

Fecundity and reproductive potential of wild female delta smelt in the upper San Francisco Estuary, California

LAUREN J. DAMON*, STEVEN B. SLATER, RANDALL D. BAXTER, AND ROBERT W. FUJIMURA

California Department of Fish and Wildlife, Bay-Delta Region, 2109 Arch-Airport Road, Suite 100, Stockton, CA 95206, USA

*Correspondent: Lauren.Damon@wildlife.ca.gov

Delta smelt (*Hypomesus transpacificus*), an annual fish that is endemic to the upper San Francisco Estuary, has suffered substantial decline in recent decades. This decline has led to delta smelt becoming a listed species under the California and United States Endangered Species Acts. Managing this endangered species requires a clearer understanding of its life history: specifically egg production and other spawning characteristics in the wild. In this study, we examined near-ripe female delta smelt collected from 2012 through 2015 to identify the relationship of fecundity and length. We found the length-fecundity relationship to be: $F = 0.0183FL^{2.7123}$ ($R^2 = 0.569$), where F is fecundity and FL is fork length (mm).

Fecundity ranged from 813 to 3919 eggs per clutch. We regularly observed females with eggs in two or three developmental stages, affirming that delta smelt were serial spawners, capable of producing multiple clutches of eggs. The minimum size of post-spawn fish was 55 mm FL, but the majority (98%) of post-spawn fish were >61 mm FL. Additionally, females continued to grow throughout the spawning season, with the largest females being ready to spawn first and producing the largest clutches. Small females produced fewer and smaller clutches, resulting in decreased reproductive potential compared to large females. This information aids species management, supports recent modeling, and may help explain reduced recruitment in some years.

Key words: delta smelt, *Hypomesus transpacificus*, annual fecundity, clutch, length, eggs, serial spawning, growth, climate change

Delta smelt (*Hypomesus transpacificus*) is a small fish that was once abundant in the upper San Francisco Estuary (SFE). It suffered a substantial decline in recent decades (Moyle et al. 1992; Sommer et al. 2007) and is currently listed and managed under both the United States and California Endangered Species Acts. (USFWS 1996; CDFW 2016). Management of this species is complicated, as it is endemic to a watershed that has undergone numerous anthropogenic alterations, which have changed the amount and timing of freshwater flow available to fishes (Nichols et al. 1986; Cloern and Jassby 2012). Delta smelt

were previously described as having an annual life cycle, low fecundity, and spawning only once before dying (Moyle et al. 1992). The life history framework by Winemiller and Rose (1992) suggests this would be an unsuccessful life history strategy in the absence of another mechanism to increase egg production or egg survival. Other species in the Osmeridae family exhibit various such mechanisms. For example, surf smelt (*H. pretiosus*) select spawning substrate based on tides and grain size to ensure egg survival (Penttila 1978); whereas long-fin smelt (*Spirinchus thaleichthys*) and rainbow smelt (*Osmerus mordax*) live and grow for multiple years, resulting in substantially increased fecundity (Lawton et al. 1990; Chigbu and Sibley 1994). Therefore, we hypothesize that one or more life history characteristics of delta smelt are missing or incompletely described. In this study, we investigate delta smelt clutch fecundity at length, annual fecundity, and provide evidence that delta smelt is a serial spawner (i.e. produces multiple clutches during the annual spawning season) in order to improve understanding of its reproductive biology and reconcile its life history strategy.

Fecundity of fishes is a key life history characteristic, and is critical to understanding the reproductive potential of a species. Fecundity is defined as the number of eggs produced by a female over some time period (Bagenal 1978; Murua and Saborido-Rey 2003). In fishes, annual fecundity is the number of eggs released in a year by a female and can be used in stock assessments (Kjesbu et al. 2003; Murua et al. 2003). Increasing annual fecundity is one way to improve production of offspring, but it's not the only way. Fish exhibit a variety of behaviors and mechanisms to increase reproductive success, the collective combination of these are referred to as life history strategies (e.g. Winemiller and Rose 1992). Lowerre-Barbieri et al. (2011) describe general teleost reproductive development patterns, summarized here and in Table 1. Semelparous species have a single spawning event in their lifetime, and contain a finite number of eggs, which are present in the ovary and equal to their lifetime fecundity. In contrast, iteroparous species have multiple spawning events and their lifetime fecundity is not finite. Iteroparous species can initiate eggs into development, either continuously or in groups. Since eggs are constantly being generated, their lifetime fecundity cannot be determined by the number of eggs in the ovary at any one time. Continuous initiation of eggs into development is referred to as asynchronous development, characterized by eggs at various stages of development within the ovary. Group-synchronous development is a special case of asynchronous development, in which the eggs develop in easily distinguishable 'clutches', with a clear gap between egg sizes, as displayed by an oocyte size frequency graph (Kjesbu et al. 2003; Murua and Saborido-Rey 2003). Species displaying group-synchronous egg development are described as serial spawners. The annual fecundity of iteroparous, group-synchronous fish is calculated by the number of eggs in a clutch (i.e. clutch fecundity) multiplied by the spawning frequency during the year. The spawning frequency is the number of clutches produced and released during a spawning season, and is dependent on the length of the spawning season and the spawning interval, which is time between spawning events for individual females (i.e. time necessary for the next batch of eggs to mature; see Table 1 for terms and definitions).

Many factors influence annual fecundity, such as environmental conditions (Lowerre-Barbieri et al. 2011), food supply (Hunter and Leong 1981), fish size (Kjesbu et al. 1996), and the duration of the spawning period (Hunter et al. 1985; Bennett 2005; Brown et al. 2013). It is generally observed that within species fecundity and egg size increase with fish size, but trade-offs between fecundity and egg size can occur as needed to suit the environmental conditions (Chigbu and Sibley 1994). Among serial spawners, relatively large fish tend to spawn earlier in the spawning season, because they reached adult size and can direct energy

TABLE 1.— Definitions of terms related to Delta smelt fecundity and life history used throughout this paper.

Term	Definition	Reference
Annual fecundity	Number of eggs released per female per year.	Murua et al. (2003)
Atresia (or Atretic)	The process of egg degeneration and resorption. Can occur in any number of eggs at any stage of maturity, or within the entire ovary (gonadal atresia).	Bagenal (1978), Hunter and Macewicz (1985), Tyler and Sumpter (1996)
Clutch	Group of eggs in the same developmental stage present in the ovary to be released at one event.	Lindberg et al. (2013)
Clutch fecundity	Number of viable eggs in a clutch.	This study
Fecundity	Loosely used to describe the number of potential offspring produced by a female over some time period.	Bagenal 1978 and Murua Saborido-Rey (2003)
Serial spawner	Species that repeatedly develops and releases clutches of eggs over a spawning season.	Hunter et al. (1985)
Serial spawning	Repeatedly developing and releasing clutches of eggs over a spawning season.	Hunter et al. (1985)
Spawning frequency	The number of spawning events in a spawning season.	Lowerre-Barbieri et al. (2011)
Spawning interval	The time between spawning events, also referred to as refractory period in some species.	Lowerre-Barbieri et al. (2011)
Spawning period	The time in which an individual fish is capable of spawning. Also known as 'spawning window'.	Lowerre-Barbieri et al. (2011)
Spawning season	The time that spawning can occur for the population (population spawning window).	Lowerre-Barbieri et al. (2011)
Subsequent clutch	The clutch of eggs that are developed in a female that has spawned a previous clutch of eggs.	This study
Subsequent spawner	An individual that has spawned at least one clutch of eggs and is preparing to spawn an additional clutch.	This study

into gonad maturation instead of growth, prior to the onset of spawning conditions. This can result in a longer spawning period and substantially increased annual fecundity, if larger fish are able to increase spawning frequency relative to smaller fish (Bagenal 1978; Kjesbu et al. 1996; Murua et al. 2003). Thus, being relatively large confers reproductive benefits.

The spawning season of delta smelt appears to be linked to water temperature (Bennett 2005; IEP 2015), and has been reported to occur when temperature ranges from 7–22°C based on the presence of larval fish in field surveys (Wang 2007). Delta smelt eggs ripen following a rise in water temperature in late winter, and spawning success decreases in the spring when water temperature exceeds 20°C (e.g., Bennett 2005; IEP 2015). Delta smelt experience a temporally variable ‘spawning window’ influenced by meteorological and hydrological conditions in the SFE during winter and spring. Fish commonly experience environmental stress, such as temperatures outside of their optimal range or limited food availability, and respond in a variety of ways. Maturing females may temporarily halt egg maturation or, in extreme or prolonged instances, resorb their clutch of eggs (Mager 1996; Tyler and Sumpter 1996). The process of egg degeneration and resorption, called atresia, commonly occurs at low levels in many fish species, and most often involves only a few eggs or a small portion of an ovary. In such cases, atresia is not considered a major factor in fish fecundity, and the effects are typically negligible (Hunter and Macewicz 1985; Tyler and Sumpter 1996). However, when fish resorb an entire clutch of eggs, a process referred to as gonadal atresia, this can signal a sudden end of the spawning season. If many fish in the population experience gonadal atresia, the population’s annual fecundity may be severely diminished (Tyler and Sumpter 1996). In contrast, the extension and gradual change of spawning season temperatures results in increased population annual fecundity, and has been linked to year class strength in delta smelt (Bennett 2005; MacNally et al. 2010; IEP 2015).

Studies conducted on captive delta smelt provide considerable insight into reproductive biology (Baskerville-Bridges et al. 2005; Lindberg et al. 2013; LaCava et al. 2015). In captivity, delta smelt commonly live and spawn for multiple years, growing to greater than 100 mm FL. Lindberg et al. (2013) report that one-year old fish can grow up to 90 mm, but shows an overlap of several millimeters between one- and two-year olds between about 86–93 mm (cf., Lindberg et al. 2013). In culture, two-year old fish produce substantially more eggs per clutch than first year spawners, and females as small as 52 mm FL produced viable eggs (Lindberg et al. 2013). Captive females spawn (manually or naturally) all the ripe eggs present in the ovary at one time over a day or so, and can do so several times during an annual spawning season, separated by spawning intervals. This implies that delta smelt are serial (i.e. batch) spawners that release distinct, rather than continuous, clutches (Lindberg et al. 2013; LaCava et al. 2015). Up to four clutches per female have been observed in a season for individually tagged captive fish, each separated by a spawning interval of several weeks (LaCava et al. 2015).

Wild delta smelt were previously described as mostly semelparous, spawning only once and then dying, with a second spawning event possible only for the few individuals that lived beyond the first year (Mager 1996). However, new evidence suggests that delta smelt are iteroparous, capable of spawning multiple times in a single spawning season. Captive delta smelt produce multiple clutches in one spawning season (Lindberg et al. 2013; LaCava et al. 2015), and recent histological samples from wild fish contained post-ovulatory follicles in addition to developing eggs (Kurobe et al. 2016). Post-ovulatory follicles indicate a prior spawning event (eggs have been released) and the developing clutch of eggs indicates another spawning event is possible in the future. Post-ovulatory follicles can only

be seen using histological methods, which are time and cost intensive. An alternative gross anatomical approach is possible once histology has confirmed microscopic characteristics. This approach allows for a quick and easy assessment of fish in the field, which is necessary for the adaptive management of a species. Prior spawning event gross anatomical characteristics include remnant hydrated eggs and a flaccid abdomen (Kjesbu et al. 2003). Remnant hydrated eggs left-over from a previous spawning event appear much larger than the developing, non-hydrated eggs. Such eggs will eventually become atretic (Tyler and Sumpter 1996). Left-over eggs have been used to distinguish between immature and spent fish, and to indicate non-virgin individuals in species that are known to serial spawn (Hunter and Goldberg 1980; Hunter and Macewicz 1985; Hunter et al. 1992). The ability to serial spawn (i.e. spawning multiple egg clutches in a season) would reconcile delta smelt life history strategy better with life history theory (see Winemiller and Rose 1992).

Understanding delta smelt clutch fecundity and spawning frequency in the wild is critical for improving methods to manage and recover the species (IEP 2015), to accurately model life history (Rose et al. 2013a, 2013b), and to forecast effects of climate change on the species (Brown et al. 2013, 2016). In this study, we used field and laboratory data from wild caught delta smelt to answer the following questions:

- Is clutch fecundity a function of length and does this relationship vary by year?
- At what temperatures do wild delta smelt spawn?
- What number of ≥ 89 mm FL fish (possible age-2+) have been collected in recent years?
- At what minimum size do we observe delta smelt spawning in the wild?
- Does the size of females change over the spawning period?

MATERIALS AND METHODS

Specimens for analyses were collected during the California Department of Fish and Wildlife (CDFW) Spring Kodiak Trawl (SKT) Survey, which is a long-term fish monitoring program. This survey was initiated in 2002 to target maturing and spawning delta smelt. Monthly sampling occurred each year from January through May (Sommer and Mejia 2013), but did not occur in a few instances: April and May 2002, January 2003, and May 2005. During each monthly survey, a surface tow was conducted with a Kodiak trawl net for 10-minutes at 40 discrete stations in the SFE (Figure 1). The Kodiak trawl net had a fully stretched mouth opening of 7.62 m wide by 1.83 m deep. Water quality data, including surface water temperature ($^{\circ}\text{C}$), was collected at each station using a handheld YSI Model 30 digital meter. All delta smelt caught were measured to the nearest millimeter FL while fresh and then the gender and gonad stage were determined in the field for the purposes of reporting to resource managers (Table 2). This information is used to determine the potential to entrain adult delta smelt and their offspring at water export facilities in the Delta. The staging process first involves gently squeezing the abdomen of each fish to check for release of gametes, since ripe individuals will release milt or eggs with minimal pressure applied to the abdomen (Mager 1996; Lindberg et al. 2013). After the external examination, the abdomen was dissected to examine gonads, and then the fish was preserved and retained.

Egg Staging and Fecundity Analyses.—The fecundity (egg count and size) portion of this study was conducted during the 2012 to 2015 SKT with a subset of the females based on their gonadal stage. Delta smelt that were caught during this period were measured and then staged using a modified staging protocol. All individuals had their abdomen gently



FIGURE 1.— Station locations of the California Department of Fish and Wildlife’s Spring Kodiak Trawl Survey in the upper San Francisco Estuary. Stations are sampled once each month from January to May.

TABLE 2.—Gonadal staging criteria for female Delta smelt using macroscopic characteristics. These criteria have been adapted from Mager (1996) and R. Mager (Department of Water Resources, personal communication).

<u>Stage</u>	<u>Macro-characteristics</u>	<u>Phase</u>
1	Left ovary translucent and grainy in texture. Right ovary difficult or impossible to find.	Developing
2	Same as stage 1 when observed without a microscope	Developing
3	Yellow or orange eggs, less than 1.0 mm in diameter and visible to the naked eye.	Near-Ripe
4	Enlarged abdomen. Hydrated, orange eggs that are 1 mm in diameter. Eggs released from vent with gentle pressure to abdomen.	Ripe
5	Failed to spawn for some reason and eggs to be resorbed (atresia).	Atretic
6	Evidence of a prior spawn. Loose abdomen or left-over, hydrated eggs. May or may not contain a developing clutch of eggs.	Post-Spawn

squeezed to check for release of gametes per standard protocol. Females that did not release eggs but had eggs visible through the vent were considered near-ripe and temporarily set aside to be used for the fecundity analysis. Females that released eggs were not used for fecundity analysis because eggs may have been lost during or prior to capture. The gender and gonad stage data were still recorded following the normal protocol for consistency with the long-term data. For the set aside near-ripe females, a systematic subsample of every other female was preserved intact in 10% formalin or 70% ethanol, and sent to the CDFW Bay-Delta Region's Stockton office for laboratory processing. The remainder of the sample was preserved in liquid nitrogen and sent to University of California, Davis for another study.

In the Stockton laboratory, three incisions were made to create a flap on the left side of the body to expose the ovaries. Care was taken to not cut into the ovaries or damage eggs. Many of the specimens were photographed while the ovaries were exposed and intact to document their appearance prior to fecundity processing. In most cases, each ovary was kept separate for fecundity processing. For egg counts, ovaries were removed from the body cavity, and transferred to a Petri dish. Using a dissecting scope, the eggs were separated from ovarian tissue, sorted by general stage (size and yolk presence), and then the secondary-growth eggs were counted and placed back into an individually numbered vial. Both ovaries from all females contained eggs in two or three different stages of vitellogenesis, as visually determined by color and amount of yolk. Egg stages were as follows: 1) a primary-growth stage where eggs were not distinguishable without magnification and no vitellogenesis was observed (<500 micrometer (μm) dia.); 2) a secondary-growth stage in which eggs were readily distinguishable without magnification, vitellogenic, and approaching size at ripeness (>500 μm dia.); and 3) a post-vitellogenic stage of large and discolored over-mature or atretic eggs (>1000 μm dia.; Figures 2A-C; Bagenal 1978; Mager 1996; Tyler and Sumpter 1996; Murua and Saborido-Rey 2003; Brown-Peterson et al. 2011; Lowerre-Barbieri et al. 2011). To confirm, post-hoc, that egg stages exist rather than a continuum of egg sizes, we measured diameters on a random subsample of about 140-220 eggs from the eight fish used for the 2015 fecundity analysis (Nichol and Acuna 2001; Kjesbu et al. 2003; Brown-Peterson et al. 2011). Since this occurred after the secondary-growth counts were complete, primary-growth egg loss was possible. To measure the eggs, we took photographs of them under a dissecting scope (Olympus Model DP25) and measured the maximum diameters (μm) using Olympus cellSens Standard 1.8.1 software, without regard for their visual condition. Egg size frequency was plotted to determine the size ranges for the three egg stages (Hunter et al. 1985; Nichol and Acuna 2001; Kjesbu et al. 2003; Murua and Saborido-Rey 2003).

To determine clutch fecundity, all of the eggs in the secondary-growth stage from both ovaries were counted for each fish (Bagenal 1978; Hunter et al. 1992; Murua et al. 2003). Eggs in the primary-growth stage were noted but not counted: their presence indicates a form of asynchronous development and those eggs likely would not be released along with those in the secondary-growth stage. Therefore, primary-growth eggs would not contribute to the current clutch fecundity (Bagenal 1978; Mager 1996; Tyler and Sumpter 1996; Murua et al. 2003; Brown-Peterson et al. 2011; Lowerre-Barbieri et al. 2011). We counted post-vitellogenic eggs separately (Figure 3), because they were not considered viable eggs and were likely to be resorbed (e.g., Bagenal 1978; Hunter and Macewicz 1985; Tyler and Sumpter 1996). Since histological analysis was not feasible in this study, we used the presence of post-vitellogenic eggs as evidence that a female had already spawned at least once. Other studies drew similar conclusions from the presence of post-vitellogenic eggs (Hunter and Macewicz 1985; Hunter and Macewicz 2003; Nichol and Acuna 2001). These females were categorized



FIGURE 2.—Photo of wild delta smelt eggs in three different stages of development, including (A) primary-growth, (B) secondary-growth, and (C) post-vitellogenic.

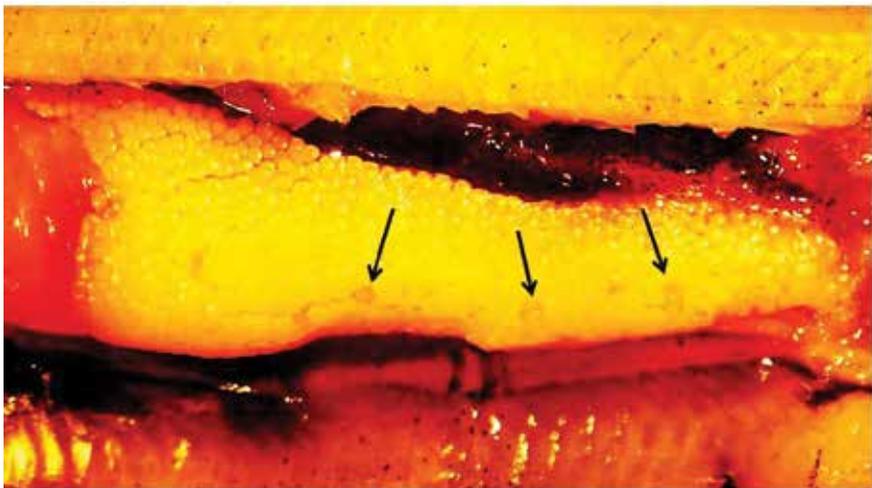


FIGURE 3.—Photo of the left ovary during dissection of a delta smelt used for the California Department of Fish and Wildlife’s delta smelt fecundity study. Arrows point to post-vitellogenic eggs that were left over from a previous spawning event.

as post-spawners and females without the third stage eggs as pre-spawners. Post-spawning fish with a vitellogenic clutch were referred to as subsequent-spawners with a subsequent clutch, whereas pre-spawning fish with a vitellogenic clutch were referred to as first-spawners with their first clutch. Since not all post-spawning fish also contained eggs in the secondary-growth stage (a subsequent clutch), we use post-spawn to describe fish that have spawned at least once, and subsequent spawner as defined above to describe post-spawning fish that likely would have released a subsequent clutch of eggs shortly, if the fish had not been captured.

The length-fecundity relationship of delta smelt in culture has been reported as non-linear (Bennett 2005; Lindberg et al. 2013). Therefore, we described the length-fecundity relationship as: $F=a*FL^b$, where F =fecundity, FL =fork length (mm) (Bagenal 1978; Lauer et al. 2005). To test for inter-annual differences among slopes and intercepts for the years 2012-2015, we linearized the data using a log10 transformation so an analysis of covariance (ANCOVA) could be used. In the absence of significant differences among years, the data for all years could be pooled into a single model (Lauer et al. 2005). An ANCOVA was also used to test for significant differences in slopes and intercepts of fecundity at length relationships between females carrying their first and subsequent clutches of eggs. We used the GLM procedure in SYSTAT 13 to run all the ANCOVA tests.

Temperature Analysis.—To determine the temperature range for spawning among delta smelt, we used water temperature data at the time of capture for the entire SKT period of record (2002-2015). We plotted all ripe and post-spawn females in a histogram with binned temperature ranges, and also determined what temperature range 95% of the ripe fish (Table 2, Stage 4) were caught, using the 2.5 and 97.5 temperature percentiles (SYSTAT 13).

Atresia Analysis.—To determine if gonadal atresia signals the end of the delta smelt population's spawning window, we examined the relative frequency of females caught during all years of the SKT that were undergoing gonadal atresia (i.e., Table 2, Stage 5). In order for a female to be classified as Stage 5 according to our gonadal staging criteria, the majority of the clutch must appear atretic. Based on field macroscopic observations, atresia appeared to either affect the entire clutch or none at all, which reduced uncertainty in classifying females as Stage 5. Small amounts of egg atresia were common in fish and likely went unnoticed using our methods. The effect of egg atresia on clutch fecundity was assumed negligible (Hunter and Macewiz 1985; Tyler and Sumpter 1996).

Length Analyses.—For the length analyses, we used only individuals caught from routine SKT surveys from 2003 to 2015. We did not use lengths from 2002 because all of those fish were measured post-preservation, making their lengths inconsistent with the rest of the dataset. To determine if potential two-year old fish had been caught by the SKT, we plotted the fork length of all fish by month and examined the scatterplot to see if there were distinct outliers representing a separate year class. We used the age cut-off of 90 mm reported in Lindberg et al. (2013) as an approximate criterion for putative two-year old fish.

To show the distribution of change in length through the spawning season, female fork lengths were plotted by month (January through May) in a box plot. The center horizontal line within each box represents the median value. The lower and upper ends of the box represent the 25% and 75% quartiles of the data. The whiskers show the range of values that fall within 1.5 times the lower and upper quartile values. Values exceeding the whiskers are represented by asterisks or empty circles, when exceeded by 1.5 times or 3.0 times, respectively. Females were separated into two categories, pre- and post-spawners. To determine if females grew during the spawning season, we tested the hypothesis that fork length distributions for pre- and post-spawners remained the same throughout the season, January

through May. We used the nonparametric Kruskal-Wallis test, and followed with post-hoc pairwise comparisons using Conover–Inman’s test if significant. We used nonparametric tests because the data did not meet the assumptions of normality or homoscedasticity.

All statistical test results were considered significant at $P < 0.05$. All analyses were conducted using SYSTAT 13 (SYSTAT Software).

RESULTS

Egg Staging and Fecundity Analyses.—We examined near-ripe females ($n=129$) ranging in length from 56 to 90 mm FL (mean=71.2, $SD=5.6$) to determine their clutch fecundity. The number of secondary-growth eggs per female from both ovaries ranged from 813 to 3,919 (mean=1,999, $SD=566.5$).

We found fecundity increased significantly with female length for all years ($P < 0.001$), but found no significant differences in slopes or intercepts among years (Figure 4; slopes: $F_{3, 121}=1.448$; $P=0.232$; intercepts: $F_{3, 124}=0.804$; $P=0.494$); therefore, we pooled data to describe the length-fecundity relationship. The pooled FL and fecundity data for the period 2012-2015 produced the relationship $F=0.0183FL^{2.7123}$ ($R^2=0.569$; Figure 5).

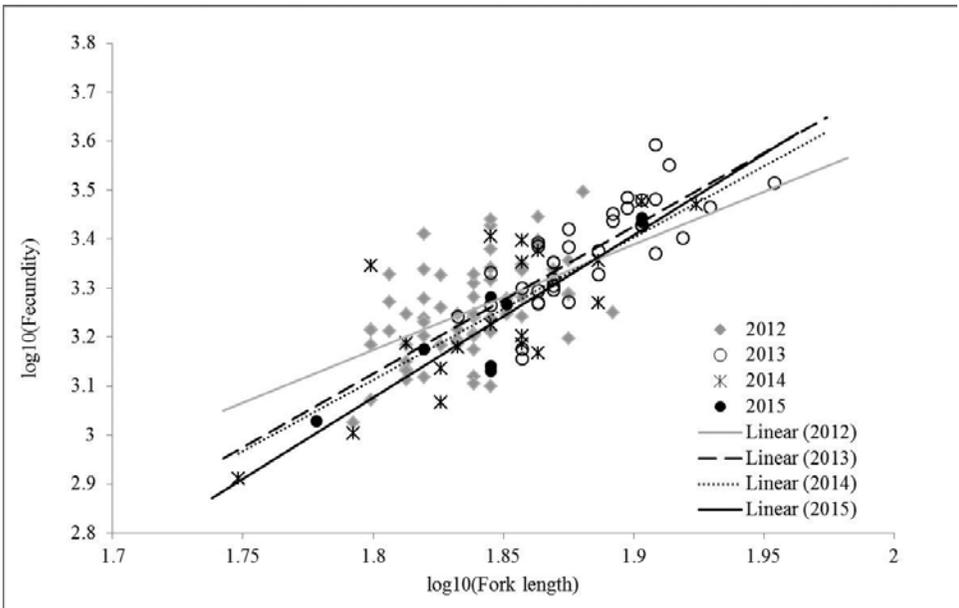


FIGURE 4.—Log₁₀ fecundity at fork length data of delta smelt collected in the upper San Francisco Estuary during January-May for years 2012-2015.

Of the 129 females examined for fecundity, 36 individuals contained post-vitellogenic eggs, and were categorized as subsequent spawners. The earliest observation of a subsequent spawner occurred in February (n=2), and the frequency of such observations increased across months with the highest occurrence in May, late in the spawning period (Table 3). The number of post-vitellogenic eggs per individual, when present, ranged from 1 to 72 (n=36, mean=2, SD=8) and they were found in various locations, including both ovaries, and both sides of each ovary.

We found no significant difference in clutch fecundity at length between first- and subsequent-spawn female delta smelt (Figure 6; ANCOVA, slopes: $F_{1, 125}=0.101$; $P=0.751$; intercepts: $F_{1, 126}=1.086$; $P=0.299$). However, as a group, subsequent spawners contained on average 377 more eggs than first spawners. The mean number of eggs was higher in all years for subsequent spawners than first spawners.

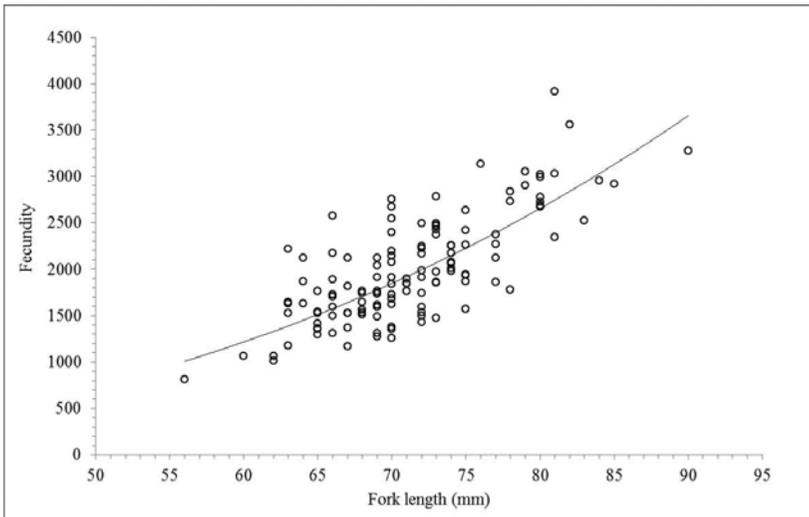


FIGURE 5.—Fecundity at fork length data of delta smelt collected in the upper San Francisco Estuary during January-May for years 2012-2015. The trend line represents the length-fecundity relationship $F = 0.0183FL^{2.7123}$ ($R^2 = 0.569$, $n=129$) of the pooled data.

TABLE 3.—Number and size range (mm FL) of near-ripe female delta smelt on their first or subsequent clutch of eggs by month of collection. Delta smelt were used in this study's fecundity analysis and collected during routine monthly sampling during January-May for years 2012-2015.

	<u>First</u>	<u>Subsequent</u>	<u>Total</u>
January	2 (72-73)	0	2 (72-73)
February	41 (56-84)	2 (65-85)	43 (56-85)
March	37 (63-77)	5 (63-81)	42 (63-81)
April	6 (62-82)	9 (65-90)	15 (62-90)
May	7 (68-78)	20 (69-83)	27 (68-83)

All females examined in this study contained two ovaries, with the left ovary much larger than the right ovary, as Mager (1996) observed. The right ovary contained, on average, 7% of the total eggs, with a range of 1 to 21%. In 2015, maximum egg diameter ranged from 153 to 1022 μm ($n=1510$, $\text{mean}=640$, $\text{SD}=154.2$). We found no difference in the egg diameters between the left and right ovaries ($t\text{-test}=0.820$, $\text{df}=1,387$, $P=0.412$). The egg diameter frequency distribution appeared bimodal (Figure 7), but heavily weighted toward the upper mode.

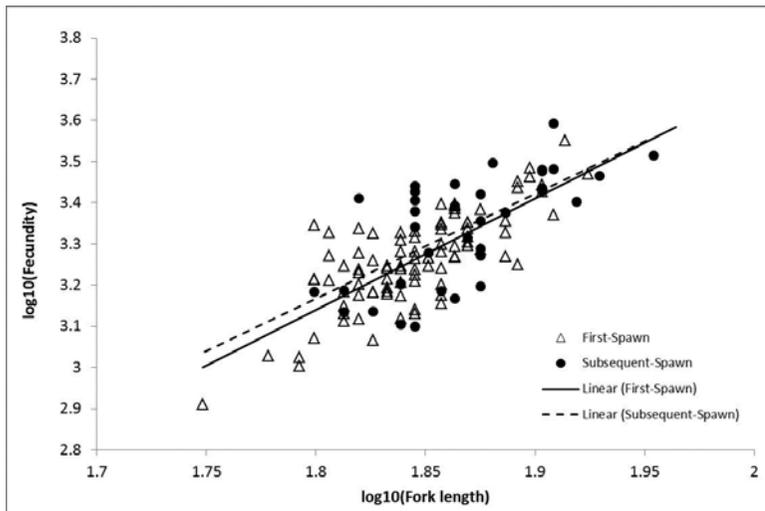


FIGURE 6.— \log_{10} fecundity at fork length (mm) data of first- or subsequent-spawn female delta smelt collected in the upper San Francisco Estuary during January-May for years 2012-2015.

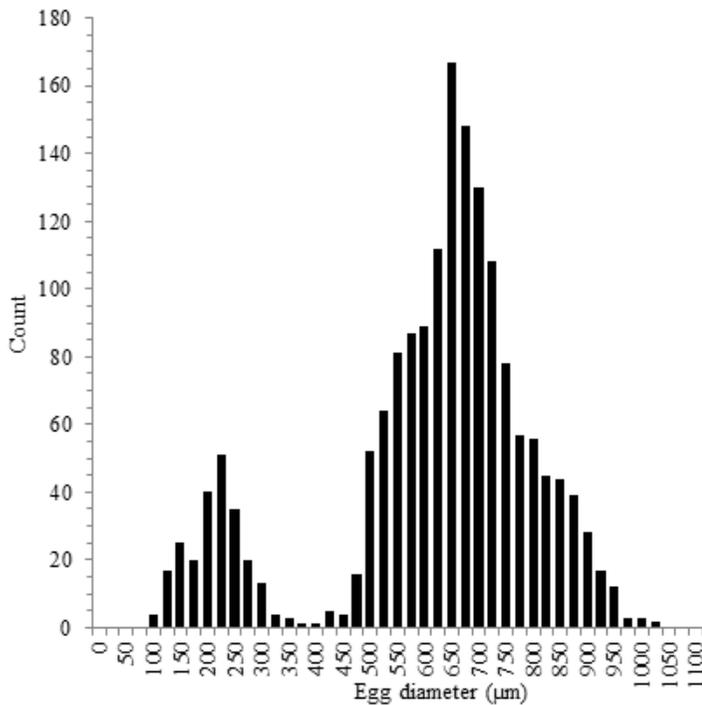


FIGURE 7.— Frequency distribution of egg diameters (μm) from ovaries of eight near-ripe delta smelt collected in 2015. Roughly, 140-220 egg diameters per fish were measured from the same eggs included in the fecundity analysis.

Temperature Analysis.—A total of 4,063 female delta smelt were caught and examined during routine SKT surveys from 2002 to 2015. Ripe and post-spawn females ($n=1,171$) were collected at temperatures ranging from 8 to 20°C during 2002-2015, and both were present in the full range (Figure 8). For ripe females only, we excluded the upper and lower 2.5 percentiles and found that roughly 95% of the ripe females ($n=521$) occurred between 9.2 and 17.9 degrees. Therefore, we determined that 9-18°C approximates the range when most spawning takes place (Figure 8).

Atresia Analysis.—We found that gonadal atresia occurred in 7 of the 14 years on record, but in only 26 of the 4,063 females examined (Stage 5; Table 4). We rarely detected gonadal atresia in females examined early in the spawning season (January and February), but the occurrence increased in later months. The highest occurrences of gonadal atresia occurred in 2014, with a third and a quarter of the females examined in April and May, respectively, undergoing gonadal atresia (Table 4). In 2015, many of the fish caught in the later portion of the spawning season were atretic, but the sample sizes in that year were small.

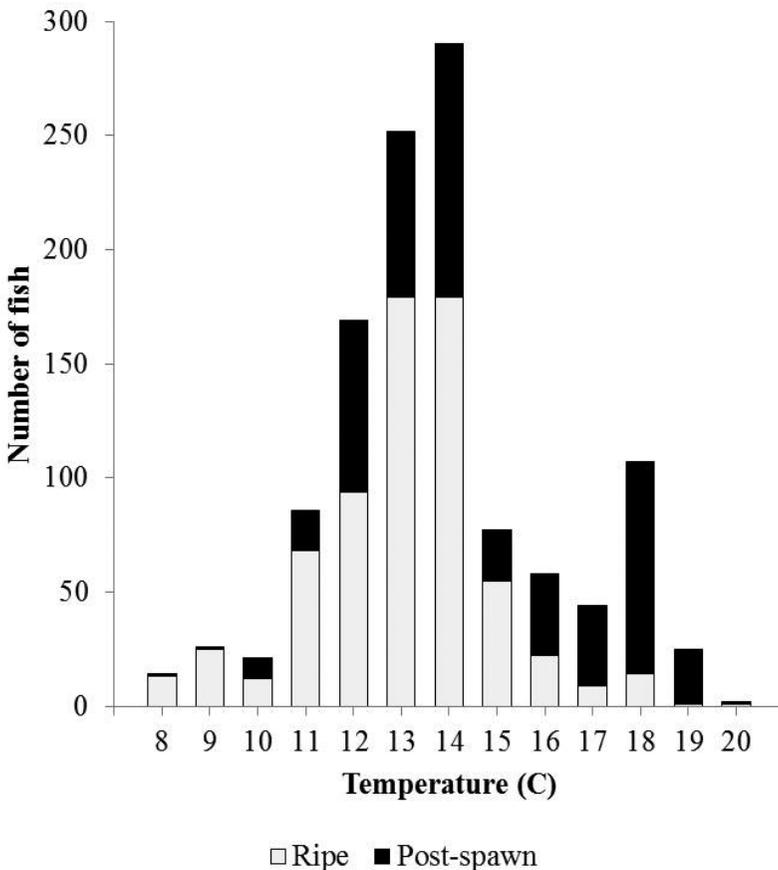


FIGURE 8.—The number of ripe (grey) or post-spawn (black) delta smelt caught in a specific temperature range during routine monthly sampling in the upper San Francisco Estuary during January-May for years 2002-2015.

Length Analyses.—Delta smelt caught during the 2003–2015 SKT ranged in size from 16 to 94 mm FL ($n=6,525$, $\text{mean}=66.2$, $\text{SD}=6.0$). Ten of these fish were equal to or greater than 89 mm, and eight were less than 40 mm (Figure 9). Females ranged in size from 47 to 92 mm ($n=3,618$, $\text{mean}=67.6$, $\text{SD}=5.9$), with the smallest post-spawn female being 55 mm FL. Majority (98%) of post-spawn fish were >61 mm FL. We found a significant difference and generally increasing pattern in fork lengths of pre-spawn females among months sampled ($H_4=560.65$; $P<0.001$; Figure 10). Only the months of March and April were not significantly

TABLE 4.—Number of adult female delta smelt by year and month that were caught during routine monthly sampling, 2002–2015. Zeros indicate no catch, whereas NA indicates there was no sampling effort. Females are grouped into two categories, healthy and atretic, based on gonadal-stage. Atretic females have ovaries that failed to spawn and are being resorbed (stage 5). Healthy females have gonads that appear to be in a normal stage of development (stages 1, 2, 3, 4, or 6).

Year	January		February		March		April		May	
	Healthy	Atretic	Healthy	Atretic	Healthy	Atretic	Healthy	Atretic	Healthy	Atretic
2002	108	0	186	0	151	0	NA	NA	NA	NA
2003	NA	NA	145	0	258	0	35	0	29	0
2004	183	0	134	0	110	0	55	0	9	0
2005	113	0	137	0	17	0	14	0	NA	NA
2006	21	0	44	0	53	0	47	1	6	0
2007	61	0	49	0	38	0	59	1	13	1
2008	54	0	13	0	49	0	19	0	14	0
2009	223	0	33	0	52	0	22	0	7	0
2010	39	0	32	0	48	0	46	0	5	0
2011	65	0	52	0	30	0	33	1	24	0
2012	139	0	161	0	148	1	95	1	99	0
2013	42	1	57	0	56	0	24	0	10	0
2014	90	0	32	0	59	2	17	9	18	5
2015	13	0	37	0	3	1	0	0	2	2
Total	1,151	1	1,112	0	1,072	4	466	13	236	8

different in pairwise comparisons ($C-I \text{ Test}=0.8022$; $P=0.4225$), and all other monthly comparisons were significantly different ($P<0.001$). We also found a significant difference in fork lengths of post-spawn females among months sampled ($H_4=12.80$; $P=0.01231$), but no consistent increase or decrease across months. However, pairwise comparisons showed that only the months of April and May were significantly different ($C-I \text{ Test}=3.1202$; $P=0.0019$); all other monthly comparisons were non-significant ($P>0.05$). Mean fork length increased by 10 mm for pre-spawn females from January to May, whereas the mean fork length for post-spawn females appeared to remain the same over the same period (Figure 10).

DISCUSSION

Delta smelt exhibited group-synchronous gonad development, indicating females undergo serial spawning (i.e. spawning more than one clutch per season) in the wild (Mager

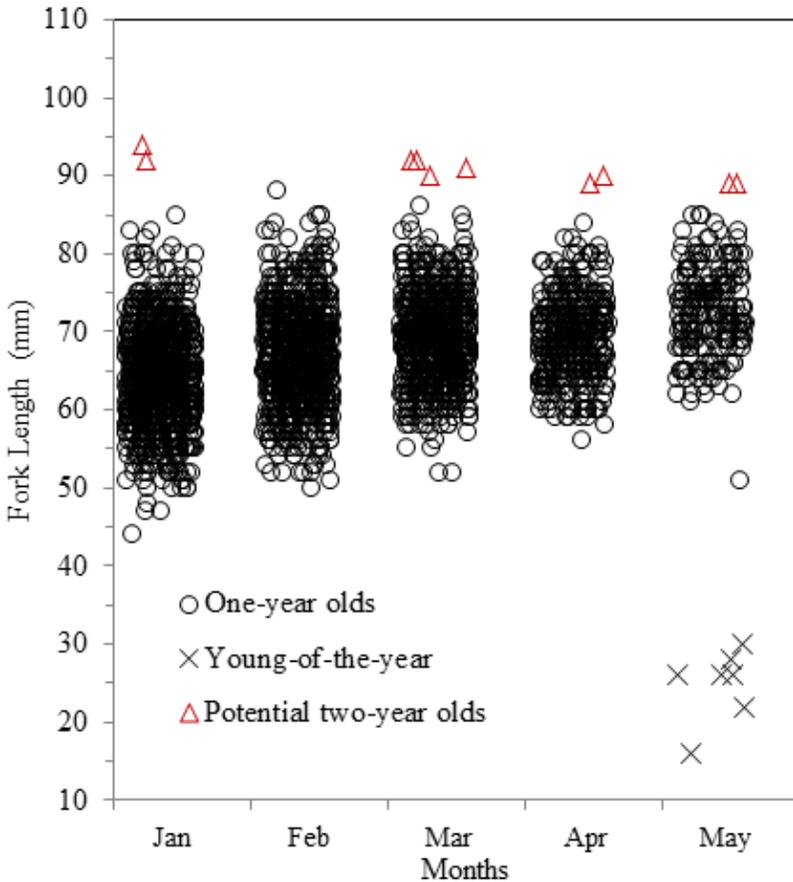


FIGURE 9. — Fork length (mm) by month of capture for all delta smelt caught during January–May for years 2003–2015. Red triangles indicate potential two-year old fish, black circles indicate one-year old fish, and black crossmarks indicate young-of-the-year.

1996). Observations of multi-stage gonadal development have long been used as evidence of serial spawning in other species (Hunter et al. 1992, Nichol and Acuna 2001). Delta smelt egg size was highly variable among individuals and occurred in two distinct modes. This resulted in a small, yet clear, gap between the sizes of primary and secondary growth egg-size stages. Post-spawn eggs were not measured in this study, but based on visual observation; we hypothesize that they would also result in a third, larger egg-size stage. Observations of multi-stage gonadal development and clearly defined egg-size stages are evidence of group-synchrony and serial spawning in other species (Hunter et al. 1992; Nichol and Acuna 2001). It is common for small fish with eggs less than 1 mm (1,000 μm) in diameter to have undefined egg-size stages, even when group-synchronous, which may explain why the gap between egg-size stages was small for delta smelt (Hunter and Macewicz 2003). Since egg diameter measurements were done post-hoc, there was likely a loss of primary-growth eggs

that resulted in a dampening of the lower mode. Given that cultured female delta smelt produce several clutches in a single spawning season, and wild delta smelt have been detected with post-ovulatory follicles, our premise that wild female delta smelt are group-synchronous and can spawn multiple clutches within a season is strongly supported (Lindberg et al. 2013).

Previous studies suggest that the onset and termination of delta smelt spawning (the spawning window) is regulated by temperature (Brown et al. 2013, 2016). We found the thermal spawning window to occur between 9°C and 18°C, which was similar to ranges found by other researchers, both in wild and culture settings (Wang 1986, 2007; Baskerville-Bridges et al. 2004; Lindberg et al. 2013). Ripe and post-spawn females occurred at both tails of the temperature range, indicating that spawning occurred within the entire range. The length of the spawning season has been proposed as one factor contributing to year-class strength or an-

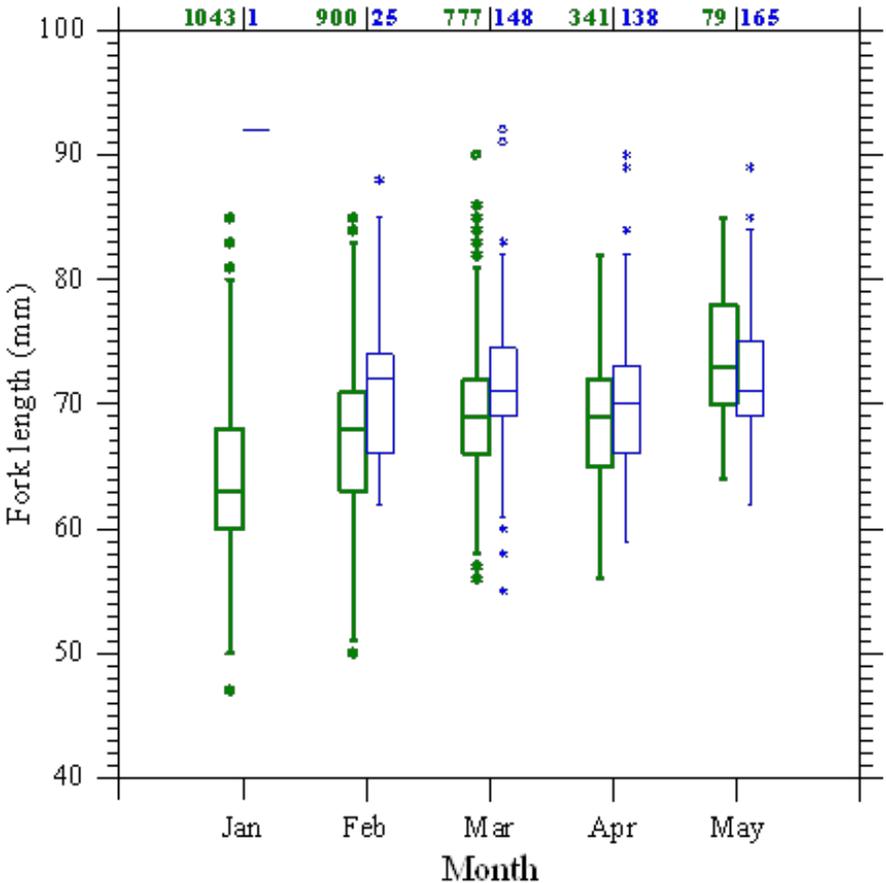


FIGURE 10.—Fork lengths (mm) by month for pre-spawn (green on left) and post-spawn (blue on right) female delta smelt caught during routine monthly sampling during January-May for years 2003-2015. Values above box plots are number of individuals. Note, the number of January post-spawners was n=1 at 92 mm FL.

nual abundance (Bennett 2005; MacNally et al. 2010; IEP 2015). Since spawning only occurs within the thermal spawning window, then extension of that window will add spawning opportunities and increased abundance of the next year-class. Shortening the spawning window will have the opposite result: limited number of clutches possible and decreased abundance of the next year-class. Since survival of wild eggs and larvae is low, another, and likely greater benefit of serial spawning is risk spreading among cohorts (i.e. individuals produced from a clutch). Since clutches are spawned sequentially, each cohort would encounter different environmental conditions, thus spreading risk and improving chances for survival. Spreading risk across multiple clutches/cohorts increases the possibility that some will encounter favorable conditions, thus improving survival and recruitment (Lambert and Ware 1984; Kisdi 2002). Risk spreading is extremely important for a small annual fish and could significantly increase recruitment success, which is particularly helpful in years of low adult abundance.

We rarely detected gonadal atresia overall, but such detections occurred most frequently in 2014, suggesting the delta smelt experienced a uniquely severe environmental stress during the spawning season that year (e.g., a sudden increase in temperature). This stress prevented a large fraction of the population from spawning in April and May (otherwise prime spawning months), and affected some individuals in March (Table 4). Due to the occurrence of gonadal atresia, the 2014 spawning season appeared to end by April; thus, the spawning window lasted only two months. The shortened and stressful spawning season is probably due to a suite of drought conditions experienced in the SFE since 2012 (Jeffries et al. 2016), and likely contributed to the drastic reduction in healthy mature females caught in 2015.

We estimated 55 mm FL to be the minimum size at maturity for wild female delta smelt. Many delta smelt remained below this minimum size just prior to and during the early portion of the spawning season as inferred by the thermal spawning window (Figure 9). This would have effects on when females could first spawn and their total egg production, since Rose et al. (2013a) found that inter-annual differences in mean length of winter fish had large effects on maturity and total egg production. At the onset of the spawning window, small fish would have to delay spawning until reaching the putative minimum maturity size. In our study, all pre-spawn females achieved spawning size around April, which would result in only one spawn per female, with subsequent spawning events being rare except in exceptional years when the thermal spawning window extends past May. In the early 1990's, there was a significant decrease in delta smelt juvenile (measured in the fall) mean fork length (Sweetnam 1999). Prior to this shift, most of the delta smelt would have approached and surpassed minimum spawning size earlier in the year, resulting in increased spawning opportunities, and probably an increase in reproductive potential (i.e., egg production) as a result.

Our delta smelt clutch fecundity results were consistent with the general historically reported range of fecundity in wild (Moyle et al. 1992; Mager 1996) and captive delta smelt, which also includes some two-year olds (Bennett 2005; Lindberg et al. 2013). Fecundity increased as a function of length, and although the length-fecundity variation was high, it was similar to the variation in cultured fish (Lindberg et al. 2013). This indicates that controlled temperature and food supply in culture had minimal effect on the length-fecundity relationship. It could also indicate that wild conditions, such as food supply, were adequate to maintain basic physiological needs. Two-year old delta smelt were rarely collected during the 2003-2015 sampling period. SKT did capture 10 potential two-year olds over 14 years of sampling; all appeared healthy and in spawning condition. However, fish in culture have been able to grow to large lengths in their first year (Lindberg et al. 2013); it is possible some or

all of the wild caught individuals were large one-year olds, but we believe this is not likely (Figure 10). In culture, two-year old fish were considerably more fecund than one-year old fish (Bennett 2005; Lindberg et al. 2013), but this was not the case for the single 90 mm female examined for fecundity in this study (Figure 5). It has been reported that two-year old delta smelt were historically present in the fall (Sweetnam and Stevens 1993), but it is unclear whether they were more abundant in the past, or lived to spawn in their second year.

The number of clutches a female can successfully develop and spawn within the spawning window drives her annual fecundity. Development of a subsequent egg clutch after a spawning event requires time, which we called the spawning interval (also referred to as a refractory period). Recent culture estimates place the spawning interval at 50 days at 12°C, with a range of 39 to 70 days (M. Nagel, University of California, Davis, personal communication). In the wild, females first became near-ripe in January and were followed about a month later by the first observations of subsequent spawners attaining near-ripe status for the second time in a season (Table 3). This suggests that the minimum spawning interval in the wild of about one month, is similar to the lower end of the range observed in culture (i.e., 39 days, M. Nagel, University of California, Davis, personal communication). There is potential that the spawning interval is a function of temperature and, like fecundity, is linked to size of the fish (i.e., larger fish need shorter intervals between spawning events). The length of the spawning window combined with the required spawning interval determines the potential number of times a female delta smelt can spawn each year. For example, if environmental conditions resulted in a 100 day spawning season (i.e., water temperature in the range of 9-18°C for 100 days per year), and the spawning interval in the wild is similar to culture (less than 50 days), the result could be a spawning frequency of three clutches for a mature female. Conversely, a spawning season of less than 50 days would yield a spawning frequency of only one clutch. In years where cool temperatures persist into spring, delta smelt could have an increased spawning frequency, resulting in a greater reproductive potential. To determine actual spawning frequency, more information is needed on the spawning interval of wild delta smelt.

We found no evidence indicating that the length-fecundity relationship differed between first spawners and subsequent spawners. Based on our length-fecundity model, growth during the spawning season would result in larger subsequent clutches. We found pre-spawn females to increase about 10 mm on average between January and May, but growth appears to subside during March and April (Figure 9), suggesting that resources are diverted to ovary and egg development during that time, rather than growth. It may be possible for growth and ovarian development to occur simultaneously, or for spawning intervals to be reduced, if food supply was increased or of higher quality.

The number of subsequent spawners detected by our study was probably biased low. Our macroscopic staging methods relied on detection of post-vitellogenic eggs retained by subsequent spawners. Females attempt to release their entire clutch, and presumably many or most are successful, leaving no post-vitellogenic eggs for detection (false negative). We do not believe many post-vitellogenic eggs were overlooked or resorbed, but these effects would also reduce detection. Microscopic methods, such as detection of post-ovulatory follicles, might have improved detections, but we do not know how long such structures remain visible after the release of eggs. Thus, the additional effort would likely produce only modest additional information. We found evidence that post-spawning females were preparing to spawn a second time as early as February, and more frequently in March and April. In each case within this monthly range, there may have been sufficient

time to complete a second spawning interval and spawn a third time during the season. The strong potential for wild spawners to release a third and perhaps a fourth clutch within a single spawning season substantially elevates delta smelt's annual fecundity, which better fits the definition of the opportunistic strategist (Winemiller and Rose 1992).

Climate change is a growing concern for delta smelt because their survival, growth, maturity, and spawning season duration are all affected by temperature (Brown et al. 2013, 2016). Increased water temperature due to climate change is likely to expedite the spawning season, by shortening it and causing it to occur earlier in the year. This will result in a reduction of spawning opportunities and some individuals not reaching full maturity at the onset of spawning. Given the food limited conditions in nursery habitat during the summer and fall (Slater and Baxter 2014), growth rates are not likely to result in enough growth to counter the earlier spawning season. Ultimately, climate change and warming temperatures will result in decreased delta smelt reproductive potential, by reducing the total annual fecundity of the population each year.

Our results indicate that delta smelt annual fecundity, and thus their reproductive potential, is maximized when females are large, ready to spawn at the start of the spawning season, and spawn multiple times. Multiple spawns in a single season also spreads risk of encountering poor or catastrophic conditions. Production of multiple clutches requires several months of suitable temperatures and an adequate food supply. Additional research is warranted to help clarify the influence of environmental conditions on the length of the spawning season and the spawning frequency possible in the wild. The increasing amount of information regarding climate change and its effects on delta smelt habitat makes this issue one of increasing importance for the management of the species.

ACKNOWLEDGMENTS

This study was conducted under the auspices of the Interagency Ecological Program for the San Francisco Estuary. We thank the field and lab staff from the California Department of Fish and Wildlife-Stockton office for their efforts collecting and processing delta smelt gonads. Their time was paramount to making this study a reality, and it required so many people that we can't list them all here. We also thank Jim Hobbs, Vanessa Tobias, Gonzalo Castillo, Larry Brown, Ted Sommer, Steve Culberson, and three anonymous reviewers for their thorough review of our manuscript, all of which greatly improved the quality. Finally we thank our colleagues at CDFW and UC Davis (Joan Lindberg, Meredith Nagel, Swee Teh, and Tomo Kurobe) for their eager brainstorming sessions and collaboration with us. Work of all authors was funded by the Interagency Ecological Program through contracts with Department of Water Resources (4600010609, Karen Gehrts contract manager) and U.S. Bureau of Reclamation (R15AC00094, Erwin Van Nieuwenhuyse contract manager).

LITERATURE CITED

- BAGENAL, T. B. 1978. Aspects of fish fecundity. Pages 75-101 in S. D. Gerking, editor. Ecology of Freshwater Fish Production. John Wiley & Sons, New York, USA.
- BASKERVILLE-BRIDGES, B., J. C. LINDBERG, J. V. EENENNAAM, AND S. I. DOROSHOV. 2004. Delta smelt research and culture program 5-year summary, 1998-2003. University of California Davis, Davis, California, USA

- BASKERVILLE-BRIDGES, B., J. C. LINDBERG, AND S. I. DOROSHOV. 2005. Manual for the intensive culture of delta smelt (*Hypomesus transpacificus*). Sacramento (CA): University of California, Davis, Report to CALFED Bay-Delta Program, ERP-02-P31
- BENNETT, W. 2005. Critical assessment of Delta Smelt. San Francisco Estuary and Watershed Science 3(2). Available from: <http://escholarship.org/uc/item/0725n5vk>
- BROWN, L. R., W. A. BENNETT, R. W. WAGNER, T. MORGAN-KING, N. KNOWLES, F. FEYRER, D. H. SCHOELLHAMMER, M. T. STACEY, AND M. DETTINGER. 2013. Implications for future survival of Delta Smelt from four climate change scenarios for the Sacramento-San Joaquin Delta, California. *Estuaries and Coasts* 36:754-774.
- BROWN, L.R., L.M. KOMOROSKE, R. W. WAGNER, T. MORGAN-KING, J. T. MAY, R. E. CONNOR, N. A. FANGUE. 2016. Coupled Downscaled Climate Models and Ecophysiological Metrics Forecast Habitat Compression for an Endangered Estuarine Fish. *PLoS ONE* 11(1): e0146724. Doi: 10.1371/journal.pone.0146724
- BROWN-PETERSON, N. J., D. M. WYANSKI, F. SABORIDO-REY, B. J. MACEWICZ, AND S. K. LOWERRE-BARBIERI. 2011. A standardized terminology for describing reproductive development in fishes. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 3:52-70.
- CALIFORNIA DEPARTMENT OF FISH AND WILDLIFE [CDFW]. 2016. State and Federally Listed Endangered and Threatened Animals of California. State of California, Natural Resources Agency. <http://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=109405&inline>
- CHIGBU, P., AND T.H. SIBLEY. 1994. Relationship between abundance, growth, egg size and fecundity in a landlocked population of longfin smelt, *Spirinchus thaleichthys*. *Journal of Fish Biology* 45,1-15.
- CLOERN, J.E., AND A.D. JASSBY. 2012. Drivers of change in estuarine-coastal ecosystems: Discoveries from four decades of study in San Francisco Bay. *Reviews of Geophysics*, 50(4), RG4001, doi:10.1029/2012RG000397.
- HUNTER, J. R., AND S. R. GOLDBERG. 1980. Spawning incidence and batch fecundity in Northern Anchovy, *Engraulis mordax*. *Fisheries Bulletin* 77:641-652.
- HUNTER, J. R., AND R. LEONG. 1981. The spawning energetics of female Northern Anchovy, *Engraulis mordax*. *Fisheries Bulletin* 79:215-230.
- HUNTER, J. R., N.C. LO, AND R.J. H. LEONG. 1985. Batch fecundity in multiple spawning fishes. Pages 61-72 in R. Lasker, editor. An egg production method of estimating spawning biomass of pelagic fish: application to the Northern anchovy, *Engraulis mordax*. US Department of Commerce, NOAA Technical Report NMFS 36.
- HUNTER, J. R., AND B. J. MACEWICZ. 1985. Measurement of spawning frequency in multiple spawning fishes. Pages 79-94 in R. Lasker, editor. An egg production method of estimating spawning biomass of pelagic fish: application to the Northern anchovy, *Engraulis mordax*. US Department of Commerce, NOAA Technical Report NMFS 36.
- HUNTER, J. R., AND B. J. MACEWICZ. 2003. Improving the accuracy and precision of reproductive information used in fisheries. Pages 57-68 in F. Haver, editor. Modern approaches to assess maturity and fecundity of warm and cold water fish and squids.. Institute of Marine Research, Bergen, Norway. https://brage.bibsys.no/xmlui/bitstream/handle/11250/112627/fh_2003_12-1.pdf?sequence=3/#page=57
- HUNTER, J. R., B. J. MACEWICZ, N. CHYAN-HUEI LO, AND C. A. KIMBRELL. 1992. Fecundity, spawning, and maturity of female Dover Sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fishery Bulletin* 90:101-128.

- [IEP] INTERAGENCY ECOLOGICAL PROGRAM MANAGEMENT, ANALYSIS AND SYNTHESIS TEAM. 2015. An updated conceptual model of Delta Smelt biology: our evolving understanding of an estuarine fish. Interagency Ecological Program for the Sacramento-San Joaquin Estuary Technical Report 90. Available at: http://www.water.ca.gov/iep/docs/Delta_Smelt_MAST_Synthesis_Report_January%202015.pdf
- JEFFRIES, K. M., R.E. CANNON, B.E. DAVIS, L.M. KOMOROSKE, M.T. BRITTON, T. SOMMER, A.E. TODGHAM, N.A. FANGUE. 2016. Effects of high temperatures on threatened estuarine fishes during periods of extreme drought. *Journal of Experimental Biology* 219 (11). <http://escholarship.org/uc/item/7d22b524>
- KISDI, E. 2002. Risk spreading versus local adaptation. *The American Naturalist* 159 (6): 579-596. <http://www.jstor.org/stable/10.1086/339989>
- KJESBU, O. S., J. R. HUNTER, AND P.R. WITTHAMES. 2003. Report of the working group on modern approaches to assess maturity and fecundity of warm- and cold-water fish and squids. 4-7 September 2001. Bergen, Norway,
- KJESBU, O. S., P. SOLEMDAL, P. BRATLAND, AND M. FONN. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 53:610-620.
- KUROBE, T., M.O. PARK, A. JAVIDMEHR, F. TEH, S. C. ACUÑA, C. J. CORBIN, A. J. CONLEY, W. A. BENNETT, S. J. TEH. 2016. Assessing oocyte development and maturation in the threatened Delta Smelt, *Hypomesus transpacificus*. *Environmental Biology of Fishes* 99:423-432.
- LACAVA, M., K. FISCH, M. NAGEL, J. C. LINDBERG, B. MAY, AND A. J. FINGER. 2015. Spawning behavior of cultured Delta Smelt in a conservation hatchery. *North American Journal of Aquaculture* 77:255-266.
- LAMBERT, T. C. AND D.M. WARE. 1984. Reproductive strategies of demersal and pelagic spawning fish. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1565-1596. <http://www.nrcresearchpress.com/doi/pdf/10.1139/f84-194>
- LAUER, T. E., S. M. SHROYER, J. M. KILPATRICK, T. S. MCCOMISH, AND P. J. ALLEN. 2005. Yellow perch length-fecundity and length-egg size relationships in Indiana waters of Lake Michigan. *North American Journal of Fisheries Management* 25:791-796.
- LAWTON, R., P. BRANDY, C. SHEEHAN, S. CORREIA, AND M. BORGATTI. 1990. Final Report on Spawning Sea-Run Rainbow Smelt (*Osmerus mordax*) in the Jones River and Impact Assessment of Pilgrim Station on the Population, 1979-1981. Pilgrim Nuclear Power Station Marine Environmental Monitoring Program Report Series No. 4. Department of Fisheries, Wildlife, and Environmental Law Enforcement. Massachusetts Division of Marine Fisheries. Sandwich, Massachusetts, USA.
- LINDBERG, J., G. TIGAN, L. ELLISON, T. RETTINGHOUSE, AND M. NAGEL. 2013. Aquaculture methods for a genetically managed population of endangered Delta Smelt. *North American Journal of Aquaculture* 75:186-196.
- LOWERRE-BARBIERI, S. K., K. GANIAS, F. SABORIDO-REY, H. MURUA, AND J. R. HUNTER. 2011. Reproductive timing in marine fishes: variability, temporal scales, and methods. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 3:71-91.
- MAC NALLY, R., J. R. THOMSON, W. J. KIMMERER, F. FEYRER, K. B. NEWMAN, A. SIH, W. A. BENNETT, L. BROWN, E. FLEISHMAN, S. D. CULBERSON, AND G. CASTILLO. 2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). *Ecological Applications* 20(5):1417-1430.

- MAGER, R. C. 1996. Gametogenesis, reproduction, and artificial propagation of Delta Smelt, *Hypomesus transpacificus*. Ph.D. Dissertation, University of California, Davis, USA.
- MOYLE, P. B., B. HERBOLD, D. E. STEVENS, AND L. W. MILLER. 1992. Life history and status of the delta smelt in the Sacramento-San Joaquin Estuary. *Transactions of the American Fisheries Society* 121:67-77.
- MURUA, H., G. KRAUS, F. SABORIDO-REY, P.R. WITTHAMES, A. THORSEN, AND S. JUNQUERA. 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *Journal of Northwestern Atlantic Fisheries Science* 33:33-54.
- MURUA, H., AND F. SABORIDO-REY. 2003. Female reproductive strategies of marine fish species of the North Atlantic. *Journal of Northwestern Atlantic Fisheries Science* 33:23-31.
- NICHOL, D. G., AND E. I. ACUNA. 2001. Annual and batch fecundities of yellowfin sole, *Limanda aspera*, in the eastern Bering sea. *Fishery Bulletin* 99(1):108-122.
- NICHOLS, F.H., J.E. CLOERN, S.N. LUOMA, AND D.H. PETERSON. 1986. The modification of an estuary. *Science* 231(4738):567-573.
- PENTTILA, D. 1978. Studies of the Surf Smelt (*Hypomesus pretiosus*) in Puget Sound. State of Washington Department of Fisheries Technical Report No. 42. Olympia, Washington, USA
- ROSE, K. A., W. J. KIMMERER, K. P. EDWARDS, AND W. A. BENNETT. 2013a. Individual-based modeling of Delta Smelt population dynamics in the upper San Francisco Estuary: I. model description and baseline results. *Transactions American Fisheries Society* 142:1238-1259.
- ROSE, K. A., W. J. KIMMERER, K. P. EDWARDS, AND W. A. BENNETT. 2013b. Individual-based modeling of Delta Smelt population dynamics in the upper San Francisco Estuary: II. Alternative baselines and good versus bad years. *Transactions American Fisheries Society* 142:1260-1272.
- SLATER, S.B. AND R. D. BAXTER. 2014. Diet, Prey Selection, and Body Condition of Age-0 Delta Smelt, *Hypomesus transpacificus*, in the Upper San Francisco Estuary. *San Francisco Estuary and Watershed Science* 12(3). <http://escholarship.org/uc/item/52k878sb#>
- SOMMER, T., C. ARMOR, R. BAXTER, R. BRUERER, L. BROWN, M. CHOTKOWSKI, S. CULBERSON, F. FEYRER, M. GINGRAS, B. HERBOLD, W. KIMMERER, A. MUELLER-SOLGER, M. NOBRIGA, AND K. SOUZA. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries* 32(6):270-277.
- SOMMER, T. AND F. MEJIA. 2013. A Place to Call Home: A Synthesis of Delta Smelt Habitat in the Upper San Francisco Estuary. *San Francisco Estuary and Watershed Science* 11(2). <http://eprints.cdlib.org/uc/item/32c8t244>
- SWEETNAM, D. A. 1999. Status of Delta Smelt in the Sacramento-San Joaquin Estuary. *California Fish and Game* 85(1):22-27. Sacramento, California, USA
- SWEETNAM, D.A. AND D. E. STEVENS. 1993. Report to the Fish and Game Commission: A Status Review of the Delta Smelt (*Hypomemus transpacificus*) in California. Candidate Species Status Report 93-DS. State of California Resources Agency.
- TYLER, C. R. AND J.P. SUMPTER. 1996. Oocyte growth and development in teleosts. *Reviews in Fish Biology and Fisheries* 6:287-318.
- UNITED STATES FISH AND WILDLIFE SERVICE [USFWS]. 1996. Sacramento-San Joaquin Delta Native Fishes Recovery Plan. U.S. Fish and Wildlife Service, Portland, Oregon. http://ecos.fws.gov/docs/recovery_plan/961126.pdf

- WANG, J. C.S. 1986. Fishes of the Sacramento-San Joaquin Estuary and Adjacent Waters, California: A Guide to the Early Life Histories. Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary Technical Report 9. FS/B10-4ATR 86-9. Sacramento, California, USA
- WANG, J. C.S. 2007. Spawning, early life stages, and early life histories of the osmerids found in the Sacramento-San Joaquin Delta of California. Tracy Fish Facility Studies. US Bureau of Reclamation. Volume 38. Byron, California, USA
- WINEMILLER, K. O., AND K. A. ROSE. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal Fisheries and Aquatic Sciences 49:2196-2218.

Submitted: 25 March 2016

Accepted: 02 August 2016

Associate Editor was K. Fleming