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Abstract:

While there is substantial information about the upstream migration of commercially and recreationally important fishes, relatively little is known about the upstream migration of small-bodied species, particularly through estuaries. In the San Francisco Estuary, there is a major need to understand the behavior of delta smelt Hypomesus transpacificus, a small pelagic fish listed under the state and federal endangered species acts. The spawning migration period may be critical as upstream movements can result in entrainment in water diversions. In general, delta smelt live in the low-salinity zone of the estuary and migrate upstream for spawning. During the fall pre-migration period, delta smelt remain primarily within the low-salinity zone in the western Sacramento–San Joaquin Delta and Suisun Bay. There were no significant upstream shifts of fish into fresher water during late fall, suggesting that delta smelt do not show pre-migration staging behavior. Following winter "first flush" flow events that appear to trigger migration, upstream movement rates are relatively rapid, averaging 3.6 km/d, a finding consistent with

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results from particle-tracking simulations, laboratory studies, and other fishes. Like some other native fishes, delta smelt apparently “hold” in upstream areas following migration; most do not spawn immediately. Overall, delta smelt fit the pattern of a diadromous species that is a seasonal reproductive migrant. Emerging data suggest that there is variability in the migration behavior of delta smelt, a pattern contrary to the reigning viewpoint that all smelt migrate in winter.

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The Spawning Migration of Delta Smelt in the Upper San Francisco Estuary

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ABSTRACT

While there is substantial information about the upstream migration of commercially and recreationally important fishes, relatively little is known about the upstream migration of small-bodied species, particularly through estuaries. In the San Francisco Estuary, there is a major need to understand the behavior of delta smelt *Hypomesus transpacificus*, a small pelagic fish listed under the state and federal endangered species acts. The spawning migration period may be critical as upstream movements can result in entrainment in water diversions. In general, delta smelt live in the low-salinity zone of the estuary and migrate upstream for spawning. During the fall pre-migration period, delta smelt remain primarily within the low-salinity zone in the western Sacramento–San Joaquin Delta and Suisun Bay. There were no significant upstream shifts of fish into fresher water during late fall, suggesting that delta smelt do not show pre-migration staging behavior. Following winter "first flush" flow events that appear to trigger migration, upstream movement rates are relatively rapid, averaging 3.6 km d^{-1}, a finding consistent with results from particle-tracking simulations, laboratory studies, and other fishes. Like some other native fishes, delta smelt apparently "hold" in upstream areas following migration; most do not spawn immediately. Overall, delta smelt fit the pattern of a diadromous species that is a seasonal reproductive migrant. Emerging data suggest that there is variability in the migration behavior of delta smelt, a pattern contrary to the reigning viewpoint that all smelt migrate in winter.

KEY WORDS

delta smelt, *Hypomesus transpacificus*, migration, *Osmeridae*, San Francisco Estuary, fish

INTRODUCTION

Animal migrations have long intrigued humans, particularly movements by food species such as waterfowl, ungulates, and game fishes. In estuaries and their tributaries, the seasonal passage of anadromous fishes represents the most dramatic migration by aquatic species. Given the impressive numbers of salmonids that migrate through estuaries and rivers of the northern hemisphere, it is relatively easy to understand why these movements have regional cultural significance (Roche and McHuchison 1998).

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Migration represents a critical part of the life history for a variety of organisms. Seasonal or ontogenetic migrations have been documented for a broad diversity of taxonomic groups, including fish, mammals, reptiles, birds, and insects (Baker 1978). Many organisms also undergo smaller-scale diel migrations, particularly in aquatic habitats. Northcote (1978) has proposed that there are three basic functional categories of migrations: (1) reproductive (spawning) migration, (2) migration toward food, and (3) refuge migration.

Much of the attention paid to fish migration through estuaries has been on large fishes including salmonids, clupeids, and sturgeon (Lucas and Baras 2001). By contrast, there is relatively little information about the upstream migration of many groups of fishes, particularly small-bodied types (Clough and Beaumont 1998). This disparity is, in part, a consequence of the economic value of large species, as well as the difficulty in using techniques such as tagging and telemetry on small fishes. Much of the available information is summarized in Lucas and Baras (2001). Some examples of studies on estuarine migration of smaller fishes include rainbow smelt *Osmerus mordax* (Murawski and others 1980; Ohji and others 2008), pond smelt *Hypomesus nipponensis* (Katayama and others 2000), and threespine stickleback *Gasterosteus aculeatus* (Snyder 1991).

The dearth of information about the upstream migration of small fishes also applies to the San Francisco Estuary (Figure 1). However, the decline in several native smelt, salmon, sturgeon, and minnows and associated listings under the state and federal endangered species acts raised major questions about the life histories of these fishes. The best example is the imperiled delta smelt, *Hypomesus transpacificus*, a small pelagic osmerid that occurs only in the upper San Francisco Estuary. The population has declined precipitously over the past decade, leading to major legal and regulatory actions to try and improve its status (Service 2007; Sommer and others 2007). In recent years, there has been substantial progress in understanding the life history of this species (Moyle and others 1992; Bennett 2005), although details of its upstream migration have remained elusive (Swanson and others 1998). Delta smelt is 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). Basic physiological and environmental requirements have been described for several life stages (Swanson and others 1998, 2000; Baskerville–Bridges and others 2004; Feyrer and others 2007; Nobriga and others 2008).

Migration frequently involves substantial risks both from natural (e.g., predation, starvation, extreme climate) and anthropogenic (e.g. hunting, fishing, barriers) sources (Baker 1978). Indeed, even small-scale movements on the order of a few kilometers can have a major impact on fish survival and reproduction (Lucas and Baras 2001). For delta smelt, migration and subsequent spawning are perhaps the most critical periods in its life cycle (Moyle 2002; Bennett 2005). Because the delta smelt is an annual species that exists in a single estuary, the persistence of the population may depend on successful migration and spawning of the adults through the Sacramento–San Joaquin Delta (Delta), the upstream region of the San Francisco Estuary that is the most frequently available spawning habitat (Figure 1). The hydrodynamics of the Delta's highly interconnected channels are especially complex and highly altered, so upstream migrating fish encounter unusually difficult navigation challenges. For example, if upstream migrating delta smelt swim into the San Joaquin River, they are much more likely to be entrained by the large Central Valley Project (CVP) and State Water Project (SWP) water diversions, which supply water to about 25 million California residents and a multi-billion dollar agricultural industry (Grimaldo and others 2009). This logic is, in part, the basis behind recent major water export restrictions to protect upstream spawners (USFWS 2008). From a management perspective, it is, therefore, essential to understand how delta smelt migrate, and what factors influence them during this period (Martin and others 2007).

The primary objective of this paper was to characterize, at least in a general sense, the spawning migration of delta smelt, including the periods immediately before and after upstream movement. Specific study

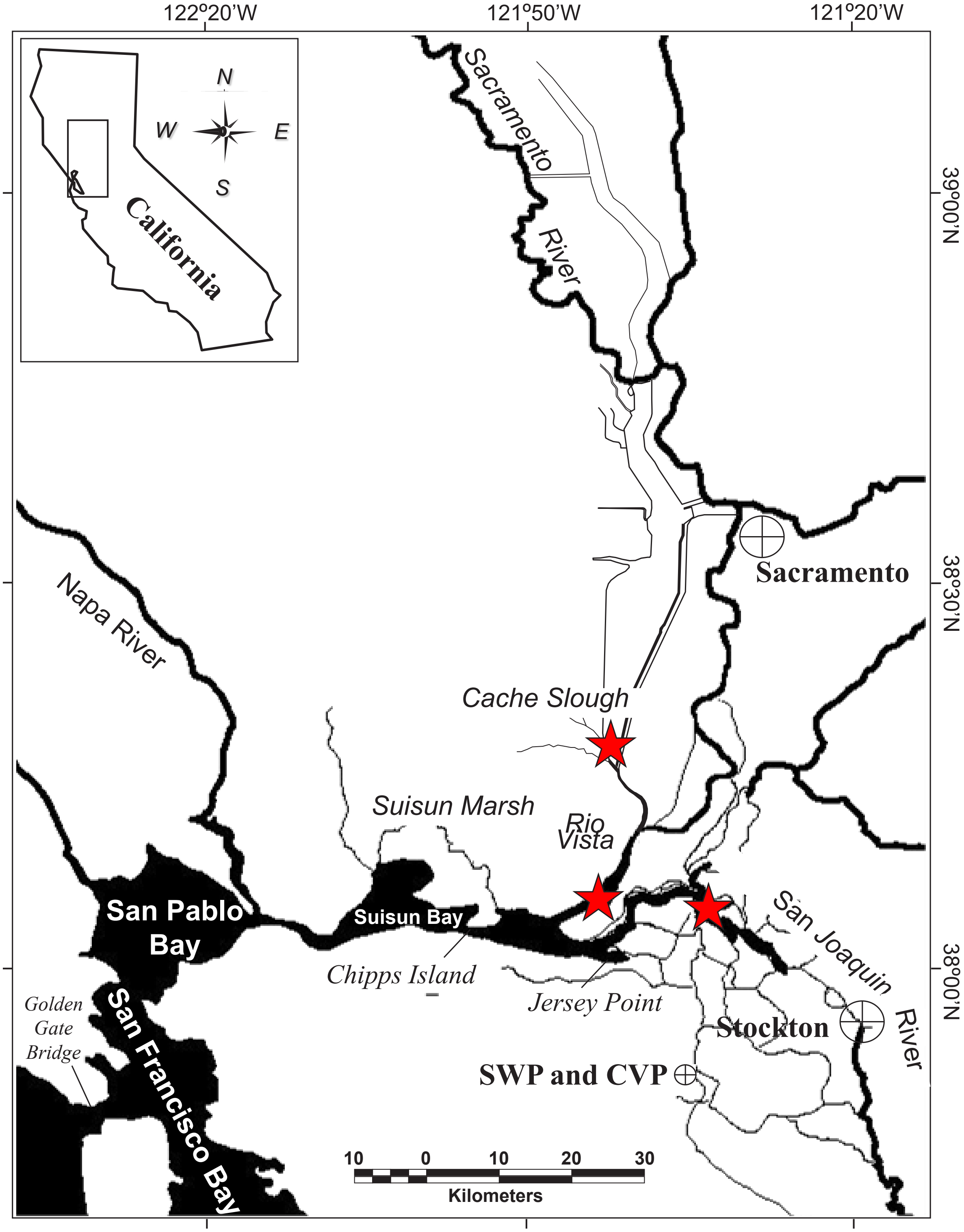

Figure 1 The San Francisco Estuary, including key landmarks noted in the text. The Sacramento–San Joaquin Delta is the area between Chipps Island, Sacramento, and just south of Stockton. The general locations of the three sampling regions described in Table 3 are identified with red stars. Liberty Island is located immediately north of the symbol for Cache Slough.

questions included the following:

1. Where is the starting location for migration?
2. How quickly do delta smelt migrate?
3. Does spawning occur immediately after migration?
4. Is there evidence that there is variability in the migratory behavior of delta smelt?

Because of the limited nature of the data available on delta smelt, our study was not intended as a comprehensive description of delta smelt migration. Instead, we reasoned that answering these questions would be useful as a framework for adaptive management of this imperiled fish. Given the rarity of delta smelt, and associated constraints on field collection, we also hoped that our analyses of existing data would help to set priorities for future research.

METHODS AND MATERIALS

Evaluating the migration of delta smelt was particularly challenging because the fish is very small (usually <100 mm FL), fragile, increasingly rare, and has a protected legal status. In addition, the San Francisco estuary is large and spatially complex, with multiple tributaries, embayments, and braided channels (Figure 1). These issues meant that it was not feasible to use traditional migration study techniques such as telemetry and mark–recapture. We therefore relied on a combination of data analyses from long- and short-term fisheries surveys, and modeling to infer details about migration patterns. We acknowledge that these techniques have higher uncertainty than direct methods such as telemetry, but emphasize that our approaches represented the best available methods given the constraints.

Data Sources

The Fall Midwater Trawl Survey (FMWT) samples fishes in open water and other offshore habitats monthly each September to December at 116 stations throughout the northern region of the estuary. The survey at each location takes a 10- to 12-min tow with a 13.4 m^2 midwater trawl of variable meshes starting with 20.3-cm mesh at the mouth of the net and 1.3-cm mesh at the cod end (Stevens and Miller 1983; Feyrer and others 2007). The survey represents one of the best long-term fishery data sets for the San Francisco Estuary and covers the majority of the range of delta smelt. The FMWT samples delta smelt distribution and relative abundance during the period leading up to—but not including—their spawning migration. Thus, it provides a long-term data set on where delta smelt are distributed in the estuary when they start their migration. The survey has been conducted since 1967 with the exception of 1974 and 1979.

The Spring Kodiak Trawl Survey (SKT) has been conducted since 2002 as a survey to assess the distribution of adult delta smelt during the time they ripen and spawn (Source: *http://www.delta.dfg.ca.gov/data/skt/*). It samples 39 locations from Napa River upstream though Suisun Bay and the Delta (Figure 1). The survey has been conducted every 2 to 4 weeks in winter and spring starting in January or February. At each location, a single 10-min surface sample is taken by two boats that tow a 7.6-m wide by 1.8-m high Kodiak trawl. The mesh ranges in dimension from 5.1-cm knotted stretched mesh at the mouth and decreases by 1.3 cm through a series of five panels to 0.6-cm knotless stretched mesh at the cod end. Delta smelt collected by this survey are counted, measured, and classified in terms of six spawning condition levels (*http://www.delta.dfg.ca.gov/data/skt/eggstages.asp*; Mager 1996).

Initiated in 1995, the 20-mm Survey typically samples larvae during each neap tide between March and July (Dege and Brown 2004). A total of 48 sites have been sampled continuously; they include freshwater to mesohaline habitats of the estuary. Three, 10-min oblique tows are conducted at each location using a 5.1-m long, skid-mounted net, with a 1.5-m^2 mouth, a 1.6-mm mesh body, and a removable 2.2-L cod-end jar. This survey provides a basic indication of some of the major spawning areas, although it is important to note that tides and river flow can redistribute larvae after spawning occurs.

The SWP salvage is a data set based on the collection of juvenile and adult delta smelt at the

Harvey O. Banks water diversion's fish screens (Sommer and others 1997; Kimmerer 2008; Grimaldo and others 2009). Salvage of delta smelt from the fish screens is highly seasonal, with most adult collections during winter migration, and juveniles during spring rearing and downstream migration. A limitation of the salvage data is that they are geographically localized in an upstream area of the Delta. However, these data are also considered an important source of information about the species because the fish salvage facilities have historically had the largest delta smelt catch of any of the sampling programs. Relatively high catch at the fish screens is consistent with water diverted by the SWP and its nearby counterpart, the CVP, which have combined exports of up to 35% to 65% of Delta inflow, depending on season. Modeling studies by Kimmerer (2008) found that entrainment (calculated from salvage) can be a substantial portion of the delta smelt population in some years, increasing our confidence that the salvage data have some statistical relevance.

Since 1959 the California Department of Fish and Game (DFG) has conducted annually the Summer Townet Survey (TNS). The survey was designed to index the abundance of age–0 striped bass, but also collects delta smelt data that have been used to analyze abundance, distribution, and habitat use (Kimmerer 2002; Bennett 2005; Nobriga and others 2008). The TNS samples up to 32 stations using a conical net (1.5-m^2 mouth; 2.5-mm cod-end mesh) towed obliquely through the water column.

Data Analyses

The starting distribution of delta smelt during the pre-migration period (Study Question 1) was evaluated using the approach of Dege and Brown (2004) to calculate the location of the centroid of the distribution of delta smelt in the FMWT. The analysis used the weighted catch of delta smelt from 54 core (i.e., consistently sampled) stations to calculate the centroid based on the distance from the mouth of the San Francisco Estuary (Golden Gate Bridge). The data for each of the four survey months (September through December) were plotted in two different ways to examine different aspects of the pre-migration period. First, we plotted the results on an annual basis and relative to two locations (Rio Vista at km 100 and Chipps Island at km 75) commonly used as reference points for water management in the region. This approach allowed us to evaluate the geographic range of delta smelt before migration, and how it changed monthly and annually. As will be evident below for Question 2, these data provided the baseline for estimates of migration rates. Our second analytical method was to examine fish distribution relative to salinity. This approach is particularly useful in estuaries, where the salinity field can shift substantially, based on seasonal changes in inflow. Delta smelt are strongly associated with the low-salinity zone (Moyle 2002; Bennett 2005; Feyrer and others 2007), so it makes sense to evaluate their distribution in this way. The salinity metric that we used was X2, the distance of the 2 practical salinity units (psu) salinity isohaline from the Golden Gate Bridge (Jassby and others 1995; Kimmerer 2002; Feyrer and others 2007). For each month, we plotted the delta smelt distribution centroids relative to X2. We used a Generalized Linear Model (GLM) to test whether there were statistically significant relationships between fish distribution centroids and X2. In addition, we used an ANOVA to test whether the slope intercepts varied by month. This approach allowed us to examine whether delta smelt remained in the same salinity zone throughout the pre-migration period. We were particularly interested in whether there was a shift in distribution towards fresher water during later months of the pre-migration period, a possible sign of "staging" behavior. Many fishes exhibit staging behavior before migration (Salo 1991; Moyle 2002). Salmonids, a phylogenetic relative of osmerids, show staging behavior, so it is possible that delta smelt have similar early movements.

Our second question was to evaluate how quickly delta smelt migrate. We developed estimates of migration rates based on pre-migration distribution and SWP salvage data. To calculate migration time, we relied on analyses of salvage data by Grimaldo and others (2009), the best available high-frequency data on the timing of migration. Their studies showed that adult salvage peaks relatively shortly (about 1 to 4 weeks) after the onset of seasonal rain brings a “first flush” of fresh water into the Delta. Note that one of the key environmental changes during first flush is pulses of turbidity entering the system (Wright and Schoellhamer 2004). Delta smelt distributions are closely associated with turbid water (Feyrer and others 2007; Nobriga and others 2008), so it is likely that high turbidity throughout the migration corridor is necessary for successful migration. This assumption does not preclude the idea that first flush contains some other migration cue that is independent of turbidity; at the very least, turbidity is a reasonable and measurable indicator of first flush in the hydrologically complicated upper estuary. Thus, we estimated migration time as the number of days between first flush (as indicated by a rise in south Delta turbidity to 12 nephelomethric turbidity units [ntu]) and the salvage peak at the SWP fish screens (reported by Grimaldo and others 2009). High winter turbidity levels near the SWP Delta salvage facilities tend to reflect high turbidity levels through the delta smelt migration corridor (DWR, unpublished data). Nine recent years (1993, 1995, 1999, and 2000–2005) were selected based on their relatively distinct turbidity pulses and higher salvage, which allows for more accurate identification of peaks. These years include a fairly wide range of conditions except for extreme wet years, so we believe that the data set was fairly representative of migration patterns. Finally, we calculated the distance traveled as the number of river kilometers between the December centroid of the FMWT distribution of spawners (Study Question 1) and the SWP fish screens, which are 155.1 km from the Golden Gate Bridge. Estimates of migration rate using this approach were used to examine whether there was evidence of an effect of flow rate. Flow was based on average daily Delta outflow values, which were obtained from the DAYFLOW database (*http://www.iep.water.ca.gov/dayflow/index.html*). We tested whether estimated migration rates were related to average Delta outflow during the migration period (from first flush to the salvage peak at the SWP) using Kendall–Tau correlation.

We used particle-tracking simulations to determine if our estimated fish migration rates were within the range of what would be expected based on reasonable swimming behaviors from the literature. We used the Delta Simulation Model II (DSM2) hydrodynamic model and its associated particle-tracking model (DSM2 ptm) to simulate a delta smelt spawning migration. These models are quasi–3D mathematical models developed by the California Department of Water Resources (DWR) as a water distribution planning tool (Culberson and others 2004; Kimmerer and Nobriga 2008). In DSM2, the upper estuary is divided into a grid with 416 nodes and 509 links. Model limitations were explored and discussed extensively by Kimmerer and Nobriga (2008).

The DSM2 ptm default models neutrally buoyant particles, but it can provide limited particle behavior (Culberson and others 2004). We used this feature to model particles that stayed in the upper 10% of the water column during flood tides, and the lower 10% of the water column during ebb tides. This is one of several behaviors that delta smelt and other estuarine fishes use to maintain geographic positions within the estuary or to change position quickly (Bennett and others 2002). Moreover, it is fairly likely that delta smelt use this type of behavior to migrate upstream (Swanson and others 1998). The vertically migrating behavior causes particles to tidally “swim” upstream against net downstream water flows. We acknowledge that other smelt may exhibit other behaviors, such as lateral migration to move upstream; however, lateral movement simulations are not possible using the DSM2 ptm.

We conducted 30-day (d) simulations using three levels of Delta flow (340, 1,070 and 1,899 $m^3 s^{-1}$) and a constant water diversion rate (SWP and CVP combined) of 170 $m^3 s^{-1}$. We performed one model run at each flow level. We selected these Delta flow levels because they covered the range of all but the wettest conditions during the recent nine years when we analyzed salvage data (see previous method above). It also represented a sufficiently low water export scenario such that upstream particle movement was not strongly influenced by the net upstream flows that result when diversion rates are high relative to inflow rates (Kimmerer and Nobriga 2008). We inserted 2,000 particles into the model at Chipps Island (75 km from the Golden Gate Bridge) and tracked the change in their position for 30 days, using particle flux into the SWP diversion (Figure 1). We summed the number of particles entrained at the SWP for each simulation—migration rate was calculated as the time for 50% of the total at the SWP.

Our third question was to examine whether spawning tends to occur immediately after migration, or whether the spawners first hold in upstream areas, similar to some other migratory fishes (Lucas and Baras 2001; Moyle and others 2002). We first used salvage data described for Study Question 3 to estimate the timing of migration. Second, we used the SKT to determine the percentage of females in post-spawn ("spent") condition. The estimates were conducted for 2002–2005 since the SKT did not begin until 2002. We reasoned that a long gap between estimated migration date and the post-spawning stage was evidence for pre-spawning holding behavior.

Historically, delta smelt have been assumed to have a fairly "linear" life history pattern, with upstream migration of adults in winter, followed by downstream migration of juveniles in spring and summer (Moyle 2002; Bennett 2005). The previous study questions were based largely on this assumption. However, we evaluated the fourth study question because there is evidence that some anadromous fishes show variable migration patterns. For example, Clark (1968) and Secor (1999) described how favorable upstream habitat conditions likely promote residency of other species near spawning areas.

We hypothesized that there is at least some diversity in delta smelt migration. To evaluate this hypothesis, we compiled delta smelt catch data for three regions of the estuary during recent years (2002–2008) and a historical period of equal length (1967–1973). The data were summarized for the stations in the core distribution of delta smelt in the west Delta ("Stations 704 and 706"), as well as for two upstream areas assumed to support some spawning: Cache Slough ("Station 716") and the south Delta ("Stations 812 and 815") (Figure 1). If the hypothesis of variability in migration were true for delta smelt, we would expect that some delta smelt would be collected year-round in the upstream spawning areas. For each region and time period, we recorded whether delta smelt were collected in one of the following surveys: FMWT, SKT, 20-mm Survey, or TNS. We selected presence or absence rather than fish density as our metric because of the patchy distribution of the delta smelt (Feyrer and others 2007; Newman 2008), and because we relied on data from multiple survey methods, a requirement since no one survey effectively samples all life stages of delta smelt (Bennett 2005). Note that there was no 20-mm Survey or SKT sampling during the historical period. Because there was a gap in these surveys in a key spawning area (August in Cache Slough), we conducted a supplemental analysis of beach seine data collected by Nobriga and others (2005) for Liberty Island, the largest body of water in the Cache Slough region. The surveys were conducted during 2001 and 2003 in all months except for November through February. As for the other survey data, we determined whether delta smelt were present in a given month.

RESULTS

Analyses of the FMWT showed that the distribution of delta smelt varied by year, but the pre-migration distribution over the past two decades has consistently been in west Delta and Suisun Bay, the region immediately downstream of Chipps Island (Figure 2). In general, the pre-migration distribution occurs in the low-salinity zone of the estuary as illustrated by the strong association between fish distribution and X2 during fall (Figure 3). The monthly relationships for September (centroid = 7.0 + 0.902 X2; $p < 0.005$), October (centroid = –2.2 + 1.04 X2; $p < 0.001$), November (centroid = –5.1 + 1.08 X2; $p < 0.001$), and December (centroid = 25.4 + 0.745 X2; $p < 0.005$) were each highly significant based on generalized linear models. In general, the fish distributions also tended to be fairly well-associated with X2 over a wide range of X2 values. One possible exception is during December, when fish centroids mostly deviate above the simple linear relationship. Put another way, the data show that in late fall of most years, there may be a subtle shift into fresher water (i.e., upstream from the low-salinity zone) during the pre-migration period. However, an ANOVA showed no significant differences in the slope or intercept of the relationships between fish centroids and X2, so there is no statistical support for a December shift in distribution.

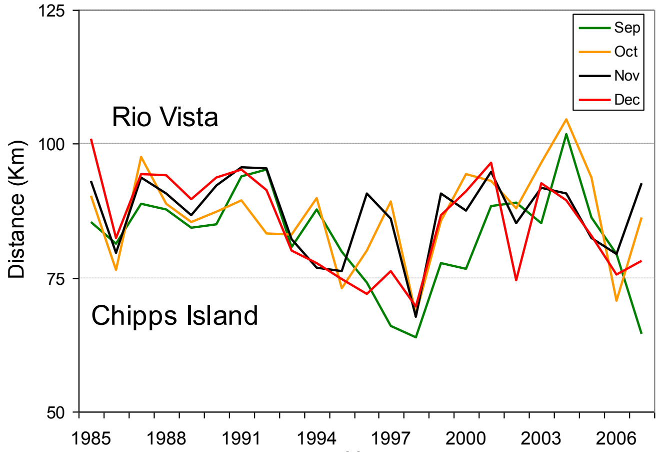

Figure 2 Monthly geographic distribution of delta smelt during the fall pre-migration season. The results are based on the centroid of the distribution from the FMWT using the method of Dege and Brown (2004). The distances were calculated as the number of kilometers from the Golden Gate Bridge. The west Delta is shown as the region between Rio Vista and Chipps Island, the downstream limit of the Delta.

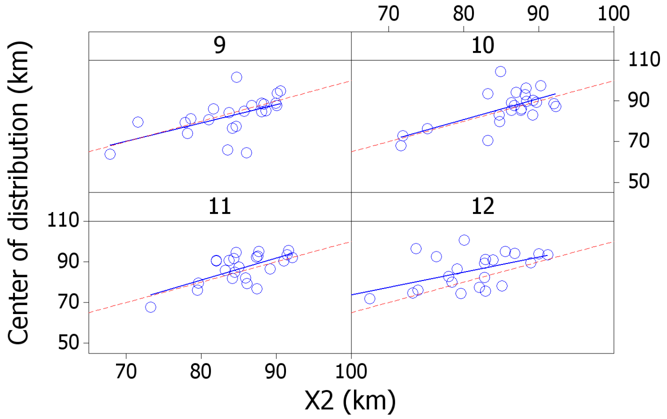

Figure 3 Monthly distribution of adult delta smelt in relation to salinity for the FMWT survey. The fish distribution data represent the centroid of the distribution from the FMWT (Dege and Brown 2004). Salinity is based on X2, the location of the 2 psu isohaline (Jassby and others 1995). The units for each data series represent the distance in kilometers from the Golden Gate Bridge. Hence, smaller values represent a seaward location and larger values represent a landward location. The red dotted lines show when the centroid and X2 values are equal. Centroid values above the red line represent fish distributions upstream of X2. Centroid values below the red line represent distributions downstream of X2. The blue lines show the fitted lines for the data, based on GLMs.

Estimates of migration rates varied across years (Table 1). The average migration rates for the years we evaluated were around 3.6 km d^{-1} with a range of 1.8 to 6.3 km d^{-1}. Average Delta outflow from first flush to the salvage peak at the SWP fish screens was not significantly correlated with the estimated migration rates (Kendall–Tau correlation coefficient = 0.33, $p = 0.25$).

The average migration rate estimate was fairly consistent with our particle-tracking simulations. The model runs showed that particles swimming only up and down in the water column at slack tides could migrate 80 km upstream from Chipps Island to the SWP in 18.3 days for the 340 m^3 s^{-1} simulation, 21.6 d for the 1,070 m^3 s^{-1} simulation, and 24.9 d for the 1,899 m^3 s^{-1} simulation (Figure 4). These simulations, therefore, represent average migration rates of 4.4, 3.7, and 3.2 km d^{-1}, respectively.

In all years analyzed, peak migration appears to have occurred well before most fish spawned. From 2002 through 2006, most spawners were collected at the SWP in January, but spent females were not observed in the SKT until February, and not in substantial numbers until March (Table 2). Hence, it appears that there is at least a one month gap between the primary upstream migration and spawning.

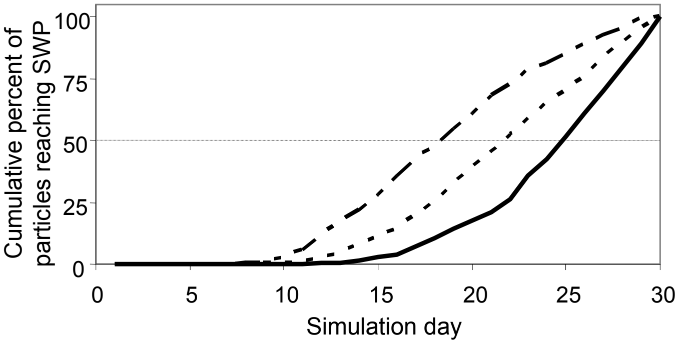

Figure 4 The cumulative percent of particles entrained into the SWP's Banks diversion based on a 30-d simulation that tracks the upstream "migration" of particles released in the Delta at Chipps Island for three levels of flow: 340 m^3 s^{-1} (broken line), 1,070 m^3 s^{-1} (dotted line) and 1,899 m^3 s^{-1} (solid line). The total number of the initial 2,000 particles entrained at the SWP during each simulation was 422, 770, and 452, respectively, after 30 days. The horizontal dotted line shows when 50% of the particles were entrained.

Table 1 Estimated upstream migration rates for delta smelt. The migration distance was calculated as the difference between the location of the State Water Project (SWP) Skinner Fish Facility (155.1 km from the Golden Gate Bridge) and the centroid of delta smelt distribution (Figure 2). The migration time was estimated based on the days between the first flush event and the timing of the salvage peak at the SWP (Grimaldo and others 2009).

Year	December FMWT centroid (km)	Estimated Distance traveled to SWP (km)	Time to SWP after first flush (d)	Estimated migration rate (km d^{-1})	Mean Delta flow during the migration period (m^3 s^{-1})
1993	80.1	75	12	6.3	1636
1995	74.8	80	16	5.0	4053
1999	86.7	68	36	1.9	1821
2000	91.1	64	29	2.2	1901
2001	96.5	59	33	1.8	412
2002	74.6	80	13	6.2	969
2003	92.6	62	17	3.7	1536
2004	89.3	66	19	3.5	1246
2005	82.8	72	39	1.9	802
Mean				3.6 (+1.8 SD)	

Table 2 Comparison of peak migration based on collection at the SWP (see Table 1) with the percentage of spent females in subsequent monthly SKT surveys. Sample sizes (number of fish) are shown in parentheses.

Year	Peak arrival of spawners at SWP	Percent spent			
		January	February	March	April
2002	January 2	0 (108)	0 (186)	14.6 (151)	n/a
2003	January 6	n/a	4.8 (145)	23.3 (158)	37.1 (35)
2004	January 19	0 (182)	0 (134)	2.7 (110)	23.6 (55)
2005	January 27	0 (113)	7.3 (137)	41.2 (17)	14.3 (14)

For recent years, the data show that delta smelt were present in all months in the west Delta (Table 3), which is the pre-spawning center of distribution for the species (Figure 2). The historical data for the west Delta stations do not include the entire year, but indicate that delta smelt were collected in all months when sampling was conducted. The recent results are similar for the Cache Slough region, a known upstream spawning area where fish were collected in all recent months (when samples were collected) including summer and fall, well outside the spawning season for this species (Table 3). The Cache Slough data are consistent with shorter-term sampling in Liberty Island, the largest contiguous area of open water in that region. Beach seine sampling in Liberty Island collected delta smelt in all months from March through October. Both the west Delta and Cache Slough catches contrast strongly with the recent results for the south Delta (Table 3), where fish were clearly absent during the warmer summer months. The historical data for the south Delta regions cover only half of the year, but indicate that delta smelt remained in upstream areas of the south Delta during summer.

DISCUSSION

Overall, our observations for delta smelt are consistent with the findings of Ohji and others (2008) that

Table 3 Presence of delta smelt for sampling in three regions of the estuary during two time periods. The general locations of the west Delta, Cache Slough, and south Delta sampling are shown in Figure 1. "X" indicates the presence of delta smelt for one or more stations or survey methods, "0" represents no detected delta smelt, and "n/a" indicates that there was no sampling during that month or period.

Month	Recent years			Historical years			Survey
	2002–2008			1967–1973			
	West Delta	Cache Slough	South Delta	West Delta	Cache Slough	South Delta	
1	X	X	X	n/a	n/a	n/a	SKT
2	X	X	X	n/a	n/a	n/a	SKT
3	X	X	X	n/a	n/a	n/a	SKT
4	X	X	X	n/a	n/a	n/a	SKT, 20 mm
5	X	X	X	n/a	n/a	n/a	SKT, 20 mm
6	X	X	X	X	n/a	X	20 mm, TNS
7	X	X	X	X	n/a	X	20 mm, TNS
8	X	n/a	0	X	n/a	X	TNS
9	X	X	0	X	n/a	X	FMWT
10	X	X	0	X	n/a	X	FMWT
11	X	X	0	X	n/a	X	FMWT
12	X	X	0	X	n/a	X	FMWT

the migration patterns of Osmerids are complex and variable. Based on our data and previous studies, delta smelt should be considered a diadromous seasonal reproductive migrant, fishes that show migrations between freshwater and marine (or estuarine) environments. Although some individuals migrate entirely within freshwater (potadromy), most of the population starts the migration period in brackish water. Like many species that migrate, delta smelt move upstream seasonally for reproduction, but there is some variability in this general pattern, as will be discussed in further detail.

Pre-Migration. Consistent with previous descriptions of the life history of delta smelt (Moyle 2002; Bennett 2005), the pre-migration distribution appears to be focused on the low-salinity zone. Because the fish live in an estuary, this distribution is not geographically static; it shifts upstream and downstream with tides and depending on annual variation in flow. Implicit in our analyses is the assumption that the FMWT samples the majority of the range of delta smelt. As will be discussed in further detail, an unknown portion of the population occurs in the Cache Slough region (Figure 1), an area that the FMWT did not sample consistently. Nonetheless, we believe the FMWT provides the best available information to analyze long-term patterns and associations.

Our results suggest that delta smelt is different than several other anadromous fishes such as salmon and sturgeon, which show "staging" behavior prior to the major upstream migration. For example, salmonids frequently show initial distribution shifts from the ocean into brackish or freshwater portions of estuaries (Salo 1991; Moyle 2002). Our results did not show statistical support for an upstream shift in fall before the major winter spawning migration (Figure 3). This pattern is not surprising, because delta smelt has a relatively small range and migrates relatively short distances (Moyle 2002; Bennett 2005), so there may be little adaptive need for staging.

Migration. Evidence suggests that delta smelt migrate in response to "first flush" events (Grimaldo and others 2009). Typically, pulses of delta smelt are observed at the fish facilities within 1 to 4 weeks of the flow and turbidity increases (Table 2). Moreover, delta smelt tend to be collected at the SWP in single unimodal peaks (Grimaldo and others 2009), suggesting a somewhat coordinated migration strategy. This degree of coordination may be adaptive for a highly variable and turbid estuary, where finding mates may otherwise be challenging. Upstream migration in response to inflow also is consistent with observations from other Pacific coast osmerids (D. Hay, Pacific Biological Station, Fisheries and Oceans Canada, pers. comm., 2007; P. Chigbu, University of Maryland, pers. comm., 2007) and several fishes native to the San Francisco Estuary (Harrell and Sommer 2003).

Average migration rates in recent years have been around 3.6 km d^{-1} and were not correlated with Delta flow. We acknowledge that our estimates based on the pre-migration population distribution (e.g., the "centroid" in Figure 3) may not be fully representative of how far individual fish migrate. However, our results seem realistic in light of laboratory studies, particle-tracking simulations, and results for other fishes. Laboratory studies indicate that delta smelt can probably swim for long periods at rates of 1 to 2 body lengths per second (Swanson and others 1998). This means that in slack water, adult delta smelt could potentially swim 5 to 10 km d^{-1}. Although this level is higher than our estimates, our migration rates still seem reasonable given the conclusion by Swanson and others (1998) that the fish probably do not make long-distance movements using constant swimming behavior. The particle-tracking model simulation generated average migration estimates of 3.2 to 4.4 km d^{-1}. This level is quite consistent with our estimates for delta smelt based on salvage data (Table 3). Our model result depended on a specific assumed swimming behavior ("tidal surfing"), which has not yet been established for delta smelt. However, it is highly likely that the species uses a selective tidal swimming behavior to move upstream (Swanson and others 1998). For example, young longfin smelt in the San Francisco estuary show different behaviors during ebb and flood cycles that allow them to maintain their position (Bennett and others 2002). Our particle-tracking model simulations indicate that vertical migration represents a plausible behavior for tidal surfing, but our model did not allow us to determine if lateral migration would produce similar or better results.

Our estimated migration rates are within the range reported for other North American fishes (Table 4). Fish size affects migration speed and distance (Nøttestad and others 1999), and, as expected, our estimates are much lower than those of adult salmonids (Salo 1991). Although delta smelt is smaller than any of the types summarized in Table 4, our estimates were fairly consistent with several other fishes.

Table 4 Reported upstream migration rates of selected North American fishes. Note that each species is capable of faster short-term swimming.

Species		Migration rate (km d^{-1})	Sources
Chum salmon	*Oncorhynchus keta*	4 – 80	Salo (1991)
Atlantic lamprey	*Petromyzon marinus*	0.008	Bigelow and Schroeder (1953)
Green sturgeon	*Acipenser medirostris*	1.2 – 2.2	Benson and others (2007)
Herring	*Alosa aestivalis* *Alosa pseudoharengus*	8 – 21	Jessop (1994)
American shad	*Alosa sapidissima*	1.6 – 3.1	Leggett (1976)
Colorado pikeminnow	*Ptychocheilus lucius*	6.6	Irving and Modde (2000)
Striped bass	*Morone saxitilis*	23.6	Carmichael and others (1998)
Walleye	*Sander vitreus*	0.8	Ryder (1968)
Delta smelt	*Hypomesus transpacificus*	1.8 – 6.3	This study

Note that migration rates of 5 km d^{-1} have been characterized as a "fast pace" for small fishes (Lucas and Baras 2001). As a consequence, we believe that it is realistic to characterize delta smelt migration rates as relatively rapid. This contrasts Moyle's (2002) characterization of delta smelt migration as "gradual, diffuse" and that it "may take several months for an individual to reach a spawning site." We were unable to find good upstream migration rate data for other osmerids. Murawski and others (1980) reported that rainbow smelt movements between spawning areas in a Massachusetts estuary was in the range of 0.5 to 9 km d^{-1}. However, it is unclear from the rainbow smelt study whether movements represented active migration, or a "wandering" interchange between spawning areas (Rupp 1968, as cited in Murawski and others 1980).

Post-Migration. The data suggest that delta smelt do not spawn immediately after migrating upstream. Grimaldo and others (2009) showed that December–March flow pulses trigger upstream migration; however, spawning does not begin until late February, with typical peaks from March through May (Bennett 2005). Our analyses using the SKT data indicate that delta smelt hold upstream for long periods after migration, probably at least a month before spawning. This conclusion is consistent with the behavior of several other native fishes, including some races of Chinook salmon (Healy 1991), sturgeon (Moyle 2002) and Sacramento splittail (Moyle and others 2004). We wish to emphasize that apparent holding behavior does not mean that delta smelt do not show additional pre-spawning movements (e.g., Rupp 1968, as cited in Murawski and others 1980).

The year-round presence of delta smelt in upstream areas indicates that their migratory patterns vary. This does not appear to be a new trend, because there is historical information that young delta smelt persisted in the Delta months after the winter–spring spawning period (Erkkila and others 1950; Nobriga and others 2008). These results do not necessarily mean that fish remaining upstream in summer are the same individuals spawned in spring—the range of delta smelt is small, and it is unclear how much of the pattern results from residence of juveniles in upstream spawning areas and how much results from periodic movements of fish within its range. In any case, the emerging story is somewhat different from previous accounts of this species, which focused on a uniform upstream migration of adults, followed by downstream migration of juveniles (Moyle 2002; Bennett 2005). Prolonged upstream residence may be supported by high turbidities and prey densities (Sommer and others 2004; Lehman and others 2010) in the Cache Slough region. The year-round presence of delta smelt in the Cache Slough region may be evidence of contingents in the population. Migratory fishes frequently have alternative life histories that may be influenced by habitat use at early life stages (Clark 1968; Secor 1999). The "contingent hypothesis" proposes that these fishes have divergent migration pathways that could help the species survive in variable and heterogeneous environments. This type of strategy has already been identified for pond smelt, a congener of delta smelt in Japan (Katayama and others 2000).

Recommendations. Conservation of migratory species such as delta smelt depends largely on understanding links between different periods of their life cycles (Martin and others 2007). Just a decade ago, the upstream migration portion of the life cycle of delta smelt was largely unknown (Swanson and others 1998). A review of migration by different taxonomic groups indicates that this information gap is apparently fairly common among smaller estuarine fishes (Lucas and Baras 2001). Although there are still substantial uncertainties, we believe that recent local studies and results from similar species provide basic insight into delta smelt migration. Understanding this part of its life history is critical, especially considering its recent collapse to record and near-record low abundance (Sommer and others 2007) and its relatively high vulnerability to extinction (Bennett 2005). Nonetheless, there are still key information gaps that require additional study. A major priority is the development of improved telemetry and marking techniques to deal with this small, fragile species. Such methods might allow researchers to determine whether delta smelt use lateral or vertical migration as part of "tidal surfing" to migrate upstream. In addition, detailed otolith studies to determine migration patterns such as the frequency of occurrence of delta smelt in different salinity ranges (Katayama and others 2000; Hobbs and others 2007). Based on similar studies of other species (Secor 1999; Kerr and others 2009), our expectation is that delta smelt show highly diverse migration pathways, including freshwater residence, brackish water residence, and various strategies in between.

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