Title

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Eastward Migration or Marshward Dispersal: Understanding Seasonal Movements by Delta Smelt

Dennis D. Murphy[1] and Scott A. Hamilton[2]

ABSTRACT

Differing and confounding understandings of the seasonal movements of the delta smelt (*Hypomesus transpacificus*) in the San Francisco Estuary persist nearly 2 decades after its listing as threatened under the federal and state endangered species acts. The U.S. Fish and Wildlife Service and the U.S. Bureau of Reclamation have characterized the delta smelt as a species that migrates extensive distances from Suisun Bay and the Sacramento and San Joaquin rivers confluence in the fall and winter, eastward and upstream to the central and east Sacramento–San Joaquin Delta to spawn, with the next generation returning to downstream rearing areas in the following spring (OCAP Technical Support Team unpublished; USBR 2012). This description of inter-seasonal movements of 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 proximate marshlands and freshwater inlets (e.g., Moyle et al. 1992; Bennett 2005). In an effort to resolve this disagreement over the movements of delta smelt, we use publicly available data on its distribution drawn from trawl surveys to generate maps from which we infer seasonal patterns of dispersal. In the fall, before 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 real-world 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.

KEY WORDS

delta smelt, *Hypomesus transpacificus*, distribution, dispersal, spawning migration, inter-seasonal movement

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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 (estuary), is a species for which an absence of data on dispersal has fed controversy over appropriate conservation actions needed to recover and restore its habitats, and over the allocation of resources required to protect it. 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 estuary suggest that different delta smelt life stages use different areas of the estuary's water bodies and channels. However, since with few exceptions, delta smelt are not directly observed in those habitats and cannot readily be marked or tagged, many uncertainties remain about the details of delta smelt movements (Sommer et al. 2011).

Individual survey samples that capture delta smelt offer limited direct information regarding dispersal by the species. Sequential analysis of data from multiple trawl-based surveys parsed by life-stage can provide evidence of continuously shifting populations. 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 the sequential trawl surveys and used to infer inter-seasonal patterns in its movements.

Based on publicly available long-term data sets on the distribution of the species, two dramatically differing perspectives have emerged in the literature and in federal agency planning documents and presentations on adult delta smelt movement before 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). These studies depict 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. Juvenile fish that emerge to become the next generation distribute themselves into adjacent open waters where they feed and grow for several months, followed by a repeat of the cycle of dispersal toward marshland and freshwater spawning locations.

The other perspective on delta smelt movement is described by Sommer et al. (2011) as a uniform, upstream migration from open waters in western portions of the Delta's low-salinity zone toward its eastern freshwater limits. Department of the Interior agencies illustrate the premise of large-scale, seasonal, directional movement by delta smelt in a pair of maps. Figure 1A illustrates a seasonally bimodal distribution of delta smelt in which the fish feeds and matures in the western Delta and Suisun Bay from the early spring to the late autumn and early winter, at which time pre-spawning adults undergo a unidirectional migration to a distinct eastern distribution for spawning (OCAP Technical Support Team unpublished). The next generation returns to previously occupied west estuary waters to repeat the cycle. The second map (Figure 1B) 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 before spawning, followed by a return to the more western distribution by the next generation (USBR 2012). The presentations that accompanied both maps described those seasonal shifts in distribu-

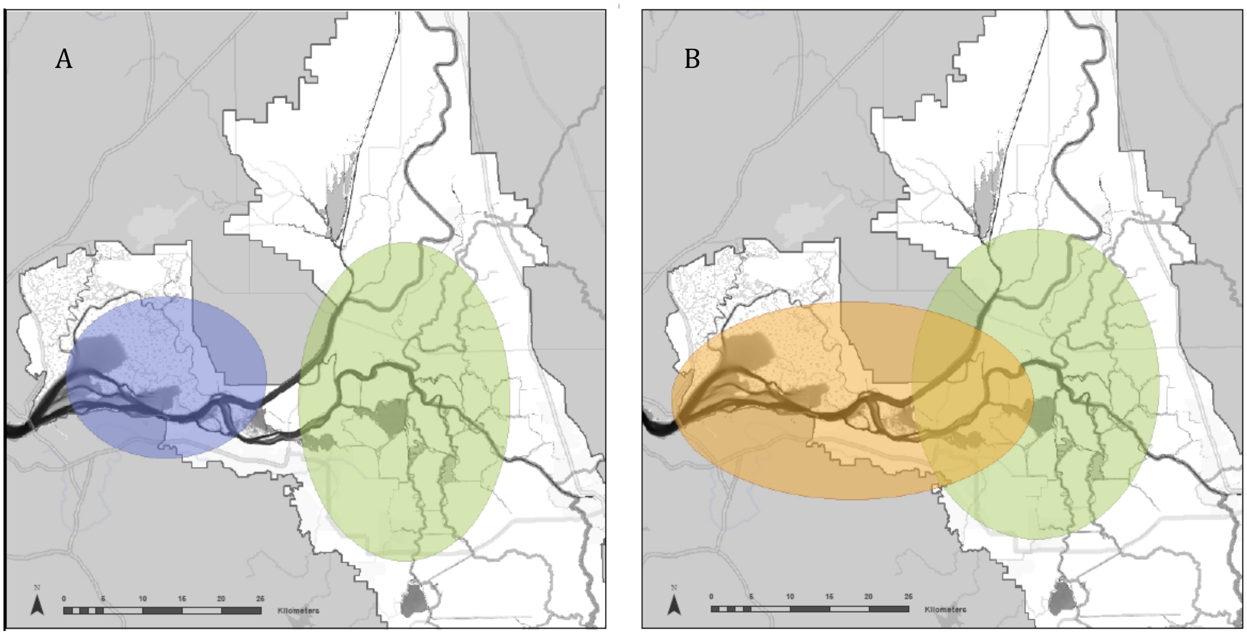

Figure 1 Conceptual mapped and inferred distributions of delta smelt seasonal dispersal in the San Francisco Estuary redrawn from a presentation by (**A**) the OCAP Technical Support team (unpublished) and (**B**) a guidance document from U.S. Bureau of Reclamation (2012). (**A**) portrays a migration of adult delta smelt from the Suisun Bay and the area of the Sacramento and San Joaquin rivers confluence (blue oval) to the central Sacramento–San Joaquin Delta in the winter and spring (green oval) before spawning. Offspring migrate back from the central Delta, returning to the western distributional footprint by summer. (**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.

tion as constituting migration events by spawning delta smelt.

Here we use state agency-generated survey data to produce maps of delta smelt distribution across seasons and to understand of where delta smelt are most commonly found during each of their several recognizable life stages. 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 inferences concerning the fish's inter-seasonal movements. We contrast our findings with those presented in a recent assessment of the spawning migration of delta smelt in the upper estuary by Sommer et al. (2011).

We also consider the relevance of information on delta smelt distribution and dispersal to the multiple conservation planning efforts in the Delta. It appears that the first perspective has informed ongoing conservation planning efforts that target delta smelt, including recovery actions that directly target delta smelt, restoration efforts that seek to restore essential components of its diminished habitats, and management of flows through the Delta (USFWS 2008; USBR 2012; BDCP 2013). 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, marshward spawning dispersal phenomenon indicates the need for focused conservation actions in sub-regional context. In contrast, a long-distance migration phenomenon would expose delta smelt to distinct suites of environmental stressors during movement from one geographic limit of its west-to-east range to the other, and would invoke a different conservation agenda.

Here we address three assertions regarding the dispersal of delta smelt that are critical to the choice of a conceptual model. The assertions can be framed as hypotheses that, if not falsified with available data, would support the mass, upstream migration conceptual model for delta smelt:

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.
2. In migrating seasonally to areas of the eastern Delta, delta smelt effectively vacate Suisun Bay and Suisun Marsh.
3. After spawning, sub-juvenile delta smelt are predominantly distributed across the central Delta.

We test these (*de facto*) hypotheses and draw inferences about 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 about the seasonal movements of delta smelt.

METHODS

Data Sources and Treatment

Since it is not possible at present to track delta smelt directly, inferences about 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 Wildlife carries out multiple surveys of fishes in the estuary, returns from which include delta smelt in temporal samples that span the fish's life cycle. Surveys include the 20-mm Survey, Summer Townet Survey (TNS), Fall Midwater Trawl Survey (FMWT), and Spring Kodiak Trawl Survey (SKT), 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; Bennett 2005). Bennett (2005) has discussed in detail the varying strengths and weaknesses of several of those surveys as population assessment tools for delta smelt. 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 to 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 ongoing surveys mentioned previously largely 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.

We differentiated the life history of the delta smelt into five separate life stages—larvae, sub-juveniles, juveniles, sub-adults, and mature adults (Table 1)—based on prior descriptions of the species' life history by Moyle (2002) and Bennett (2005). We chose a 15-mm body length to differentiate between larvae and sub-juveniles, because at 16 to 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 or 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 SKT, 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, CDFW, pers. comm., 2012).

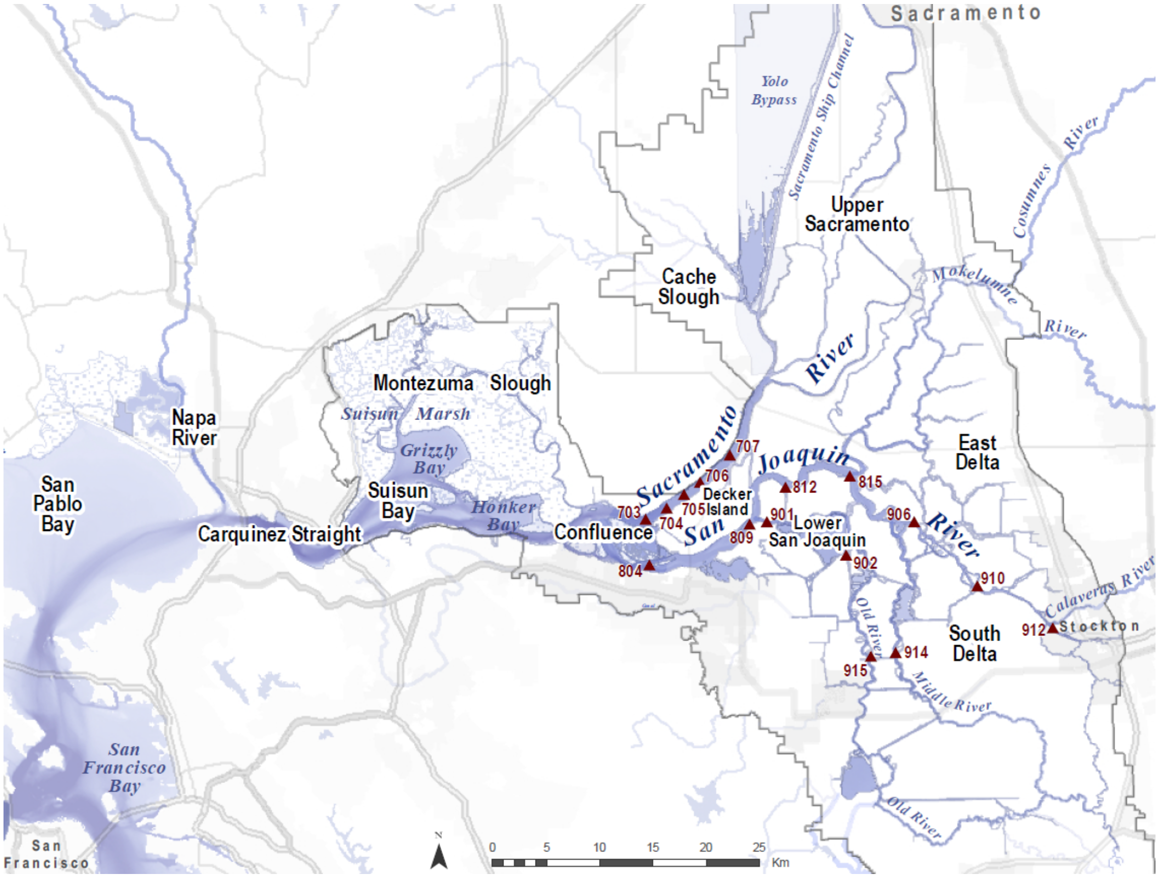

Figure 2 The San Francisco Estuary, including features and geographic designations referenced and described throughout this presentation. Numerical designations accompanying triangles identify trawl survey locations referenced in the text.

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 the Spring Kodiak Trawl database were classified by California Department of Fish and Wildlife (CDFW) following Mager (1986). Descriptions of reproductive stages are available at *http://www.dfg.ca.gov/delta/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, <30 mm	Apr–Aug	1995–2012
Juveniles	20 mm	30 to 55 mm	May–Aug	1995–2012
Juveniles	TNS	30 to 55 mm	Jun–Aug	1987–2011
Sub-adults	FMWT	>55 mm	Sep–Oct, Nov, Dec	1987–2012
Mature adults: pre-spawning	Kodiak Trawl	Reproductive stages: females 1–3, males 1–4	Jan–May	2002–2012
Mature adults: spawning	Kodiak Trawl	Reproductive stages: females 4, males 5	Jan–May	2002–2012
Mature adults: spawning	Beach Seine		Mar–Apr	1987–2009

Although data are available for juvenile and adult delta smelt from the FMWT 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 Survey was first conducted in 1995, and was intended to provide data on larval, sub-juvenile, and juvenile delta smelt. Data from the SKT 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, CDFW, pers. comm., 2010). To avoid introducing anomalies that might be caused by the addition of new stations to established survey frames, we only included data from sampling stations that were sampled consistently (that is, stations that were sampled in at least 90% of the years) from any of the monitoring programs.

Distribution by Life Stage

We calculated the average catch per unit effort (CPUE) of delta smelt for each sampling event for each life stage and station 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 station and period within a year, then multiplying by 10,000 to determine the catch per 10,000 m^3 for each life stage, region, and year:

$$CPUE_{lspy} = \Sigma C_{lspy} / \Sigma V_{spy} \bullet 1000 \quad (1)$$

Then, we calculated the percentage of delta smelt observed at each station in a year by dividing the result from Equation 1, summed over each station, by the total across all stations in that 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 (Table 2). To produce Table 2, the data from the FMWT survey stations were combined and reported for the most proximate 20-mm station.

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 about the census number of delta smelt, which can vary substantially in returns from different monitoring programs and discordantly between life stages from within an 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. Stations that accounted for less than 0.2% of the observed distribution were not depicted. The extent of the range of each survey is shown as a solid surrounding line. Areas without shading within the surrounding line supported very few delta smelt during the period analyzed.

To test the first hypothesis—that there is uni-directional 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 Sacramento and San Joaquin 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 first hypothesis presumes 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 questioned whether the percentage of pre-spawning adults in the area of the Sacramento and San Joaquin rivers confluence and further west (as identified above) were significantly different from zero. We used a one-tailed *t*-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 progressively move 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 before analyses (Zar 2009). Transformed values were checked for normality with a one-sample Kolmogorov–Smirnov test. We used a non-parametric Wilcoxon signed–rank test for data that addressed 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. We ran all *t*-tests (or non-parametric equivalents) 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 publicly 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 before dispersal to spawning areas, and (2) mature adults at or immediately before 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 3 through 7. During summer months the majority of delta smelt feed, grow, and mature in four adjacent geographic locations: in Suisun Bay, in Suisun Marsh (Montezuma Slough), at the Sacramento and San Joaquin rivers confluence, and in the lower Sacramento River (Figure 3). Data from the TNS shows that nearly 90% of the delta smelt sampled in the summer are found in that circumscribed area (Table 2). Delta smelt are essentially absent from the east and south Delta during this period. It should be noted that before 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 north of the mouth of the Napa River.

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 exhibiting a substantial presence in the Cache Slough area (Figure 4). 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 SKT from January through May, it appears that a trend toward increased delta smelt numbers in areas

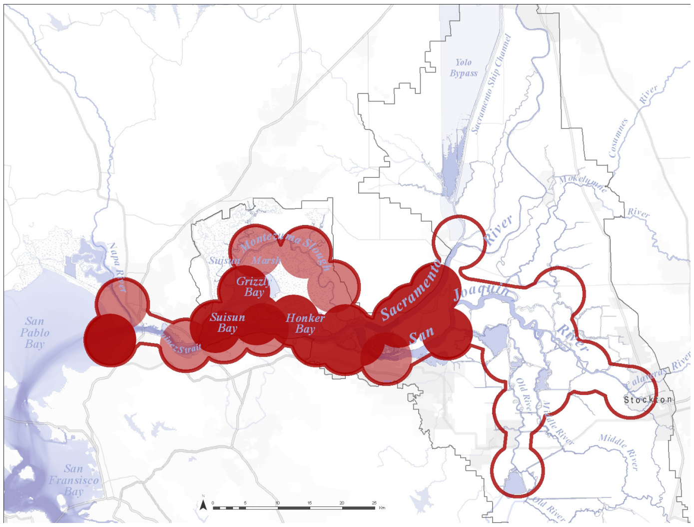

Figure 3 Distribution of delta smelt juveniles in summer (July) in the Summer Townet Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4-km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

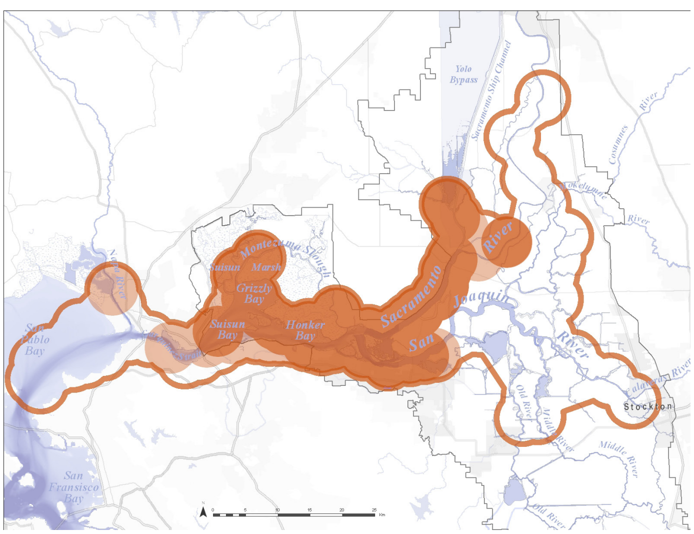

Figure 4 Distribution of delta smelt sub-adults in fall (September to November) in the Fall Midwater Trawl Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed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

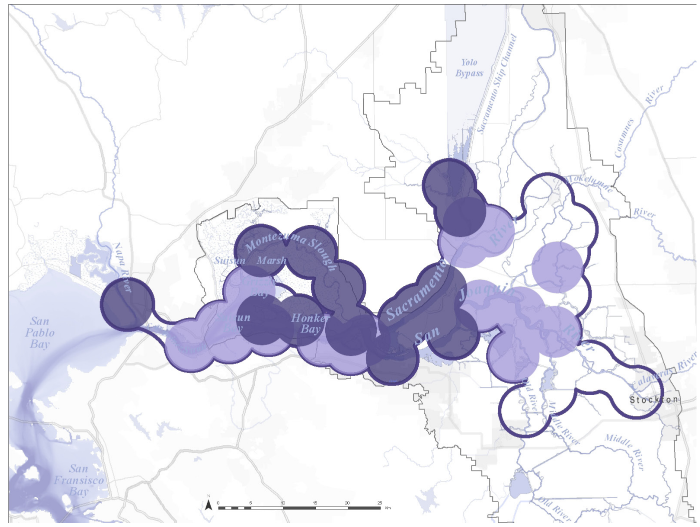

Figure 5 Distribution of delta smelt adults in winter (January to May) in the Spring Kodiak Trawl. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4-km buffer was used for all stations. Source: CDFW survey data.

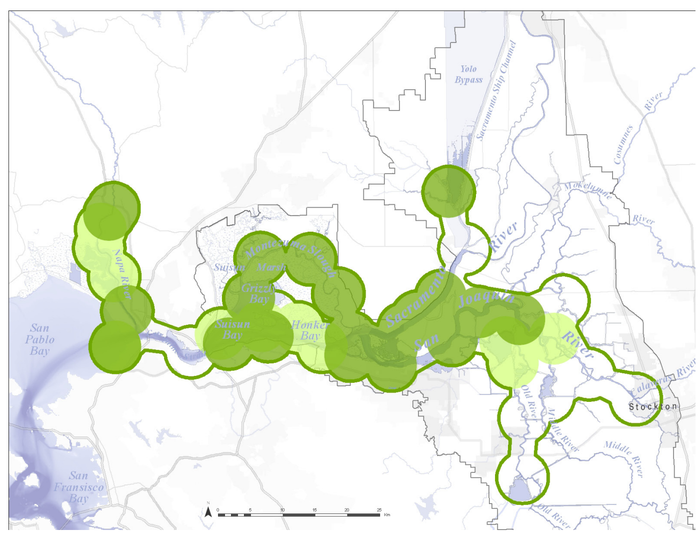

Figure 6 Distribution of delta smelt sub-juveniles in spring (April to June) in the 20-mm Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4-km buffer was used for all stations. Source: CDFW survey data..

beyond the four summer population loci 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 5).

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 SKT are generally observed in the same locations as their pre-spawning predecessors, although there are 80% fewer spawners than pre-spawners observed in the SKT, suggests that some of the fish have moved away from open-water survey sites. Data from the beach seine surveys suggest that adults are found beyond the boundaries of the SKT, with observations of delta smelt well up the Sacramento River. The differences between the two surveys suggest that the mid-channel SKT under-samples spawning adults.

Data derived from beach seine surveys indicate that a northerly dispersal of spawning delta smelt adults is more frequent than dispersal in east or southeast directions (Figure 7), with just incidental observations along the San Joaquin River. The sub-juveniles produced by the spawning adults are dispersed widely throughout the Delta (Figure 6), 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 6 months: north and south Suisun Bay, the Sacramento and San Joaquin rivers confluence, and the lower Sacramento River, particularly around Decker Island, and notably, in the Cache Slough complex of channels.

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. We use inference, however, to interpret those information gaps. We can infer 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 those months precede the redistribution of adults for spawning, and since Cache Slough was not routinely surveyed in the historical TNS, it might be reasonably concluded that a year-round "population" of delta smelt exists in near-freshwater circumstances in the Cache Slough area (Sommer et al. 2011). The question of year-round occupancy of the Napa River is uncertain, because neither the TNS nor the FMWT samples upper reaches of the Napa River. Data from the 20-mm Survey indicate that spawning occurs well up the Napa River, but the lack of data from other surveys prevents us from concluding a year-round delta smelt presence there.

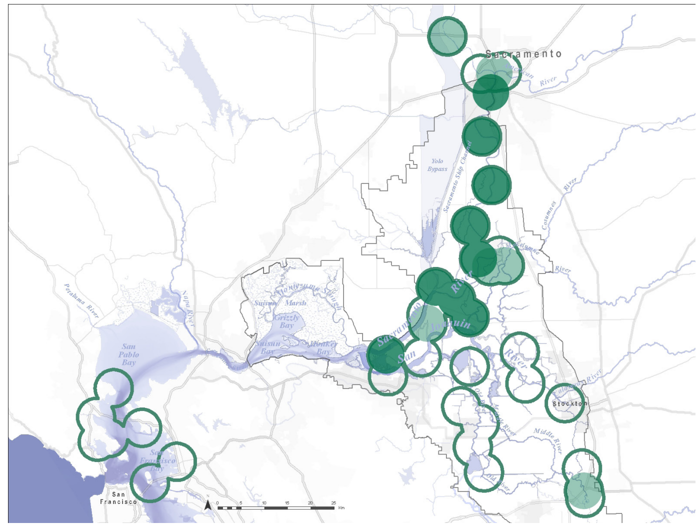

Figure 7 Distribution of delta smelt adults in spring (March to April) from the Beach Seine Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4-km buffer was used for all stations. Source: USFWS survey data.

When the five maps (Figures 3–7) are considered 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

Table 2 Average distribution of delta smelt observed in Interagency Ecological Program monitoring surveys by location. Source: *http://www.dfg.ca.gov/delta/data/20mm/stations.asp*

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
San Pablo Bay										
323	0.0%	0.0%	0.1%	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%
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%
Carquinez Straight										
405	0.2%	1.9%	1.8%	1.6%	0.0%	0.1%	0.2%	0.0%		0.0%
411	1.5%	1.8%	0.7%	0.8%	0.4%	0.3%	0.4%	0.1%		0.1%
418	0.3%	1.1%	2.1%	2.2%	2.2%	0.5%	0.3%	0.4%		0.2%
Subtotal	1.9%	4.9%	4.6%	4.7%	2.6%	0.9%	0.9%	0.5%		0.3%
South Suisun Bay										
501	0.7%	2.9%	3.5%	1.5%	1.5%	6.8%	1.8%	0.3%		0.2%
504	2.5%	1.0%	1.7%	2.0%	0.3%	0.6%	0.6%	0.2%		0.1%
508	1.9%	3.6%	5.8%	6.9%	2.8%	2.4%	1.1%	0.6%		0.4%
Subtotal	5.1%	7.5%	11.0%	10.4%	4.6%	9.8%	3.5%	1.2%		0.7%
Montezuma Slough										
606	3.6%	1.5%	0.8%	2.9%	7.6%	15.7%	21.7%	14.9%		9.4%
609	5.2%	1.7%	1.3%				26.6%	10.6%		6.7%
610	3.8%	1.5%	0.9%	0.2%	0.2%	1.5%	2.1%	1.4%		0.9%
Subtotal	12.5%	4.7%	3.0%	3.1%	7.8%	17.3%	50.4%	26.9%		17.0%
North Suisun Bay (including Grizzly & Honker Bays)										
513	3.6%	6.2%	9.6%	9.1%	8.8%	4.6%	1.2%	1.9%		1.2%
602	3.6%	16.2%	13.3%	4.1%	1.2%	4.1%	1.4%	0.5%		0.3%
519	1.8%	7.0%	6.5%	2.9%	7.3%	16.0%	4.9%	2.5%		1.6%
Subtotal	9.0%	29.4%	29.4%	16.1%	17.3%	24.7%	7.5%	5.0%		3.1%
Confluence										
520	3.8%	2.3%	1.9%							
703	7.1%	7.3%		10.3%	8.4%	6.5%			1.5%	0.6%
801	2.8%	1.7%	2.4%	1.3%	0.4%	0.2%	0.8%	0.3%		0.2%
804	3.4%	0.9%	1.5%	0.5%	0.5%	0.1%	0.9%	0.2%	0.0%	0.1%
Subtotal	17.1%	12.2%	5.8%	12.1%	9.3%	6.7%	1.7%	0.6%	1.5%	0.9%
Lower Sacramento River (Decker Is)										
704	9.8%	16.5%	20.6%	15.2%	16.3%	9.7%	8.1%	8.0%		5.0%
705	1.9%	0.5%								
706	11.4%	9.7%	16.7%	17.8%	18.6%	13.8%	6.5%	2.3%		1.5%
707	3.8%	1.5%	5.7%	6.1%	13.3%	7.0%	2.7%	9.2%	27.2%	16.5%

Table 2 Average distribution of delta smelt observed in Interagency Ecological Program monitoring surveys by location (Cont.)

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%

in several areas of the Delta: north Suisun Bay, the Sacramento and San Joaquin 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 the onset of spawning—to be addressed. The percentages of sub-adult delta smelt in the early fall (September and October) and pre-spawning adults that are located east of the Sacramento and San Joaquin 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 there maturing to spawning condition, the percentage of the surveyed population there actually decreases; with an average of 24% fewer delta smelt later in their life cycle being detected in surveys east of the confluence (with the west–east difference significant at the 95% level).

We addressed the second hypothesis—that delta smelt vacate Suisun Bay and the Sacramento and San Joaquin rivers confluence before spawning—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). We can reject the hypothesis that delta smelt vacate the western portion of the estuary to spawn.

We also rejected the third hypothesis: that sub-juvenile delta smelt are found predominantly in the central Delta. Data from the 20-mm 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 that 39% of sub-juvenile delta smelt are present 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 maps (Figures 3–7), 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 to that area. Also, the area is on the very northwest edge of the Delta, and is not usually considered part of the central Delta. Removing these

Table 3 Percentage of delta smelt sub-adults sampled east of the confluence in September and October in the FMWT compared with the percentage of pre-spawning adults in the subsequent SKT

Cohort Year	Percentage east of confluence during Sep–Oct in FMWT	Percentage east of confluence during subsequent Jan–May in SKT	Percent 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 SKT

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%

four stations from the central Delta station grouping used in Table 5, reduces the average observed presence of delta smelt in the actual central Delta from 39% to just 12%.

Collectively, rejecting the three hypotheses strongly supports the perspective that delta smelt spawning movement is multi-directional—likely toward local freshwater inputs—rather than manifest as a uni-directional eastward migration.

A pair of synthetic maps depicts inter-seasonal dispersal by delta smelt (Figures 8A and 8B). Juvenile delta smelt are found primarily in four areas in late spring: (1) in the Napa River estuary, (2) in areas from the western portion of Grizzly Bay through Suisun Bay to the Sacramento and 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 Deep Water Ship Channel. Delta smelt adults, just before and into the period of spawning, exhibit a distribution at relatively high densities:

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

Year	Central Delta Stations 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%

(1) from the area around Suisun Bay and adjacent to Montezuma Slough, and (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 are apparent in the distribution of delta smelt within its geographic range between life stages.

DISCUSSION

Five trawl-based fish surveys sample extensive, partially overlapping portions of the Sacramento–San Joaquin River Delta and adjacent areas of the San

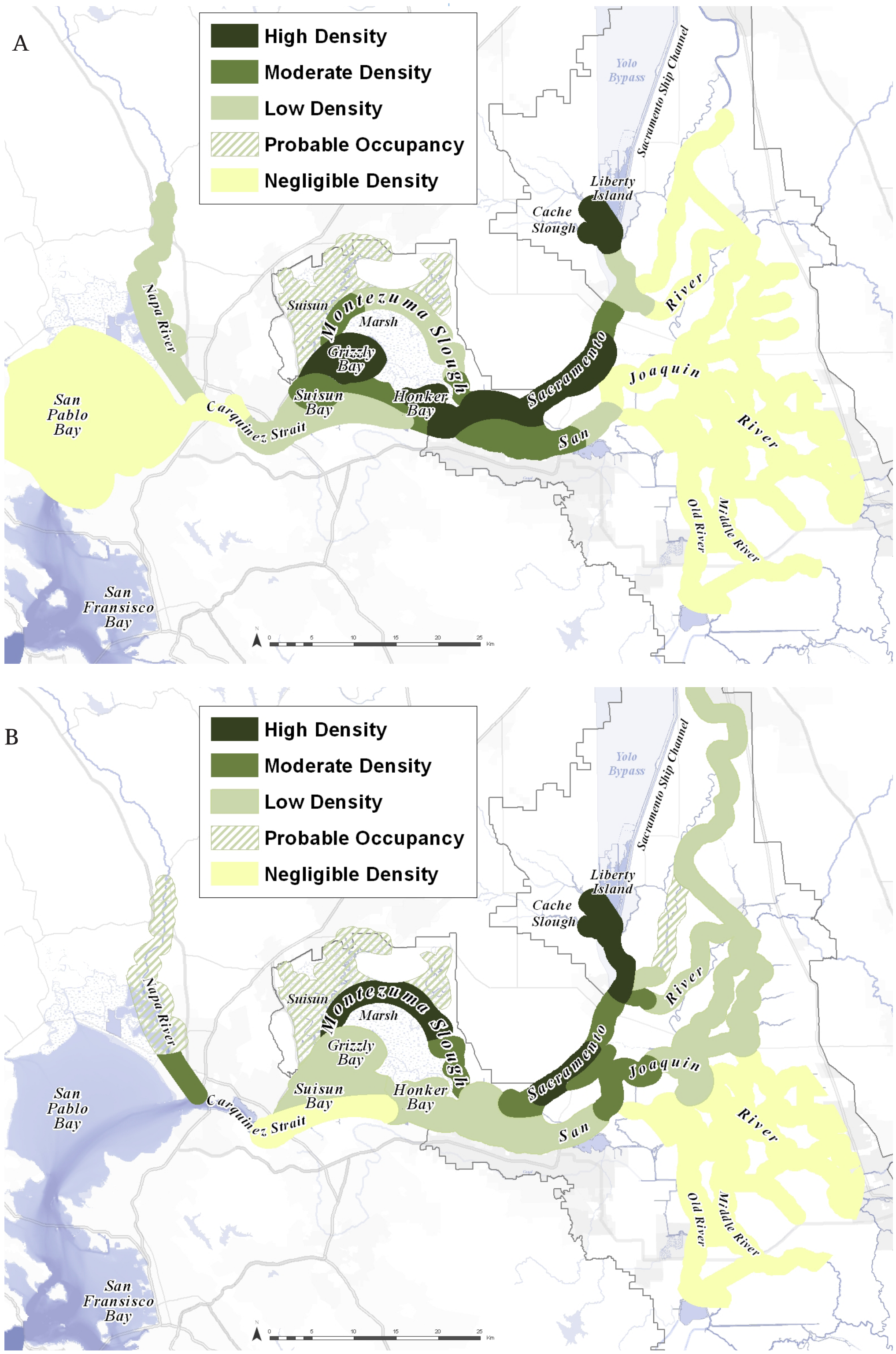

Figure 8 Synthesized distribution of delta smelt in summer and fall (**A**) before dispersal to spawning areas, and in spring (**B**) after dispersion. The dark areas show the predominant range during each period. The high and moderate density areas combined account for 90%, on average, of the observed presence of delta smelt. Areas of negligible density combined account for less than 1% of delta smelt during the survey period. Light green areas represent 9% of the presence of delta smelt. Source: CDFW survey data.

Francisco Estuary. The known distributional range of delta smelt has been informed largely by those surveys (Merz et al. 2011). Delta smelt range from the just east of the Carquinez Strait, through Grizzly and Suisun bays, and the adjacent Suisun Marsh, up-Delta past the Sacramento and San Joaquin rivers confluence, on the lower Sacramento River, in the Cache Slough and Liberty Island complex of waterways, and in the Sacramento Deep Water Ship Channel. Beach Seine surveys have established that delta smelt are present in the Sacramento River north of Walnut Grove. 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 as a disjunct presence in lower reaches of the Napa River.

The pertinent issue addressed here is the distribution of delta smelt adults before spawning and their movement to locations at which spawning presumptively occurs. Two alternative perspectives have been offered regarding movement by delta smelt from "rearing" areas to spawning locations. One describes a uni-directional, upstream migration by delta smelt from rearing areas in the west Delta to freshwater areas 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 inform our understanding of what constitutes habitat for delta smelt—its spatial extent, and its temporal patterns of habitat occupancy—as well as determining the conservation actions that might benefit delta smelt, prioritizing those actions, and identifying the locations where management actions might yield the greatest benefits to delta smelt.

Our analyses using data generated by seasonal surveys refute the assertion that delta smelt undertake uni-directional movement in late autumn and early winter toward eastern spawning areas in the Delta. Spatial data are consistent with delta smelt dispersal from bay, embayment, and channel areas occupied by pre-spawner delta smelt toward freshwater inlets on nearby shores and in marshes, with only a relatively small fraction of delta smelt exhibiting movement east to freshwater, including up and into the Sacramento or San Joaquin rivers. The mapped survey data indicate that most of the delta smelt that rear in Suisun Bay appear to disperse north to Montezuma Slough and Suisun Marsh to spawn. Fish in the Cache Slough complex of channels and wetlands appear to stay in that general area. And delta smelt in the lower Sacramento River likely disperse in multiple directions: up the Sacramento River, east toward the San Joaquin River, and west into Montezuma Slough. Drawing from Table 2, the percentage of delta smelt sampled in Suisun Bay decreased from 34.5% in December to 11% in January through May, whereas the percentage in Montezuma Slough increased from 17.3% in December to over 50% in January through May. In September and October, 12.4% of sampled delta smelt were sampled from the Cache Slough complex; that percentage declined in November and December, but rebounded to 12.3% for the period from January through May. 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 Bay 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 and San Joaquin rivers confluence in the spring. This finding is consistent with earlier observations of the distribution of young fish. Citing Radtke (1966) and Wang (1986), 2 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, life-stage-specific 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 OCAP Technical Support Team (unpublished) and U.S. Bureau of Reclamation (2012). The most parsimonious conclusion that can be drawn from surveys that sample delta smelt before, during, and after the winter to early spring spawning period is that the fish move from open water to adjacent shoals and shoreline areas, which exhibit the physical attributes—especially the freshwater inputs and appropriate substrates—that are necessary to support successful spawning.

Sommer et al. (2011) also describe the annual dispersal patterns of delta smelt. Their study computes the average position of delta smelt in temporal samples (the centroid of the distribution of the fish) from a subset of FMWT stations, and suggests 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. This is interpreted as evidence of upstream migration. The findings presented here call into question use of the centroid of the distribution of delta smelt to assess their interseasonal movement. The west-to-northeast orientation of the Delta's uplands interface and channel complexes that delta smelt occupy can provide for an eastward component to fish spawning movements that could also be inshore, north (or south) toward freshwater inputs. Moreover, the presence of multiple demographic loci obviates the utility of defining a single delta smelt centroid, the geographic shifting of which can misrepresent actual site-specific movement patterns. But, perhaps most importantly, the slight eastward shifts in the centroid of the delta smelt distribution described by Sommer et al. (2011) do not support the assertion that delta smelt undergo a mass migration to the freshwater edge of the Delta—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. As support for an eastward, "upstream" migration by delta smelt, Sommer et al. (2011) turn to previous studies for corroboration (Swanson et al. 1998; Dege and Brown 2004), but neither of those studies offer data or analyses that address the issue of migration *per se*.

Use of the term "migration" to characterize seasonal, spawning-related movements in delta smelt without presentation of an unambiguous definition of the term may have contributed to a confounded narrative about seasonal delta smelt movements. The federal resource agency maps presented herein illustrate movement phenomena that meet the vernacular use of the term "migration," with fish moving extensive distances across the Delta to reproduce. And, Sommer et al. (2011) used the term in their description of a long-distance west-to-east dispersal phenomenon. But, Moyle (2002) and Bennett (2005) also referred to migration in describing delta smelt moving from open waters to adjacent shorelines—a less commonplace use of the term. In strict technical usage, both short- and long-distance dispersal can constitute migration (Dingle and Alistair Drake 2007; Lack 1968; Ramenofsky and Wingfield 2007). Wilcove (2007) differentiates migratory movements from "daily searches for food and shelter" or "the dispersal movements of offspring, as they establish their own territories." 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 also technically correct to invoke the term migration to describe the delta smelt's far less ambitious dispersal from open waters to adjacent shorelines. Nonetheless, we have used the term "dispersal" to reflect the seasonal movement of the fish between rearing and spawning areas, and to differentiate such movements from the long-distance, uni-directional movements that are essential to the conceptual model employed by the federal resource agencies (OCAP Technical Support Team unpublished; USBR 2012).

The findings presented here on seasonal dispersal have implications for understanding delta smelt ecology and behavior. 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, with the presence of four or more geographically discontinuous delta smelt spawning loci in the Delta, as indicated here, and absent mass directional movements, a different demographic picture can be inferred. Substantial demographic mixing is certain in the limited-dispersal scenario. This is consistent with Hobbs et al. (2007), who used trace elemental fingerprinting to determine natal areas of delta smelt. Under a limited-dispersal model, 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 constrained; while the stepping-stone exchange necessary to genetically tie the demographic units of delta smelt east of the Carquinez Strait is realized (see Fisch et al. 2011).

In light of the spatial and temporal patterns of delta smelt distribution presented here, characterization of delta smelt habitat is possible. Extensive areas depicted as being seasonally occupied in the federal agency maps, and 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 (and see Figure 4 in Merz et al. 2011). According to survey data, much of the area in the large eastern polygons in Figures 1A and 1B are infrequently occupied and currently may not provide habitat for delta smelt. 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. 2005), 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 observations have implications for delta smelt conservation and for resource managers. The distribution of delta smelt during each of the life stages serves to delineate 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 that environmental stressors in that area need to be closely examined. An ambitious effort to restore tidal marshes and wetlands in the Delta, which are believed to contribute to producing prey for 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 loci of delta smelt occurrences in the north Delta. The lack of evidence that delta smelt make an extensive easterly migration to spawn could 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.

The maps presented here indirectly address Sommer et al.'s (2011) concern about the effects that entrainment of delta smelt at water export facilities in the south Delta may have on the species' status and trends. They also indicate that conclusions about population-level effects of entrainment at export pumps may warrant re-evaluation (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, 2011; Miller 2011), and therefore consequential to the status and trends of delta smelt, is not so clear (see also Castillo et al. 2012). While available distribution data suggest relatively wide dispersal of larvae and young juvenile delta smelt away from natal spawning areas—and hence some proportion of the very youngest delta smelt may be lost at the water export pumps—available survey data do not seem to support the contention that large numbers of delta smelt migrating upstream pass perilously close to the export facilities or are drawn to them during annual, long-distance spawn movements.

CONCLUSIONS

Using available survey data, we have presented a complex picture of the distribution and dispersal of delta smelt before spawning. A diffuse collection of delta smelt population loci exist in and adjacent to the northern Delta's open waters, individuals from which undertake landward movements to spawn. These movements are consistent with the long-understood idea that delta smelt mature in the estuary's brackish water and spawn in fresher water. The maps offer no support for a uni-directional, easterly spawning migration by delta smelt from open water in the west of the Delta to fresher water 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 reducing the numbers of delta smelt—and the appropriate recovery measures that should be taken in efforts to conserve the species.

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