Migratory Life Histories and Early Growth of the Endangered Estuarine Delta Smelt
(Hypomesus transpacificus)

By

EVA ELISABET BUSH

BS (University of California, Davis) 2012

THESIS

Submitted in partial satisfaction of the requirement for the degree of

MASTERS OF SCIENCE

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

_____

Dr. Peter B. Moyle, Chair

_____

Dr. Nann A. Fangue

_____

Dr. James Hobbs

Committee in Charge

2017

i

Abstract

The Sacramento-San Joaquin Delta in California, is a complex estuarine ecosystem managed both for human use as well as for fish, including threatened and endangered species. The abundance of the endangered Delta Smelt (*Hypomesus transpacificus*) is at an all-time low and now the centerpiece of conflict between human and environmental use of limited fresh water resources. We used otolith strontium isotopes to determine the life histories of 1109 adult Delta smelt collected by the California Department of Fish and Wildlife Spring Kodiak Survey over 7 non-consecutive years, representing variable climatic conditions. We found that Delta Smelt exhibit partial migration through three different life history phenotypes, which include a freshwater resident fish, a brackish water resident fish, and a migratory phenotype, hatching in fresh water then occurring in brackish water during the juvenile and sub-adult stage. The yearly contributions from each phenotype were found to vary with freshwater flows and temperature. The relative abundance of each life history phenotype varied inter-annually with the migratory phenotype being most abundant in all years, while the freshwater resident phenotype was important in several years of low overall Delta smelt abundance. The brackish residents only made up a small part of the population in most years, but appear to make an important contribution in the year of highest spring flows, but with high temperatures. Together, the freshwater and brackish water residents provided population stability, contributing more to the overall population when abundance indices were low. Inter-annual variations in early (30 day) growth rates can also be discerned among years, but not over the years combined. This study provide evidence that suggest Delta Smelt could benefit from cooler water temperatures in fresh water, particularly during the summer months when temperatures peak. Overall, the three phenotypes provide the Delta smelt with some resiliency but the continued decline of population suggests the life history variability is insufficient.

Table of contents

List of figures

List of Tables

Introduction

Delta Smelt were historically an abundant pelagic species in the San Francisco Estuary, while exhibiting the population density fluctuations expected with a species living in California's highly variable climate (Bennett 2005). The population began to decline in the 1980s, and was first listed as threatened under the California (CESA) and Federal Endangered Species Acts (FESA) in 1993; it was subsequently up-listed to Endangered by the state in 2009 following a second step-change decline in the early 2000s (Mac Nally et al. 2010, Thomson et al. 2010). The up-listing to endangered resulted in additional restrictions on fresh water exports at the State Water Project (SWP) and Central Valley Project (CVP) pumps in the South Delta (USFWS 2008). These additional restrictions have been controversial because the annual abundance of Delta Smelt in the Fall Midwater Trawl has not been strongly correlated with freshwater outflow to the estuary (Kimmerer 2002; Moyle et al. 2016) and restrictions on exports have not resulted in recovery of the species (IEP-MAST 2015; Moyle et al. 2016). The Delta Smelt have been described as a semi-anadromous species; however, recent analyses have found Delta Smelt residing in the north delta year-round (Sommer et al. 2011, Sommer and Mejia 2013). If Delta Smelt readily reside in the freshwater reaches of the Delta throughout the life cycle, this life history phenotype could have significant ramifications for management of the species. Variability in life history could have a stabilizing effect on population abundance, as recruitment success of one phenotype could make up for less successful recruitment of another (Kerr et al. 2010; Kerr & Secor 2012). However; the benefit of phenotypic variability may be limited by direct and indirect anthropogenic impacts such as effects of invasive alien species and changes in water infrastructure that alter the flow regime of the Delta (Hobbs et al. *in press*, Hammock et al. 2015; Moyle et al. 2016). Furthermore, the resilience of such a life history may be further eroded by the unprecedented drought in California.

Large and small scale migrations occur in many taxa and ecosystems worldwide and have long been of interest to ecologists as both an ecological and evolutionary response to shifting food availability and reproduction (Thomson 1926; Elton 1927). Migration has been extensively studied in birds, mammals and fish all over North America (Dingle 1996; Chapman, K. Hulthén, et al. 2012; Thomson 1926; Elton 1927). From an evolutionary perspective, individuals adopting a migratory life history must show an increase in fitness, through enhanced foraging and reproductive success, that outweighs the metabolic cost and increased predation risk associated with migrations (Jonsson & Jonsson 1993). Migrants can be classified as facultative (migrate in response to deteriorating environmental conditions) or obligate (individuals migrate, regardless of cues). Furthermore, populations can exhibit both resident and migratory phenotypes, known as partial migration. In partial migration, the distinction between obligate and facultative migration is blurred due to the plasticity of the phenotype within populations (Dingle & Drake 2007; Hayes et al. 2012). In fish, partial migration is found around the world, from marine species making cross-ocean migrations to freshwater species making short migrations between rivers and lakes (Chapman, Skov, et al. 2012; Chapman et al. 2011; Brönmark et al. 2014; Dingle 1996). For the purposes of this investigation, partial migration is defined as a type of intrapopulation phenotypic variation where migration occurs in a fraction of the total population and the remainder is resident in the natal or nursery region.

The San Francisco Estuary (SFE) is the largest estuarine habitat along the Pacific coast. It supplies a wide variety of species with habitats ranging from freshwater in the very upper part of the estuary to the brackish Delta and marine conditions in the San Francisco Bay. The variety of habitats is also structural, from tidal marsh and wetlands to open water areas. This patchwork of dynamic habitat has facilitated evolution of different life history strategies (LHS) influencing movement

among species and within-species. Probably the most well studied aquatic species in California exhibiting different types of within species LHS in regards to migration is the steelhead/rainbow trout (*Oncorhynchus mykiss*) but there are others in the SFE, such as Striped Bass (*Morone saxatilis*) and Sacramento Splittail (*Pogonichthys macrolepidotus* which have been extensively studied (Feyrer et al. 2004; Merz et al. 2013). A broad understanding of the nature of movements, even local non-migratory movements, can have management implications for several native species, including the critically endangered Delta Smelt (*Hypomesus transpacificus*).

Studies suggest that the opportunity to migrate from one type of habitat to another for better foraging is capitalized on by either faster growing individuals, who due to their size, are less likely to become prey during migration (Hayes et al. 2012; Jonsson & Jonsson 1993) or slower growing individuals migrating to better foraging opportunities (Kitamura et al. 2006). In general, fecundity commonly increases with body size in female fishes and difference in body size between migrants and residents is a common observation for both sexes (Chapman, K. Hulthén, et al. 2012; Jonsson & Jonsson 1993). In females, both the amount and the size of eggs increases with increased body size, making it more profitable, from a fitness standpoint, for the female to migrate to find better foraging opportunities (Bagenal 1973; Brönmark et al. 2014). Furthermore, in populations exhibiting partial migration, it is common to see more female than male migrants (Chapman, Kaj Hulthén, et al. 2012; Jonsson & Jonsson 1993). In populations of sea-run Brown Trout (*Salmo trutta*) females grow faster attaining larger sizes prior to migrating to riskier, but more food-rich areas, while the smaller males remain in the safer, but less food-rich areas (Jonsson & Jonsson 1993). The more abundant or higher quality the forage is; the greater fitness advantage is expected in return.

In some species, size or growth rate appears to be a determining factor for migration whether male or female. For example, Steelhead in Scotts Creek, California appear to have an age or size threshold for anadromy, with only individuals greater than 250 mm undergoing smoltification and migrating to sea (Hayes et al. 2012). In Japan, the partial migratory population of Threespined Stickleback (*Gasterosteus aculeatus*) exhibits a bimodal distribution of body length which was a strong driver of life history strategy. Migratory individuals exhibited slower juvenile growth and shorter body length and left the fluvial pond in search of more productive foraging in the ocean (Kitamura et al. 2006). In Lake Ogawara, Japan, the pond smelt *(Hypomesus nipponensis)* a congener of the Delta Smelt, exhibits partial migration, with individuals inhabiting fresh, brackish and ocean waters. Spawning takes place in small streams inland in late winter-early spring. At spawning the population exhibits a bimodal size distribution, where members of the migratory contingent are much larger than the residents. In early life, prior to migration, there is no size difference however. This suggests growth in freshwater is not the determining factor for migration in this species, but migrants to the estuary and ocean experienced rapid growth in those habitats (Katayama et al. 2000).

Delta Smelt life history was first described by Moyle et al. (1992). Delta Smelt inhabit downstream, oligohaline areas from spring until late winter and very early spring, at which time they migrate upstream to freshwater to spawn, normally after the first large storm increases the freshwater flows from the upper watershed into the estuary. The adults die shortly after spawning, and the larvae hatch out in the freshwater, to then migrate downstream. For some time, it was thought that adult Delta Smelt were unable to control their movements during migration and that the spawning migration up the Sacramento River was a long process. However, while many spawning-ready (ripe) females have been found in brackish water, not many individuals had a

brackish natal otolith chemistry signature indicating that successful spawning rarely took place there (Hobbs et al. *in prep*) indicating that successful spawning more likely occurred in fresh water. In a study conducted during the peak migration, which occurs after the first high flow event of the year, Delta Smelt were found to use lateral movement between the shoals and channel, corresponding to tidal cycles, and rapidly migrated upstream against the prevailing current by riding the tides (Bennett & Burau 2015). This strategy may be effective in mitigating the high energetic cost of migration.

Although Delta Smelt have on occasion been found in fresh water sampling year round, the general understanding has been that all Delta Smelt make obligatory migrations on an annual basis (Moyle 2002; Sommer et al. 2011; Moyle et al. 1992). This perception has driven actions to protect the species and the low-salinity habitats it inhabits. These actions have been largely unsuccessful, in part because managers have failed to account for large-scale changes to the SFE which have adversely affected Delta Smelt. The migration, both as juvenile and spawning adults, make them vulnerable to anthropogenic habitat alterations, such as entrainment by extensive water diversions in the Delta (Sommer et al. 2011).

The growing evidence that migration is not the exclusive strategy has led to the understanding that Delta Smelt movements are complex and that the genetically homogenous population exhibits a partial migration life history strategy in which some individuals are resident in fresh water. Whether this is a recent phenotypic shift in life history strategy in response to shifting environmental cues is difficult to tell. Here we take a closer look at the hypothesized partial migration of Delta Smelt, using samples archived from select CDFW SKT surveys (Figure 1) By combining otolith growth metrics and otolith strontium isotope chemistry approaches, we try to assess migratory characteristics of the Delta Smelt population. We predict that migratory Delta

Smelt grew faster due to the productive nursery habitat in the low-salinity zone. Further we hypothesize that the partial migration life history strategy provides population resilience. We examine growth and life history phenotype among several year-classes occurring over years with conditions ranging from high freshwater outflow to low flows from persistent drought. We ask the following questions: (1) Does the composition of life history phenotypes vary among years? and (2) Do growth rates in the early stages of life (first 30 days) determine the life history strategy? To answer these questions, we analyzed otoliths from smelt belonging to year classes from the two high flow, but temperature varying years (2006 and 2011) from smelt year classes from adjacent dry years (2005, 2010) and from the drought year classes of 2012, 2013 and 2014 (Figure 1).
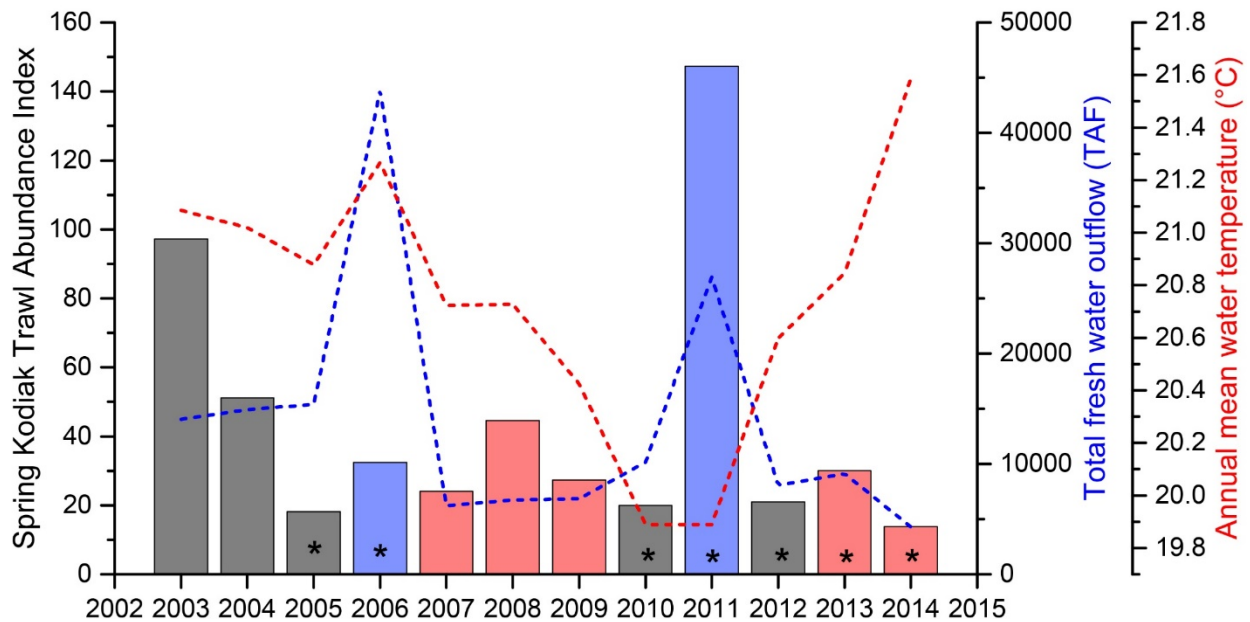
Figure 1. Smelt abundance indices from the Spring Kodiak Trawl sampling program of CDFW, 2002-2014 with fresh water outflow (dotted blue line) and annual mean water temperature (dotted red line). Blue bars indicate wet years, the grey above and below normal and the red indicates dry years. Asterisks indicate years from which Delta Smelt samples were processed.

Materials and Methods

Fish Sample Collection

Adult Delta Smelt were collected during the spawning season (January-May) in 2006-2007, and 2011-2015 by the California Department of Fish and Wildlife's (CDFW) Spring Kodiak Trawl Survey (SKT) (*https://www.wildlife.ca.gov/Conservation/Delta/Spring-Kodiak-Trawl*). These adult spawning fish were hatched out the previous year and represent the year classes 2005-2006 and 2010-2014. The SKT survey uses a 7.6-m wide by 1.8-m deep Kodiak trawl towed between two boats at the surface for 10-minutes per tow among 40 fixed sampling stations located from the Napa River in the west to the San Joaquin River in the south and the Sacramento Deep Water Ship Channel to the north, encompassing the presumed distribution of adult Delta Smelt (Figure 2).
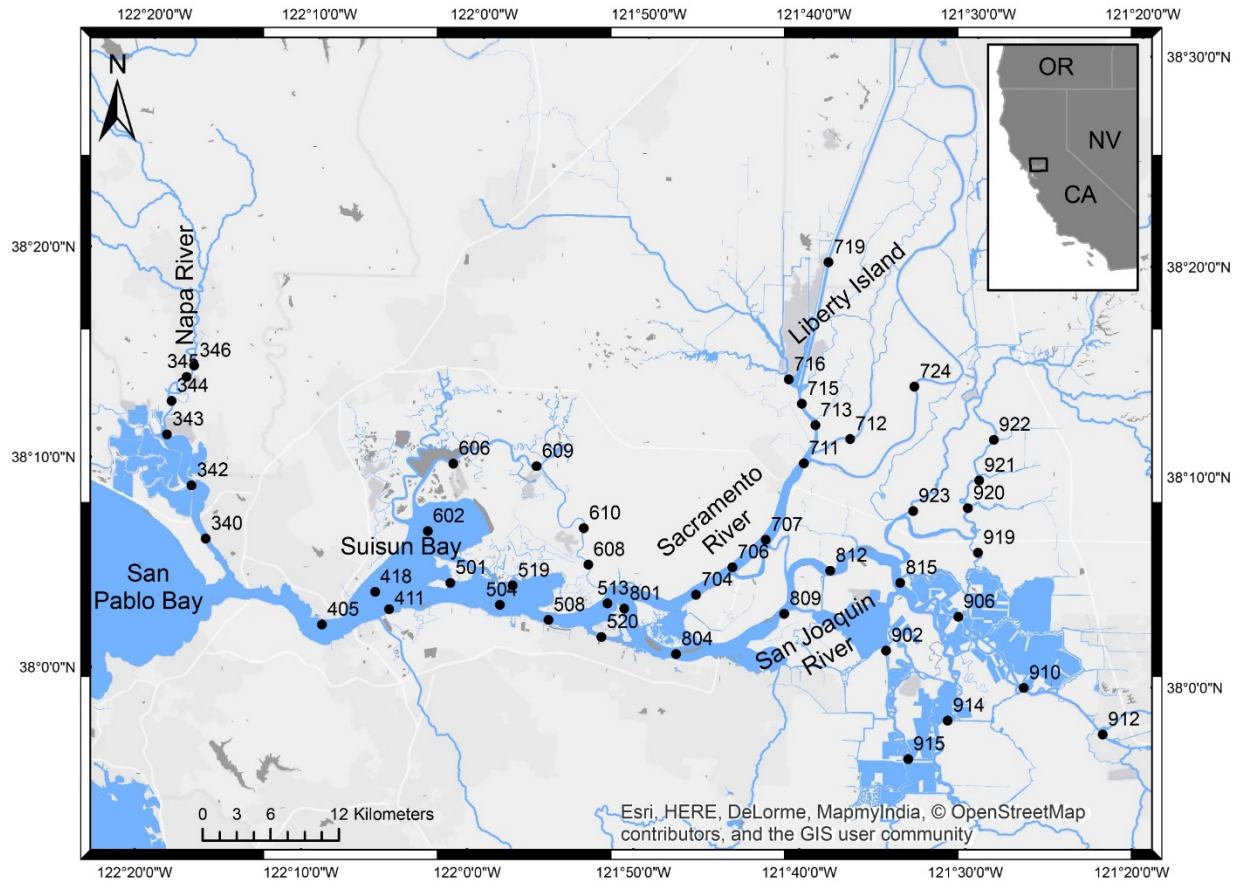
Figure 2. Map of the Delta and part of the San Francisco Estuary showing all the SKT stations, covering most of known Delta Smelt habitat.

An annual index of abundance is calculated by summing the catch per unit effort over the first four monthly surveys. For otolith analysis, subsamples of archived fish were selected to represent the spatial distribution and relative abundance in freshwater and the LSZ. First, catch was summed by station, then stratified by salinity and summed for freshwater and the LSZ by monthly survey. Sub-samples were selected based on the proportion of catch by salinity and survey targeting up to 200 individuals per year (Table 1).

Table 1. Catch and sub-sample shown by region as a percentage of total catch. The sub-samples were attempted to mirror the total catch whenever possible, however some years the samples passed on by CDFW did not mirror the actual catch and the samples received where used.

	Cohort	2005	2006	2010	2011	2012	2013	2014	All Years
	SKT Survey year	2006	2007	2011	2012	2013	2014	2015	-
Catch region	Low-salinity zone	146	206	138	430	105	176	31	1232
	Freshwater	395	495	296	738	231	216	72	2443
	% Low-salinity zone	27	29	32	37	31	45	30	34
	% Freshwater	73	71	68	63	69	55	70	66
	total catch								3675
Sub-Sample	Low-salinity zone	30	50	27	84	64	125	44	424
	Freshwater	31	98	159	114	126	113	44	685
	% Low-salinity zone	49	34	15	42	34	53	50	38
	% Freshwater	51	66	85	58	66	47	50	62
	total samples analyzed								1109

Otolith Processing and Analysis

Sagittal otoliths were dissected from the heads of Delta Smelt and stored dry in ThermoScientific Cell Culture Plates. Before mounting, the membrane remains surrounding the otoliths were removed by soaking in 95% ethanol for a minimum of 24 hours. Once the membrane was removed, otoliths were mounted onto microscope glass slides with Crystal Bond® thermoplastic resin in the sagittal plane. Otoliths were sanded sulcus side up until the outermost rings were visible, turned and sanded with wet-dry sandpaper (Buehler 800 and 1200 grit) until the core rings were visible and then polished with a polishing cloth and 0.3-micron polishing alumina.

Otoliths were digitized with a 12 Megapixel digital camera attached to an Olympus CH30 compound microscope at a magnification of 20X, using AM Scope (www.amscope.com). Otolith

increments were enumerated and the increment width and radial distance (µm) from the core to each daily ring was measured using Image-J NIH software *(http://imagej.nih.gov/ij/)*.

Two people independently quantified otolith increments; the mean, median, average percent error and the coefficient of variation of each individual fish were assessed. If the age reading by the three readers for an individual fish was greater than 10% average error, the sample was selected for processing of the second otolith for age analysis.

The samples were then mounted on petrographic slides (20 per slide) for otolith microchemistry. Otolith strontium isotope ratios (^{87}Sr:^{86}Sr) were analyzed using methods established protocols (Hobbs et al. 2005; Hobbs et al. 2010) at the UC Davis Interdisciplinary Center for Plasma Mass Spectrometry (http://icpms.ucdavis.edu). A multi-collector inductively coupled plasma mass spectrometer (*Nu Plasma HR* from Nu Instrument Inc.) was interfaced with a Nd:YAG 213 nm laser (New Wave Research UP213) for in situ strontium isotopic measurement by laser ablation (LA-MC-ICP-MS technique). A laser beam of 40-µm diameter traversed across the otolith from the core to the edge at 10-µm per second, with the laser pulsing at 10-Hz frequency and 5-10 J/cm^2 photon output. The laser profile began ~100µm before the core and scanned to the dorsal edge to ensure the analysis encompasses the entire life history (Figure 3).
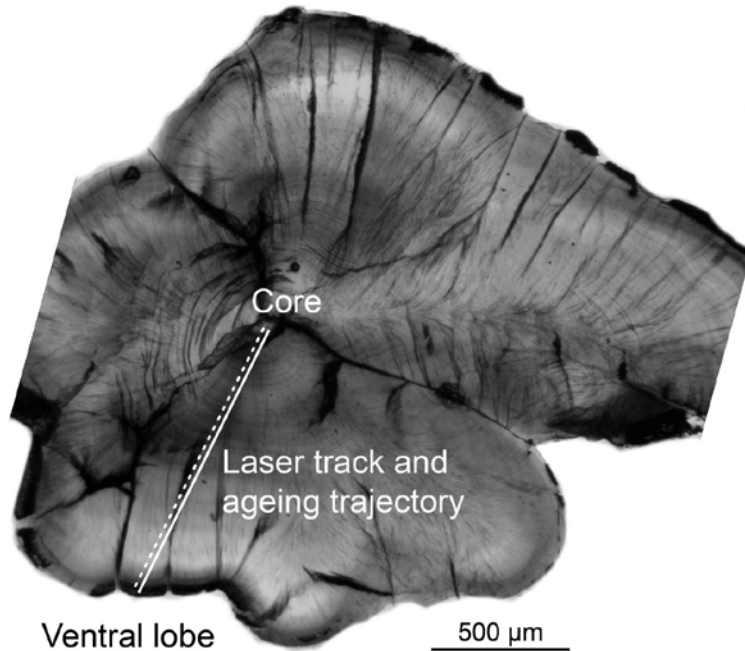
Figure 3. Microscope image of Delta Smelt otolith at a magnification of 4x, showing the laser trajectory and ageing trajectory.

Helium was used as the carrier gas to maximize sensitivity and minimize sample deposition at the ablation site, and was mixed with Argon gas between the laser sample cell and the plasma source. Gas blank and background signals were monitored until ^{84}Kr and ^{86}Kr stabilized after the sample change (i.e. exposing sample cell to the air) and were measured for 30 seconds. Strontium isotope ratios (^{87}Sr:^{86}Sr) were internally normalized by the measured ^{86}Sr:^{88}Sr ratio relative to assumed ratio of 0.1194, which corrects for mass discrimination. The signal on mass 85 was monitored to account for any ^{87}Rb interference on ^{87}Sr. During each daily analysis, an aragonite coral, and ocean-caught fish otolith (white seabass) standard was analyzed with the same laser parameters at the beginning and end of each day with at least three replicate line-scans per standard. The analytical accuracy was evaluated by comparing the results of replicate analyses of the coral and otolith standards at the beginning and end of analytical sessions to the modern seawater ^{87}Sr:^{86}Sr value of 0.70918 (McArthur et al. 2001).

Strontium Isotope Isoscape of the SFE

To create a strontium isotope ratio profile of the estuary, water samples were collected at the surface at each SKT station in 2012 and 2015 using an acid rinsed polypropylene syringe from a bucket of water collected at the surface of the water column. Water was filtered through a 0.45 μm syringe filter (Whatman[TM] Puradisk) into a 250-mL polypropylene container and the sample was acidified (1mL of 3% nitric acid) to stop bacterial growth. At the UC Davis ICPMS lab, water samples were initially screened for alkaline earth metals (such as strontium) and analytical interferences (such as rubidium) on an Agilent 7500ce (Agilent Technologies, Inc.) Quadrupole inductively coupled plasma mass spectrometer (Q-ICP-MS). After elemental screening, the samples were transported to a class 100 (less than 100 particles per cubic foot of air) clean room facility. Within this environment, an aliquot of each water sample was made at volume totaling approximately 1 nanogram of total strontium. This volume (ranging 3 – 70 mL) was evaporated to dryness and reconstituted in sub-boiling double-distilled nitric acid (8M) for Sr chromatographic separation. Strontium was isolated from all other water constituents by rinsing water samples through a micro-column packed with Sr spec resin (Eichrom Inc.) The purified strontium was subsequently oxidized with concentrated sub-boiling double-distilled nitric acid to remove organics from column and dried to a powder. This powder was reconstituted in 2% sub-boiling double-distilled nitric acid and analyzed with the Nu Plasma HR (MC-ICP-MS) to determine the $^{87}Sr:^{86}Sr$ ratio.

Samples were introduced into the Nu Plasma with a desolvating nebulizer system (DSN-100) providing an order of magnitude sensitivity increase by evaporating most of the sample matrix (water vapor) away. Ratios include 50-60 data points and each data point was integrated for 10 seconds. Baselines were measured for 30 seconds by ESA deflection (ion beams were defocused

away from detectors). Strontium isotope ratios (^{87}Sr:^{86}Sr) were internally normalized as described in the otolith analysis section, with the exception of the Krypton correction on ^{86}Sr. In this case, ^{84}Sr:^{86}Sr was assumed to be 0.00675476 (natural abundance of these isotopes) and is used to estimate subtraction of ^{84}Krypton and ^{86}Krypton. Kr was subtracted until the ^{84}Sr:^{86}Sr ratio equals the canonical value while iterating the mass-bias correction. Replicate analyses of NIST SRM 987 (strontium carbonate) were conducted bracketing every six samples normalizing for instrument drift over the course of the day and analytical artifact between sessions. An in-house modern coral standard was processed in parallel with each water sample set and resulted in ^{87}Sr:^{86}Sr = 0.709182±0.000017 (2σ, n=8).

Water quality was also collected using a YSI 6600. Water quality parameters included salinity (psu), electrical conductivity (μs/cm), and temperature (Celsius °C). To describe the relationship between strontium isotope ratios and salinity, we fit a smoothing spline to data. In addition, a conservative linear mixing model using three freshwater endmembers (North Delta- Cache-Lindsey Slough Complex ^{87}Sr:^{86}Sr = 0.70642, Sacramento River upstream of confluence with the North Delta ^{87}Sr:^{86}Sr = 0.70583 and along the San Joaquin River near Jersey Point ^{87}Sr:^{86}Sr = 0.70721) was used with the ^{87}Sr:^{86}Sr = global ocean value of 070918.

Environmental Data

Two key environmental features; temperature and outflow, were calculated to assess their impact on the growth rates and expression of life history phenotypes. Data for freshwater outflow was retrieved from the IEP's DAYFLOW model (http://www.water.ca.gov/dayflow/). Daily freshwater flows (OUTFLOW) in total acre-feet was used to describe inter-annual differences during study years. Daily water temperature data was retrieved from CDEC

(http://cdec.water.ca.gov/) for the Rio Vista station (RIV). Data for the study years were averaged daily (15-min intervals over 24 hours). Summer water temperatures in Celsius (mean June 1 to August 31) were derived from 15-min continuous interval data at three stations, Rio Vista (RIV), Mallard Slough (MAL) and Martinez (MTZ) CDEC (http://cdec.water.ca.gov/). Delta Smelt are known to be adversely affected by warm summer water temperatures (Komoroske et al. 2014, Komoroske et al. 2015, Jeffries et al. 2016) thus the period from June through August was used to encompass the warmest period of time.

Life history assignment by strontium isotope ratios

Life history phenotype was based on the ^{87}Sr:^{86}Sr profile from the core to the edge of the otolith. Several life history patterns were apparent from visual examination of profiles reflecting different natal origins and age-at-migration. Natal and adult ^{87}Sr:^{86}Sr regions in the otolith were assigned to salinity zone based on the water ^{87}Sr:^{86}Sr-Salinity relationship using the QDFA analysis.

Water strontium isotope ratio data analyzed in this study was combined with data from the literature and our data from previous studies (Ingram and DePaolo 1993, Hobbs et al. 2010). To characterize the empirical relationship between strontium isotope ratios and salinity, we fit a Loess regression smoothing spline (span = 0.4) to water ^{87}Sr:^{86}Sr and corresponding salinity. A priori, we choose freshwater (<0.5 ppt) and the Low-Salinity Zone-LSZ (0.5 to 6 ppt) as two zones to distinguish using ^{87}Sr:^{86}Sr as these zones are considered the critical habitat for Delta Smelt (Sommer & Meija 2013; Feyrer et al. 2007). However, Delta Smelt have been encountered in habitats with salinity exceeding 20 ppt (Komoroske et al. 2016) so we devised a method to resolve the ^{87}Sr:^{86}Sr for salinity greater than 6 ppt *(Hobbs et al, in prep).* Since ^{87}Sr:^{86}Sr do not fractionate when incorporated into otoliths, assignment to salinity zone based on otolith ^{87}Sr:^{86}Sr would be

similar. Based on 10+ years of laser ablation MC-ICPMS of the in-house coral standard, our laser ablation based accuracy is within $\pm$1-ppm 2σ (0.0001) of the true value 0.70918. Therefore, to further resolve salinity zones greater than 6 ppt, we combined water sample $^{87}Sr:^{86}Sr$ values corresponding to 1-ppm incremental bins in water $^{87}Sr:^{86}Sr$ above the value for 6 ppt ($^{87}Sr:^{86}Sr$ = 0.70890) to define two additional salinity zones, a mesohaline-salinity zone (6-15-ppt) and polyhaline-salinity zone (>15-ppt) for the San Francisco Estuary. To evaluate statistical precision of salinity zone assignment via $^{87}Sr:^{86}Sr$ we used quadratic discriminant function analysis (QDFA) in R using the MASS package using a jackknife leave-one-out test (R Core Team 2013).

Otolith Growth Analysis

Otolith increment widths (30-day increments) were modelled in R using a mixed effects regression following the statistical approach outlined in Morrongiello and Thresher (Morrongiello & Thresher 2015). In this modelling approach, the intrinsic ontogenetic (age, sex) effects on otolith growth were distinguished from extrinsic effects (life history phenotype) in the modeling procedure. First models were run to determine the optimum random effects structure. The random effects included individual FishID, year-class and age, with intercepts only effects for FishID, year-class and age-FishID slope and intercepts and age-year-class slope and intercepts (Table 2). In addition, a quadratic term for age was included to account for the non-linear pattern in otolith growth (Table 2&3). The latter was kept and built on, by next adding cohort and lastly the interaction of age and cohort.

15

Table 2. Description of parameters used.

Parameter	Code	Description
Fixed Effects		
Age	Age	Age (months) when otolith increment was formed
Sex	Sex	Male or Female
Cohort	fCohort	Yearclass (birthyear)
Life History Phenotype	fLHS	Freshwater resident or migratory (reared in low-salinity habitat) types from otolith 87Sr:86Sr
Random Effects		
FishID	fishid	Unique fish identification for each fish
Month	fMonth	Month when otolith increment was formed. Quantifies seasonal growth variability
Age	Age	Random Age slope on each FishID, Month, Life History Phenotype

Table 3. Hierarchical Models used to fit random and fixed effects.

Random Effects	
M1	FishID
M2	Age*FishID
M3	Age+Age^2*FishID
M4	Age+Age^2*FishID+Cohort
M5	Age+Age^2*FishID+Age*Cohort
M6	Age+Age^2*FishID+Age^2*Cohort
Model M6 selected for refit	
Fixed Effects Models	
M8	Age*LHS+Age^2

Table 4. Best random effect model results from AIC.

Model	df	Δ_AICc	Res.LL
M6	17	0.00	-109.94
M5	17	74.98	-147.43
M4	15	141.69	-182.8
M3	14	337.49	-281.7
M2	11	517.33	-374.63
M1	9	761.03	-498.49

Next the intrinsic fixed effects were tested with age, age^2 and sex and their interactions terms as predictors of 30-day otolith growth intervals from age 0 to 210 days post hatch.

The mixed effects model allows us to account for the inherent autocorrelation in otolith growth data. Adjacent otolith increment measurements within a fish (*e.g*., first 30 with the second 30) are more correlated to each other than to those of other fish because of individual-specific differences in growth rates. The fish sampled are also seen as a random draw of all possible fish in a population, therefore the random intercept for FishID induces a correlation among increment measurements within a fish and allows each individual to have an independent model intercept from the model's overall intercept. All analyses were performed using the lme4, AICcmodavg, and effects package in R 3.0.2 (R Core Team 2013). 30-day growth increments and Age were log-transformed to satisfy linear model assumptions and all predictor variables were mean-centered to facilitate model convergence and interpretation of interaction terms. Analyses of random effects were performed by fitting the desired model structure using restricted maximum likelihood estimates of error (REML). Models with increasing fixed effect complexity were fitted using maximum likelihood estimates of error. We assessed the relative support for each candidate set of models using Akaike's information criterion (AIC). AIC values were rescaled as the difference between each model and

the model with lowest AIC. Best models were then reanalyzed using REML to produce unbiased

parameter estimates (Zuur et al. 2009).

Results

Strontium Isotope to Salinity relationship

The strontium isotope ratios (^{87}Sr:^{86}Sr) of fresh waters (<0.5 ppt) were consistently below 0.7075, and the Cache-Lindsey-Sacramento River Deep Water Ship Channel (SRDWSC) region in the North Delta had ^{87}Sr:^{86}Sr less than 0.7066 (Figure 4). ^{87}Sr:^{86}Sr increased rapidly across the isohaline from <0.5 ppt to ~ 6 ppt, after which the rate of change slowed, assymptoting near a salinity of 15-ppt (Figure 4). The continuous gradient of ^{87}Sr:^{86}Sr-salinity was accurately classified into 4 distinct salinity zones; freshwater (FW, <0.5 ppt), low-salinity zone (LSZ, 0.5 – 6 ppt), mesohaline-salinity zone (MSZ, 6-15 ppt) and a polyhaline-salinity zone (PSZ, >15 ppt) based on ^{87}Sr:^{86}Sr variability, with 94% of samples classified into the correct salinity zone using a quadratic discriminant function analysis (QDFA) jackknife procedure. Samples that were not correctly assigned to salinity zones had ^{87}Sr:^{86}Sr occurring at the boundaries between salinity zones.
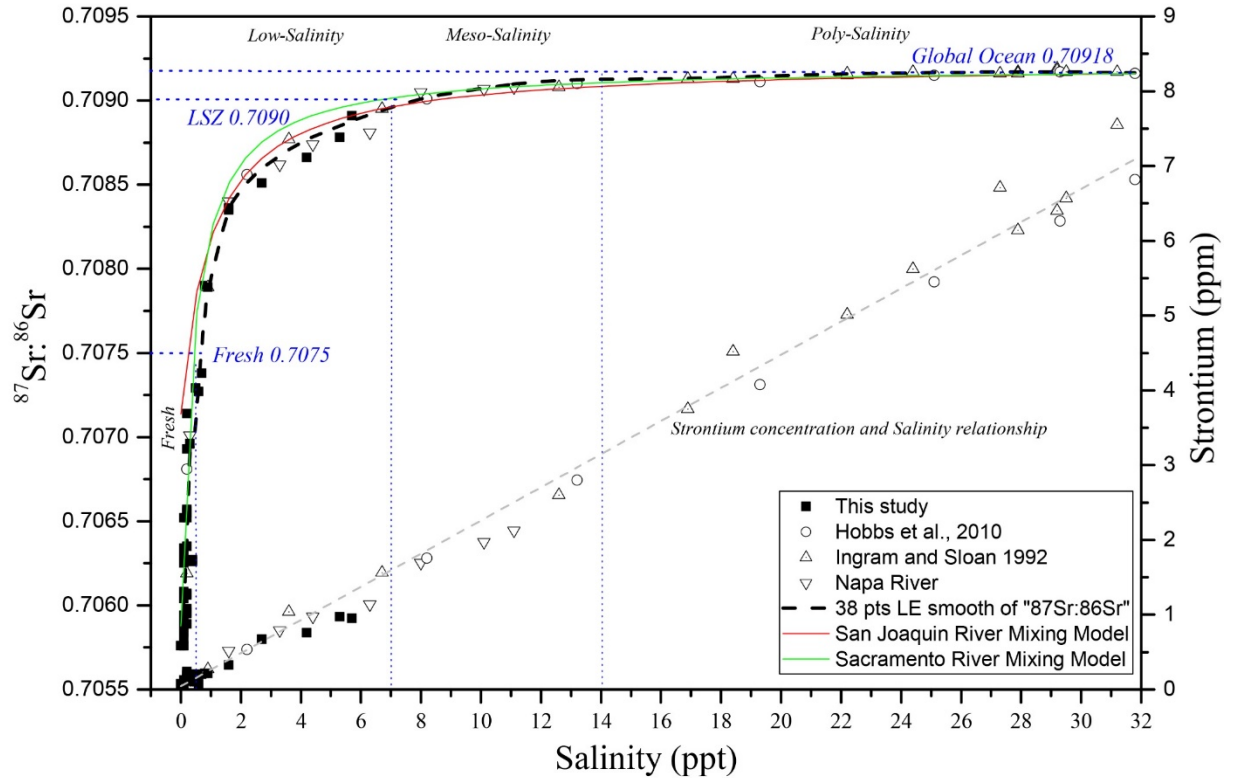
Figure 4. The strontium isoscape for the San Francisco Estuary. Solid squares represent water samples collected in this study, open circles data from Hobbs et al 2010, open triangles from Ingram and Sloan 1992. Red line depicts the San Joaquin River mixing model, black dashed line Loess smoothed empirical ^{87}Sr:^{86}Sr, green line the Sacramento River mixing model and the grey dashed linear regression line the salinity-strontium concentration.

Life History Phenotype Composition

Delta Smelt exhibited three distinct life history phenotypes, including; (1) a freshwater (year-round) resident where the ^{87}Sr:^{86}Sr from the core to the edge was consistently less than 0.7075 ($\bar{x}$ = 0.7063), (2) a brackish water resident fish, where the ^{87}Sr:^{86}Sr was consistently greater than 0.7075 ($\bar{x}$ = 0.7085), and (3) a migratory phenotype, hatching in freshwater ($\bar{x}$ = 0.7065) then occurring in brackish ($\bar{x}$ = 0.7084) water during the juvenile and sub-adult stage (Figure 5).
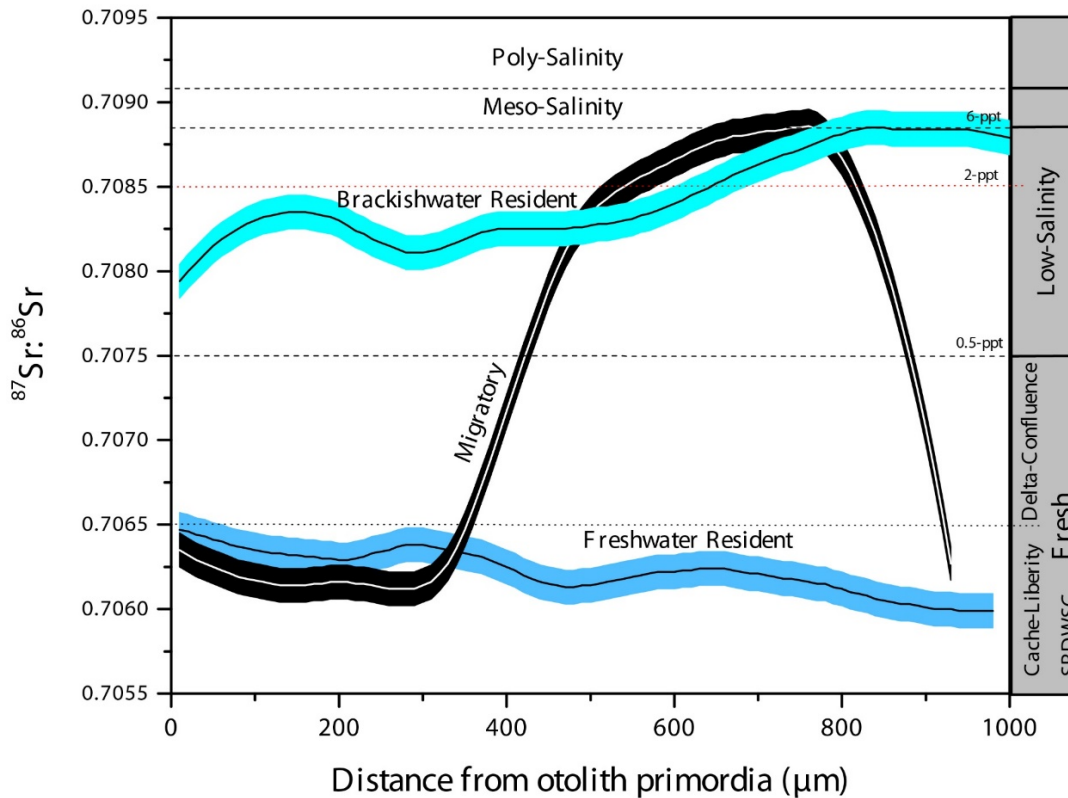
Figure 5. Representative ^{87}Sr:^{86}Sr life history profiles for adult Delta Smelt (Loess smoothed $w=$ 0.4, ±2σ). Salinity zones ^{87}Sr:^{86}Sr transition value depicted by horizontal dashed lines derived from the Loess smoothed empirical fit of water ^{87}Sr:^{86}Sr in Figure 2. Dotted horizontal lines depict important habitats for Delta Smelt. Distances from core of 200,400,600 and 800µm correspond to ages of 46, 81, 130 and 250 days-post-hatch and back-calculated lengths of 21, 36, 51 and 67 mm-FL.

The percentage of life history contingents varied among regions of the estuary and between years of the study. All fish collected in the low-salinity zone region were either brackish origin fish or migratory phenotypes (Table 5). No freshwater resident fish were found in the low-salinity zone, but brackish origin fish were found in fresh water, presumably migrating upstream to spawn. In each year, a majority of the catch occurred in fresh water (63-73%). We attempted to sub-sample fish from the catch distribution to provide a representative and robust estimate of the percentage of contingents. In 3 of the 7 study years we were able to accomplish this; however, for the SKT

21

2011 our sub-sample was significantly skewed towards freshwater catches due to biased sample archival (Table 1). In that year samples were archived by CDFW staff, and more were archived from the freshwater stations. This increased our sample from the freshwater stations; thus we could not adequately match the catch distribution (Table 1). Since the freshwater stations catches include all spawning migrants coming back as well, this should not affect the phenotype calculations however.

Table 5. Contribution of phenotypes by percent of sample. Table shows breakdown of phenotype contribution in the subsample by survey year. FWR indicates fresh water residents, MIG migrants and BWR indicate brackish water residents.

Cohort	SKT Survey year	FWR %	MIG %	BWR %
2005	2006	15	72	13
2006	2007	2	75	23
2010	2011	47	52	1
2011	2012	18	80	2
2012	2013	42	52	6
2013	2014	16	79	5
2014	2015	8	89	3
All Years	-	23	70	7

The migratory contingent made up the majority of the Delta Smelt catch in each study year (52% - 89% - sub-sample, Table 5, Figure 6). The freshwater contingent was found in all study years, but was highly variable between years, making up only 2% of the catch for 2007 and 47% - sub-sample for 2011 (Table 5, Figure 6). The Brackish Water contingent varied between 1% of the subsample in 2011, to 23% in the 2007 survey (Table 5, Figure 6). The composition among wet years was different, with the 2006-year class comprised of a significant percentage of brackish origin fish (Figure 6). Freshwater residents comprised a larger percentage of the catch for 2011 and 2013 (47 and 42% respectively) compared to 2007 and 2015 (2% and 8% respectively).
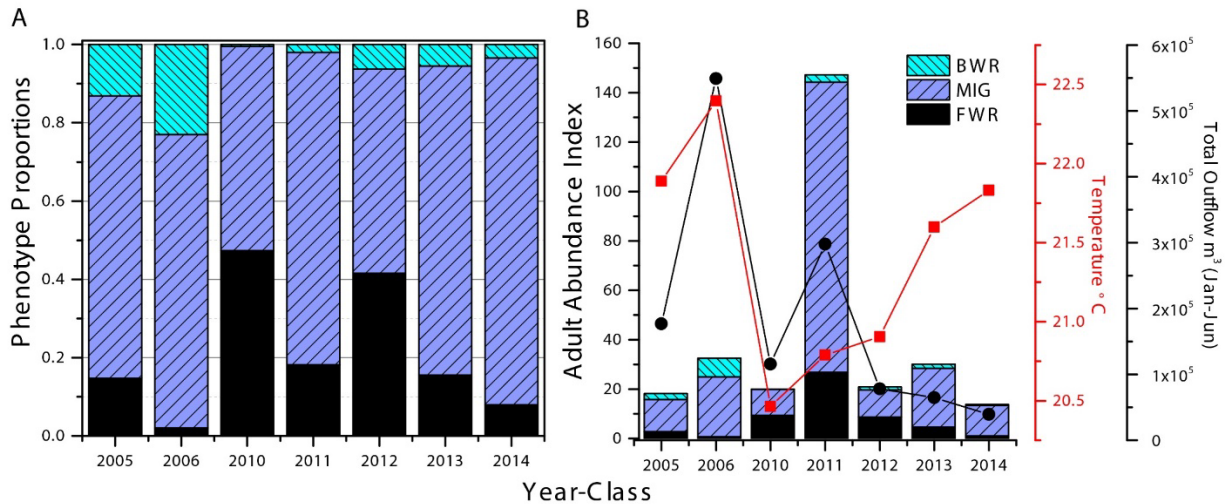
Figure 6. A. Life history phenotypic composition of the adult Delta Smelt population B. Life history phenotypes scaled to the adult abundance index. BWR= brackish water residents, MIG = migratory, FWR = freshwater resident fish. 2006 and 2011 were years of high freshwater flows.

The relative abundance of life history phenotypes (proportion scaled to the SKT index) varied with freshwater outflow (Total January-June) and with July mean water temperature (Figure 6). Years 2006 and 2011 had higher freshwater outflow, but water temperatures were high in 2005 and 2006 and 2013-2014 (Figure 6). The relative abundance of the brackish water resident fish and the migratory phenotype was positively associated with freshwater outflow, while the freshwater resident exhibited a negative trend with outflow (Figure 7). Temperature could explain the low abundance in 2006 which would improve our understanding of outflow-abundance trends. July 2006 was the warmest month in the time series and was strongly negatively correlated with the abundance of freshwater resident fish (Kendall's tau = -0.84, p = 0.0004), while the brackish water residents and migratory phenotype showed no trend with temperature (Figure 7). The high abundance of all three life history phenotypes in 2011 coincided with high flows and cool summer temperature. This was in contrast with 2006 with high flows and warm temperatures in early spring as well as warm summer temperatures, which were associated with low abundance of the migratory phenotype and extremely low abundance of freshwater resident phenotype (Figure 7).
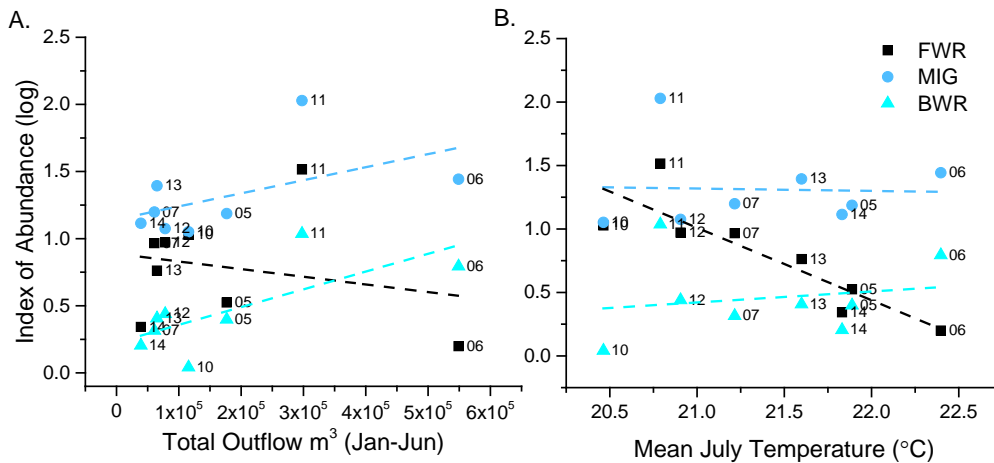
Figure 7. The effect of freshwater outflow and temperature on abundance of life history phenotype. FWR = Freshwater Residents, MIG = Migratory, BWR = Brackish Residents. Dashed lines depict regression lines for each phenotype.

Growth Model Results

The best random effects structure included the random slope and intercepts for age^2 and FishID, age^2 and Yearclass (Table 3&4). Next, we fit additional hierarchical models of complexity for the fixed effects, sex and Life History Strategy (LHS), with sex entered as an interaction term with age as well as added effect for LHS. Through a comparison of models using AIC the best fitting model lowest AIC score was used to evaluate fixed effects in the model. The overall best fitting model included age, age^2 and LHS interaction and Age^2 (Table 3&4). For all fish in this study, age was the most important intrinsic factor determining growth rate variation in Delta Smelt, as typically found for ontogenetic age affects in otolith growth studies. Life history phenotype was used as an additional model variable to explain the remaining variance, but there was not a significant effect of LHS on growth (Figure 8).

Growth rates did vary among year classes through 90 days post hatch, after which growth slowed ontogenetically and no differences among yearclasses were observed (Figure 9). Growth to age 30 and age 60 was reduced in the 2013 and 2014 yearclasses (Figure 9a-b), but was similar among all yearclasses after age 90 (Figure 9c).

24
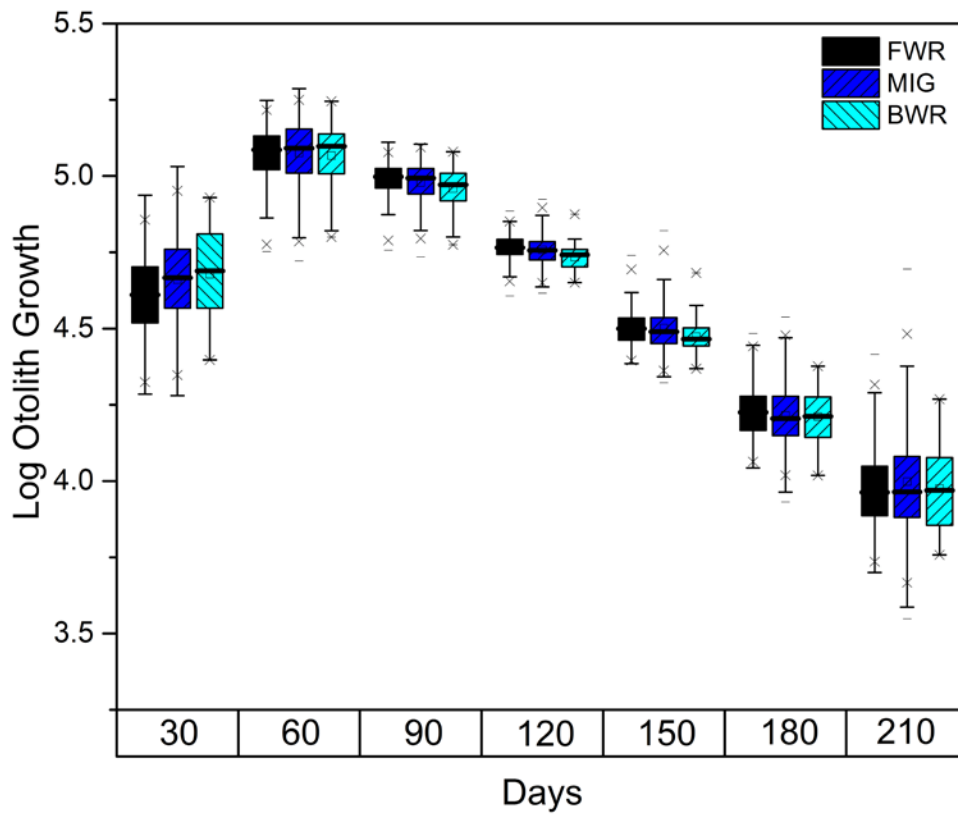
Figure 8. Box-plot of otolith growth over the first 6 months for the three different life history phenotypes. FWR = Freshwater Residents, MIG = Migratory, BWR = Brackish Residents.
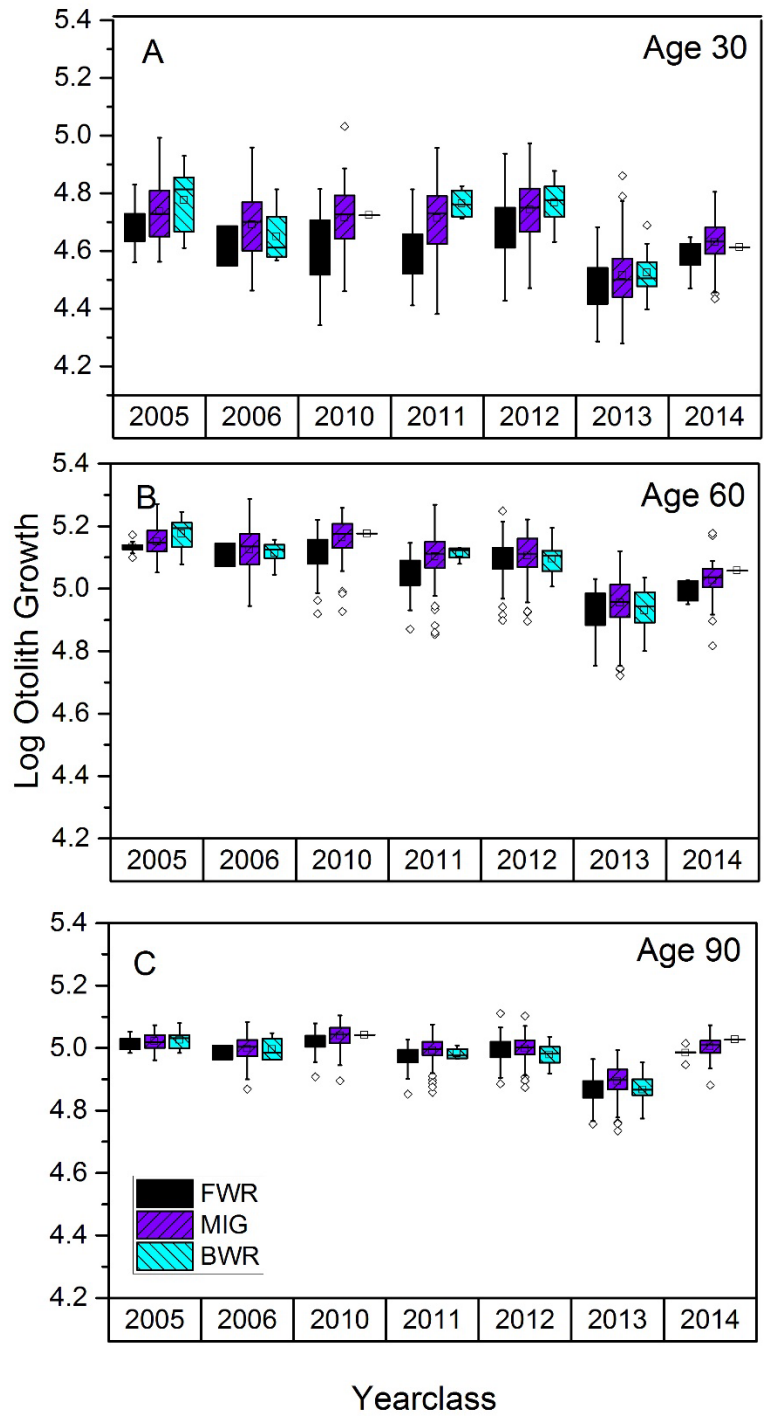
Figure 9. Growth rates by year class and life history strategy. The brackish resident (BWR) and migratory contingent (MIG) are consistently growing faster than the freshwater contingent (FWR) in the first 30 days. By 60 days the rates converge and no discernable differences remain.

Discussion

In this study, we used otolith $^{87}Sr:^{86}Sr$ to identify three distinct life history phenotypes in Delta Smelt. The abundance patterns of each life history phenotype responded differently to freshwater flows and temperature. The contribution of each life history phenotype to the population varied, but was not related to freshwater outflow alone, but rather to the combination of high freshwater flow and low summer time temperatures. Both 2006 and 2011 were high freshwater flow years, but only 2006 did not see an increase in Delta Smelt abundance, likely due to the unusually high spring time temperatures and rapid decrease of flows through the dry season. Often, years of high flow into an estuary coincide with high primary and secondary productivity, as well as high recruitment of juvenile fish, which has also been established in the SFE (Kimmerer 2002a, Kimmerer 2002b). During the sample years used for this study (2006-2007, 2011-2015), this held true only for the 2011 year-class for the population as a whole, which almost reached pre-decline levels of abundance. The proportion of the freshwater resident contingent of Delta Smelt did not change with freshwater outflow. Instead, warm summer water temperatures appeared to be a likely driver of spatial distribution and life history strategy limiting their use of this habitat. This observation is consistent with long-term changes in summer distributions; the Delta Smelt no longer reside in the Central or South Delta during summer months when water temperatures exceed ~22°C (Nobriga et al. 2008). This was also seen in 2005-2006 when daily mean water temperatures at Rio Vista exceeded 22°C during summer and few freshwater resident fish where found. It is unclear if the low number of freshwater residents in 2006 indicates that more individuals migrated due to the very early heat or stayed behind with increased mortality. The partial migration life-history strategy may obscure effects of warm summer temperatures on fish abundance. If spring conditions favor a resident strategy, a subsequent hot summer could reduce the abundance of this

27

phenotype as in 2006 (Figure 6). However, if spring conditions favor a migratory life-history strategy, then warm summer conditions in fresh water will affect fewer fish and will have less of an effect on the population, especially in the Low-Salinity Zone, where water temperatures are generally cooler, as seemed to happen in 2011 (Figure 6).

Laboratory studies of juvenile Delta Smelt acclimated to 16ºC show that they experience a mortality rate of over 50% when water temperature exceeds 24ºC. These same studies show that physiological impairment is exhibited at 22ºC (Komoroske et al. 2014; Komoroske et al. 2015; Brown et al. 2016). The Spring-Summer survival of Delta Smelt during the 20-mm Survey-Summer Townet Survey period, when they migrate from freshwater larval nursery areas to the Low-Salinity Zone, was lower in 2005 and 2006 when the mean daily temperatures exceeded 22°C early on, compared to 2010 and 2011 (IEP-MAST 2015). Thus warm temperatures in fresh water are likely a driver of Delta Smelt recruitment success. Delta Smelt critical thermal maximum temperatures depend on life stage, with larval smelt being most tolerant, suggesting the early life stages are adapted to warm conditions (Komoroske et al. 2014). However, while in fresh water juveniles are often found near their tolerance level during summer months and may be vulnerable to short-term warm water pulses (heat waves) which would push them above tolerance levels, causing high mortality.

The abundance of the freshwater contingent did not appear to coincide with higher adult abundance indices for Delta Smelt. The contribution of the freshwater contingent was similar between 2010 and 2011; however, only the 2011 year-class experienced significantly greater abundance (Figure 1). Interestingly, the total catch in the Spring Kodiak Trawl did not fluctuate from year to year as much as the abundance index (Figure 1). The SKT index is calculated using only a core set of 39 stations, with stations 719 and 799 not included in the abundance index. During the years of this

study, these non-index stations made up a large portion, and in some years, the majority of the total catch of Delta Smelt (Table 6).

Table 6. Showing the percent of the catch made up by non-index stations during the study years. The Spring Kodiak Trawl Index is made up from 39 core stations. The catch at 719 and 799 are not included in the index calculations.

Cohort	2005	2006	2010	2011	2012	2013	2014
SKT Survey	2006	2007	2011	2012	2013	2014	2015
Total Catch	575	706	445	1206	340	355	108
719/799 Catch	353	383	244	301	159	104	16
Catch (%)	61	54	55	25	47	29	15

Fish caught at these two stations were mainly freshwater resident fish, with a few migrants. Other IEP surveys have added stations in the Sacramento Deep-Water Ship Channel and Delta Smelt have been caught as far upstream as Washington Lake, the turning basin of the Sacramento Deepwater Ship Channel. Considering the shift in spatial distribution from the Central and South Delta to the North Delta that is apparent in the IEP surveys, a significant proportion of the population may now occur outside of the core index stations. The large jump in population size between the 2010 and 2011 year classes, brings to question if we have an accurate estimate of the population, given the freshwater resident contingent of the population and the apparent importance of that phenotype in supporting the population when environmental conditions are right, providing stability to the population long term. Thus, the freshwater resident phenotype contributed a large portion to the population during the drought years.

The migratory life history contingent was nevertheless the most common phenotype in every year examined in this study, indicating that this life history strategy remains the dominant one. Both the migratory and brackish resident phenotypes in the population responded positively to freshwater outflow, which implies that freshwater flow is an important driver of Delta Smelt

29

populations. Since the invasion of the voracious overbite clam however, the presumed increased productivity does not translate into added foraging opportunities for fish. The decline of foodweb productivity in the LSZ of the upper SFE has been well documented and is believed to be a major driver of the overall decline in Delta Smelt abundance (Kimmerer et al. 1994; IEP-MAST 2015). The LSZ essentially is no longer a functional nursery habitat; juvenile fish caught in this habitat are in poor health and exhibit reduced growth rates (Hammock et al. 2015). Arriving into a food-limited habitat after expending energy in migration puts further stress on juvenile fish. In many years, high summer temperatures are yet an additional stressor requiring additional food for increased metabolic demands. Laboratory studies show metabolic rates of Delta Smelt increase at increasing temperatures (Jeffries et al. 2016), meaning they require more food to meet their energetic needs. This suggests that the migratory life history phenotype is now at a disadvantage from a bioenergetics perspective and is likely experiencing increased mortality as a result. Large numbers of larvae occurring in a food-deprived LSZ could also be an important phenomenon explaining low abundance during high outflow years. It seems likely that Delta Smelt are either subject to thermal stress as a freshwater resident or to limited food abundance in the LSZ as a migrant.

In 2006, we found a large number of fish which appear to have been born in low-salinity habitats (Figure 6). There are two potential explanations for this apart from brackish water spawning and hatching. The fish may have been born in fresh water and rapidly transported to the Low-Salinity Zone post-hatch, or maternal contribution of Low-Salinity Zone strontium to the offspring may obscure our natal origin identifications. While the latter cannot be ruled out, it is unlikely because Delta Smelt embryos have a very small volume of yolk from which to derive maternal contributions and the otolith core at hatch is very small. Recent laboratory rearing experiments

have confirmed that Delta Smelt can successfully hatch and rear at low salinities, thus it is likely this is a viable life history strategy. In 2006, ~15% of the spawning adult Delta Smelt were found in the Napa River at a single station, which was the highest catch in the Napa River during this study. Spawning in the Napa River has been previously reported in Delta Smelt during high outflow years and offspring from the Napa River had natal ^{87}Sr:^{86}Sr indicative of low-salinity exposure at hatch (Hobbs et al. 2005b). Since monitoring did not start within the Napa river until the early 2000s there is no catch data available for the other years of outflows of that magnitude (1967, 1969, 1983, 1995, 1998). Regardless, high early winter flows would likely influence adult fish distributions and possibly cue fish to spawn downstream of the Napa River confluence. Furthermore, when spawning occurs in the Napa River offspring can become trapped by the receding salinity field as spring flows and high exports move the LSZ upstream past the mouth of the Napa River. Thus high outflow may have indirect effects on recruitment success by facilitating spawning in marginal habitats or dispersing larvae into stressful rearing conditions (Hobbs et al. 2005b). It is also worth noting that apart from the 2006 year-class sampling where the brackish life history fish were found in Napa, the overwhelming majority of the brackish residents are found in the Montezuma Slough in Suisun Marsh, which is part of the North Delta Arc of habitat, a concept first developed by Moyle et al. (Moyle et al. 2012) (Figure 10).

The limited numbers of fish with low-salinity natal origins would suggest that this is not a successful life history strategy at this point, however. Interestingly, we did observe brackish water origin fish in fresh water, indicating that they too might migrate back into fresh water to spawn. During the sampling years for this study no freshwater resident fish captured in low-salinity waters were observed; thus the strontium isotope signatures appears to be a robust indicator of salinity history.

With higher yearly freshwater flows, the growth rates did not respond as predicted. Growth rates did vary between year classes. The highest growth rates occurred in the 2011 year-class, particularly during the fall, while the 2006 year-class experienced lower growth rates. The elevated growth rates in 2010 and 2011 corresponded with lower water temperatures and prolonged flows, while in 2006 temperatures increased very quickly and flows tapered off significantly in the summer. This would suggest Delta Smelt benefit from cooler water temperatures, particularly during the summer months when temperatures peak. Successful spawning and hatching in Delta Smelt was found to be temperature dependent and temperatures over 20°C provided poor larval survival (Bennett 2005). Elevated growth rates also appeared to be associated with lower temperatures seasonally. Growth rates were fastest during the spring months in all years (March-May). Growth is typically fast in the early life stages of fish, but we accounted for the ontogenetic effect of age and life stage in our growth models. Thus, faster growth in spring was likely associated cool water temperature.

Partial migration is common in estuarine species and generally considered to provide resilience in fish populations, giving the population protection against catastrophic population decline and providing the ability to rebound once environmental conditions are again favorable (Gillanders et al. 2015; Hart et al. 2015; Dingle 1996; Chapman, K. Hulthén, et al. 2012). If a habitat is not favorable for rearing and growth one year and reproduction suffers in one life history phenotype, the remaining strategies may support the population as a whole. If we define resilience as the ability to come back to previous population levels it is also worth considering that there is a threshold below which this is not possible. This threshold occurs if stock recruitment passes below a certain point, a point which differs for different species and populations depending on their reproductive behavior and life history (Myers et al. 1994). The environmental stochasticity the

population is exposed to can also be an important factor. The uncertainty of the rate of change in salinity and temperature in the estuary makes it important to ensure that all life history strategies remain.

What gives resilience in a population is the presence of this variability, the often talked about portfolio effect, which allows a population to survive, and even thrive under highly variable environmental conditions under which they evolved (Carlson & Satterthwaite 2011; Griffiths et al. 2014). For example, despite the currently very small contribution of brackish resident to the population, environmental changes being brought on by climate change could increase its importance. The varying contributions from different life history phenotypes in different years suggests that unless Delta Smelt are given the opportunity to use all of these habitats to retain their varied life histories, the population resilience will be lessened. This puts the population at a far greater risk of extinction given that a poor year for one strategy can no longer be compensated for by another.

Historically Delta Smelt spawned in the San Joaquin river as well as the Sacramento river (Moyle 2002), but due to water exports the adults who migrate there to spawn most likely end up as salvage at the water export pumping stations (Sommer et al. 2011). This makes the connection between the San Joaquin River and the LSZ non-functional and the population has to rely on Sacramento River spawning only. The Sacramento River to LSZ connection is intact, with spawning in the Cache Slough/Liberty Island area and north and larvae moving down to the LSZ. With decreasing food availability in the LSZ and increasing temperatures in fresh water, Delta Smelt are already experiencing the stress of climate change (Kimmerer & Allen 1982; Sommer et al. 2007).

If we accept that resiliency of a population comes from a variation in life history strategies, we need to support the diversity that is there to promote population persistence. We can find habitat

with connectivity supporting all three life history strategies in the North Delta Arc of habitat (Figure 10). The 2010 and 2011 year classes showed us that the freshwater habitat will support a large part of the population if temperatures remain cool. The historic dendritic channels with shading riparian vegetation have been replaced by a network of unshaded canals designed only with water transport in mind. This together with the flooding of Liberty Island, which created a large open body of water to absorb heat, has completely changed the thermal regime of the North Delta (Figure 10&11).
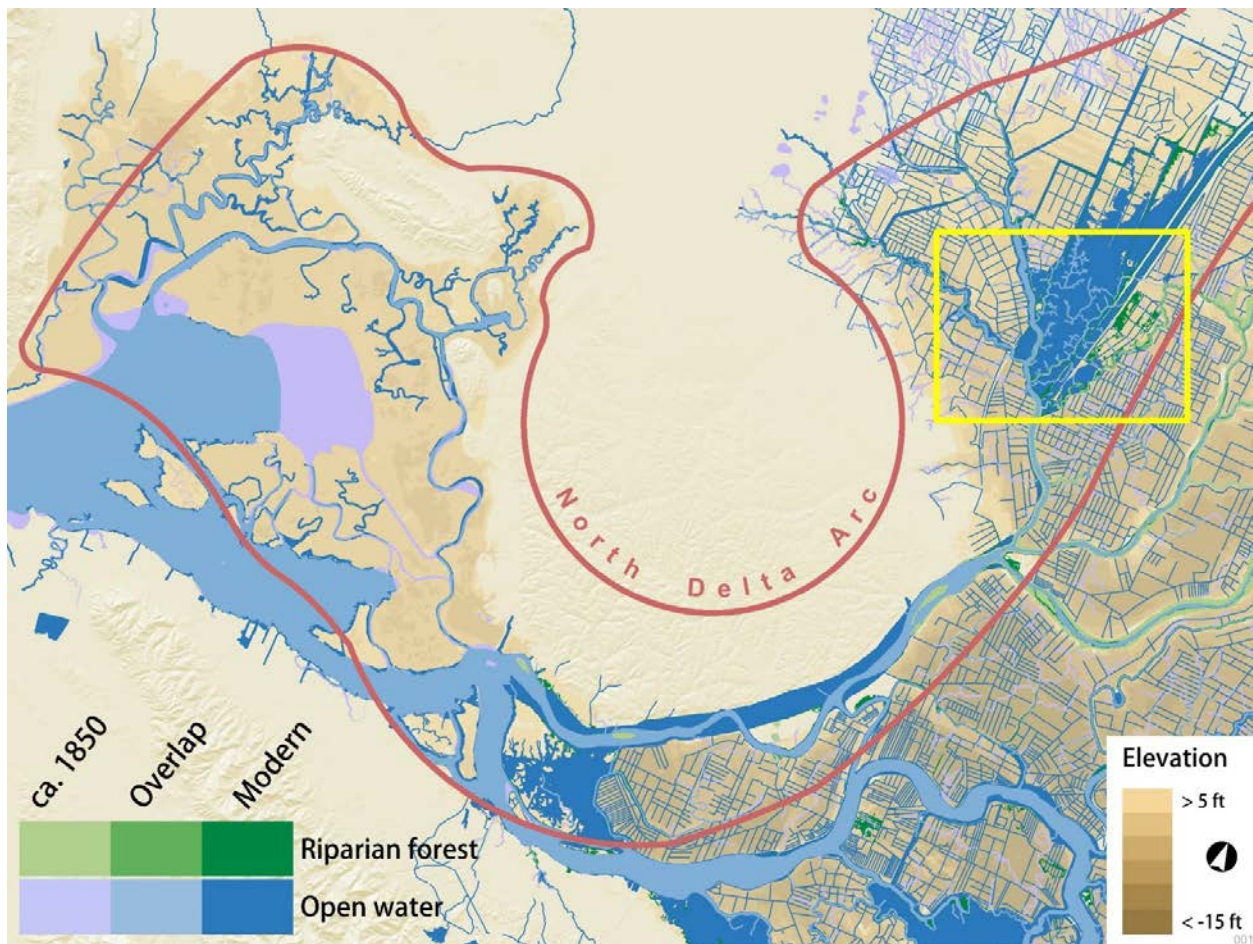
Figure 10. This map shows the North Delta Arc of habitat from Liberty Island to Suisun Bay, including Suisun Marsh (Moyle et al. 2012). It gives an overview of the network of channels created for water transport for irrigation of crops or livestock mainly. It also shows the historic range of shallow open water and dendritic channels. The yellow rectangle marks the area zoomed into in Figure 11. (Cartography by Amber Manfree, geospatial resources from Calatlas 2012, Contra Costa County 2013, Gesch et al 2002, SFEI 2012, CWS 2016, USGS 2016).
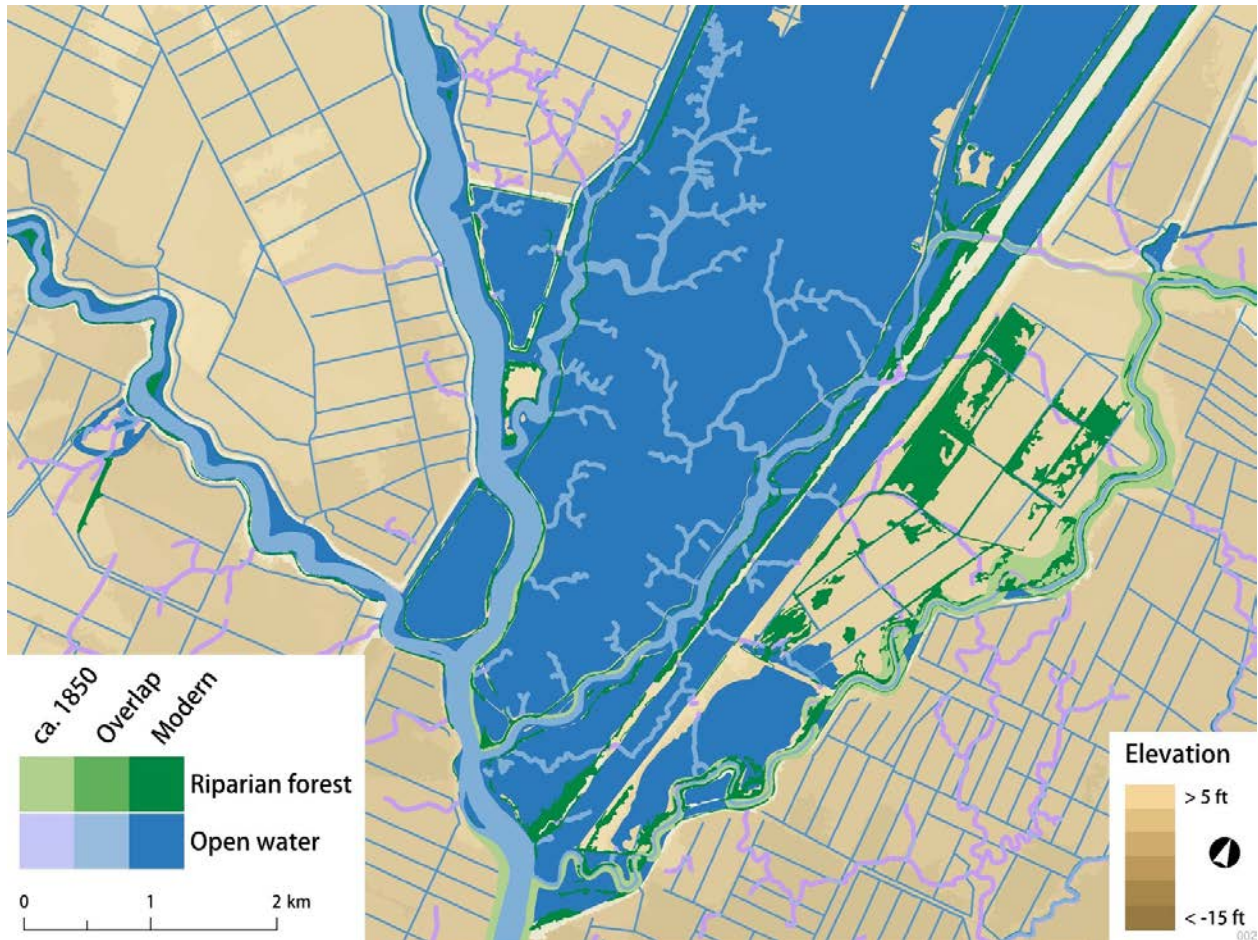
Figure 11. This map shows a close up of the flooded Liberty Island with the historic channels shown in lilac or light blue in the flooded area. The historic riparian area is shown in the lightest green color, with the historic remnants in the middle shade. (Cartography by Amber Manfree, geospatial resources from Calatlas 2012, Contra Costa County 2013, Gesch et al 2002, SFEI 2012, CWS 2016, USGS 2016).

Despite all this, this is where we find the freshwater resident population, which likely uses the adjacent Deep Water Ship Channel, as a thermal refuge during the warmest periods since it does thermally stratify in the daytime in the summer months (*Van Nieuwenhuyse, E. pers. com.*). Ongoing efforts to restore tidal marsh habitats in the Delta may increase temperatures further, as the flooding of shallow polders will likely increase water temperatures during the summer months.

This points to a need to integrate thermal refuges for Delta Smelt, and native fishes in general, into the efforts to restore tidal marsh habitat as an effective means to reduce water temperatures.

Current climate change predictions for the Sacramento-San Joaquin Delta suggest the Delta Smelt will reach a significant level of thermal stress, restriction of reproductive timing and habitat loss by 2020 (Brown et al. 2013). The recent drought (2012-2015) may have reduced this time frame and it is likely that Delta Smelt are currently exhibiting these responses to warm water temperatures. Air and water temperatures have increased significantly in the last two years and Delta Smelt abundance has reached all-time lows. The hatch date distributions and growth rates have shifted nearly a full month earlier in the calendar year than the historic average and growth rates of young fish have declined (Hobbs unpublished data). Data from this study suggests, the significant increase in abundance for the 2011 year-class was likely the result of both increased freshwater flows to the estuary and cool temperatures in 2010 and 2011. A large body of evidence now exists supporting the role of temperature in modulating the abundance of Delta Smelt, and likely other native fishes in the San Francisco Estuary. Climate predictions for the estuary do not foreshadow an optimistic future for the Delta Smelt.

Conclusions

In this study, we found that Delta Smelt exhibit a partial migration life history strategy including a migratory phenotype and resident phenotype, with year-round residents in both fresh water and brackish water. The relative abundance of each life history phenotype varied inter-annually with the migratory phenotype providing the most (70%) to population resilience, while the freshwater resident phenotype was important in several years of low abundance. Meanwhile the brackish residents only made up a small part of the population in most years, but appear to make an important contribution (23%) in the year of highest spring flows. Together, the freshwater and brackish water residents provided population stability, contributing more to the populations when abundance indices were low. Furthermore, we found the relative abundance of different phenotypes varied as a product of freshwater outflow into the estuary and water temperature. This may explain the non-linear population level response of Delta Smelt to freshwater outflow. The migratory phenotype did not experience faster growth, despite the risky migration to the low-salinity zone, thus lower food densities now found in the low-salinity zone may be limiting population resilience. The importance of freshwater nursery habitat conditions in the Delta has been sorely overlooked and may be an important driver of Delta Smelt recruitment. Improving habitat conditions in fresh water may facilitate population resilience in Delta Smelt; however, water temperature may be a difficult habitat attribute to manage. We urge managers to consider thermal refuges for Delta Smelt in the Delta to provide safe harbor during peak summer temperatures. With the progress of global warming, temperature may be the single greatest threat to persistence of Delta Smelt in the wild.

References

Bagenal, T.B., 1973. Conseil International Pour L'exploration De La Mer. *Rapports Et Proces-Verbaux Des Reunions*, 164, pp.186–198.

Bennett, W.A., 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. *San Francisco Estuary and Watershed Science*, 3(2).

Bennett, W.A. & Burau, J.R., 2015. Riders on the Storm: Selective Tidal Movements Facilitate the Spawning Migration of Threatened Delta Smelt in the San Francisco Estuary. *Estuaries and Coasts*, 38(3), pp.826–835.

Brönmark, C. et al., 2014. There and back again: migration in freshwater fishes 1. *Canadian Journal of Zoology*, 92(6), pp.467–479. Available at: http://apps.webofknowledge.com/full_record.do?product=UA&search_mode=GeneralSearch&qid=2&SID=U1HEVJS2Ecr1fhT9rII&page=1&doc=3.

Brown, L.R. et al., 2016. Coupled Downscaled Climate Models and Ecophysiological Metrics Forecast Habitat Compression for an Endangered Estuarine Fish. *PLoS One*, 11(1), p.e0146724.

Brown, L.R. et al., 2013. Implications for Future Survival of Delta Smelt from Four Climate Change Scenarios for the Sacramento-San Joaquin Delta, California. *Estuaries and Coasts*, 36(4), pp.754–774.

Carlson, S.M. & Satterthwaite, W.H., 2011. Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(9), pp.1579–1589. Available at: http://www.nrcresearchpress.com/doi/abs/10.1139/f2011-084#.VZwTlflVhBc%5Cnhttp://www.nrcresearchpress.com/doi/abs/10.1139/f2011-084.

Chapman, B.B., Hulthén, K., et al., 2012. Partial migration in fishes: causes and consequences. *Journal of Fish Biology*, 81(2), pp.456–478.

Chapman, B.B., Hulthén, K., et al., 2012. Partial migration in fishes: Causes and consequences. *Journal of Fish Biology*, 81(2), pp.456–478.

Chapman, B.B., Skov, C., et al., 2012. Partial migration in fishes: Definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, 81(2), pp.479–499.

Chapman, B.B. et al., 2011. To boldly go: Individual differences in boldness influence migratory tendency. *Ecology Letters*, 14(9), pp.871–876.

Dingle, H., 1996. *Migration: The Biology of Life on the Move*, Oxford, New York: Oxford University Press.

Dingle, H. & Drake, V., 2007. What is migration? *Bioscience*, 57(2), pp.113–121. Available at: http://bioscience.oxfordjournals.org/content/57/2/113.short.

Elton, C., 1927. *Animal Ecology*, London: Sidgewick and Jackson.

Feyrer, F. et al., 2004. Otolith aging of age-0 splittail: techniques, validations, and limitations. *Interagency Ecological Program for the San Francisco Estuary Newsletter*, 17(1), pp.24–27.

Feyrer, F. et al., 2007. Otolith microchemistry provides information complementary to microsatellite DNA for a migratory fish. *Transactions of the American Fisheries Society*, 136(2), pp.469–476.

Gillanders, B.M. et al., 2015. Partial migration: growth varies between resident and migratory fish. *Biology Letters*, 11(3).

Griffiths, J.R. et al., 2014. Performance of salmon fishery portfolios across western North America. *Journal of Applied Ecology*, 51(6), pp.1554–1563.

Hammock, B.G. et al., 2015. Contaminant and food limitation stress in an endangered estuarine fish. *Science of the Total Environment*, 532, pp.316–326.

Hart, L.M. et al., 2015. Use of otolith microchemistry and stable isotopes to investigate the ecology and anadromous migrations of Northern Dolly Varden from the Egegik River, Bristol Bay, Alaska. *Environmental Biology of Fishes*, 98(6), pp.1633–1643.

Hayes, S.A. et al., 2012. Should I stay or should I go? The influence of genetic origin on emigration behavior and physiology of resident and anadromous juvenile oncorhynchus mykiss. *North American Journal of Fisheries Management American Fisheries Society*, 32(November 2015), pp.772–780.

Hobbs, J.A. et al., 2005. Retrospective determination of natal habitats for an estuarine fish with otolith strontium isotope ratios. *Marine and Freshwater Research*, 56(5), pp.655–660.

Hobbs, J.A. et al., 2010. The use of otolith strontium isotopes (87Sr/86Sr) to identify nursery habitat for a threatened estuarine fish. *Environmental Biology of Fishes*, 89(3–4), pp.557–569.

IEP-MAST, 2015. *An updated conceptual model of Delta Smelt biology: our evolving understanding of an estuarine fish*, Sacramento, Ca.: Interagency Ecological Program: Management, Analysis and Synthesis Team.

Jeffries, K.M. et al., 2016. Effects of high temperatures on threatened estuarine fishes during periods of extreme drought. *Journal of Experimental Biology*, 219(11), pp.1705–1716.

Jonsson, B. & Jonsson, N., 1993. Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, 3(4), pp.348–365.

Katayama, S. et al., 2000. Coexistence of anadromous and resident life history styles of pond smelt, Hypomesus nipponensis, in Lake Ogawara, Japan, as determined by analyses of otolith structure and strontium: calcium ratios. *Environmental Biology of Fishes*, 58(2), pp.195–201. Available at: http://link.springer.com/10.1023/A:1007682729460.

Kerr, L.A., Cadrin, S.X. & Secor, D.H., 2010. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. *Ecological Applications*, 20(2), pp.497–507.

Kerr, L.A. & Secor, D.H., 2012. Partial Migration Across Populations of White Perch (Morone americana): A Flexible Life History Strategy in a Variable Estuarine Environment. *Estuaries and Coasts*, 35(1), pp.227–236.

Kimmerer, R.W. & Allen, T.F.H., 1982. The Role of Disturbance in the Pattern of a Riparian Bryophyte Community. *American Midland Naturalist*, 107(2), pp.370–383.

Kimmerer, W.J., 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? *Marine Ecology Progress Series*, 243, pp.39–55.

Kimmerer, W.J., Gartside, E. & Orsi, J.J., 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. *Marine Ecology Progress Series*, 113(1–2), pp.81–93.

Kitamura, T. et al., 2006. Juvenile bimodal length distribution and sea-run migration of the lower modal group in the Pacific Ocean form of three-spined stickleback. *Journal of Fish Biology*, 69(4), pp.1245–1250.

Komoroske, L.M. et al., 2015. Linking transcriptional responses to organismal tolerance reveals mechanisms of thermal sensitivity in a mesothermal endangered fish. *Mol Ecol*, 24(19), pp.4960–4981. Available at: http://www.ncbi.nlm.nih.gov/pubmed/26339983.

Komoroske, L.M. et al., 2014. Ontogeny influences sensitivity to climate change stressors in an endangered fish. *Conservation Physiology*, 2(1), p.cou008-cou008.

Komoroske, L.M. et al., 2016. Sublethal salinity stress contributes to habitat limitation in an endangered estuarine fish. *Evolutionary Applications*.

McArthur, J.M., Howarth, R.J. & Bailey, T.R., 2001. Strontium Isotope Stratigraphy: LOWESS Version 3: Best Fit to the Marine Sr-Isotope Curve for 0–509 Ma and Accompanying Look-up Table for Deriving Numerical Age. *The Journal of Geology*, 109(2), pp.155–170.

Merz, J.E. et al., 2013. Longfin smelt: spatial dynamics and ontogeny in the San Francisco Estuary, California. *California Fish and Game*, 99(3), pp.122–148.

Morrongiello, J. & Thresher, R., 2015. A statistical framework to explore ontogenetic Growth variation among individuals and Persistent Link : A statistical framework to explore ontogenetic growth variation among individuals and populations : a marine fish example. *Ecological Monographs*, 85(1), pp.93–115.

Moyle, P.B. et al., 2016. Delta Smelt: Life History and Decline of a Once-Abundant Species in the San Francisco Estuary. *San Francisco Estuary and Watershed Science*, 14(2). Available at: http://www.escholarship.org/uc/item/09k9f76s.

Moyle, P.B., 2002. *Inland fishes of California*, Univ of California Press.

Moyle, P.B. et al., 1992. Life-History and Status of Delta Smelt in the Sacramento-San-Joaquin Estuary, California. *Transactions of the American Fisheries Society*, 121(1), pp.67–77.

Moyle, P.B. et al., 2012. Where the Wild Things Aren't: Making the Delta a Better Place for Native Species. , (June), p.53.

Myers, R.A. et al., 1994. In search of thresholds for recruitment overfishing.pdf. *International Council for the Exploration of the Sea*.

Nobriga, M.L. et al., 2008. Long-term trends in summertime habitat suitability for delta smelt. *San Francisco Estuary and Watershed Science*, 6(1), pp.1–13.

R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing,Vienna, Austria. http://www.R-project.org/.

Sommer, T. et al., 2007. The collapse of pelagic fishes in the Upper San Francisco Estuary. *Fisheries*, 32(6), pp.270–277.

Sommer, T. et al., 2011. The Spawning Migration of Delta Smelt in the Upper San Francisco Estuary. *San Francisco Estuary and Watershed Science*, 9(2), pp.1–16. Available at: http://www.escholarship.org/uc/item/86m0g5sz.

Sommer, T. & Meija, F., 2013. A Place to Call Home: A Synthesis of Delta Smelt Habitat in teh Upper SAn Francisco Estuary. *San Francisco Estuary & Watershed Science*, 39(3), pp.321–325.

Thomson, A., 1926. *Problems of Bird Migration*, London: Witherby.

USFWS, 2008. Formal Endangered Species Act Consultation on the Proposed Coordinated Operations of the Central Valley Project (CVP) and State Water Project (SWP) U. S. D. of the Interior, ed. , 81420–2008, p.411.

Zuur, A.F. et al., 2009. Mixed effects models and extensions in ecology with R. New York: Springer.

Geospatial References

CalAtlas California Geospatial Clearinghouse. 2012. Delta-Vision LiDAR derived elevation dataset. State of California. Available: http://atlas.ca.gov/. Accessed: 2012

Contra Costa County. 2013. Contra Costa County Mapping Information Center. Available: http://www.ccmap.us/. Accessed: January 2013.

Gesch, D., M. Oimoen, S. Greenlee, C. Nelson, M. Steuck and D. Tyler. 2002. The National Elevation Dataset. Photogrammetric Engineering and Remote Sensing 68 (1): 5-11.

San Francisco Estuary Institute (SFEI). 2012. Delta Historical Ecology GIS Data. Richmond, CA. Available: http://www.sfei.org/content/delta-historical-ecology-gis-data. Accessed: August 2015.

Center for Watershed Sciences, University of California Davis (CWS). 2016. North Delta Arc Boundary. Davis, CA. Available: by request. Contact: Amber Manfree admanfree@ucdavis.edu.

US Geological Survey (USGS). 2016. National Hydrography Dataset. Available: http://nhd.usgs.gov/data.html. Accessed: May 2016.