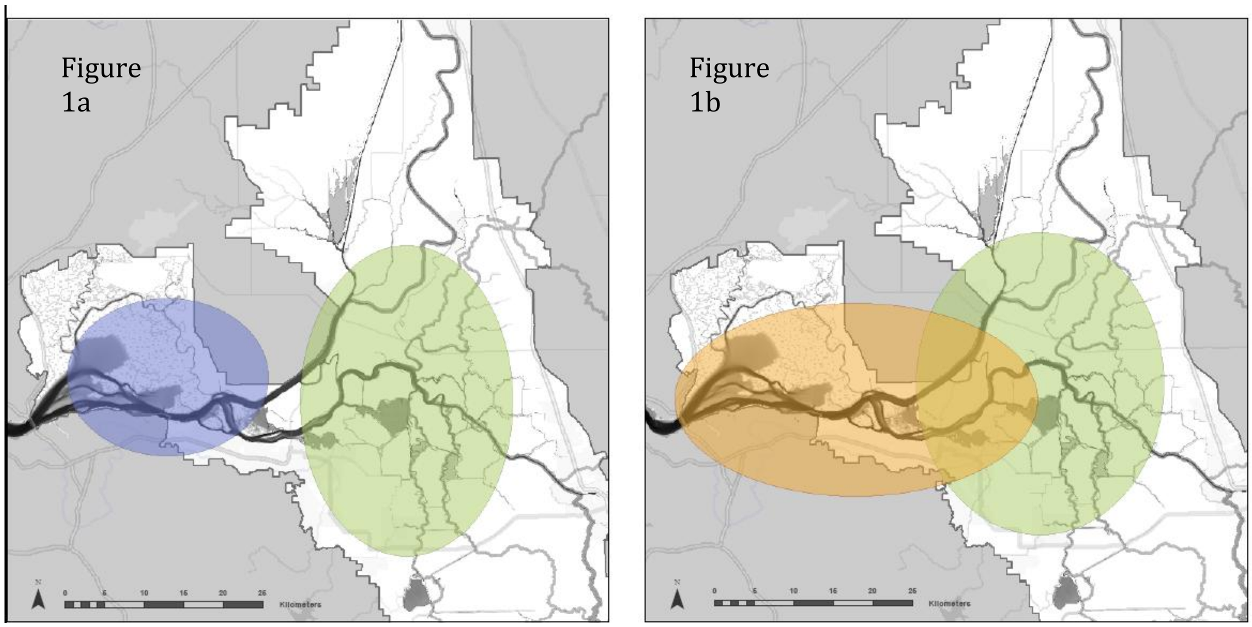

Figure 1. *Conceptual mapped distributions of and inferred seasonal dispersal by delta smelt in the San Francisco estuary redrawn from a presentation by the U.S. Fish and Wildlife Service (2010) -- left panel -- and a guidance document from U.S. Bureau of Reclamation (2012) -- right panel. The figure (a) portrays a migration of adult delta smelt from the Suisun Bay and the area of the Sacramento-San Joaquin rivers confluence (blue oval) to the central Sacramento-San Joaquin Delta in the winter and spring (green oval) prior to spawning. . Offspring migrate back from the central Delta, returning to the western distributional footprint by summer. The figure (b) depicts a shift of individuals eastward from a larger pre-spawning distribution from edge of Suisun Bay in the west to up into the lower Sacramento and San Joaquin rivers to the east (orange oval) to the central delta (green oval) where spawning presumptively occurs.*

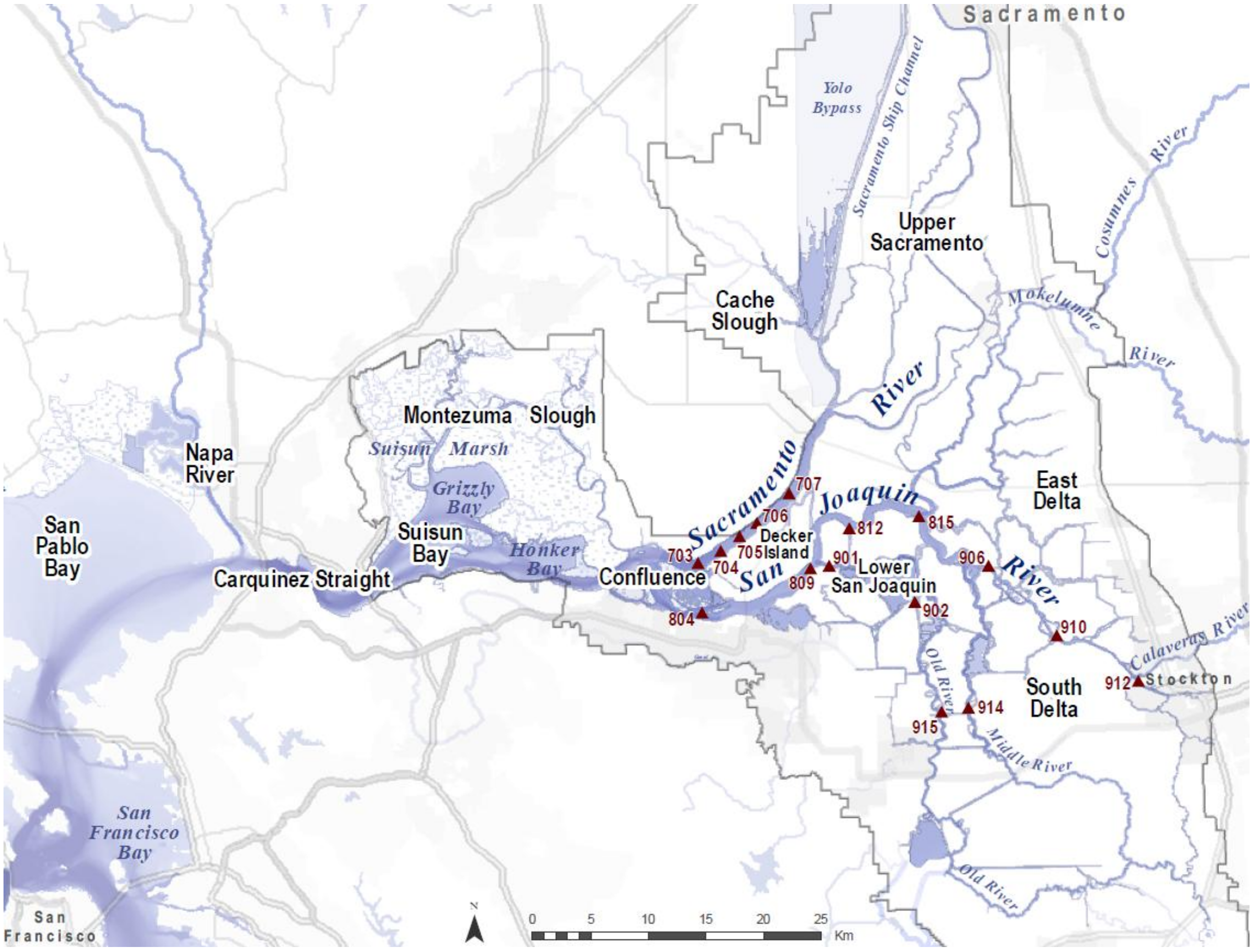

Figure 2. *The San Francisco estuary, including features and geographic designations referenced and described throughout this presentation. Numerical designations accompanying triangles identify trawl survey locations referenced in the text.*

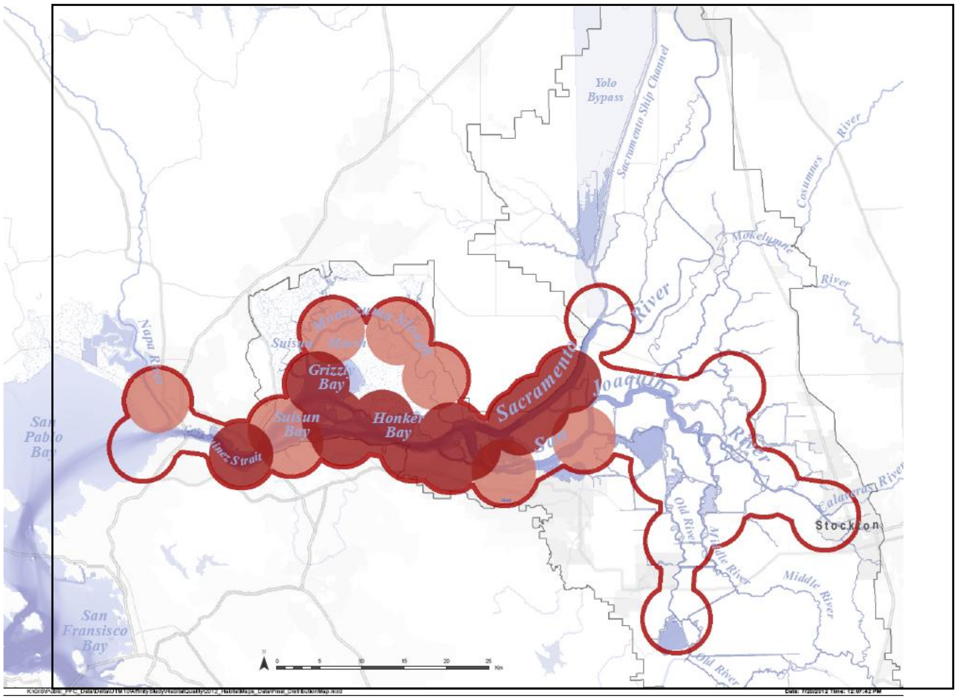

Figure 3a. *Distribution of delta smelt juveniles in summer (July) in the Summer Tow-net Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.*

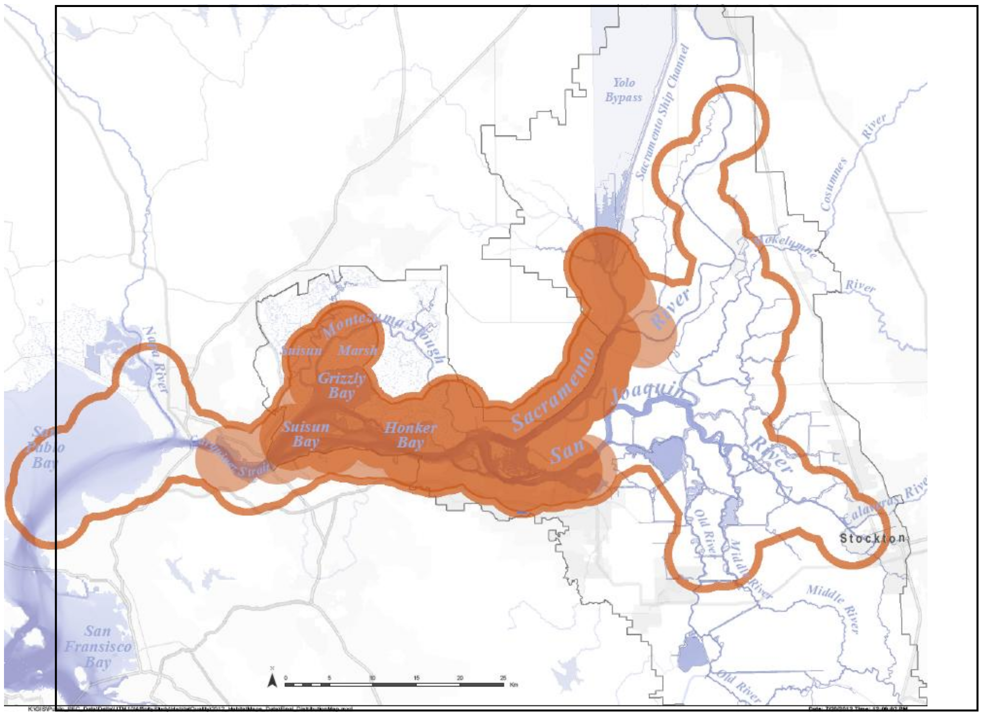

Figure 3b. *Distribution of delta smelt sub-adults in fall (September to November) in the Fall Midwater Trawl. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.*

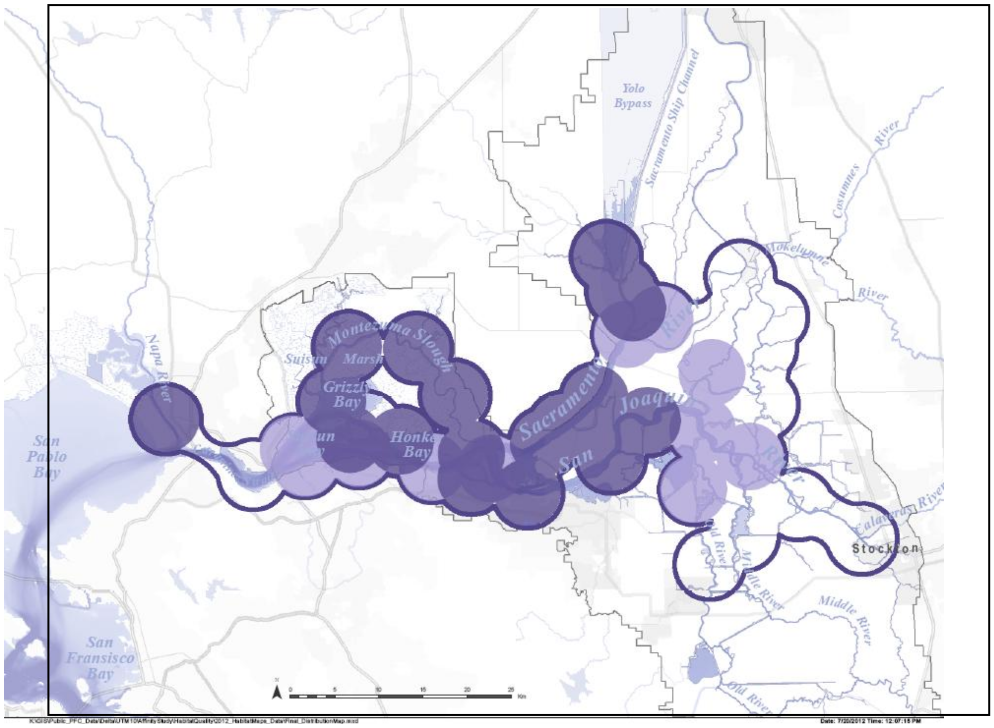

Figure 3c. *Distribution of delta smelt adults in winter (Jan to May) in the Spring Kodiak Trawl. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.*

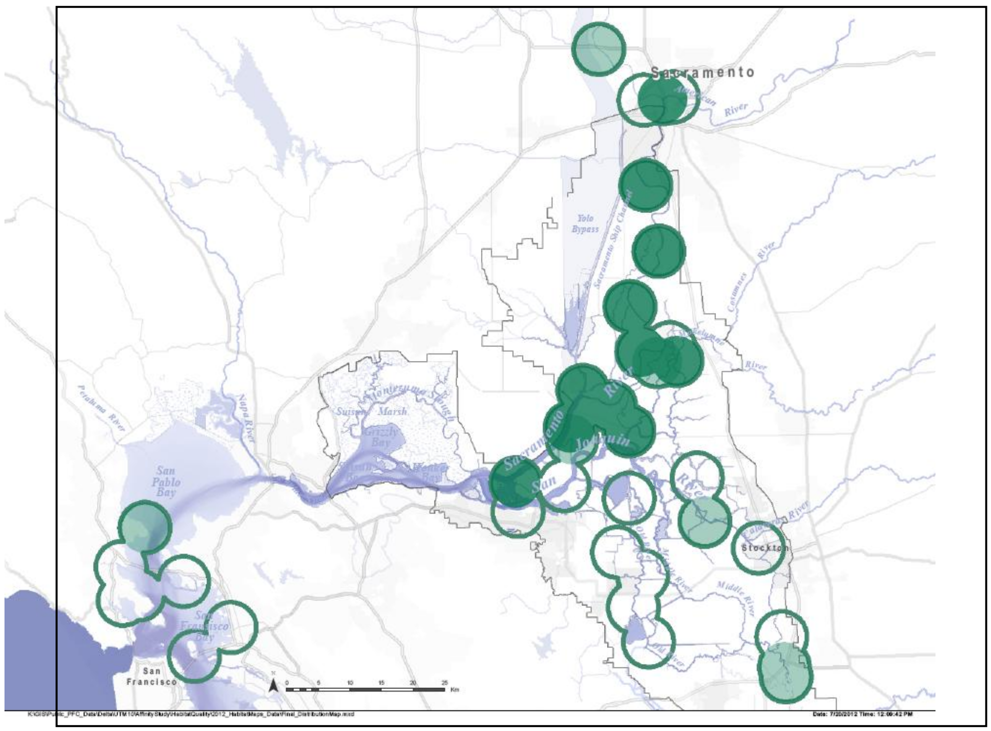

Figure 3d. *Distribution of delta smelt adults in spring (March to April) from the Beach Seine Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.*

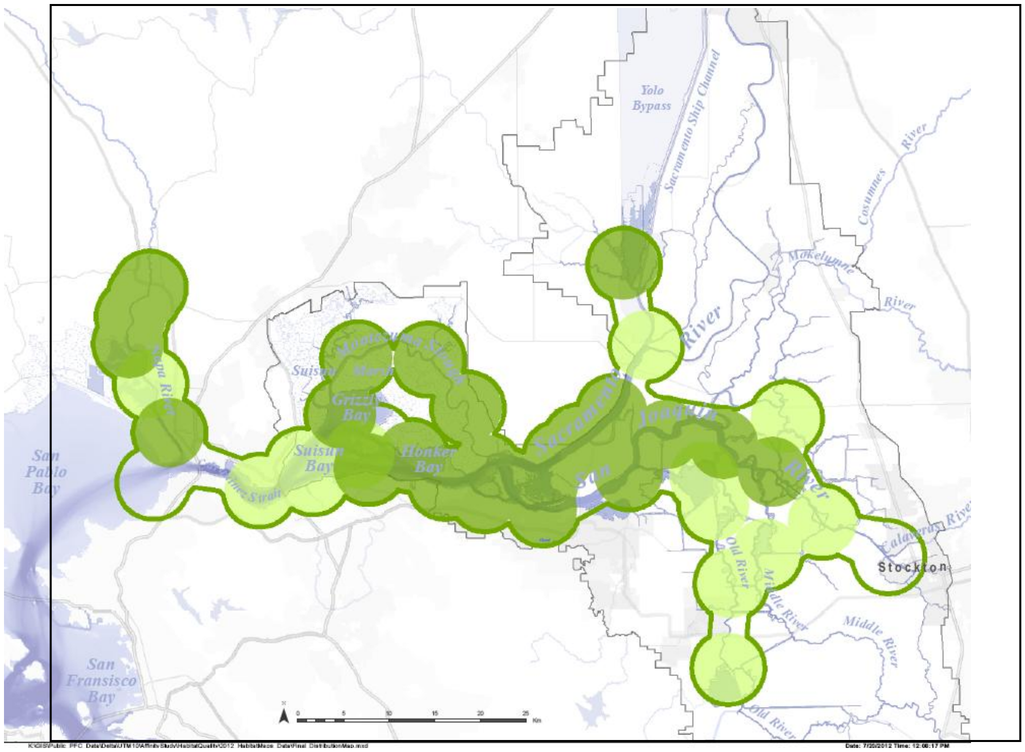

Figure 3e. *Distribution of delta smelt sub-juveniles in spring (April to June) in fall the 20 mm Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.*

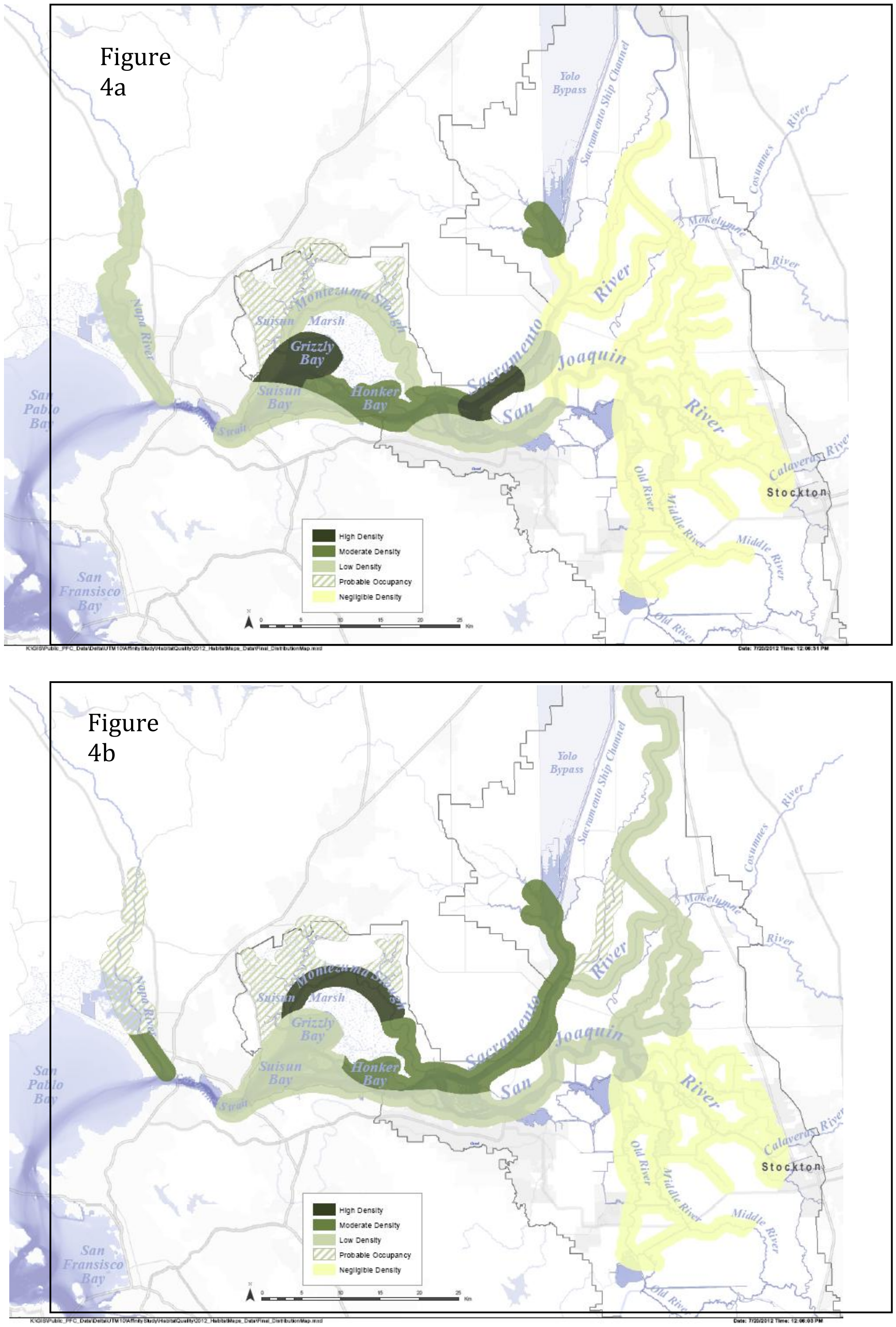

Figure 4. *Synthesized distribution of delta smelt in summer/fall (top panel) before dispersion to spawning areas, and in spring (bottom panel) after dispersion. The dark areas show the predominant range during each period. The high and moderate density areas combined account for 90%, on average, of the observed presence of delta smelt.*