

CALIFORNIA FISH AND GAME

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Photo by Christina Fischer.

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Please direct correspondence to:
Armand Gonzales
Editor-in-Chief
California Fish and Game
Armand.Gonzales@wildlife.ca.gov



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Notes from the Editor

California Fish and Game has been continuously published quarterly since 1914. In this issue, the journal begins a new feature of reprinting select past article for historical perspective, or using the past to study the present. Our first reprint was published in the first edition of the first volume of the journal and was authored by George C. Pardee, ex-governor of California. Pardee's essay entitled *Fish and Game Conservation Dependent on other Natural Resources*, describes the establishment at the time, of institutions in California intended to oversee the conservation of resources like water, forests, and animals and the opposition then encountered by those institutions. The historical perspective that natural resources belong to all of us and they should be conserved for the benefit of all citizens is still relevant today, as is the awareness that there is still opposition to this perception.

I would like to clarify a topic that has come up a few times regarding formatting manuscripts for publication in the *California Fish and Game*. The question has come up mostly in relation to formatting common names of fishes and whether to capitalize or not, e.g. Longfin Smelt, as required by the America Fisheries Society. The answer is provided by the Council of Science Editors Style Manual (CSE 2014) which serves as this journal's standard for style unless specifically stated otherwise in Bleich et al. 2011. The CSE states: "Vernacular names of animals and plants are generally written in lowercase, except for proper name components, which are capitalized. This style is widely followed for nearly all plants, invertebrates (including insects and crustaceans), fish, and mammals and is reflected in a variety of vernacular name lists developed by professional societies." The CSE acknowledges that the style is not universal and is handled differently by different journals, and that no cross-disciplinary authority (e.g., International Union of Biological Sciences) has made a recommendation for all biological sciences. So for *California Fish and Game*, use lowercase for vernacular names of all animals (including fish), and plants, but use uppercase for any proper name components.

In the final edition of every volume, the journal publishes indexes of Reviewers of Manuscripts, Subject Matter Index, and Author Index for *California Fish and Game*. Following this tradition, these indexes are included in this edition. I would like to take this opportunity to thank the reviewers for their generosity of time and knowledge in helping the journal maintain its high scientific standards. I would also like to thank the authors for submitting their work to *California Fish and Game*. It is the contributions from authors, and our rigorous peer-review that earns this journal its credibility and respect amongst scientists worldwide.

Armand Gonzales
Editor-in-Chief

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Environmental extremes and biotic interactions facilitate depredation of endangered California Ridgway's rail in a San Francisco Bay tidal marsh

CORY OVERTON*, STEVEN BOBZIEN, AND MARCIA GREFSRUD

U.S. Geological Survey, Western Ecological Research Center, Biological Research Division; Dixon Field Office, 800 Business Park Drive, Dixon, CA 95620, USA (CO)

*East Bay Regional Park District; 2950 Peralta Oaks Ct, Oakland, CA 94605, USA (SB)
California Department of Fish and Wildlife; 1416 9th Street, 12th Floor, Sacramento, CA 95814, USA (MG)*

*Correspondent: coverton@usgs.gov

Key words: apparent competition, *Falco peregrinus*, high tide, peregrine falcon, predation, *Rallus obsoletus obsoletus*, Ridgway's rail, San Francisco Bay, tidal marsh

On 23 December 2015 while performing a high tide population survey for endangered Ridgway's rails (*Rallus obsoletus obsoletus*; formerly known as the California clapper rail) and other rail species at Arrowhead Marsh, Martin Luther King Jr. Regional Shoreline, Oakland, California, the authors observed a series of species interactions resulting in the predation of a Ridgway's rail by an adult female peregrine falcon (*Falco peregrinus*). High tide surveys are performed during the highest tides of the year when tidal marsh vegetation at Arrowhead Marsh becomes inundated, concentrating the tidal marsh obligate species into the limited area of emergent vegetation remaining as refuge cover. Annual mean tide level (elevation referenced relative to mean lower low water) at Arrowhead Marsh is 1.10 m, mean higher high water is 2.04 m (NOAA National Ocean Service 2014) and the average elevation of the marsh surface is 1.60 m (Overton et al. 2014). Tidal conditions on the day of the survey were predicted to be 2.42 m. Observed tides at the nearby Alameda Island tide gauge were 8 cm higher than predicted due to a regional low-pressure system and warmer than average sea surface temperatures (NOAA National Ocean Service 2014). The approximately 80 cm deep inundation of the marsh plain was sufficient to completely submerge tidal marsh vegetation and effectively remove 90% of refugia habitats.

At approximately 0945 hours, about 15 minutes into the survey, a moderate (12-20) flock of diving ducks, mostly lesser scaup (*Aythya affinis*), and a mixed flock of shorebirds consisting of least sandpipers (*Calidris minutilla*), western sandpipers (*Calidris mauri*), and willets (*Catoptrophorus semipalmatus*) were observed from approximately 200-250 m away swarming in low flight over the water. The behavior was classic predator avoidance flocking as the birds were being cooperatively hunted by a pair of adult peregrine falcons. The relative size difference between the falcons' size indicated a male (smaller)

and female (larger) pair (Figure 1). The male falcon initially appeared to be in pursuit of the shorebirds and would exhibit relatively low and level flight causing the swarming behavior near the water surface. Meanwhile, the female falcon performed several shallow stoops into the flock of diving ducks. Approximately three unsuccessful falcon attacks in rapid succession were observed. During the last failed attack, swarming by the diving ducks disturbed a Ridgway's rail that was hiding in what little hybrid cordgrass (*Spartina* spp.) remained above the tide. The rail made a low and short flight of approximately 1 m and then returned to the water (Figure 2). Suddenly, the falcons abandoned their pursuit of the shorebirds and diving ducks and began relentlessly stooping at the swimming rail. The first approximately six attacks were avoided by the rail which briefly dived under water or was simply missed by the two falcons. On a subsequent pass, the female falcon was able to capture the rail from the water surface and carry it into the air (Figure 3). Within seconds, several immature and mature western gulls (*Larus occidentalis*) mobbed the female falcon carrying the rail (Figure 4). As the pair of falcons flew out of visual range, the male aggressively engaged and drove away the gulls. The male falcon did this by flying above and behind the female and diving at any gull that approached within 5 to 10 m of the female. Two or three diving maneuvers by the male successfully deterred pursuit by the gulls.

These observations provide evidence of several important species interactions in San Francisco Bay tidal marshes, as well as environmental conditions that drive some of these interactions. First, the cooperative hunting behavior of peregrine falcons clearly suggests that



FIGURE 1. —A pair of peregrine's after the successful cooperative capture of a Ridgway's rail. The female was identified as the larger of the falcons and carried the rail away with the smaller male following behind. Photo credit: Marcia Grefsrud/CDFW.



FIGURE 2.—Ridgway's rail flushing from sparse, flooded *Spartina* at Arrowhead Marsh, Oakland, CA. During the highest tides, available cover for concealment is reduced and individuals concentrate in the little exposed vegetation that remains. Photo credit: Marcia Grefsrud/CDFW.



FIGURE 3.—A female peregrine falcon's successful capture and flight with the Ridgway's rail. Photo credit: Marcia Grefsrud/CDFW.



FIGURE 4. —Western gulls chasing the female peregrine falcon as she carries a captured Ridgway's rail away. Photo credit: Marcia Grefsrud/CDFW.

pair-bonded individuals (mated pairs) benefit from an intraspecific mutualism that advantages each member of the pair through increased capture success, decreased energy used defending successful kills due to safeguarding by mates, decreased prey loss due to kleptoparasitism, and increased provisioning from food sharing. Cooperative hunting is uncommon in birds but has been observed, with some of the above benefits, in Aplomado falcons (*Falco femoralis*), (Hector 1986). A second biological interaction of importance is the rapid opportunistic prey switching behavior that occurred following the exposure of the Ridgway's rail. The hunting time and energy expended by the peregrine falcon pair to capture and kill the rail was likely much lower than the effort expended in their continued air to air pursuit and unsuccessful attacks on the diving ducks and shorebirds. While the ducks and shorebirds relied on swarming behavior, presence of conspecifics, and speed to evade the falcons, the rail appeared to initially depend on concealment to avoid detection. The effectiveness of relying on a concealment strategy decreases substantially in San Francisco Bay during the winter when extreme high tides correspond with winter storm events and low pressure systems (NOAA National Ocean Service 2014, Overton et al. 2014). These high tides are typically the most extreme of the year and occur during daylight (noting that summertime high tides may be of near equal height but occur at night). The combination of diurnal high tides and relatively homogenous vegetative cover results in a rapid decrease in suitable refuge habitat, and increases rail exposure to raptor predation events during these winter high tides (Figure 2). In addition, the presence of shorebirds and diving ducks, many species of which reach greatest abundance during the winter (Page et al. 1999), that flock together over the marsh plain prior to the falcons' arrival may serve as a source of apparent competition (Holt 1977) that indirectly reduce the likelihood of the rail surviving. The flocks of massed shorebirds and diving ducks were the initial targets of the falcons, as well as the apparent source of the disturbance that flushed the concealed rail from sparse cover, ultimately resulting in its depredation. Although this does not prove apparent competition, as it is possible that falcons would intensively hunt inundated tidal marshlands that contain the secretive rail even without

the much more visible shorebirds and waterfowl being present, it is apparent in this case that the survival of the rail was negatively influenced by the presence of such alternative prey for the falcon. Other sensitive species in San Francisco Bay, such as California least tern (*Sterna antillarum browni*) and snowy plover (*Charadrius nivosus*), have been preyed upon by peregrine falcons and may be similarly affected by indirect biotic interactions.

Although these types of interactions may result from environmental conditions (i.e., extremely high tides) that exist for just a few hours per year in the San Francisco Bay, the fragmented and diminished condition of tidal marsh habitats, together with sea level rise, cumulatively increase the risks to rail populations by reducing the extent of suitable transition vegetation communities between intertidal and upland ecotones.

Concerns are heightened given the limited number of Ridgway's rails, its relatively poor escape capability, and its vulnerability to extant hazardous environmental conditions. Loss of this transition zone habitat may limit the ability of rails to find refuge and escape predation from avian predators (Casazza et al. 2016).

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Breeding chronology, movements, and life history observations of tricolored blackbirds in the California Central Coast

CHRISTOPHER R. WILSON*, ROBERT J. MEESE, A. CHRISTY WYCKOFF

Santa Lucia Conservancy, 26700 Rancho San Carlos Rd, Carmel, CA 93923 (CRW, ACW)

Department of Environmental Science & Policy, University of California, One Shields Ave, Davis, CA 95616 (RJM)

Current Address: Conservation Ecology LLC, 6 Penny Court, Hendersonville, NC 28739 (CRW)

**Correspondent: chris@conservationecologyllc.com*

The tricolored blackbird (*Agelaius tricolor*; hereafter, tricolor) has experienced population declines and is currently under review for listing under both the California and Federal endangered species acts. Tricolors form the largest breeding colonies of any extant North American land bird, and are mostly found within the California Central Valley. However, smaller numbers of tricolors breed in other parts of lowland California, including the California Central Coast where the species is little-studied. From 2012 to 2014, we studied radio-tagged tricolors at four breeding colonies in Monterey County. The relative cover of the tricolors' primary grassland foraging habitat within 5 km of colony sites was lower than reported elsewhere. Birds arrived at colony sites from early-April to mid-May and remained up to 90 days. Nest-building occurred between 5 April and 18 June, with asynchronous nest-building at individual colonies occurring over periods up to 35 days. The largest colonies each year ranged from 600 to 800 birds. Twenty-five percent of radio-tagged birds moved between the study colonies during the breeding season, suggesting itinerant breeding. After breeding, 15% of tagged birds were observed near colony sites while 21% dispersed up to 37 km north and northeast towards known over-wintering areas (northern San Joaquin Valley, San Francisco Bay-Delta, and coastal Marin County). We also recorded, apparently for the first time, 1) arboreal foraging in oak woodlands, 2) use of lichen (*Ramalina* or *Usnea* spp.) as nest material, and 3) likely predation by long-tailed weasels (*Mustela frenata*). Given the observed variability in nesting chronology, our findings suggest that surveys of prospective breeding colonies should occur throughout the entire breeding season to accurately assess presence

or absence of nesting tricolors. Additionally, inter-colony movements of tricolors suggest that continued use of any one location may depend upon the suitability and productivity of nearby colonies. Management regimes for the species must therefore ensure cooperation among multiple land-management entities controlling nearby tricolor habitats.

Key words: tricolored blackbird, *Agelaius tricolor*, California Central Coast, itinerant breeding, radio-telemetry, arboreal foraging

The tricolored blackbird (*Agelaius tricolor*, hereafter, tricolor) is a medium sized passerine that forms the largest breeding colonies of any extant land bird in North America (Neff 1937; Cook and Toft 2005). It occurs in its greatest abundance in California's Central Valley and surrounding foothills, where the largest breeding colonies occur and where the species has been most intensively studied. Smaller breeding colonies occur in the coastal and Sierra Nevada foothills of southern and central California and very small numbers of breeding birds occur in Oregon, Washington, Nevada, and Baja California (Neff 1937, Cook and Toft 2005, Meese et al. 2014).

A century ago the species was considered one of the most abundant birds in California; however, the tricolor has experienced a dramatic population decline from an extrapolated 2-3 million birds in the 1930s (extrapolated from Neff 1937) to about 145,000 birds in 2014 (Meese et al. 2015). This decline led to a 6-month emergency listing of the species as endangered under the California Endangered Species Act in December 2014 (State of California 2014) and the species is currently in formal status review for listing under both the Federal and California Endangered Species Acts (USFWS 2015; State of California 2015).

The tricolors' decline appears to be tied to loss of food supplies and habitat. Tricolors require insect prey during the breeding season for egg formation and nestling development (Payne 1969), and breeding colonies are often in proximity to insect-rich grasslands or rangelands, the bird's primary foraging habitat. Loss of grassland foraging habitat has been implicated in the decline of the species (DeHaven et al. 1975; Beedy and Hamilton 1997) and lack of insect prey has been implicated with recent chronic poor reproductive success (Meese 2013). Beedy et al. (1991) reported wetland loss and fragmentation as a principal reason for the tricolors' decline. Tricolors historically nested in largest numbers in cattail (*Typha spp.*) or bulrush (*Schoenoplectus spp.*) marshes in the California Central Valley. However, this area experienced wetland losses >90% between 1850 and 1980 (Frayer et al. 1989) and today the largest colonies typically appear in non-native upland substrates, primarily Himalayan blackberry (*Rubus armeniacus*), milk thistle (*Silybum marianum*), and cultivated triticale fields near dairies (Meese et al. 2014).

Triennial statewide tricolor breeding surveys, conducted since 1994, are the primary means for monitoring this species' numbers. The three most recent surveys indicated that the breeding population in the Central Coast declined by 91% between 2008 and 2014, the largest proportional decline in the state during that period; over half the nesting birds counted in this seven-county region in 2014 were in Monterey County (Meese 2014). Besides the triennial statewide breeding surveys and a breeding bird atlas of Monterey County (Roberson and Tenney 1993), no other tricolor research has been reported for the Central Coast region.

To improve understanding of the species' life history and population decline, we undertook breeding and post-breeding season studies in the Central Coast region during 2012-2014. Our objectives were to document numbers of breeding birds, habitat use, breeding chronology, and movements.

MATERIALS AND METHODS

Study areas.—We studied four tricolor breeding colonies in Monterey County, California, April to July each year from 2012 to 2014 (Figure 1). Two colonies, Cienega Pond (36°26'27.20"N, 121°47'35.89"W) and Ohlone Pond (36°28'9.02"N, 121°47'37.64"W), were at 446 m and 435 m elevation, respectively, within the Santa Lucia Mountains near the town of Carmel Valley. These two colonies occur on the Santa Lucia Preserve (SLP), a 20,000 acre private residential development containing an 18,000 acre protected natural area managed by the Santa Lucia Conservancy, a non-profit land trust. The Cienega Pond breeding substrate was primarily bulrush (*Schoenoplectus spp.*) with smaller amounts of cattail (*Typha spp.*), which together covered about 30% of the 10,277 m² pond. The Ohlone Pond breeding substrate was dominated by bulrush, which covered about 70% of the 2,503 m² pond.

Two additional colonies, Fort Ord Nettle Patch (36°36'3.96"N, 121°43'3.00"W) and Laguna Seca Pond (36°34'17.04"N, 121°46'4.80"W) were located about 20 km north of the SLP colonies, in the Sierra de Salinas range, near the edge of the Salinas Valley at 129 m and 116 m elevation, respectively. The Fort Ord Nettle Patch was located within the Fort Ord National Monument managed by the Bureau of Land Management and the Laguna Seca Pond was located within the Laguna Seca Recreation Area managed by the Monterey County Parks Department. The Fort Ord Nettle Patch breeding substrate was stinging nettle (*Urtica dioica*), which covered 310 m², and the Laguna Seca Pond breeding substrate was a mix of cattail and bulrush, which covered about 73% of the 11,488 m² pond.

The four colonies ranged between 9 km and 12 km from the Pacific Ocean and the maximum inter-colony distance was 20 km. All colonies were adjacent to grasslands and all except Fort Ord Nettle Patch were within 200 m of an equestrian facility. Cienega Pond and Laguna Seca Pond were also adjacent to golf courses. In 2014, these four colonies contained an estimated 25% of the birds found in the entire seven-county Central Coast region (Alameda, Santa Clara, San Mateo, Santa Cruz, Monterey, San Luis Obispo and Santa Barbara Counties) according to triennial statewide survey data (Meese 2014).

Habitat characterization.—Tricolors most often forage for insect prey within 5 km of colonies (Orians 1961, Beedy and Hamilton 1997, Airola et al. 2015). To characterize available upland foraging habitats within 5 km, we utilized the California Wildlife Habitat Relationships (WHR) System classification (Meyer and Laudenslayer 1988) available in the 2013 Existing Vegetation - CALVEG polygon GIS data for Zone 6, the Central Coast. We aggregated the WHR vegetation classes into groupings of similar physiognomic structure, with the assumption birds in different areas would utilize the groupings similarly. These groupings were: forest (montane hardwood, montane hardwood-conifer, redwood), grassland (annual grassland), shrubland (chamise-redshank chaparral, coastal scrub, mixed chaparral), other (barren, lacustrine), urban, and woodland (blue oak woodland, coastal oak woodland, valley oak woodland).

Breeding chronology and abundance.—We monitored tricolor nesting activity and abundance at the breeding colonies beginning the first 10 days of April each year, from the start of nesting until breeding activity ceased and most birds departed from

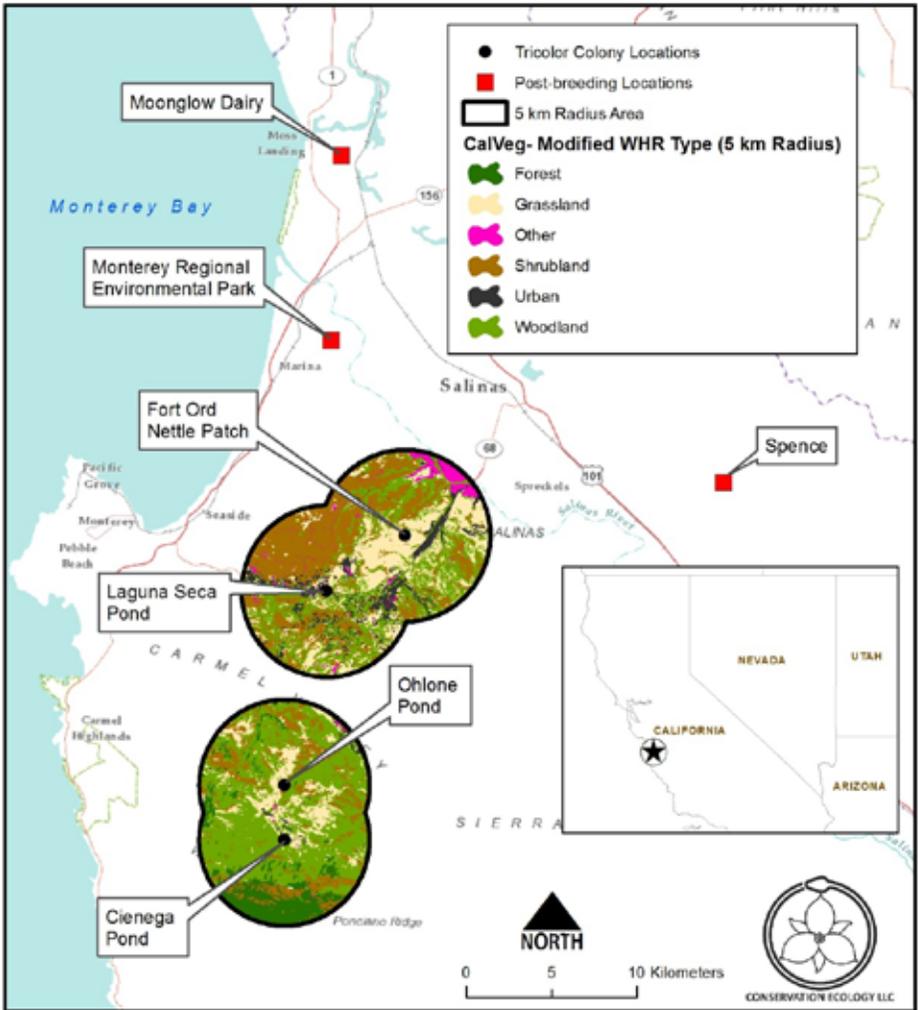


FIGURE 1.—Locations of tricolored blackbird breeding colonies, surrounding habitat types, and post-breeding locations. Monterey County, California.

colonies. For each 10-day interval, colonies were visited one to seven times. Observations at nesting substrates were conducted for at least 20 mins from a distance of 5 m to 15 m away. The birds did not flush or show defensive or nervous behavior in response to our presence. Tricolors carrying nesting material (and partially constructed nests) were indicative of active nest construction. Colony abundance was estimated during each visit as the sum of all birds visible on nesting substrate, birds flying to and from the colony, and birds foraging in nearby areas visible from the colony. On most occasions, birds were counted by a single observer. Counts by multiple observers were averaged.

Movements.—We used radio-telemetry to document tricolor breeding and post-breeding movements. Tricolors were captured one week after breeding began in the study area, using walk-in traps baited with cracked corn (Meese and Simmons 2010). Advanced Telemetry Systems model A1030 transmitters weighing 1.8 g (about 3% and 5% of mass of

males and females, respectively) were attached to birds using the backpack method described in Rappole and Tipton (1991). Over the three year study, transmitters were attached to a total of 48 birds: 22 (46%) males and 26 (54%) females (5 males and 5 females in 2012; 8 males and 10 females in 2013; and 9 males and 11 females in 2014). Estimated battery life of transmitters was 90 days and the unobstructed, straight-line detection distance was about 2 km. Captured birds were also banded with aluminum USGS bands on the left leg and Darvic color bands on both legs. All tricolor radio-tagging and banding occurred at Ohlone Pond and birds were banded and released within 1 hour of their capture.

During monitoring visits to colony sites, radio-tag detection was determined by scanning transmitter frequencies using the Advanced Telemetry Systems model R410 receiver and a 3-element Yagi antenna. As the breeding season progressed each year and fewer tagged birds were detected at colonies, we began conducting broader vehicle-based searches within the Santa Lucia Preserve and western Monterey County. These broader searches involved scanning tag frequencies using an omnidirectional antenna mounted to the roof of a moving vehicle, then stopping and searching specific areas of interest with the unidirectional Yagi antenna. Searches targeted grasslands, vegetated ponds, ranches, equestrian facilities, and dairies in the vicinity of: California State Route 1, between Andrew Molera State Park and the town of Moss Landing (a driving distance of about 70 km); Carmel Valley Road, between the towns of Carmel-by-the-Sea and Carmel Valley (about 20km); and California State Route 68, in the vicinity of Toro County Park, Fort Ord National Monument, and Laguna Seca Recreational Area (about 8 km). These broader searches generally occurred at least once per 10-day interval. On 22 June 2013 we searched for radio-tagged birds by airplane, scanning colony sites (and vicinities), the Salinas Valley southeast to King City, and coastal areas between Watsonville and Monterey (about 2,000 km²). Transmitter locations detected from the air were later (within 2 days) searched from the ground, using the vehicle-based methods. For temporal analyses of observations, we chose one date representing the transition from breeding to post-breeding, generally reflecting 1) the end of nest building activity, 2) substantially declining numbers of birds at colony sites, and 3) movements of tagged birds away from colony sites (>5 km).

RESULTS

Foraging habitat.—For the four colony sites combined, the three most dominant habitat types within 5 km were woodland (43%), shrubland (25%), and grassland (21%); forest, urban, and other habitat types made up the remainder (<11% combined).

Breeding chronology and abundance.—Annual first-arrivals of birds to colony sites occurred between early-April and mid-May, and colonies were occupied for <30 days to 90 days (Figure 2). Nest-building occurred between 5 April to 18 June at four sites in 2012, but at only two sites in 2013 and 2014 (Table 1). Ohlone Pond was the only site with nest building observed each year. In 2012 and 2013, nest building was observed at active colonies over periods of 5 to 35 days.

The largest colonies each year contained: 600 birds at Laguna Seca Pond in 2012, 800 birds at Ohlone in 2013, and 600 birds at Laguna Seca in 2014 (Figure 2). For all colonies combined, the highest number of birds during a single 10-day interval each year was: 910 birds during late-May 2012, 827 birds during mid-Apr 2013, and 600 birds during mid-May 2014.

Breeding and post-breeding movements.—Over the three years, the latest nest-building activity was on 18 June, the earliest pronounced movements (5 km or

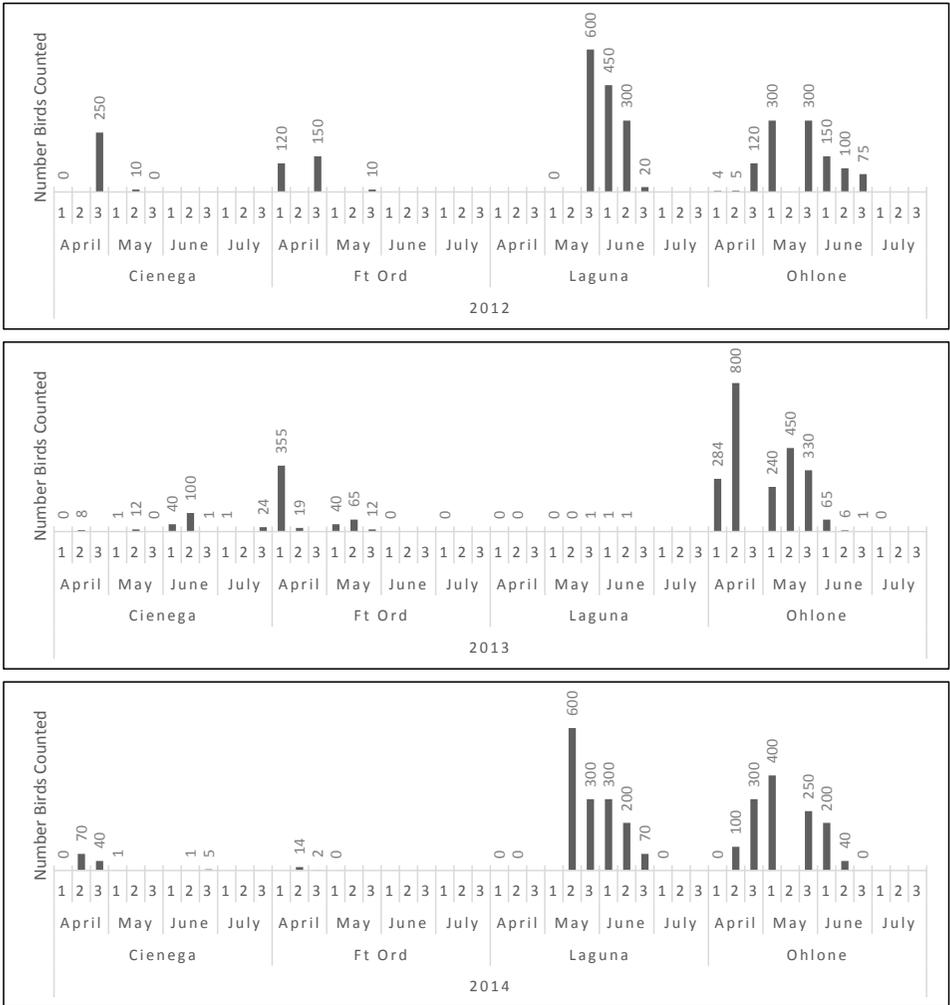


FIGURE 2.—Maximum number of tricolored blackbirds counted during 10-day intervals at four breeding colony locations, 2012 - 2014. A count of zero indicates the site was surveyed, but no birds were observed.

more) of tagged birds away from colonies was 22 June, and the last 10-day interval of June was when most colonies were completely abandoned. Thus, we considered movements of tagged birds occurring on or before June 19 to represent the breeding season and movements on or after 20 June to represent the post-breeding season.

Twelve birds (25% of total tagged) moved among colony sites during the breeding season (Table 2). These birds moved from Ohlone Pond to Cienega Pond (3 km), or to Laguna Seca Pond (11 km). Three of the 12 returned to Ohlone Pond during the same breeding season. Proportionally more males (32%) than females (19%) made inter-colonial movements.

Post-breeding locations of 17 radio-tagged birds were recorded between 22 June and 30 July (Table 3). Seven birds (15% of total tagged) were only observed at or near the breeding colonies. Six of these birds were observed within the Santa

TABLE 1.—Nest-building dates at four tricolored blackbird colonies.

Tricolor Study Colonies				
Year	Cienega Pond	Ft Ord Nettle Patch	Laguna Seca Pond	Ohlone Pond
2012	9 April	9 April	31 May	2 May
	24 April	24 April	2 June	10 May
	30 April		18 June	14 May
	7 May			17 May
				18 May
2013	5 April			10 April
	10 April			19 April
				13 May
				15 May
2014			12 May	18 April

Lucia Preserve, within 3 km of the Ohlone Pond capture site, and were located at Ohlone Pond, Cienega Pond, in and around the grazed pastures of nearby equestrian facilities, and in surrounding annual grasslands. Another bird remained at the Laguna Seca Pond where it was previously observed during that year's breeding season.

Ten (21% of total) radio-tagged birds dispersed from breeding sites and were found at three locations to the north and northeast (Figure 1, Table 3). Six of these birds were observed near the Monterey Regional Waste Management District (MRWMD) wastewater treatment plant (36°42'8.63"N, 121°46'5.96"W), in grazed pasture and grasslands, 26 km North of Ohlone Pond. Two birds were located at the Moonglow Dairy adjacent to Moro Cojo Slough (36°47'51.91"N, 121°45'49.59"W), near the town of Moss Landing, in grazed pasture, 37 km north of Ohlone Pond (including one bird previously observed at the MRWMD site during the same year). Two other birds were located outside the town of Spence, CA (36°37'53.64"N, 121°30'33.06"W) along the base of the eastern foothills of the Salinas Valley, among agricultural fields and grazed pasture, 31 km northeast of Ohlone Pond.

Additional life-history observations.—On four occasions during late-April to early-May of 2012, one occasion in late-July 2013, and three occasions mid-April to early-May 2014, we observed tricolor flocks of 12 to 100 birds foraging in coast live oak (*Quercus agrifolia*) and valley oak (*Quercus lobata*) trees within the Santa Lucia Preserve. Several of these flocks were mixed with red-winged blackbirds (*Agelaius phoeniceus*) and European starlings (*Sturnus vulgaris*). Additionally, during mid-April of 2012, about 20 tricolors were observed foraging in the crowns of coast live oak trees near the Fort Ord Nettle Patch (Don Roberson, Monterey Audubon Society, personal communication.). We believe this arboreal foraging behavior observed in 2012 represent birds feeding on California oakworm caterpillars (*Phryganidia californica*), a species known to fluctuate widely (Furniss and Carolin 1977) and which was relatively abundant that year (C. R. Wilson and R. J. Meese, personal observation.)

On one occasion in late-April 2012, about 30 tricolors were observed returning to Cienega Pond from the direction of an extensive woodland and forested area, many carrying nesting material consisting of lace or beard lichen (*Ramalina* or *Usnea* spp.). We believe this is the first reported use of lichens as nest materials by this species.

Finally, during early-May 2012, we observed a group of three juvenile long-tailed weasels (*Mustela frenata*) hunting on the ground within the Fort Ord Nettle Patch, while nesting tricolors were present. Although predation was not observed and the weasels were not observed climbing vegetation in the vicinity of nests, it appeared they were likely searching on the ground for nestlings or fledglings that had fallen from nests.

TABLE 2.—Locations of radio-tagged tricolored blackbirds that moved among breeding colonies during the breeding season. Individual birds are labeled M (male) or F (female) followed by capture sequence number. CP = Cienega Pond, LS = Laguna Seca Pond, OP = Ohlone Pond. No tagged birds were observed at the Fort Ord Nettle Patch.

Individual Birds												
	2012					2013				2014		
Date	F01	F02	F03	M01	M05	F08	M10	M11	M13	F17	M14	M22
3 May	OP	OP	OP	OP	OP	-	-	-	-	-	-	-
4 May	OP	OP	OP	OP	OP	-	-	-	-	-	-	-
6 May	OP	OP	OP	OP	OP	-	-	-	-	-	-	-
7 May	OP	OP	OP	OP	OP	OP	OP	OP	OP	-	-	-
8 May	OP	OP	OP	OP	-	-	-	-	-	OP	OP	-
9 May	-	-	-	-	-	-	-	-	-	OP	OP	-
10 May	OP	OP	OP	OP	OP	OP	OP	OP	OP	-	-	-
12 May	-	-	-	-	-	-	-	-	-	OP	LS	-
13 May	-	-	-	-	-	OP	OP	CP	OP	-	-	-
14 May	OP	OP	OP	OP	-	-	-	-	-	OP	LS	-
15 May	OP	OP	OP	OP	-	OP	OP	CP	OP	-	-	-
16 May	OP	OP	OP	-	-	-	-	-	-	-	-	-
17 May	OP	OP	-	OP	-	-	-	-	-	-	-	-
18 May	OP	OP	-	OP	-	OP	OP	-	OP	-	-	-
20 May	-	-	-	-	-	OP	OP	OP	OP	OP	-	-
21 May	OP	OP	-	-	-	-	-	-	-	OP	-	OP
22 May	OP	OP	LS	LS	-	OP	OP	-	OP	OP	LS	CP
23 May	LS	-	LS	LS	-	-	-	-	-	OP	-	-
24 May	LS	OP	LS	-	LS	OP	OP	-	OP	-	-	-
26 May	-	LS	-	LS	-	-	-	-	-	-	-	-
27 May	-	-	-	-	-	-	-	-	-	OP	-	-
28 May	-	-	-	-	-	OP	OP	-	OP	OP	-	-
29 May	-	OP	-	-	-	-	-	-	-	OP	-	-
30 May	-	LS	LS	-	LS	OP	LS	-	OP	-	-	-
31 May	-	LS	LS	-	LS	-	-	-	-	-	-	-
1 June	-	OP	-	-	-	-	-	-	-	OP	-	OP
2 June	-	OP	LS	-	LS	-	-	-	-	OP	-	-
3 June	-	-	-	-	-	-	-	-	-	OP	-	-
4 June	-	-	-	-	-	CP	-	-	-	-	-	-
6 June	-	-	LS	-	-	-	-	-	-	OP	-	-
7 June	-	-	-	-	-	CP	-	-	-	-	-	-
8 June	-	-	-	-	LS	-	-	-	-	-	-	-
9 June	-	-	-	-	-	-	-	-	-	LS	-	-
11 June	-	-	-	-	-	CP	-	-	-	-	-	-
12 June	-	-	-	-	-	-	-	-	-	-	LS	-
14 June	-	-	-	-	-	CP	-	-	-	-	-	-
17 June	-	-	-	-	-	-	-	-	-	CP	-	-
18 June	-	-	-	-	-	CP	-	-	CP	-	LS	-
19 June	-	-	-	-	-	-	-	-	-	-	LS	-

DISCUSSION

The four tricolor colonies studied here were adjacent to grasslands; however, the percent coverage of grasslands within a 5 km radius of each colony was lower than reported elsewhere. For example, in a recent study in the Sierra Nevada foothills, Airola et al. (2015) found tricolor colonies occurred in areas containing 55% grassland and 21% combined woodland-forest-shrub cover within a 5 km radius. Our coastal study site exhibited 21% grasslands and 68% combined woodland-forest-shrub cover within a 5 km radius. Lack of grassland

cover near breeding colonies may result in reduced availability of required insect prey and smaller colonies, since insects preferred by foraging birds are more often found in grasslands (Payne 1969). Tricolors in our study appeared to offset reduced grassland foraging opportunities by foraging for larval insects in woodland habitats, and such arboreal insect-gathering has not, to our knowledge, been reported before. Also, the abundance and use of woodland habitat in our study may explain the opportunistic gathering of lichen as a nest material.

In Monterey County, tricolor nesting at most colonies is known to begin around mid-April, with an occasional colony starting as early as late-March (Roberson and Tenney 1993). However, we observed colonies forming as late as late-May, and nest-building continuing as late as 18 June. Additionally, there was variability in how long individual colonies were occupied, ranging from <30 to 90 days. This variability in colony initiation and duration has important implications for surveys meant to determine site occupancy, specifically that site surveys extending throughout the breeding season (late-March to late-June) are necessary to accurately assess the presence or absence of breeding tricolors in a particular area.

Tricolor reproductive success is known to be strongly positively-associated with insect abundance in surrounding foraging habitats (Meese 2013). Low rainfall has been implicated in low insect abundance (Orians 1961) and loss of suitable nesting substrate due to pond drying (Roberson and Tenney 1993; Meese 2014). During 2013 and 2014, Monterey County and much of California experienced extreme drought and water levels at our breeding pond locations were markedly lower than in 2012. Consequently, the maximum numbers of tricolors observed in 10-day periods each year, and number of observed nest-building events, declined over the three-year study. These observations are not unexpected, given the state's drought and overall downward population trend of tricolors indicated by the Tricolored Blackbird Statewide Surveys from 2008 to 2014 (Meese 2014).

At least 25% of radio-tagged birds in our study engaged in inter-colony movements during the breeding season. Although we did not confirm if these radio-tagged birds actually nested, their movements among colonies suggests itinerant breeding (i.e., breeding more than once per year in different locations) as described by Hamilton (1998). Based largely on banding studies, tricolors are known to be itinerant breeders in the Central Valley, first breeding at locations in the San Joaquin Valley and then moving north to new breeding locations within the Sacramento Valley, low Sierra foothills, and northeastern California (Hamilton 1998). Nevertheless, our study appears to be the first to: 1) use radio-telemetry to study movements of tricolors, 2) document apparent itinerant breeding movements outside of the Central Valley, and 3) document such movements over relatively short distances of 3 to 11 km. The selective advantages of such movements are unknown and require additional study, but perhaps some birds were unable to acquire sufficient resources at one colony site for the entire breeding season, or were prospecting among colonies to assess availability of nesting and foraging resources or access to mates. Whatever the motivation for the movements, itinerant breeding may be more common than previously reported. The availability of multiple proximate nesting locations may allow the species to compensate for early-season nesting failures and variation in habitat and forage conditions over time (Beedy and Hamilton 1997).

Some previous workers have reported tricolors as synchronous breeders, with most eggs in a colony being laid within one week (e.g., Orians 1961). However, five of eight colonies in our study had nest-building intervals >1 week (9 to 35 days). Our study colonies were thus frequently asynchronous and breeding occurred over extended periods. However, our study colonies had relatively small numbers of birds compared to colonies studied by others (e.g., Orians 1961, Payne 1969), and small colonies may simply facilitate gathering

finer details on the nesting cycle. We did not observe predation of either eggs or nestlings, thus we believe that most of the observed nest-building asynchrony was due to the periodic arrival of additional breeding birds from other locations, as the telemetry results suggest.

Tricolors are present in Monterey County year-round, and during fall and winter they form nomadic mixed-species foraging flocks near dairies, horse and cattle feedlots, and open grasslands (Roberson 2002). Unfortunately, due to the limited battery life of the transmitters used in our study, we were able to follow tagged birds only briefly at the beginning of the post-breeding season. During this time, the birds exhibited a variety of post-breeding movements, with at least 13% remaining at the Santa Lucia Preserve and foraging in horse pens, pastures, and lawns associated with equestrian facilities, and with nighttime roosting in the nearby emergent-marsh ponds on the property. The remainder of post-breeding observations (23% of total tagged) were at northerly points within Monterey County, in rangelands, agricultural fields, or near dairies. Two tagged birds were found at the Moonglow Dairy, which is a well-known tricolor enclave during fall and winter months (Roberson and Tenney 1993; Roberson 2002). We suspect that some of the tagged birds eventually moved farther north and northeast to known wintering areas in the northern San Joaquin Valley and San Francisco Bay-Delta area (DeHaven et al. 1975), or coastal locations in Marin County (Meese et al 2014). Tricolors are also known to concentrate in rangelands along Highway 1 between Point Sur and Andrew Molera State Park during fall and winter months (Roberson 2002). The breeding colonies at the Santa Lucia Preserve are the closest known to this overwintering area, but none of our tagged birds were found along this section of Highway 1. Post-breeding movements and overwintering ecology of tricolors need further study before significant insights to aid in conservation of the species can be developed.

Our study shows that, at least in this part of the species' range, inter-colony synergism may also be integral to tricolor productivity. Therefore, management to maintain or enhance disparate nesting and foraging habitat is essential given the decline of tricolor populations and continued threats to the species (Meese and Beedy 2015). The breeding colony locations in our study area, including much of the surrounding existing and nascent foraging habitats, are currently managed by three different entities. Coordination and cooperation amongst these entities will be essential to slowing the rate of population decline of tricolors on the Central Coast.

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Year-class strength predicts commercial catch 11 years later for white seabass, *Atractoscion nobilis*, off southern California

EDWIN LEUNG AND LARRY G. ALLEN*

California State University Northridge, Department of Biology, 18111 Nordhoff St., Northridge, CA 91330-8303.

*Correspondent: larry.allen@csun.edu

Key Words: white seabass, *Atractoscion nobili*, Marine Resources Protection Act of 1994, year-class strength, abundance, survivorship, recruitment, commercial catch, otoliths

Fisheries in the past have undergone collapse due to over-exploitation of a target species beyond natural replenishment. White seabass (*Atractoscion nobilis*) has been a commercial fishery species in Southern California since the late 1800s and a popular recreational species since the mid-20th century (Hervas et al. 2010). A decline in their numbers was seen in the early 1900s and by 1982 caused the commercial white seabass fishery to move operations offshore and abide by management regulations. The change in white seabass recreational catch was dramatic and attributed to overfishing, declining from a peak of 64,000 individuals in 1949 to 284 in 1978 (Vojkovich and Reed 1983, Vojkovich & Crooke 2001).

Over the last two decades, the population of white seabass along the coast of California appears to be rising. The Marine Resource Protection Act in 1994 imposed restrictions by limiting fishing depth along the California coast and Channel Islands in addition to the state wide ban in the use of gill and trammel nets, resulting in a significant increase in white seabass numbers between 1995-2004 (Pondella and Allen 2008). White seabass commercial take was low in 1997 with 26 t and in 1998 greatly increased to 70 t (California Cooperative Fisheries Investigations [CalCOFI] 1999). Recent reports indicate that the combined commercial and recreational catch during 2008 was 342 t (CalCOFI 2009), and increased slightly to 364 t in 2010 (CalCOFI 2011).

Year-class strength is an index that uses measures of abundance, survivorship, or recruitment rates to summarize the success of a species for a given year (Landsman et al. 2011, Neuheimer and Gronkjaer 2012). Population structure can experience distinctive phases year to year, shifting in relation to increases or decreases in sea surface temperature (Tolonen et al. 2003, Lappalainen et al. 2009). Larval and juvenile stages are arguably more susceptible to variations in the environment (Tolonen et al. 2003, Raventos 2009). By organizing individuals into cohorts, it has been revealed that specific age groups benefit the most from variation in environmental conditions, contributing the most to the overall fitness of the population through increased growth and survival (Martinson et al. 2012). For species that are heavily exploited, life history information is sometimes sparse, but it is essential to the development of effective management plans and aiding stock assessments (Campana and Thorrold 2001, Fairclough et al. 2011).

The objective of this paper is to report a significant relationship between the year-class strength and commercial catch in white seabass over the last two decades. Valero and Waterhouse (2016) recently concluded that the fishing effort for white seabass has remained constant over the observed time period of catches used in this study.

We aged individuals using otoliths to determine year-class strength, thus providing insight into the population structure. Otoliths used were collected as part of an independent assessment of the abundance of juvenile white seabass off Southern California (Allen et al. 2007). Sagittal otoliths that were in good condition and intact were used for aging. One hundred otoliths were randomly sampled from each collection year, starting from 1997 to 2008 ($n=1200$). Length, width, and depth of each otolith were measured using Mitutoyo digital calipers (± 0.01 mm) with weight recorded using an Ohaus Voyager Pro analytical balance (± 0.001 g). Otoliths were mounted on wooden blocks using commercially available cyanoacrylate adhesive in preparation for cross-section. A Buehler Isomet low-speed saw equipped with two 0.3 mm diamond-edge blades was used to create 0.5 mm thick cross-sections. Each section was mounted onto glass slides using Crystalbond 509 mounting adhesive and polished for clarity by alternating between 400 and 600 fine grit sandpaper.

Cross-sections were digitally photographed using an Olympus SZX7 zoom stereo microscope with a QImaging QICAM digital camera attachment. Aging of otoliths (to the year) was based on two blind reads, i.e. having no prior knowledge of the fish itself, to prevent biased estimates of age. If the initial and second read did not agree, a third read was made to reach an agreement on age. Final age was taken as an average if an agreement was not met after three reads. Reasonable assumption of annual bands will follow an understanding of age validation reported in Williams et al. (2007) and Romo-Curiel et al. (2014).

Aged individuals were organized into cohorts to represent the age structure of the population based on birth years, which were determined by subtracting how old each individual was when caught from the year it was caught. Due to sampling method, which was size and age selective, only juvenile fish that were five years of age and younger were used in the analysis.

Using a traditional catch-curve regression (Ricker 1975), we conservatively estimated annual mortality and survivorship for white seabass. Counts for each cohort were then adjusted for annual mortality using a modified equation for mortality and survivorship from Allen et al. (1995): where N_0 = number of fish in a year-class at $t=0$, N_t = estimated number of recruits at t years in the past, corrected for mortality, and S = annual estimated survivorship (complement of mortality).

Year-class strength (annual recruitment index) was estimated by taking the average number of individuals across age groups within each represented birth year. Only fish born after 1996 and before 2007 were used in the analysis, as this time period had the highest resolution due to large numbers of fish in the samples that were born in those years. Time-lag comparisons were made to assess if there was a relationship between year-class strength and commercial catch of white seabass. All statistical analysis was conducted using SYSTAT 13.1.

Fifteen individuals from the original 1200 were excluded from the analysis due to damaged otoliths. Sagittal otoliths from the remaining 1185 individuals revealed a population structure of fish primarily ages 1 to 5, with the oldest individual aged at 11 years (Figure 1). During the 1997–2008 sampling period, the peak number of fish spawned occurred in 1997, 2000, and 2004 (Table 1). Annual mortality (M , 0.6), survivorship (S , 0.4), and instantaneous annual mortality ($-Z$, 0.991) for white seabass was estimated conservatively by catch-curve regression.

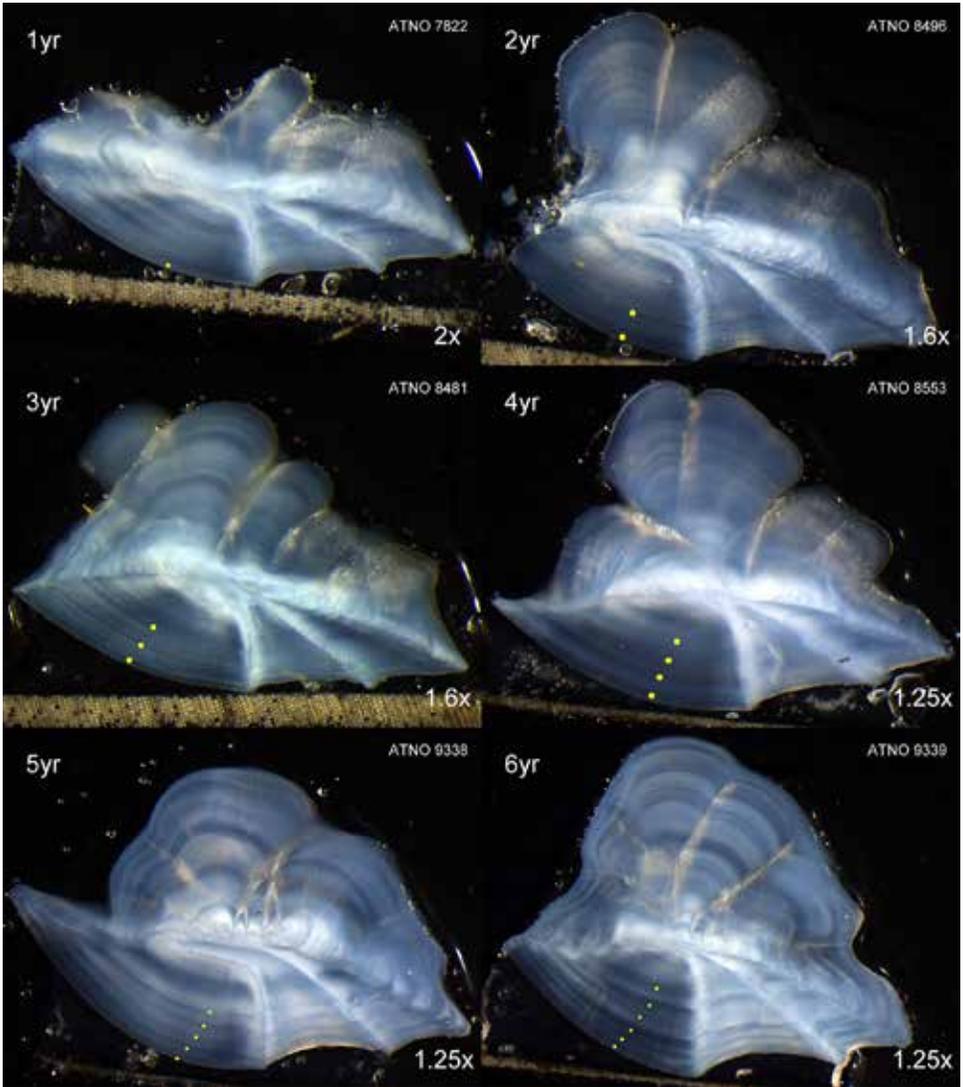


FIGURE 1.—Cross-sectioned sagittal otoliths of juvenile white seabass (*Atractoscion nobilis*) representing ages 1-6 years. White dots denote annual rings.

TABLE 1.—Cohort structure of white seabass (*Atractoscion nobilis*) for the 1996-2007 sampling period based on n = 1149 individuals representing ages 1-5 years.

Age	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
1	88	80	39	51	52	30	10	50	46	16	47	24
2	10	42	29	16	55	46	35	32	69	38	42	
3	11	16	16	10	34	12	17	13	12	15		
4	4	11	2	7	1	3	2		3			
5	3	1	3	2	1		1	2				
Total	116	150	89	86	143	91	65	97	130	69	89	24

Year-class strength estimates in 1996 and 1997 had the highest values, partly coinciding with the strong 1997-1998 El Niño (Figure 2). However, year-class strength overall was not significantly correlated with mean yearly summer sea-surface temperature ($r^2=0.065$, $p=0.42$), multivariate ENSO index ($r^2=0.004$, $p=0.85$), Pacific Decadal Oscillation ($r^2=0.048$, $p=0.49$), nor North Pacific Gyre Oscillation ($r^2=0.025$, $p=0.62$).

On-the-other-hand, commercial catch of white seabass was positively correlated with year-class strength in the presence of a time lag (Figure 3). Specifically, cross correlation

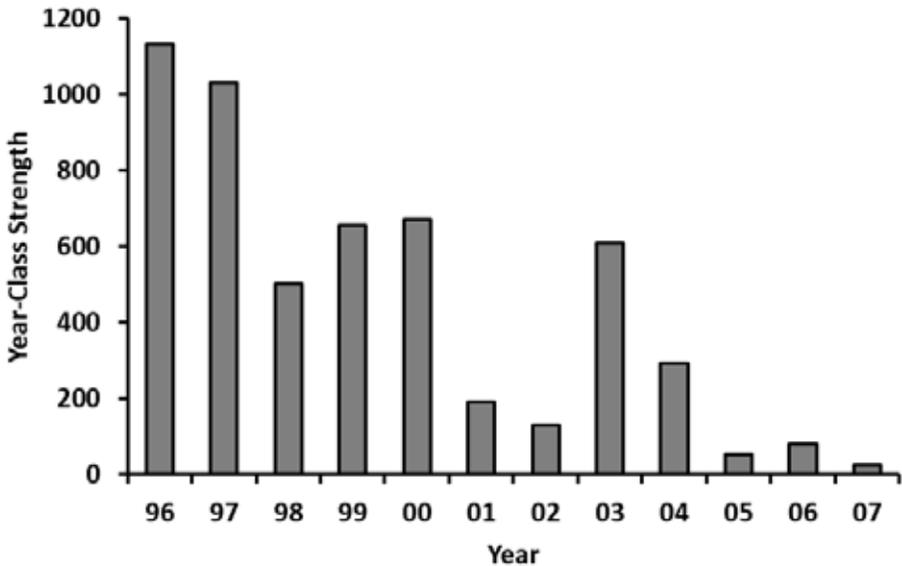


FIGURE 2.—Estimated year-class strength (corrected for mortality) of *Atractoscion nobilis*, 1996-2007.

analysis revealed a significant time lag of 11 years in the time series (Figure 4). This 11-year time lag resulted in a significant relationship between 2008-2015 commercial landings and 1996-2007 year-class strength ($n=9$, $r^2=0.48$, $p=0.038$, Figure 5).

White seabass have undergone an increase in Catch Per Unit Effort (CPUE) and juvenile abundance that could be attributed to the strong 1997 El Niño event in Southern California (Allen et al. 2007, Williams et al. 2007). Our results also suggested that the year-class strength for white seabass was the greatest in 1996 and 1997. There remains concern that the increase in white seabass abundance may not persist as the positive influence from the 1997-1998 El Niño year classes may begin to diminish. The strong year-class strength of white seabass from the 1997 El Niño has been reflected in the gradual increase in commercial landings, where the commercial catch of white seabass is made up primarily of individuals at least 10 years of age. The 2011-2012 annual review of the white seabass management plan reports that half of the fish sampled commercially were likely older than 12.5 years and likely older than 9 years from the recreational fishery (Department of Fish and Wildlife 2013).

The linear model predicting the relationship between commercial catch and year class strength was found to be $y=137.4x+107072$ (Figure 5). This model can be used to predict present and future commercial catches of white seabass for years in which year class strength (x) has been estimated (1996-2007). This model currently predicts that catch

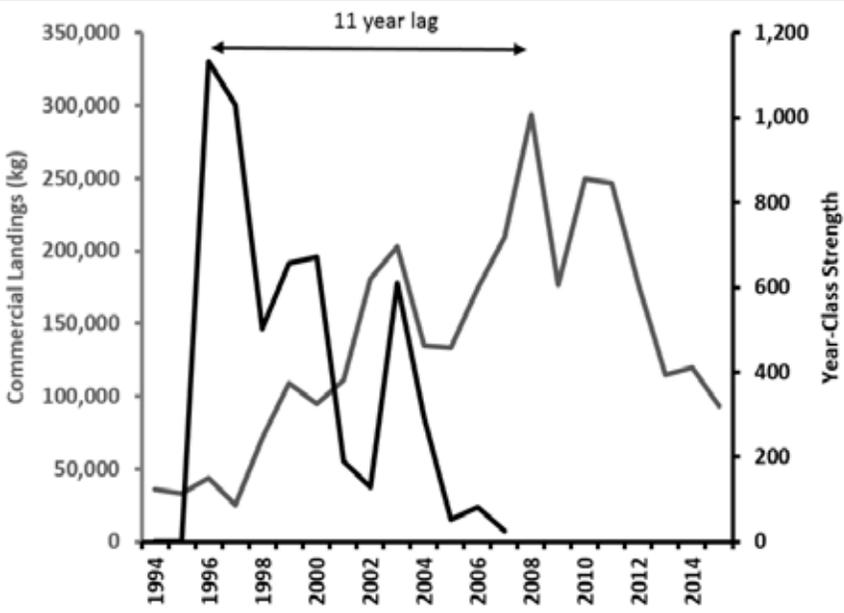


FIGURE 3.—Comparison between 1994–2015 commercial landings (gray) and 1996–2007 year-class strength (black) for white seabass, with a time lag of 11 years indicated by the arrowed line.

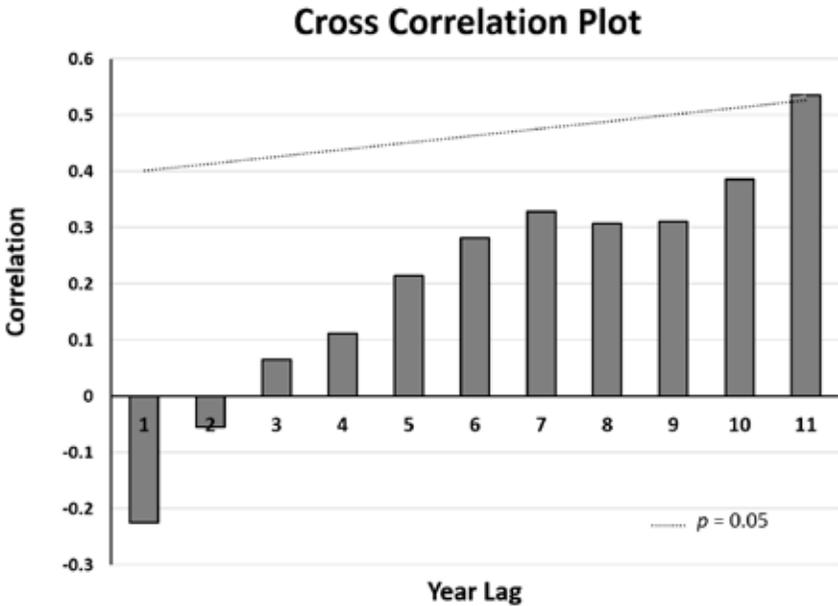


FIGURE 4.—Plot of Cross Correlation analysis between commercial landings and year-class strength for white seabass with time lag of up to 11 years. Dotted line represents the $p=0.05$ significance-level.

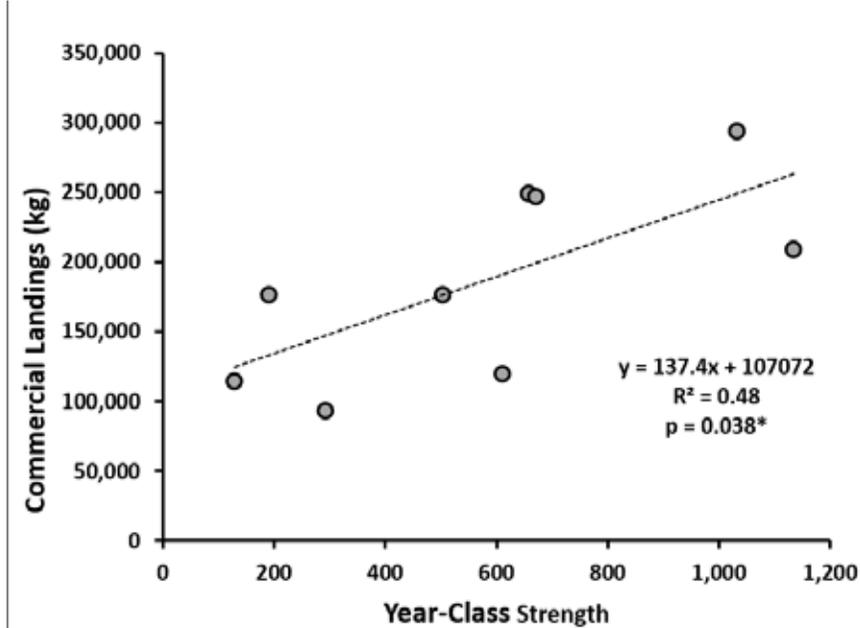


FIGURE 5.—Relationship between 2008-2015 commercial landings (y) and 1996-2007 year-class strength (x) for white seabass with time lag of 11 years ($n=9$, $r^2=0.48$, $p=0.038$). Trend line is dotted and represents the proposed linear model of $y=137.4x+107072$.

in 2016, once reported, should be about 114,200 kg, 118,300 kg in 2017, and 110,400 kg in 2018 (all estimates are ± 759 SD) based on the year class strength data presented here.

In summary, the present study determined the population structure of white seabass over an 11-year period (1997-2008) and revealed that year-class strength was the greatest in 1996 and 1997. Year-class strength was strongest during the 1997 El Niño, though was not significantly correlated with sea surface temperature or any climate index. Commercial landings for the species have shown a steady increase following the strong 1997 El Niño event, resulting in a significant relationship between year-class strength and commercial landings with an eleven-year time lag. We conclude that year-class strength estimation is an informative tool in assessing population structure of this managed species over time and may be used as a general predictor of catch over a decade later (11-years). Thus the information provided in our study can inform the white seabass fishery, update management approaches, and help ensure the persistence of white seabass into the future.

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Length-weight and length-length relationships, and condition factor of the pelican barracuda *Sphyraena idiestes* Heller and Snodgrass, 1903 (Perciformes: Sphyraenidae) in the Gulf of California, Mexico

F.O. LÓPEZ-FUERTE, U. JAKES-COTA*, A.F. GONZALEZ-ACOSTA AND S. FLORES-RAMÍREZ

Universidad Autónoma de Baja California Sur. Departamento Académico de Economía, Laboratorio de Sistemas Arrecifales, La Paz, Baja California Sur, México. (FOLF)

Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas. Departamento de Pesquerías y Biología Marina. Avenida Instituto Politécnico Nacional s/n, Colonia Playa Palo de Santa Rita, C.P. 23096, La Paz, Baja California Sur, México. (UJC, AFGA)

Universidad Autónoma de Baja California Sur. Laboratorio de Ecología Molecular y Genética Aplicada a Conservación, La Paz, Baja California Sur, México. (SFR)

*Correspondent: ujakesc@gmail.com

Key words: length-weight relationship, length-length relationship, condition factor, pelican barracuda, *Sphyraena idiestes*, Gulf of California

The pelican barracuda (*Sphyraena idiestes*) is a fish species commonly found in the southeastern Pacific and occasionally in the Gulf of California (González-Acosta et al. 2013). Recently, information on maximum and minimum lengths and weights, growth and trophic ecology, have been reported for the first time for pelican barracuda from the northern Mexican Pacific, including 15 (10 immature) specimens from four localities in the Gulf of California (González-Acosta et al. 2015). New records from the western coast of the Gulf of California show the pelican barracuda is captured locally throughout the year, with abundant peaks during the autumn-winter seasons (October-February; F. O. Lopez-Fuerte, personal observation). Thus, the aim of this study is to provide updated information on the length-weight (LWR) and length-length (LLR) relationships and condition factor for this species in the Gulf of California.

From December 2015 to April 2016, monthly field trips were conducted to catch pelican barracuda specimens in coastal waters near Santa Rosalia, Baja California Sur, Mexico (27°19'45.14" N, 112°15'13.40" W). Fish were captured using a fishing line and trolls deployed along the coastline, or from a 27-ft fishing boat. All fish caught (n=140: 76 males, 64 females) were identified as *S. idiestes* following Béarez's (2008) identification keys. The standard length (SL) and total length (TL) of each specimen were measured to the nearest millimeter using a fish measuring board. The weight of each specimen was recorded to the nearest 0.1 g. Sex was determined through macroscopic observation of the gonads.

All data collected were subjected to statistical analysis by calculating the length-weight relationship (Le Cren 1951), which can be expressed as: $W = aTL^b$, where W = weight (g) and TL = total length (cm). In this case, the relationship between TL and W was calculated for males and females separately by transforming W and TL data to logarithmic values and fitting them to the linear equation: $\log W = \log a + b \log TL$, using the least squares method with a as the interception between the regression line and the y-axis, and b the slope of the regression line. Extreme data values were identified and eliminated from the analysis by graphing log-transformed length and weight data (Froese et al. 2011). A student's t -test (Zar 2010) was conducted to assess whether the LWR b -values differed from those indicative of isometric growth ($b = 3.0$).

The TL - SL relationship was determined by simple linear regression ($TL = a + b SL$). In addition, the relative condition factor was calculated as: $Kn = W We^{-1}$, where W = weight (g) and We = the weight predicted by the LWR (Le Cren 1951). To test whether Kn values differed between months, a one-way analysis of variance (ANOVA) was performed. All statistical analyses were conducted using the R program (R Core Team 2016).

Sample size (n), TL and W value ranges, and LWRs' (a and b) parameters for *S. idiaestes* are presented in Table 1. Male pelican barracudas (40.5-54 cm TL and 35-46.5 cm SL) comprised 54.2% of the total sample. The male group showed a significant positive power function between TL and W ($r^2=0.90$), and between TL and SL ($TL=3.19 + 1.08 SL$; $r^2=0.93$). Female pelican barracudas (40.5-60 cm TL and 35.5-53 cm SL) comprised 45.8% of the overall sample and displayed a robust positive power function between TL and W ($r^2=0.91$) and between TL and SL ($TL=1.91 + 1.11 SL$; $r^2=0.96$). The overall sample showed a significant positive power function between TL and W ($r^2=0.91$). Regression analyses describing the relation of TL and W derived a b value distinct from 3.0 for males ($b=2.57$; t -test, $P<0.05$), which indicates an allometric growth pattern; whereas for females the b value did not differ from 3.0 ($b=3.04$, t -test, $P>0.05$), suggesting isometric growth.

TABLE 1.—Length-weight (LWR) and length-length (LLR) relationships for *Sphyraena idiaestes* caught in waters off Santa Rosalia, Baja California Sur, Mexico between December 2015 and April 2016.

Sex	n	TL range (cm)	W range (g)	a	95% IC of a	b	95% IC of b	r ²
Males	76	40.5-54	262-592	0.0206	0.0100 0.0429	2.57	2.37 2.75	0.90
Females	64	40.5-60	259-959	0.0032	0.0014 0.0074	3.04	2.83 3.25	0.91
Pooled	140	40.5-60	259-959	0.0057	0.0034 0.0950	2.90	2.76 3.03	0.91

n, number of specimens; TL , total length; W , weight; a , intercept; b , regression slope; r^2 , coefficient of determination; IC, confidence intervals.

The male pelican barracudas' relative condition factor did not change from month-to-month ($F_{(4, 71)}=1.54, p>0.05$), but fluctuated close to 1 throughout the study period (Figure 1). In contrast, the relative condition factor of females varied significantly in different months ($F_{(4, 59)}=11.27, p<0.05$), reaching values close to 1 from December 2015 to February 2016 that decreased in March (0.84) before attaining their highest values in April (1.04) (Figure 1).

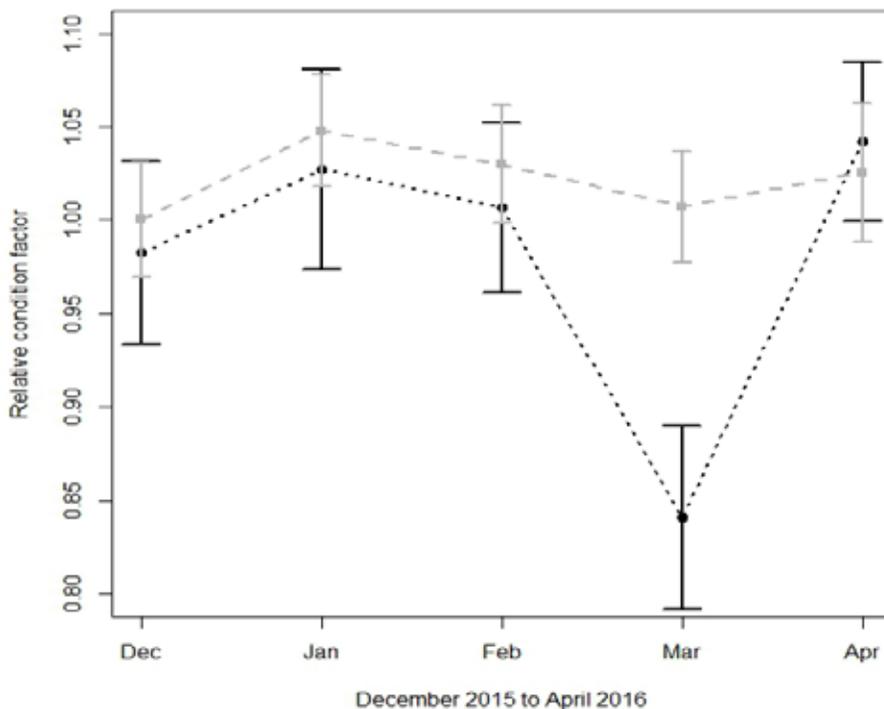


FIGURE 1.—Monthly variation of the relative condition factor (K_n) of *Sphyræna idiaestes* caught in waters off Santa Rosalia, Baja California Sur, Mexico between December 2015 and April 2016. The vertical lines indicate 95% confidence intervals of K_n . The circles and dotted black line correspond to females, while the squares and hatched grey line correspond to males.

The LWR b values obtained for male and female pelican barracudas are within the range of 2.5-3.49 reported for other barracuda species (González-Acosta et al., 2015), including *S. idiaestes*. However, the b value for the male pelican barracudas reported here was significantly different from 3, indicating allometric growth. This condition suggests that individuals become thinner as they grow in length (Anderson and Neumann 1996). Comparatively-speaking, the b value determined for females was not significantly different from 3, which suggests an isometric growth and indicates that their body shape does not change during development (Ricker 1975, Froese 2006). The differences observed in the b -value (3.19) reported previously for the pelican barracuda by González-Acosta et al. (2015) and those reported here for males (2.57), females (3.04) and pooled data (2.9) (Table 1), may result from the combined effect of the use of SL vs. TL (in the present study), as well as sample size ($n=15$ vs. $n=140$), interval lengths, sex ratio and sampling location.

Also, the differences in the overall mean Fulton's condition factor of 0.574, previously reported for this species (González-Acosta et al. 2015) could be the result of the sample size and the seasonal abundance pattern of the pelican barracuda. *Kn*-mean values reported here (0.989 for males and 0.984 for females), indicate suitable environmental conditions for *S. idiaestes* in this area in relation to sexual maturity as well as the good fitness of the specimens examined. Froese (2006) pointed out that in adult fish the condition factor shows consistent temporal changes: decreasing during periods of food shortage and increasing towards the spawning season, before plummeting during the females' spawning season and rising again immediately after it. Therefore, in the Gulf of California, the spawning of female *S. idiaestes* could occur in March, when the species displays the lowest *Kn*-value (Figure 1) with significant weight loss (Le Cren 1951). The macroscopic examination of the gonads in our specimens allowed us to confirm such condition, since their size increased from mid-February to early March. Therefore, the highest *Kn*-values for the females recorded in April 2016 could correspond to an immediate period of recuperation once spawning has taken place.

This study provides updated information on the LWR and LLR parameters and the relative condition factor previously reported for *S. idiaestes*, supported by a larger sample size than those previously used. However, further studies are needed to obtain length and weight data from specimens distributed along the species size range.

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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 (Moyle et al. 1992; Sommer et al. 2007). 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, evidence of reproductively mature female, 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

The 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 Federal 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 longfin 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 the 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

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

spawn earlier in the spawning season, because they reached adult size and can direct energy 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 ovary (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 the 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 were 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 mea-



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 personal communication with R. Mager (California Department of Water Resources, 2000).

Stage	Macro-characteristics	Phase
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

sured and then staged using a modified staging protocol. All individuals had their abdomen gently squeezed to check for release of gametes like normal. 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 laboratory in Stockton, California. 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 8 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



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.

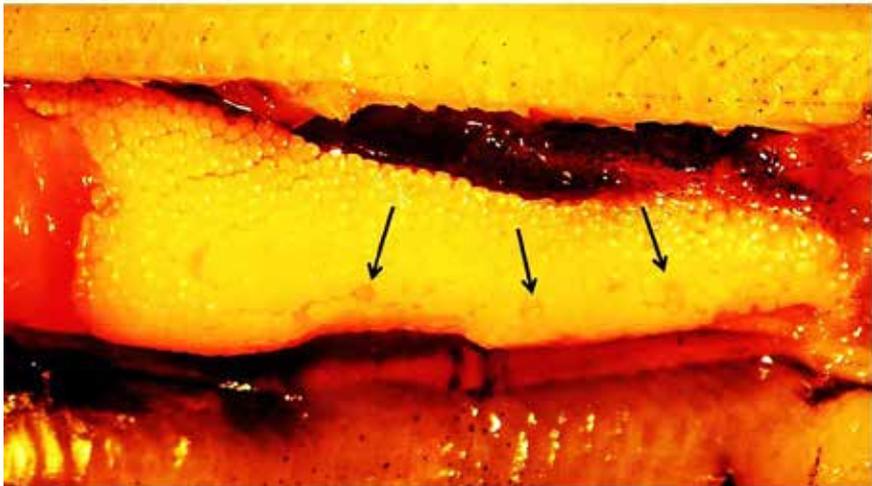


FIGURE 3.—Photo of the left ovary during dissection of a delta smelt used for the California Department of Fish and Wildlife’s delta smelt fecundity study. Arrows point to post-vitellogenic eggs that were left over from a previous spawning event.

1985; Hunter and Macewicz 2003; Nichol and Acuna 2001). These females were categorized 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 Macewicz 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 and 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).

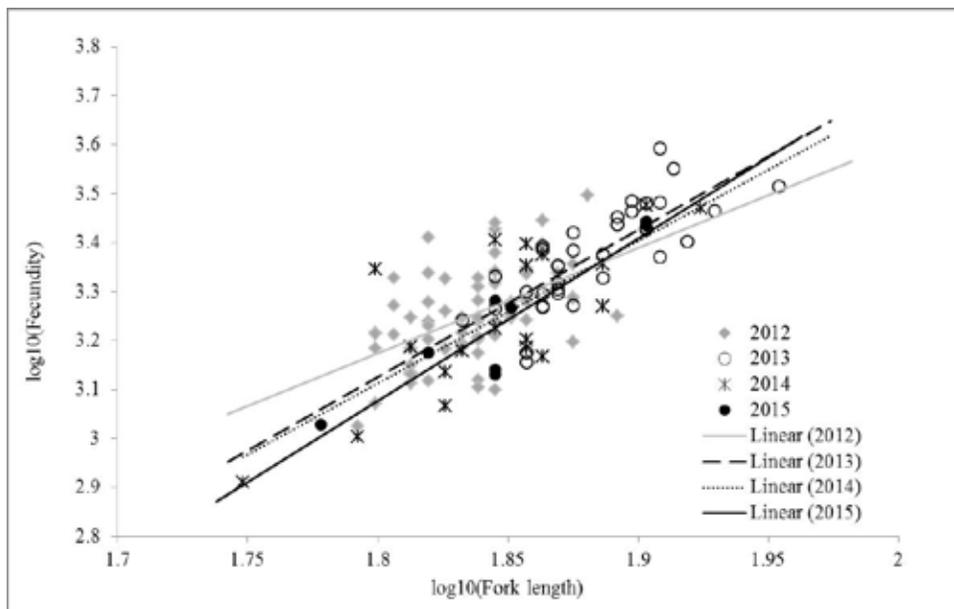


FIGURE 4.—Log₁₀ fecundity at fork length data of delta smelt collected in the upper San Francisco Estuary during January-May for years 2012-2015.

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 ($n=36$, $\text{mean}=2$, $\text{SD}=8$) 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.

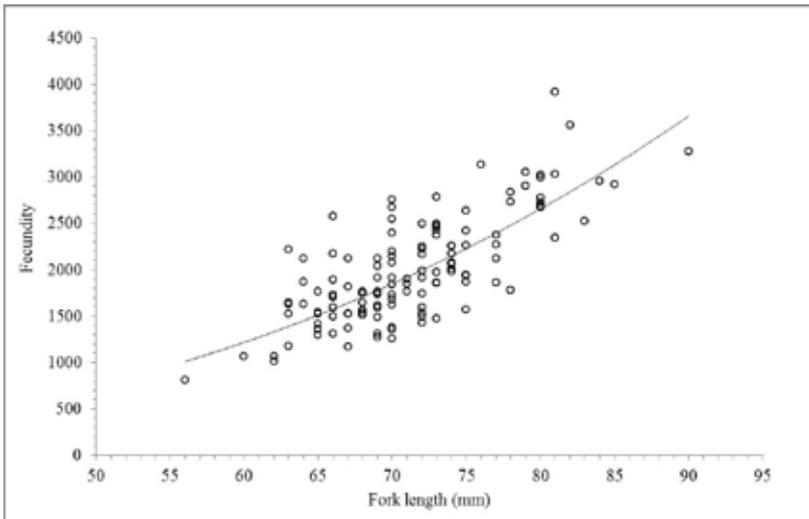


FIGURE 5.—Fecundity at fork length data of delta smelt collected in the upper San Francisco Estuary during January-May for years 2012-2015. The trend line represents the length-fecundity relationship $F = 0.0183FL^{2.7123}$ ($R^2 = 0.569$, $n=129$) of the pooled data.

TABLE 3.—Number (and range of fork lengths, mm) 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.

	First	Subsequent	Total
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.

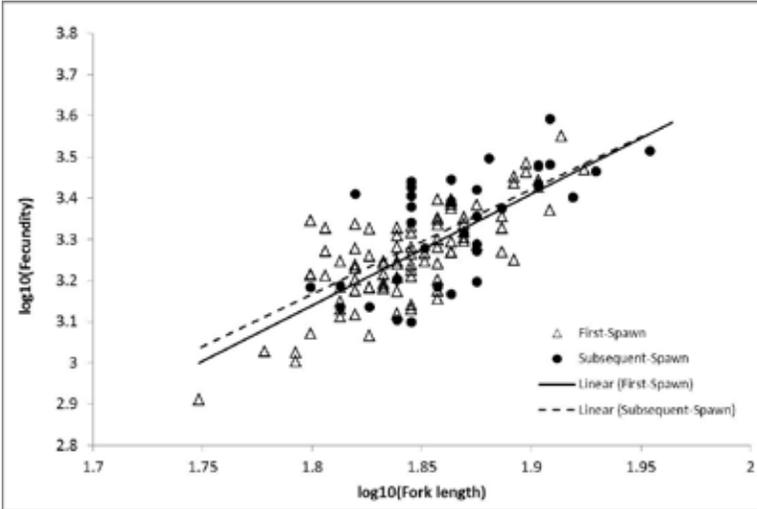


FIGURE 6.— \log_{10} fecundity at fork length (mm) data of first- or subsequent-spawn female delta smelt collected in the upper San Francisco Estuary during January-May for years 2012-2015.

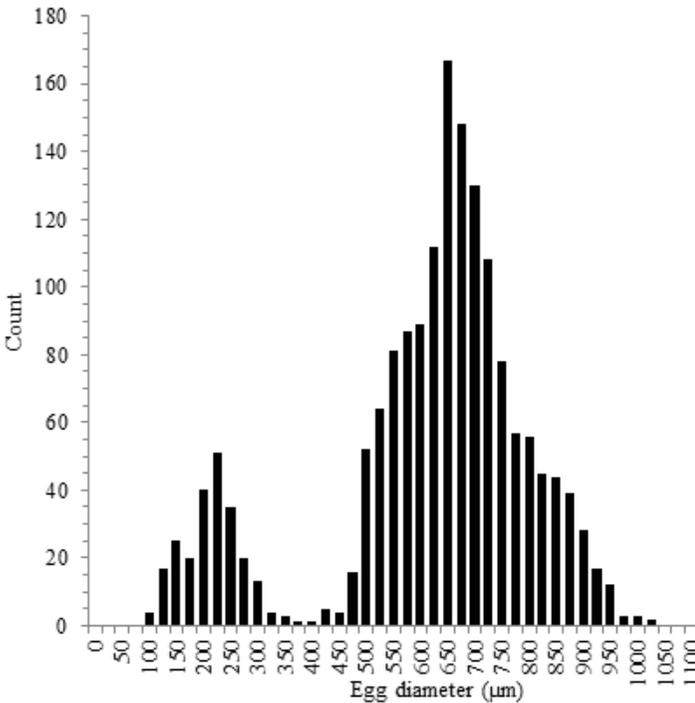


FIGURE 7.— Frequency distribution of egg diameters (μm) from ovaries of 8 near-ripe delta smelt collected in 2015. Roughly, 140-220 egg diameters per fish were measured from the same eggs included in the fecundity analysis.

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.

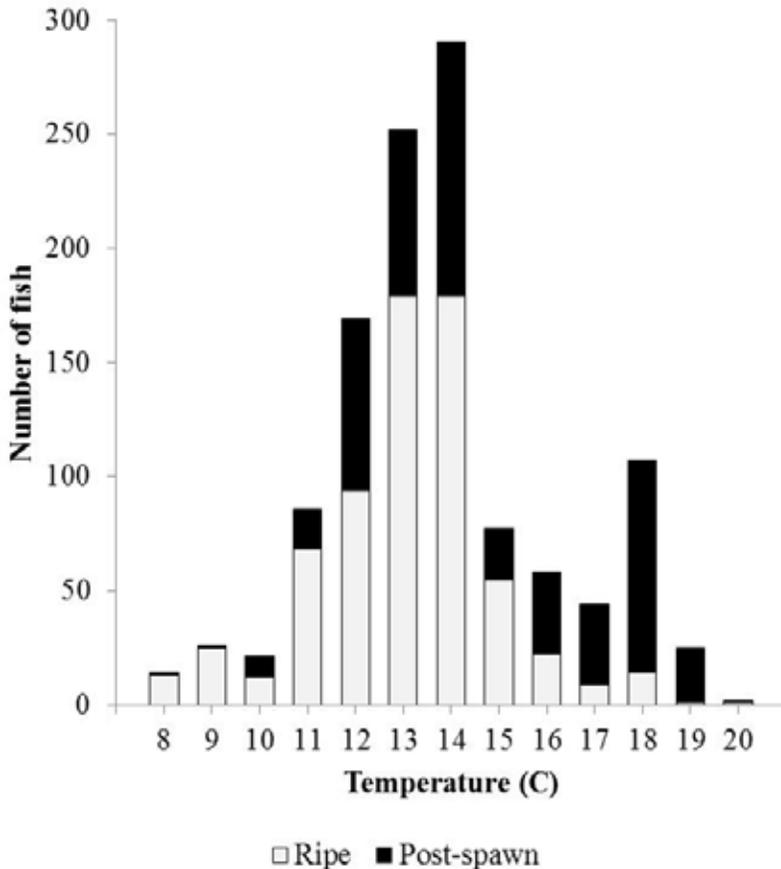


FIGURE 8.—The number of ripe (grey) or post-spawn (black) delta smelt caught in a specific temperature range during routine monthly sampling in the upper San Francisco Estuary during January-May for years 2002-2015.

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

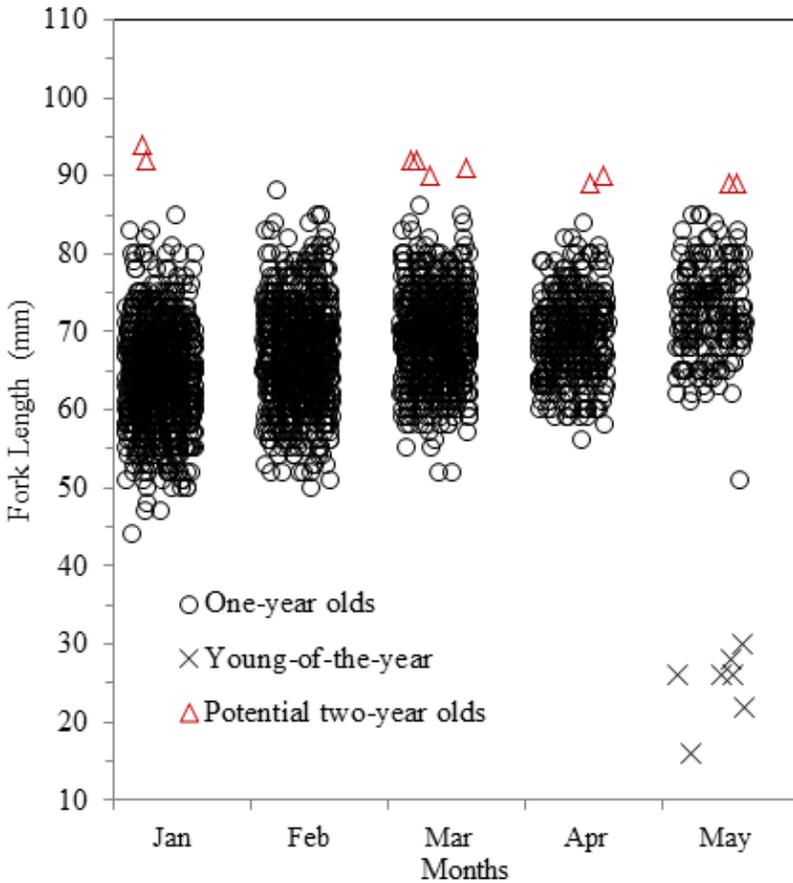


FIGURE 9. — Fork length (mm) by month of capture for all delta smelt caught during January-May for years 2003-2015. Red triangles indicate potential two-year old fish, black circles indicate one-year old fish, and black crossmarks indicate young-of-the-year.

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-

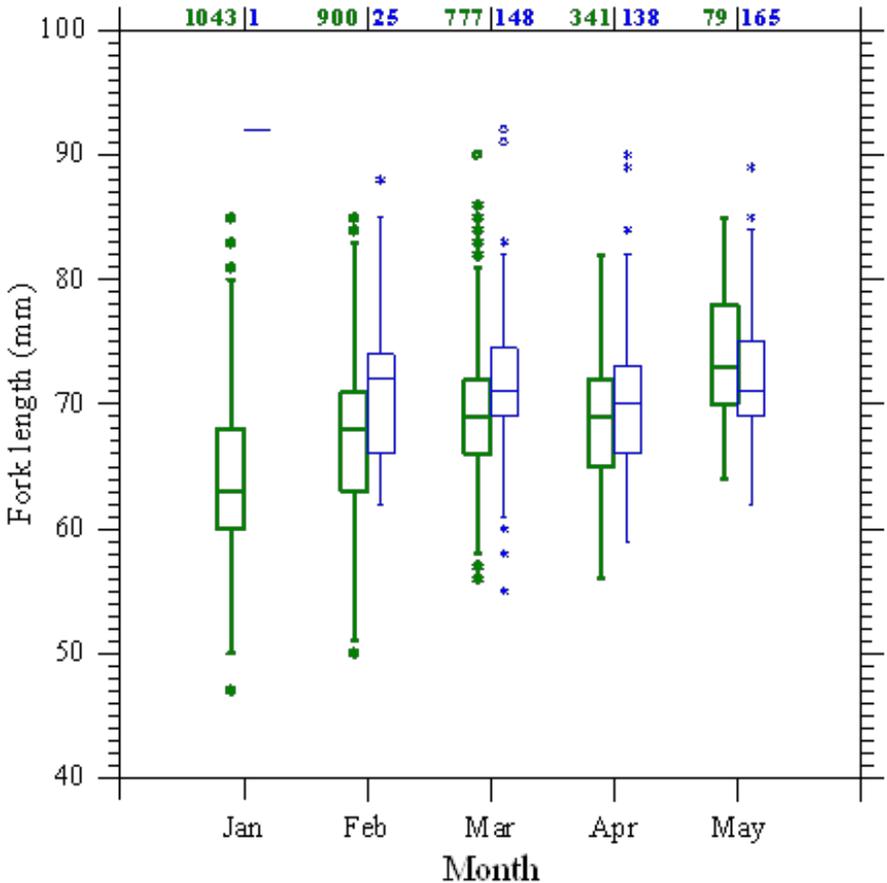


FIGURE 10.—Fork lengths (mm) by month for pre-spawn (green on left) and post-spawn (blue on right) female delta smelt caught during routine monthly sampling during January-May for years 2003-2015. Values above box plots are number of individuals. Note, the number of January post-spawners was n=1 at 92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

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From the Archives

George C. Pardee served as Governor of California from 1903 - 1907. According to the California State Library, "His exposure to innovative environmental conservation efforts in Germany heavily influenced his political decisions; as Governor, he was a strong supporter of conservation measures." Pardee wrote the following essay in 1914, which appeared in Volume I, Issue I of *California Fish and Game*.

Fish and Game Conservation Dependent on Conservation of Other Natural Resources

BY EX-GOVERNOR GEORGE C. PARDEE

Everybody who has given the subject much thought admits that fish and game ought to be conserved, not preserved, for the public benefit. Practically every state in the union has some sort of fish and game laws, some sort of a fish and game commission.

We commonly speak of such laws and such commissions as "fish and game preservation" laws and commissions. That, however, is a misnomer. For of what good to the public would preserved fish and game be?

Like all other natural resources, our fish and game should be conserved, that is, used, at such times and in such quantities and under such conditions as the public needs require, but without unnecessary waste or destruction.

Preserved game and fish, like preserved forests or preserved water-powers, are of no practical public good. Preserved fish and game die; so do preserved trees; preserved water-powers run to waste. Conserved—that is, used and protected—fish and game, forests, waterboot-powers and all other natural resources are, of course, of practical benefit to the public. And, therefore, fish and game conservation—not preservation—commissions are of practical benefit to the public.

We do not permit anybody to destroy the publicly-owned forests. There is an unenforceable California law against the "cold-storaging" of water-powers. It is the duty of the Fish and Game Commission to see to it that our animated natural resources are not destroyed or wasted.

Our game, however, can not be conserved, or even preserved, if the cover in which and the food on which it lives be not conserved. Our fish can not be conserved, or even preserved, if the waters in which they live be not kept at least free from pollution. If our wild places be permitted to be fire ravaged and destroyed, if our streams and bays be made the dumping grounds for noxious materials, then there will be no use for game and fish conservation laws, no need for a fish and game conservation commission—there will be no fish and game to be conserved.

Everybody, therefore, who believes—as almost everybody does—in the conservation of fish and game, must, if he takes a second thought, believe just as thoroughly in the



conservation—that is, the use without unnecessary waste or destruction or impairment of the necessary use of—our forests and our waters. The fish and game conservationist, therefore, must be a forest and water and waste places conservationist, whether they be publicly or privately owned. For it is just as much an injury to the public including the hunter and fisherman, amateur or professional, if our forests are destroyed, no matter whether they be publicly or privately owned. For upon the continued existence of our forests, whether publicly or privately owned, depends very largely the full running of our streams, without which our fish and game can not be fully conserved. And as forests may be forever used without being destroyed, it follows, of course, that the fish and game conservationists must deprecate the destruction of privately-owned forests and must oppose the further giving away of our publicly-owned forests into private ownership, which has always ended in their destruction.

Water is a natural resource, the most necessary of them all, which belongs to the people and can not be alienated from them. It is only the right to use water that can become private property. Upon the proper employment of this right to use, when it becomes private property, depends not only the fisherman's and hunter's vocation and sport, but also the prosperity and comfort, even the necessities, of all the people. The general public, therefore, as well as the fishermen and hunters, is interested in seeing to it that our water resources are conserved, that is, used, at such times, in such quantities, under such conditions as the public necessities require, without any unnecessary waste, without monopolies that will interfere with the public good.

How shall the public see to it that its water resources are conserved? Shall this important function be given over to the Fish and Game Commission, which is a commission with a highly specialized function, viz., that of conserving fish and game? Shall it be made the duty of the already over-burdened Railroad Commission to see to it that the right to use our waters is not improperly or wastefully acquired or exercised? Somebody, representing the public, must do it. To whom better than to a water commission, making a specialty of this highly important and very special matter, can the conservation of our waters be entrusted? In other words, the work of the Fish and Game Commission ought to be aided and supplemented by a water conservation commission, in addition to the already existing forestry conservation commission.

The work of a water commission is as highly specialized as is that of a fish and game commission, or a fire conservation commission, or a railroad commission. Recognizing that it is impracticable, if not impossible, to create one commission with special knowledge in all these diverse and very important matters, other states have created, as California has, a separate commission for each of them.

At the last session of our legislature, an act was passed creating a water commission, with power to see to it that the water resources of the state shall be conserved, that is, used at such times and in such quantities and under such conditions as the public necessities for power, irrigation, domestic purposes, etc., may require, but without unnecessary waste, and without monopoly detrimental to the public.

The passage of this law through the legislature was vigorously fought by an organized and expensive lobby, which was financed by an association of power and water companies. And no sooner was this water commission law passed by the legislature and signed by the governor than the same interests that opposed its passage organized and financed an expensive referendum campaign against it. For getting signatures to the referendum petition, which was circulated, among other places, in the redlight districts of San Francisco, Oakland and other cities, the hired petition circulators were paid 5 and 10 cents for each of the twenty-odd thousand signatures, forged and unforger, to the referendum petition.

As conservationists of the fish and game natural resources of this state, every fisherman and hunter, amateur and professional, is interested in the ratification by the people, at the November election, of this referendum water commission law. For every citizen who is interested in the conservation of our fish and game is, of course, interested equally in the conservation of our waters, on the saving of which the conservation of our fish and game largely depends.

Further than that, every fisherman and hunter, amateur and professional, is interested, along with all other law abiding citizens, in the honest carrying out of our laws. One of these laws, which it has become quite fashionable to violate, because it appears to be entirely safe to do so, is the referendum. For it is claimed that wholesale forgeries and perjuries were committed in the matter of the petitions by which the redlight abatements, the blue sky, the non-sale of game, and the water commission laws were suspended on referendum. In fact, regarding the first of these referendumed laws, the district attorney of San Francisco has been quoted in the daily press as asserting that not only were many, many forged names attached to the petition by which it was suspended by referendum, and that many perjuries were committed in the verification of those signatures, but also that there was in his possession sufficient evidence of these crimes against the people to send the forgers and perjurers to the penitentiary. But, up to date, so far as appears to be publicly known, but one of these law breakers has ever been indicted, and the penitentiary seems to have no terrors to his fellow conspirators against the people.

Every honest California hunter, every honest California fisherman, and every other honest Californian interested in the conservation of our animated natural resources is, of course, interested in seeing crime suppressed and criminals punished. As it appears to be impracticable, if not impossible, to get sent to the penitentiary either those who forge signatures to referendum petitions or those who instigate and pay for those forgeries and perjuries, there appears to be but one other way in which honest men and women can rebuke such crimes. And that is by voting to ratify laws the referenduming of which is tainted with crime. In this way only, it appears, can honest people do their part toward rendering such crimes against the public and themselves useless and unremunerative and, therefore, unfashionable.

For if neither the actual lawbreakers shall be punished nor the instigators and financiers of the crimes shall be rebuked, then, of course, the referenduming of laws by criminal means will become a fixed, organized, unremunerative, and recognized vocation. And instead of California being a government of the people, by the people, for the people, it will become a government of the people by perjury and forgery for those who are willing to employ organized bureaus of forgers and perjurers.

It is not so much a question as to whether the honest citizen agrees with the policy of the referendumed redlight abatement, blue sky, non sale of game, or water commission laws, as it is a question of whether the honest men and women of California are willing to be governed by forgery and perjury.

Everybody, therefore, who votes against a law that has been referendumed by forgery and perjury, votes to make remunerative and, therefore, fashionable organized bureaus for the government of California by forgery and perjury. And everybody who votes against a law referendumed by a crime-tainted petition, simply because he disagrees with the policy of that law, is debarred from making any objection or outcry if and when a law, with the policy of which he agrees, is referendumed by forgery and perjury.

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**REVIEWERS OF MANUSCRIPTS CONSIDERED FOR PUBLICATION IN
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- M. Adkison..... California Department of Fish and Wildlife
- L. G. Allen..... California State University, Northridge
- C. W. Barrows..... University of California, Riverside
- T. Beedy..... Beedy Biological Consulting
- R. Bellmer..... California Department of Fish and Wildlife
- M. Brett..... California Department of Fish and Wildlife
- L. Brown..... U. S. Geological Survey
- C. Burton..... California Department of Fish and Wildlife
- G. M. Cailliet..... Moss Landing Marine Laboratories Pacific Shark Research Center
- J. Claisse..... California State Polytechnic University, Pomona
- N. Clipperton..... California Department of Fish and Wildlife
- M. Cover..... California State University, Stanislaus
- J. Croteau..... California Department of Fish and Wildlife
- J. Davis..... California Department of Fish and Wildlife
- R. DeHaven..... U. S. Fish and Wildlife Service
- E. J. Dick..... National Oceanic and Atmospheric Administration
- H. Espinosa Perez..... Universidad Nacional Autónoma de México
- S. Estrella..... California Department of Fish and Wildlife
- M. Fish..... California Department of Fish and Wildlife
- K. Fleming..... California Department of Fish and Wildlife
- S. Gallager..... California Department of Fish and Wildlife
- E. Gleason..... U. S. Fish and Wildlife Service
- H. Green..... California Department of Water Resources
- R. Harrison..... University of New Mexico
- D. Herbst..... University of California, Santa Barbara
- J. Hobbs..... University of California, Davis
- M. Holyoak..... University of California, Davis
- J. Hull..... U. S. Fish and Wildlife Service
- D. Johnson..... Quinnipiac University
- P. Kalvass..... California Department of Fish and Wildlife
- T. Keeler-Wolf..... California Department of Fish and Wildlife
- L. Lefebvre..... National Oceanic and Atmospheric Administration
- K. Lesyna..... California Department of Fish and Wildlife
- S. Lonhart..... NOAA, Monterey Bay National Marine Sanctuary”
- P. McIntyre..... California Department of Fish and Wildlife
- R. Mooi..... California Academy of Sciences
- J. Moore..... California Department of Fish and Wildlife
- M. Mooring..... Point Loma Nazarene University
- P. Moyle..... University of California, Davis
- M. Okihiro..... California Department of Fish and Wildlife

- D. S. Palacios-Salgado ... Universidad Autónoma de Nayarit, México
L. Patterson California Department of Fish and Wildlife
C. Pomeroy California Sea Grant
J. Rachlow University of Idaho
K. Ramey California Department of Fish and Wildlife
J. Ray California Department of Fish and Wildlife
P. Reilly California Department of Fish and Wildlife
J. Rodriguez-Romero Centro de Investigaciones Biológicas del Noroeste, México
S. Skalos University of California, Davis
A. Tripp-Valdez Instituto Politécnico Nacional, México
J. Villepique California Department of Fish and Wildlife
A. Walde Turtle Survival Alliance
K. Wasson Elkhorn Slough National Estuarine Research Reserve
D. Wright California Department of Fish and Wildlife
L. Zweig U. S. Fish and Wildlife Service

INFORMATION FOR CONTRIBUTORS

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LITERATURE CITED

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ABOUT THE COVERS

Front—. The world's first radio tagged tricolored blackbird (*Agelaius tricolor*). The bird was tagged as part of a Central California Coast study, the results of which are published on page 162 of this issue.

Rear—. Formerly known as the California clapper rail, the endangered Ridgway's rail (*Rallus obsoletus obsoletus*) is listed among the Species of Greatest Conservation Need in the 2015 edition of the *California State Wildlife Action Plan*.



Photo by Joyce Gross.



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