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Ange Darnell Baker
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California Fish and Wildlife
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Notes from the Editor

Our first issue of 2020 is an exciting one—we are debuting our new title and redesigned cover! The issue is also exciting because of the number of articles included; for the past several years, the Journal has averaged about three articles per issue. However, due to some outreach efforts for the Journal last year, we have substantially increased our submissions, which means more articles in each issue—seven in this one—a trend that we hope to continue!

Our editorial team continues to grow as needed for the increased level of submissions to the Journal. Kristin Denryter is the Coordinator for the Elk and Pronghorn Antelope Program in CDFW's Wildlife Branch in Sacramento. Before joining CDFW, she earned a BS in Biology from Madonna University, an MS in Biology from Northern Michigan University, and a PhD at the University of Northern British Columbia. Kristin's research has focused on foraging, nutrition, and energetics of ungulates, including woodland caribou in Canada and Sierra Nevada bighorn sheep in the Eastern Sierra of California, but she also has collaborated on projects involving mule deer, elk, and moose. In addition to her regular work duties and research, Kristin currently serves as Chair of the Nutritional Ecology Working Group in The Wildlife Society. We are happy to have Kristin join our talented team of Associate Editors!

Other exciting news—the first three of the Journal's Special Issues will be coming out this year! We have explored the topics of the impacts of fire, cannabis, and human recreation on fish and wildlife resources. Look for those in spring and summer of this year. We will also be asking for submissions for additional special issues later this year—including one on CESA-listed species. If you would like to find out more about our Special Issues, please see our webpage: https://www.wildlife.ca.gov/Publications/Journal/Special-Issues.

Ange Darnell Baker, PhD
Editor-in-Chief
California Fish and Wildlife Journal

California Fish and Wildlife 106(1):7-10; 2020

Notes on reproduction of the Sierra Nevada yellow-legged frog from California

STEPHEN R. GOLDBERG*

Whittier College, Department of Biology, Whittier, CA 90608, USA

**Correspondening Author: sgoldberg@whittier.edu*

Key words: atresia, oocytes, *Rana sierrae*, Sierra Nevada yellow-legged frog, spawning, spermiogenesis

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Sierra Nevada yellow-legged frog (*Rana sierrae* Camp, 1917) is known from the northern and central Sierra Nevada of California (Vredenburg et al. 2007) where it frequents elevations of ca. 2,500-3,500 m (Dodd 2013). It is mainly diurnal and breeds between late May to July (Stebbins and McGinnis 2012). It is listed as threatened by the California Fish and Game Commission under the California Endangered Species Act (CNDDB 2019), endangered by the U.S. Fish and Wildlife Service (ECOS 2019) and imperiled by NatureServe Explorer (2019). The reproductive biology of a species is an important part of its natural history and such information is crucial in conservation plans (see Bury 2006). In this paper I add information on reproduction of *R. sierrae* from a histological examination of gonadal tissues. The use of museum collections for obtaining reproductive data avoids euthanizing specimens and obviates the need for a collecting permit by state and federal authorities.

A sample of 32 *R. sierrae* from California collected 1948 to 1972 (Appendix) consisting of 6 adult males (mean snout-vent length, SVL = 60.3 mm ± 3.3 SD, range = 54–63 mm), 22 adult females (mean SVL = 70.0 mm ± 7.1 SD, range = 60–86 mm), 1 unsexed subadult (SVL = 38 mm) and 3 subadult females (SVLs 46, 50, 58 mm) from the herpetology collection of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, USA was examined. I examined frogs from Madera and Mono counties (Clade 2) and Inyo and Mariposa counties (Clade 3) as designated by Vredenburg et al. (2007). I tested for differences between adult male and female SVLs using an unpaired t-test (Instat, vers. 3.0b, Graphpad Software, San Diego, CA, USA).

A small incision was made in the lower part of the abdomen, and the left testis was removed from males and a piece of the left ovary from females. I embedded gonads in paraffin, and sections were cut at 5 µm and stained with Harris hematoxylin followed by eosin counterstain (Presnell and Schreibman 1997). Histology slides were deposited at LACM.

The testicular morphology of *R. sierrae* is similar to that of previously studied anurans as detailed in Ogielska and Bartmanska (2009a). Within the seminiferous tubules, spermatogenesis occurs in cysts which are closed until the late spermatid stage is reached; cysts then open and differentiating sperm reach the lumina of the seminiferous tubules (Ogielska and Bartmanska 2009a). A ring of germinal cysts is located on the inner periphery of each

seminiferous tubule. All 6 *R. sierrae* males in my sample were undergoing spermiogenesis. By month these were: June (N = 1), July (N= 1), August (N = 4). The smallest mature male *R. sierrae* (spermiogenesis) measured 54 mm SVL and was from June (LACM 13565).

The mean SVL of *R. sierrae* females was significantly larger than that of males (t = 3.2, df = 26, P = 0.004). The ovaries of *R. sierrae* are typical of other anurans in being paired organs lying on the ventral sides of the kidneys. In adults the ovaries are filled with diplotene oocytes in various stages of development (Ogielska and Bartmanska 2009b). Mature oocytes are filled with yolk droplets; the surrounding layer of follicular cells is thinly stretched. Monthly stages in the ovarian cycle of *R. sierrae* are in Table 1. Two stages were present (1) "Ready to spawn" in which mature oocytes predominated; (2) "Not in spawning condition" in which previtellogenic oocytes predominated. There were nine females in the "not in spawning condition" in Table 1. Two of them, LACM 91271 (June) and LACM 67392 (July) contained early diplotene oocytes and partial yolk filled oocytes. The yolking oocytes in these two females were similar to Secondary Growth Stage 5 "progressive accumulation of yolk platelets" as reported by Uribe Aranzábal (2011). It is not known when or if these two females would have reached spawning condition. The smallest mature female (LACM 13568) measured 63 mm SVL, was from July, and contained mature yolk-filled oocytes. Three slightly smaller nonreproductive females, two of which measured 60 mm in SVL (LACM 13603, 13610) and a third LACM 67392, (SVL = 62 mm), the only one to contain partially yolking oocytes (see above), were arbitrarily considered as adults. Three yet smaller nonreproductive females (LACM 13613, 13614, 1741) SVLs = 46, 58, 50 mm, respectively, were considered to be subadults. One smaller unsexed *R. sierrae,* (LACM 13572, 38 SVL mm) was also considered as a subadult. I cannot speculate as to when any of these small *R. sierrae* would have attained adult size.

Atretic follicles were observed in 13 of 22 (59%) of my mature female sample. Atresia is a widespread process occurring in the ovaries of all vertebrates (Uribe Aranzábal 2009). It is common in the amphibian ovary (Saidapur 1978) and is the spontaneous digestion of a diplotene oocyte by its own hypertrophied and phagocytic granulosa cells which invade the follicle and eventually degenerate after accumulating dark pigment (Ogielska and Bartmanska 2009b). See Saidapur and Nadkarni (1973) and Ogielska et al. (2010) for a detailed description of stages of atresia in the frog ovary. Atresia plays an important role in fecundity by influencing numbers of ovulated oocytes (Uribe Aranzábal 2011).

In conclusion, my data on females indicates *R. sierrae* is in spawning condition during July and August. Whether *R. sierrae* females complete spawning in late summer or enter hibernation while containing mature oocytes warrants additional study.

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LITERATURE CITED

Bury, R. B. 2006. Natural history, field ecology, conservation biology and wildlife management: time to connect the dots. Herpetological Conservation and Biology 1:56–61.

CNDDB. 2019. California Natural Diversity Database. State and federally listed endangered and threatened animals of California, California Department of Fish and Wildlife. Available from: www.wildlife.ca.gov (Aug 2019).

Dodd, C. K., Jr. 2013. Frogs of the United States and Canada, Volume 2. The Johns Hopkins University Press, Baltimore, MD, USA.

Ecos. 2019. ECOS Environmental Conservation Online System, U.S. Fish & Wildlife Service. Available from: www.fws.gov/endangered (Aug 2019).

NatureServe Explorer. 2019. An Online Encyclopedia of Life. Available from: explorer.natureserve.org (Aug 2019).

Ogielska, M., and J. Bartmanska. 2009a. Spermatogenesis and male reproductive system in Amphibia—Anura. Pages 34–99 in M. Ogielska, editor. Reproduction of Amphibians. Science Publishers, Enfield, NH, USA.

Ogielska, M., and J. Bartmanska. 2009b. Oogenesis and female reproductive system in Amphibia—Anura. Pages 153–272 in M. Ogielska, editor. Reproduction of Amphibians. Science Publishers, Enfield, NH, USA.

Ogielska, M., B. Rozenblut, R. Augustnyska, and A. Kotusz. 2010. Degeneration of germ line cells in amphibian ovary. Acta Zoologica (Stockholm) 91:319–327.

Presnell, J. K., and M. P. Schreibman. 1997. Humason's Animal Tissue Techniques, Fifth edition. The Johns Hopkins University Press, Baltimore, MD, USA.

Saidapur, S. K., 1978. Follicular atresia in the ovaries of nonmammalian vertebrates. Pages 225–244 in G.H. Bourne, J. F. Danielli and K. W. Jeon, editors. International Review of Cytology, Vol. 54. Academic Press, New York, NY, USA.

Saidapur, S. K., and V. B. Nadkarni. 1973. Follicular atresia in the ovary of the frog *Rana cyanophlyctis* (Schneider). Acta Anatomica 86:559–564.

Stebbins, R. C., and S. M. McGinnis. 2012. Field Guide to Amphibians and Reptiles of California, Revised edition. University of California Press, Berkeley, USA.

Uribe Aranzábal, M. C. A. 2009. Oogenesis and female reproductive system of Amphibia—Urodela. Pages 273–304 in M. Ogielska, editor. Reproduction of Amphibians. Science Publishers, Enfield, NH, USA.

Uribe Aranzábal, M. C. A. 2011. Hormones and the female reproductive system of amphibians. Pages 55–81 in D. O. Norris and K. H. Lopez, editors. Hormones and Reproduction of Vertebrates Volume 2 Amphibians. Elsevier, Amsterdam, Netherlands.

Vredenburg, V. T., R. Bingham, R. Knapp, J. A. T. Morgan, C. Moritz, and D. Wake. 2007. Concordant molecular and phenotypic data delineate new taxonomy and conservation priorities for the endangered mountain yellow-legged frog. Journal of Zoology 271:361–374.

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APPENDIX

Thirty–two *R. sierrae* from California (by county) examined from the herpetology collection of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, USA.

Inyo: LACM 67391–67393; **Madera:** 1966–1973, 13568, 13572, 26707, 91271, 91272; **Mariposa:** LACM 13599–13606, 13609–13614; **Mono:** 1741, 13565.

Table 1. Two monthly stages in the spawning cycle of 22 adult female *R. sierrae* from California.

Month	N	Ready to spawn	Not in spawning condition
June	2	0	2
July	4	3	1
August	16	10	6

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Planning shoreline infrastructure projects at Redondo Beach, California to avoid impacting a Giant Sea Bass nursery site

MICHAEL C. COUFFER*

Grey Owl Biological Consulting, Orange County, California

Present address: 716 Marguerite Avenue, Corona del Mar, California 92625, USA

**Corresponding Author: mikecouffer@gmail.com*

Key Words: Beach rehabilitation, giant sea bass, nursery site, *Stereolepis gigas*

Adult Giant Sea Bass (*Stereolepis gigas*) (GSB) are the largest bony fish inhabiting California's near-shore habitats (Love 2011). They were historically recorded at over 250 kg (551 lbs) (Domeier 2001) and have been dated to live up to 76 years of age (Hawk and Allen 2014). House et al. (2016) measured a fish by laser rangefinder at 2.75 m (9 ft) total length and estimated its weight at 381 kg (839 lbs). They range from Humboldt Bay, California to Oaxaca, Mexico, including the Gulf of California (Kells et al. 2016). After a population crash in the early 1900s, they were listed by the International Union for the Conservation of Nature (IUCN) as a Critically-Endangered species (Musick et al. 2000; Cornish 2004), and were also prohibited from intentional take in California by fishermen.

While regulatory protection of adult GSB is important, protecting their young from take is also necessary in order to manage the species throughout its entire life cycle. Until recently, almost nothing was known about the habitat preferences and behavior of the young-of-the-year (YOY) of GSB so resource regulatory agencies had little information on which to base recommendations for avoidance or minimization of take during the planning and implementation of shoreline infrastructure construction or maintenance projects. This document provides information on the occupation of GSB nursery sites and makes recommendations for avoiding or minimizing GSB take during beach sand replenishment, harbor dredging, substantial pier or jetty maintenance, or other near-shore construction and maintenance projects planned within and near GSB nursery sites.

The YOY of GSB spend just under a month as floating eggs and planktonic larvae before settling (Benseman and Allen 2018). After planktonic settlement, YOY of GSB of total lengths between 10 and 80 mm (3/8 in to 3 ¼ in) have been found to occupy habitat between 2 and 38 m (7 to 125 ft) in depth (Couffer and Benseman 2015; Couffer 2017; Benseman and Allen 2018). YOY of GSB at this size range occupy wide expanses of open sand or sandy-mud habitat away from rocks, jetties, piers, debris, and other hard structures that often hold predators large enough to eat them at this vulnerable stage (Couffer and Benseman 2015; Couffer 2017; Benseman and Allen 2018; Benseman et al. *in press*).

Benseman and Allen (2018) found that newly-settled young were most abundant over soft-bottomed habitat at depths from 2 to 18 m (6 to 60 ft) within 300 m (984 ft) of the heads of submarine canyons that began close to shore, and that density fell precipitously at distances beyond 500 m (1,640 ft) from the heads of submarine canyons. Locations found to support the YOY of GSB included Redondo Beach at the southern end of Santa Monica Bay in Los Angeles County, the shallows surrounding Newport Pier and Big Corona del Mar State Beach in the City of Newport Beach in Orange County, and La Jolla Shores in San Diego County. To date, no focused surveys for the YOY of GSB have been conducted in Mexico. No significant submarine canyons that closely approach sandy shorelines exist along the Pacific coast of the Baja California peninsula until one rounds the tip of the peninsula. The topic of nursery sites within the Mexican portion of the species' range remains unexplored. Other locations within 2 km (1.2 mi) of California's submarine canyons were surveyed to sample soft-bottomed habitat at equivalent depths that were not significantly influenced by the presence of canyons. The author assisted with this field work and coordinated trained observer and photo-verified YOY of GSB detection reports from citizen scientist divers who dived year-round and opportunistically located the YOY of GSB between 2015 and December 2019. It was rare for the YOY of GSB to be found outside of the few YOY of GSB nursery sites mentioned above. An 760 m (831 yd) stretch of habitat off Redondo Beach in Los Angeles County inshore from the Redondo Submarine Canyon was found to support the highest seasonal density of the YOY of GSB of any location known (Benseman and Allen 2018). The Redondo Beach Giant Sea Bass Nursery Site is located south of King Harbor between the Redondo Pier and Topaz Jetty (Figure 1).

Following the completion of field work for Benseman and Allen's study, the author continued focused surveys within known and possible nursery sites during all appropriate seasons to date, amassing over 320 hours of focused YOY of GSB survey bottom time. The data collected at each YOY of GSB contact included color phase, overall length, bottom time to contact, initial behavior, depth, and temperature. Specific fish locations were determined by surfacing over each YOY of GSB for a few seconds and describing an object that was directly onshore. After the dive, a GPS was used to record coordinates at the waterline below that object, and the depth of the fish recorded during the dive was used to locate the fish directly offshore from these coordinates on a 1-foot contour chart (Figure 1). Figure 1 includes the color phase, depth, and specific location of all YOY of GSB that the author has detected within the Redondo Beach Nursery Site to date.

At least one YOY of GSB was detected within a nursery site during every month of the year except April and June. November produced the highest number of detections (n = 63), followed by September (n = 45) and December (n = 40). The collated dates of 210 YOY of GSB detections showed that GSB nursery sites were primarily occupied from August to the end of December.

The California Environmental Quality Act (CEQA) provides a regulatory framework for the identification and consideration of native species' nursery sites that might be negatively impacted by construction or maintenance projects requiring state permits. The Redondo Beach Nursery Site lies outside of all protected marine habitat and is subject to potential disturbance from periodic shoreline and infrastructure maintenance projects. King Harbor requires occasional dredging to keep channels open, and periodic activities are needed to maintain Redondo's pier, jetties and harbor channels. Man-made and natural sand transport barriers and coastal processes cause sand to erode from this stretch of coastline that is not

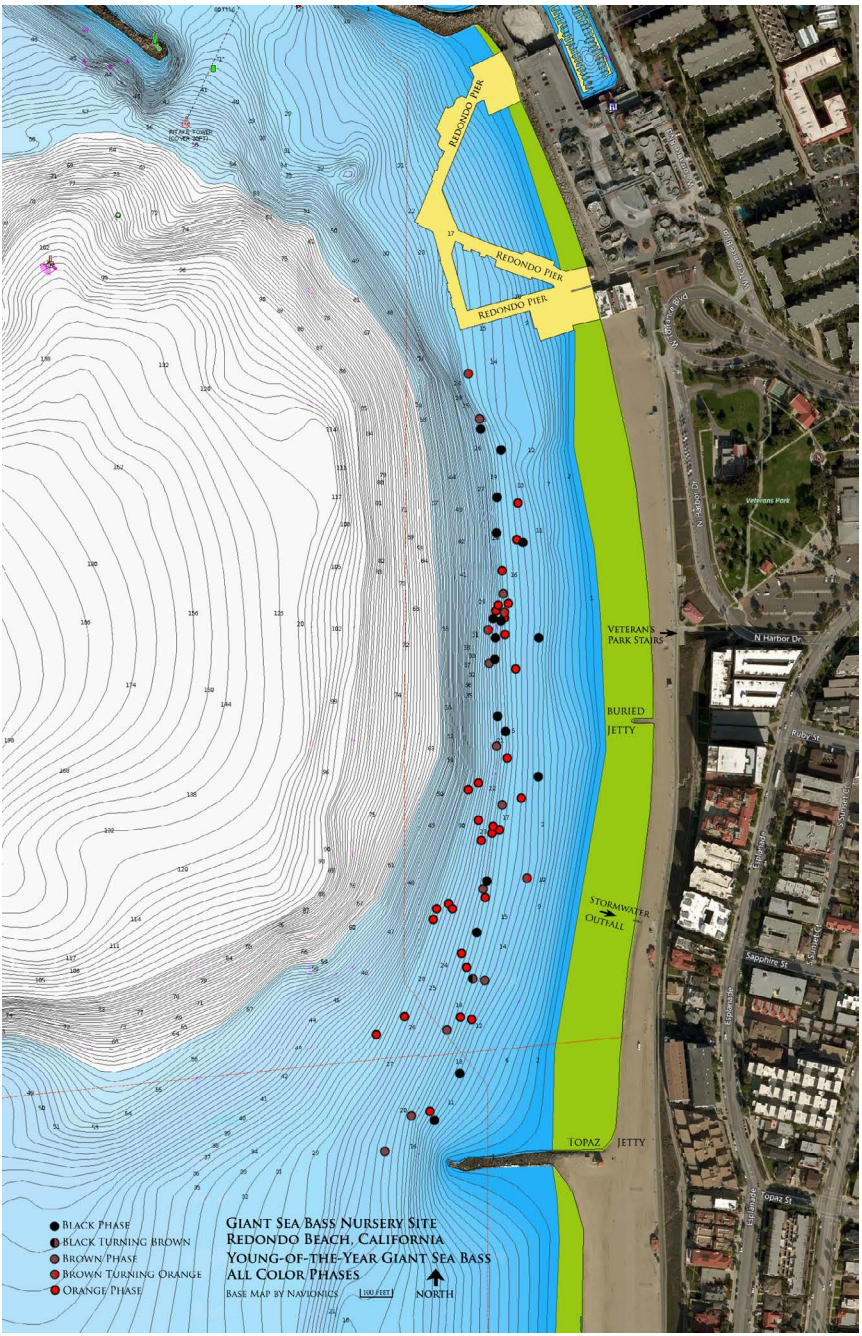

Figure 1. Young-of-the-year Giant Sea Bass detections within the Redondo Beach Nursery Site, CA, USA.

replaced by natural processes. This beach must be artificially augmented by adding sand from other sources using barges or dump trucks.

No other nursery site is subject to as many potential habitat disturbance activities as the Redondo Beach Nursery Site. The La Jolla Shores Nursery Site in San Diego County is encapsulated by the Matlahuayl State Marine Reserve where take of all living marine resources is prohibited. Big Corona del Mar State Beach in Orange County is located immediately inside the northwestern boundary of the Crystal Cove State Marine Conservation Area. The shallows surrounding Newport Pier in Orange County lie outside of all protected marine habitat, and this area is not covered by specific restrictions on fishing or shoreline infrastructure projects. Newport Pier pilings are periodically scraped free of settling organisms and pilings are occasionally replaced, but no significant shoreline infrastructure projects have been undertaken within or adjacent to these nursery sites for many years.

A year prior to Ms. Benseman's identification of GSB nursery sites, a roughly 40-day U.S. Army Corps of Engineers project barged approximately 146,304 m^3 (160,000 yd^3) of sand from Marina del Rey's harbor to Redondo Beach (G. A. Fuderer, U.S. Army Corps. of Engineers, personal communication). Beginning the week of 6 August 2012, approximately 68,580 m^3 (75,000 yd^3) of sand were pumped from the barge onto the beach shore between Topaz Jetty and Redondo Pier, which is now known to be a GSB nursery site (Figure 2). Pumping sand onto the beach is not considered to have been detrimental to recruiting GSBs within the nursery site, however, approximately 77,724 m^3 (85,000 yd^3) of sand were deposited in 9 to 15 m (30 to 50 ft) of water off Topaz Jetty where it was planned to be stored for future sand replenishment projects. Because the deposition of sand into the waters above

Figure 2. Beach sand replenishment between Topaz Jetty and Redondo Pier, CA, USA on 5 October 2012.

that nursery site coincided with YOY of GSB occupation, the timing of the replenishment project at this particular location could have had detrimental effects on recruiting GSB.

The planning and implementation phases of the 2012 Redondo Beach sand replenishment project were completed before Benseman began the first field study ever conducted of the YOY of GSB and identified the nursery sites, so the resource regulatory agencies would have been unaware of the importance of this stretch of beach for this Red-list Critically-Endangered species. It is possible that one or more of the following impacts may have resulted from depositing sediment onto the nursery site.

1) Sand dumped into 9 to 15 m (30 to 50 ft) of water on the nursery site could have displaced recently-settled YOY of GSB from their preferred habitat of algal fragments and small sand depressions where they hide from predators; unexpected displacement can expose their presence to predators. 2) Known prey species of the YOY of GSB such as mysid shrimps found within a meter of the bottom could have been buried or dispersed by falling sediment. If the horizontal and vertical distribution and/or density of mysid swarms was altered, the effectiveness of YOY of GSB feeding strategies upon them could have been reduced. 3) Project implementation fouled the sea floor with trash, and local divers organized several underwater cleanups to remove debris. The benefits of the underwater trash cleanup effort may have been offset by disturbance to the YOY of GSB occupying the nursery site by large numbers of divers working on the bottom from the surf line to recreational dive limits. 4) Large amounts of falling sediment could have fouled the gills of the YOY of GSB within the impact footprint. 5) Approximately 77,724 m^3 (85,000 yd^3) of sediment was "stored" in 9 to 15 m (30 to 50 ft) of water for future beach sand replenishment. However, large winter storm swells have altered the bottom topography to 30 m (100 ft) so any sand deposited at depths of 15 meters (30 ft) or less was probably redistributed by storms the following winter. Any attempted reacquisition of sand during the months when the nursery site supports the YOY of GSB could impact them.

The potential loss of the YOY of a Red-listed Critically Endangered fish species at the highest density nursery site for the species ever documented should be considered potentially significant. These potential impacts could have long-lasting impacts on the recruitment, population dynamics, and overall survival of GSB at this nursery site when it is most densely occupied.

After dispersal of the YOY of GSB from the nursery sites, strong winter storms can alter the topography of the nursery site bottom to a depth of at least 30 m (100 ft) before the next hatch of YOY of GSB arrives the following summer. Issues could arise if the habitat is altered when the YOY of GSB are present at the nursery sites. The Redondo Beach Nursery Site faces due west and is protected from the large south swells generated by summer storms by the Palos Verdes Peninsula which extends west to form the south-eastern rim of Santa Monica Bay. Therefore, the nursery site bottom is not significantly altered by swells for much of the period of YOY of GSB occupation.

Although the YOY of GSB have been found in California nursery sites during nearly every month of the year, these areas are very sparsely occupied for half of each year. It is recommended that beach sand replenishment and harbor dredging projects having the potential to affect nursery site bottom be implemented between 1 January and 15 July when the YOY of GSB nursery sites have been found to be the most sparsely occupied. Habitat disturbance should be avoided from 16 July through 31 December, when the majority of the YOY of GSB are arriving at and occupying the nursery sites.

Piping sand from a barge to the beach is not expected to impact the YOY of GSB; it is when a large volume of sand is deposited into the water above the nursery site that nursery site impacts could occur. Another method of sand augmentation used at Redondo Beach has been to deposit sand on the beach using dump trucks and spread the sand using rubber-tired equipment. During September of 2018, a survey for the YOY of GSB was conducted while equipment spread trucked-in sand across the beach during an incoming tide (Figure 3). Underwater survey transects to a minimum depth of 4 m (13 ft) found no visual difference in water quality between sections of the beach where sand piles were sloughing into the sea and beach sections where no sand had been deposited. No new articles of trash

Figure 3. Spreading dump truck-deposited sand at Redondo Beach with rubber-tired equipment.

were observed since the previous survey. Even during a month when the nursery site was occupied by the YOY of GSB this appears to have been a successful method for replenishing the beach with sand while having no discernible impacts on the YOY of GSB.Annual coastal cleanup events along Redondo Beach that include groups of divers have been organized for many years. Some of these events coincide with months of high density of YOY of GSB off Redondo Beach. The ability to coordinate underwater cleanups with dry beach cleanups along the entire coastline offers benefits to the habitat and to ecologically-aware members of coastal communities, and this probably outweighs the potential of disturbance to some YOY of GSB from a single day of habitat disturbance at nursery sites by groups of divers. Scuba instructors also bring classes to train and practice beach diving techniques off Redondo Beach but these classes are not believed to significantly impact the YOY of GSB. Classes typically move in groups which are closely monitored by instructors. The divers make surface swims and drop as a group, limit their movements to a relatively small area on the bottom while being watched by an instructor, and then return to shore as a group. Students do not scatter about to disturb large areas of bottom.

Both publicly and privately-funded projects require permits from federal, state, and

local governmental agencies, and often require assessments of species that are considered to have special status by resource regulatory agencies. Special status species surveys conducted for resource agencies typically follow guidelines written for the agencies by specialists who have significant experience surveying for the species. Assessments and surveys must then be conducted by qualified biologists who must follow the agency-adopted guidelines in order for their reports to be accepted by the permitting agencies. These surveys are often coupled with biological monitoring in order to assure avoidance or minimization of disturbance to special status species prior to and during construction. Effective biological monitoring of a species assumes a biologist's ability to locate individual animals within and surrounding an impact footprint in order to attempt to ascertain whether or not construction activities adversely affected those individuals. In the case of the YOY of GSB, not only would locating individuals on a daily or weekly basis be extremely difficult, but repeatedly relocating specific individuals requires close diver proximity to the fish and underwater photography of spot patterns which could increase the GSB's level of disturbance and possibly cause indirect take by a predator. Also, finding no YOY of GSB within the impact footprint would not be proof of take by the project. Rather than attempt to monitor the possible effects of construction on the YOY of GSB, a more effective approach would be to schedule construction activities that could affect the nursery site for the period between January 1 and July 15. Working during this period would either avoid impacts due to YOY of GSB absence, or if a few individuals remained it would minimize impacts by avoiding the densest seasonal presence of the YOY of GSB. Habitat disturbance within the nursery site should be avoided from July 16 to December 31 in an area extending from the shoreline to a depth of 38 m (125 ft) from the Redondo Pier to Topaz Jetty.

If it would be difficult to adjust dredging or sand deposition schedules to coincide with the season of low YOY of GSB sensitivity, changing the location of deposition of dredged material to an area that does not border a nursery site is suggested. Dredge spoils deposited into the water north of King Harbor or south of Topaz Jetty should avoid impacting the YOY of GSB.

Scheduling future Redondo Beach sand replenishment and major shoreline infrastructure projects to be implemented between January 1 and July 15 would be expected to avoid or greatly minimize impacts to the YOY of GSB at this nursery site. The large majority of the YOY of GSB are absent or at a very low density at nursery sites during this period.

It also appears that that clean sand placed on the beach by dump trucks or piped from barges and spread across the beach by rubber-tired equipment avoids or greatly minimizes impacts on GSB nursery sites at any time of year. However, no sand or sediment should be deposited into the water that could disturb the bottom at a GSB nursery site between July 16 and December 31.

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I might not have learned of the existence of GSB nursery sites were it not for the insights of Masters of Science student Stephanie A. Benseman working with her advisor Larry G. Allen of California State University at Northridge who discovered that GSB nursery sites existed and worked out how to find the often-cryptic YOY of GSB within them. Their preliminary work on the distribution and recruitment, and later, our observations of the behavior of young of Giant Sea Bass provided the basis to expand our understanding

of the early development of this species and move from reporting baseline information to this practical management tool that could enhance the recovery of the species. I would like to thank Mark A. Pavelka of the U. S. Fish and Wildlife Service (ret.), Amber S. Oneal-Heredia, Chris Lowe of California State University at Long Beach, Sharon Kramer of H. T. Harvey and Associates, and Richard Ware of Coastal Resources Management for providing valuable editorial suggestions on manuscript drafts.

LITERATURE CITED

Benseman, S. A., and L. G. Allen. 2018. Distribution and recruitment of young-of-the-year Giant Sea Bass, *Stereolepis gigas*, off southern California. Copeia 106:312–320.

Benseman, S. A., M. C. Couffer, and L. G. Allen. *in press*. Behavior of young-of-the-year of Giant Sea Bass, *Stereolepis gigas*, off the sandy beaches of Southern California. Bulletin of the Southern California Academy of Sciences.

Cornish, A. 2004. *Stereolepis gigas*. The IUCN Red List of threatened species. Version 2014. Available from: www.iucnredlist.org

Couffer, M. C., and S. A. Benseman. 2015. A young-of-the-year Giant Sea Bass *Stereolepis gigas* buries itself in sandy bottom: a possible predator avoidance mechanism. Bulletin of the Southern California Academy of Sciences 114(1):54–57.

Couffer, M. C. 2017. Individually-unique spot patterns of young-of-the-year Giant Sea Bass, *Stereolepis gigas* in captive-raised fish. Bulletin of the Southern California Academy of Sciences 116(2):98–109.

Domeier, M. L. 2001. Giant Sea Bass. Pages 209–211 in W. S. Leet, C. M. Dewees, R. Klingbeil, and E. Larson, editors. California's living marine resources: a status report. University of California, Oakland, CA, USA.

Hawk, H. A, and L. G. Allen. 2014. Age and growth of the Giant Sea Bass, *Stereolepis gigas*. California Cooperative Oceanic Fisheries Investigations Report 55:128–134.

House, P. H., Clark, L. F. B., and L. G. Allen. 2016. The return of the king of the kelp forest: Distribution, abundance, and Biomass of Giant Sea Bass (*Stereolepis gigas*) off Santa Catalina Island, California, 2014–2015. Bulletin of the Southern California Academy of Sciences 115(1):1–14.

Kells, V., Rocha, L. A, and L. G. Allen. 2016. A field guide to coastal fishes from Alaska to California. Johns Hopkins University Press, Baltimore, MD, USA.

Love, M. S. 2011. Certainly more than you want to know about the fishes of the Pacific coast: a postmodern experience. Really Big Press, Santa Barbara, CA, USA.

Musick, J. A., M. M. Harbin, S. A. Berkeley, G. J. Burgess, A. M. Eklund, L. Findley, R. G. Gilmore, J. T. Golden, D. S. Ha, G. R. Huntsman, J. C. McGovern, S. J. Parker, S. G. Poss, E. Sala, T. W. Schmidt, G. R. Sedberry, H. Weeks, and S. G. Wright. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (Exclusive of Pacific Salmonids). Fisheries 25:6–30.

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San Francisco Estuary mysid abundance in the fall, and the potential for competitive advantage of *Hyperacanthomysis longirostris* over *Neomysis mercedis*

MICHELLE AVILA AND ROSEMARY HARTMAN*

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

**Corresponding Author: Rosemary.Hartman@water.ca.gov*

Historically, the native mysid *Neomysis mercedis* was a key source of food for fish in the San Francisco Estuary (SFE). Following the introductions of the over-bite clam and many invasive zooplankton species in the mid-1980s, populations of native zooplankton species plummeted, including *N. mercedis*. In July 1993, *Hyperacanthomysis longirostris*, an invasive mysid, was first documented in the SFE, and it quickly became the most abundant mysid in the upper estuary. Since 2011, the California Department of Fish and Wildlife has sampled mysid abundance throughout the upper SFE concurrently with their Fall Midwater Trawl, which targets juvenile Striped Bass. We analyzed data from these mysid trawls to investigate environmental correlates of *N. mercedis* and *H. longirostris* abundance. We found that *H. longirostris* was found at higher temperatures significantly more often than *N. mercedis,* and there was a trend towards greater frequency of *H. longirostris* at higher salinities. Increases in water temperature over time, coupled with *H. longirostris's* smaller size at maturity and lower food needs may partially explain its success in the SFE.

Key Words: crustaceans, Delta Smelt, fish diets, invasive species, Longfin Smelt, Mysidacea, Sacramento, San Joaquin Delta, Striped Bass, temperature tolerance, zooplankton

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Mysid shrimp (or opossum shrimp), are small aquatic crustaceans that form a critical link in the San Francisco Estuary (SFE) foodweb. There are seven species of mysids found in the upper SFE (Mecum 2007). Historically, the native mysid *Neomysis mercedis* was the dominant mysid species and served as a key source of food for fish species in the area. *N. mercedis* dominated the diets of Splittail (*Pogonichthys macrolepidotus*) (Daniels and Moyle 1983), Longfin Smelt (*Spirinchus thaleichthys*) (Feyrer et al. 2003), and young Striped Bass (*Morone saxatilis*) (Bryant and Arnold 2007). They were also once an important food item for juvenile and adult Delta Smelt (Moyle et al. 1992), though their abundance in smelt gut

contents has declined in recent years (Slater and Baxter 2014). In fall months, when overall zooplankton abundance decreases, *N. mercedis* was particularly important and comprised a significant portion of Longfin Smelt and Striped Bass diets (Feyrer et al. 2003). Following the introductions of the over-bite clam, *Potamocorbula amurensis,* and many zooplankton species in the late 1980s to early 1990s, populations of native zooplankton species plummeted, including *N. mercedis* (Winder and Jassby 2011). Competition with invasive clams and zooplankton for food, and predation by introduced fish and predatory invertebrates, created a massive shift in zooplankton species composition throughout the SFE (Kayfetz and Kimmerer 2017; Winder and Jassby, 2011). In July 1993, *Hyperacanthomysis longirostris* (formerly *Acanthomysis bowmani*) (Fukuoka and Murano 2005), an invasive mysid considered semi-endemic to the Ariake Sea in Japan (Suzuki et al. 2009) was first documented in the SFE, most likely introduced through ballast water (Modlin and Orsi 1997). It quickly spread and is currently the most abundant mysid in the region (Bryant and Arnold 2007; Hennessy and Enderlein 2013).

Despite the importance of mysids to the diets of many fish species (Feyrer et al. 2003; Bryant and Arnold 2007), there are knowledge gaps concerning mysid abundance, geographic distribution, and life history in the SFE. Much of the region was not sampled for mysids until recently, and few studies have examined the causes of mysid declines (though see Winder and Jassby 2011), or the shift in dominance of the mysid community from native to nonnative species. Even basic information on environmental correlates for dominant mysid species remain unstudied (though see Kimmerer 2002 for a discussion of flow effects on *N. mercedis*). There is also little information published on the life history of *H. longirostris,* despite it being the most commonly observed mysid in the region.

The California Department of Fish and Wildlife's (CDFW) Zooplankton Study, part of the multi-agency Environmental Monitoring Program (EMP), began monthly mysid data collection in 1972, but the current sampling is limited (20 locations per month) and does not extend into habitats considered important for native fishes, such as upstream to the Cache Slough Complex, or the Sacramento River Deepwater Ship Channel (SDWSC) (Hennessy and Enderlein 2013). The Cache Slough Complex is currently the focus of large-scale restoration efforts, an attempt to improve habitat for many fish species (Department of Water Resources and Department of Fish and Wildlife 2015), so there is an interest in monitoring data on zooplankton availability.

EMP has documented peak abundances of mysids in spring and summer, with lower abundances in fall (Hennessy and Enderlein 2013), but due to the importance of food for juvenile fish in the fall for later survival (Brown et al. 2014), understanding drivers of mysid abundance during this time frame is key. The CDFW Fall Midwater Trawl survey (FMWT), added concurrent zooplankton sampling in 2008 to a subset of its long-term fish monitoring stations to address this lack of data. This paper seeks to describe the overall patterns of mysid abundance. We then answer several key questions regarding the most common taxa, *H. longirostris,* and the taxa that was historically most common, *N. mercedis*:

- What are the spatial and temporal patterns of mysid abundance in the upper SFE?
  - Was *H. longirostris* more abundant than other mysid species in the fall?
- Is *H. longirostris* out-competing the native mysid, *N. mercedis*?
  - How do water quality conditions correlate to abundance of *H. longirostris* and *N. mercedis* and are there differences between the two species?
  - How does size and fecundity differ between *H. longirostris* and *N. mercedis*?

METHODS

Sampling methods

The FMWT survey samples mysid shrimp monthly from September through December at 32 of the 122 fixed FMWT sampling stations (Figure 1). Stations were grouped into 8 geographic regions. Mysid shrimp are sampled using a 30 cm diameter, 505 µm mesh macro-zooplankton net attached to a metal frame. The net was 1.48 m long with a taper ending at the codend with a collecting jar. A flowmeter (model 2030R, General Oceanics, Miami, FL) was fitted in the mouth of the net to allow volume for the tow to be calculated. A 10-minute stepped oblique tow was conducted with the mysid net either immediately before or after the regular midwater trawl at each zooplankton sampling location. The sample was then preserved in a quart jar of 10% formaldehyde dyed with rose Bengal for later processing at the CDFW laboratory (Stockton, CA). Surface water temperature (in degrees C) and specific conductance (µS/cm) were measured using a handheld YSI meter (Yellow Springs Instruments Pro30; YSI Inc. Yellow Springs, OH). Values for specific conductance were converted to practical salinity units (psu) (Schemel 2001). Surface turbidity (in Nephelometric Turbidity Units, ntu) was measured using a portable turbidity meter (Hach 2100Q; Hach, Loveland, CO, USA).

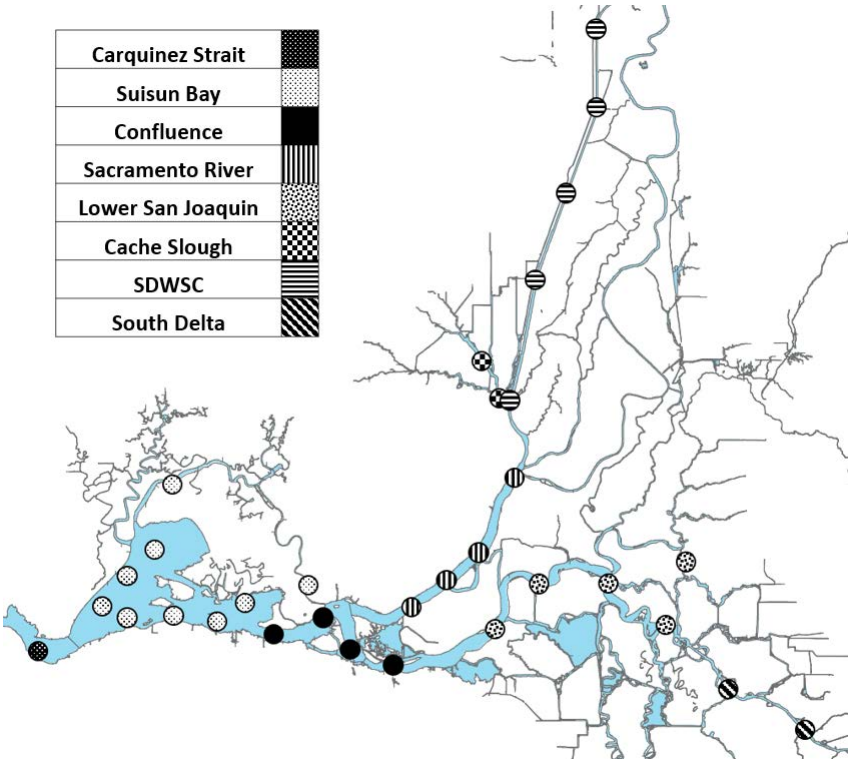

Figure 1. Map of Fall Midwater Trawl zooplankton sampling locations in the upper San Francisco Estuary, CA by region (see legend for region titles).

In the laboratory, we decanted and rinsed samples in water where mysids were removed from detritus and preserved for later processing. Processing included identification of the seven species known to occur in the SFE, measurement, and classification of individuals as juvenile, adult male, and adult female (Figures 2, 3). Species identified were: *H. longirostris, N. kadiakensis, N. mercedis, Alienacanthomysis macropsis*, *Orientomysis aspera* (formerly *A. aspera* per Fukuoka and Murano), *O. hwanhaiensis* (formerly *A. hwanhaiensis* per Fukuoka and Murano), and *Deltamysis holmquistae.* Sample processing protocols did not allow staff to positively distinguish between *N. kadiakensis* and the very similar mysid *N. japonica*; for analysis, all are assumed to be *N. kadiakensis*. Sexual classification was based on elongated fourth pleopod in males and brood pouch/marsupium in females (Figures 2, 3). If these characteristics were not fully developed it was classified as juvenile. For a key to all seven taxa, see Mecum, 2007.

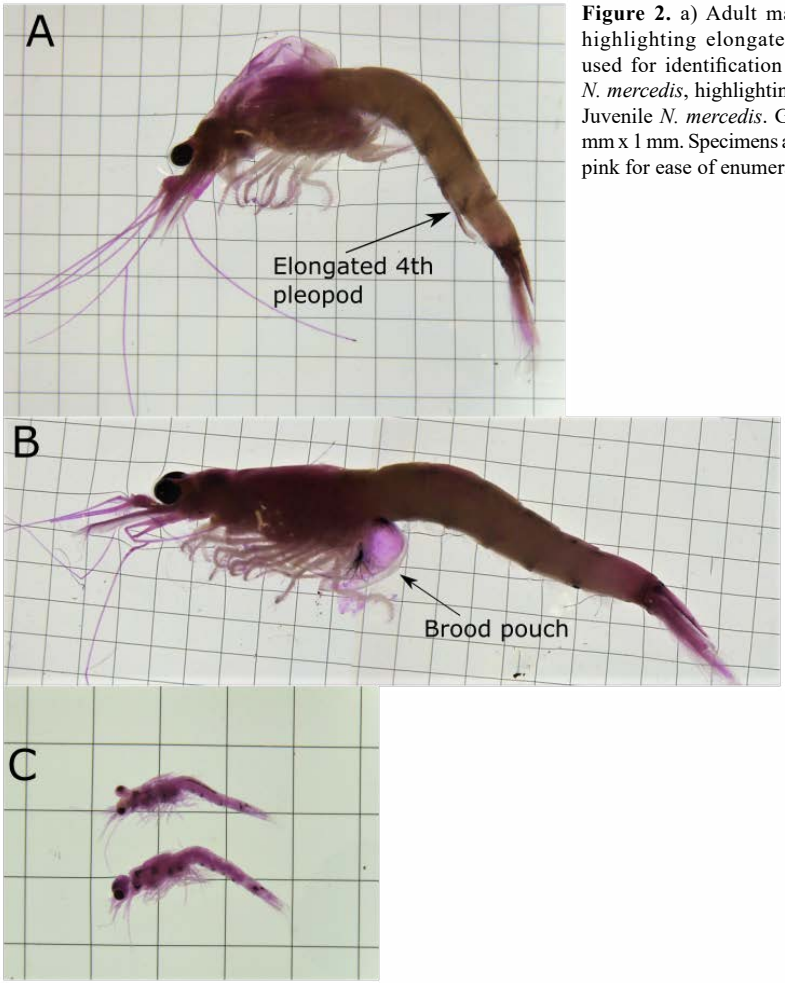

Figure 2. a) Adult male *N. mercedis*, highlighting elongated forth pleopod used for identification b) Adult female *N. mercedis*, highlighting brood pouch c) Juvenile *N. mercedis*. Grid squares are 1 mm x 1 mm. Specimens are artificially died pink for ease of enumeration.

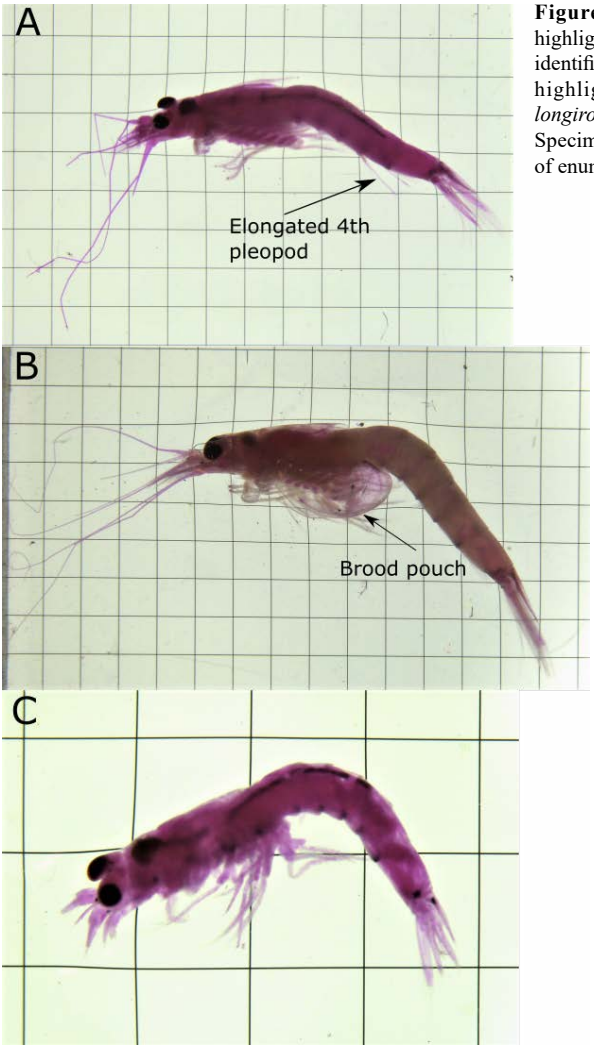

Figure 3. a) Adult male *H. longirostris*, highlighting elongated forth pleopod used for identification b) Adult female *H. longirostris*, highlighting brood pouch c) Juvenile *H. longirostris*. Grid squares are 1 mm x 1 mm. Specimens are artificially died pink for ease of enumeration.

The first 100 non-gravid (male, juvenile, or non-gravid female) mysids of each species were measured to the nearest mm (rounded up) from the tip of the eyestalk to the base of the telson; any additional mysids were identified and enumerated. The first 30 gravid females of each species were also measured, and the remainder were enumerated. Laboratory staff counted the embryos of each gravid female and classified them based on their development as: eggs were classified as stage 1, comma shaped embryos as stage 2, and embryos with visible eyes as stage 3. In samples with more than 400 non-gravid or 100 gravid mysids of a single species, laboratory staff subsampled for that species using a grid tray and recorded the fraction of the total sample processed (F_{sub}). In the case of subsampling, the total catch (N) of a species and life stage was calculated as: $N = N_{sub} / F_{\text{sub}}$.

Analysis methods

To assess our first question on spatial and temporal distribution of mysids, we used FMWT mysid shrimp catch data from 2011 to 2016 (sampling was sporadic and not standardized until 2011). Catch per unit effort (CPUE) for each species (*Sp*) at each station (*St*) was calculated as:

$$CPUE_{SpSt} = \frac{N_{SpSt}}{V_{St}}$$

Where N = Catch and V = volume sampled. From the CPUE at each station, we created an index of abundance for each species to allow us to make comparisons across years and across regions. The species-specific regional abundance index (*R*) for each month was calculated as:

$$R_{Sp} = mean(CPUE_{SpSt})$$

The overall species-specific monthly abundance index (I_{Sp}) was calculated as:

$$I_{Sp} = mean\ (R_{Sp})$$

The regional abundance indices and overall abundance were then graphed to illustrate the difference in temporal and spatial distribution for the seven species of mysid caught by the FMWT.

To explore the potential for competitive interactions between *H. longirostris* and *N. mercedis,* we examined their environmental correlates and life history patterns. To graphically display ranges of environmental parameters where these species were caught, we averaged CPUE (excluding trawls with zero catch) for surface water temperature, salinity, and turbidity. Environmental parameters were summarized for both species at intervals of 1°C for temperature, 1 psu for salinity, and 10 ntu for turbidity.

To test the statistical relationship between these environmental parameters and species' presence, two zero-inflated negative binomial models were run on the CPUE of *H. longirostris* and *N. mercedis*, using temperature, salinity, turbidity, as predictor variables. Predictor variables were centered and scaled by subtracting the mean and dividing by the variance to put all variables on a common scale. These analyses were conducted using the pscl package (Jackman et al. 2016) in R version 3.6.1 (R Project for Statistical Computing, 2019).

Mean lengths for each mysid sex and minimum and maximum size at maturity were calculated for *H. longirostris*. A binomial generalized linear model was then used to calculate the maximum likelihood estimator of the median of the distribution, using the glm function in R. A two-factor ANOVA with a Tukey post-hoc test was used to compare size of each sex classification between *H. longirostris* and *N. mercedis.*

Data on gravid *H. longirostris* were used to determine the mean number of embryos per female. Females with obviously damaged brood pouches were excluded, as well as those with less than three embryos (assumed to be damaged brood pouches). Fecundity of *N. mercedis* and other, less common, species was not examined due to an insufficient sample size of gravid females. Therefore, we compared data on *H. longirostris* fecundity to literature values of *N. mercedis* to explore whether differential fecundity might result in a competitive advantage.

RESULTS

Temporal trends

The historically common *N. mercedis* was rarely seen from 2011-2013, completely absent from catch in 2014 and through most of 2015, and much more common in 2016 (Figure 4), particularly in the Sacramento River and SDWSC (Figure 5). *H. longirostris* dominated catch numerically (Figure 4) in all but a few regions and months. *N. kadiakensis* was the second most abundant species caught. Three other species, the native *A. macropsis*, and the non-native *O. aspera* and *O. hwanhaiensis* appeared sporadically. *O. aspera* was present in 2013 through 2016 and *O. hwanhaiensis* in 2015 and 2016 (Figure 4). Only 5 specimens of *D. holmquistae* were found: 2 in 2013, 1 in 2015, and 2 in 2016. In general, overall mysid

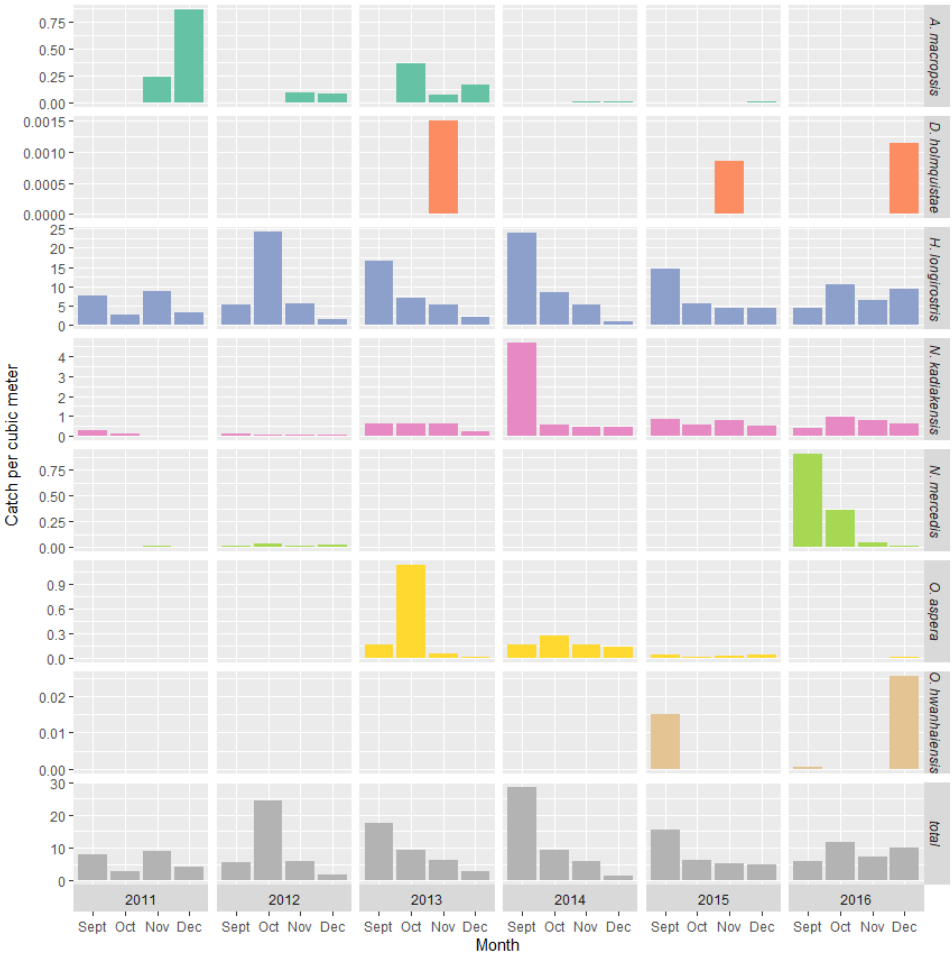

Figure 4. Monthly mean CPUE (catch per cubic meter) of the mysid species collected by Fall Midwater Trawl mysid sampling, 2011–2016, separated by species.

abundance during the FMWT survey was highest in September and lowest in December (Figure 4), though this varied by species and by year, with *O. aspera*, *O. hwanhaiensis* and *D. holmquista*e peaking later in the year.

Spatial Trends

H. longirostris was widespread in the FMWT study area across all years (Figure 5) and occurred in every region sampled. CPUE of *H. longirostris* was highest in the SDWSC, followed by the lower Sacramento River and Suisun Bay; CPUE was low in Cache Slough, the lower San Joaquin River, and the East Delta regions (Figure 5). *N. kadiakensis* occurred widely in regions of the Sacramento River downstream of the SDWSC and Cache Slough Complex and the East Delta in the San Joaquin River. *N. mercedis* occurred mainly in the SDWSC and Sacramento River. Other species were limited to downstream regions (Figure 5) generally associated with higher salinity.

Environmental correlates

FMWT mysid sampling collected *H. longirostris* across a wide range of environmental conditions, while ranges for *N. mercedis* were slightly narrower. *H. longirostris* abundance peaked at a higher temperature than *N. mercedis* (22-23 ˚C versus 20-21˚C), and although *H. longirostris* did occur at temperatures as low as 8 ˚C, both frequency of occurrence and abundance of *H. longirostris* increased with higher temperatures (Table 1, Figure 6). In contrast, *N. mercedis* rarely occurred at <17˚C or >21˚C and showed a much lower relationship between abundance and temperature than *H. longirostris* (Table 1). Abundance of *H. longirostris* was significantly higher at low salinities (Table 1, Figure 7), but they were collected at the most saline sampling location, Carquinez Strait, and frequency of occurrence of *H. longirostris* had a slight positive relationship with salinity (Table 1). *N. mercedis* CPUE was concentrated around 0-1 psu with a second, smaller peak at 15-16 psu (Figure 7), though there was no significant relationship between presence and salinity (Table 1). No *N. mercedis* were collected at >17 psu. CPUE peaked at turbidities between 31-41 ntu for *H. longirostris* and 10-20 ntu for *N. mercedis* (Figure 5) and both species were common from 10-80 ntu. This relationship between abundance and turbidity was significant for *H. longirostris*, but not for *N. mercedis* (Table 1).

Size and fecundity

Size of adult *H. longirostris* was smaller for males than females (Tukey post-hoc $p < 0.001$, Figure 9). A binomial model of size at maturity predicted the median size of adult males to be 6.3 mm (SE = 1.03, $p < 0.001$), and adult females to be 9.2 mm (SE = 1.03, $p < 0.001$). The mean number of embryos per gravid female declined in later embryonic developmental stages, with stages 1 through 3 averaging 18.4, 11.7, and 7.7 embryos, respectively. The average size of *H. longirostri*s was less than *N. mercedis* for adult males and females (Tukey post-hoc $p < 0.0001$, Figure 9). Juveniles were not significantly different in length (Tukey post-hoc $p = 0.7293$, Figure 9)

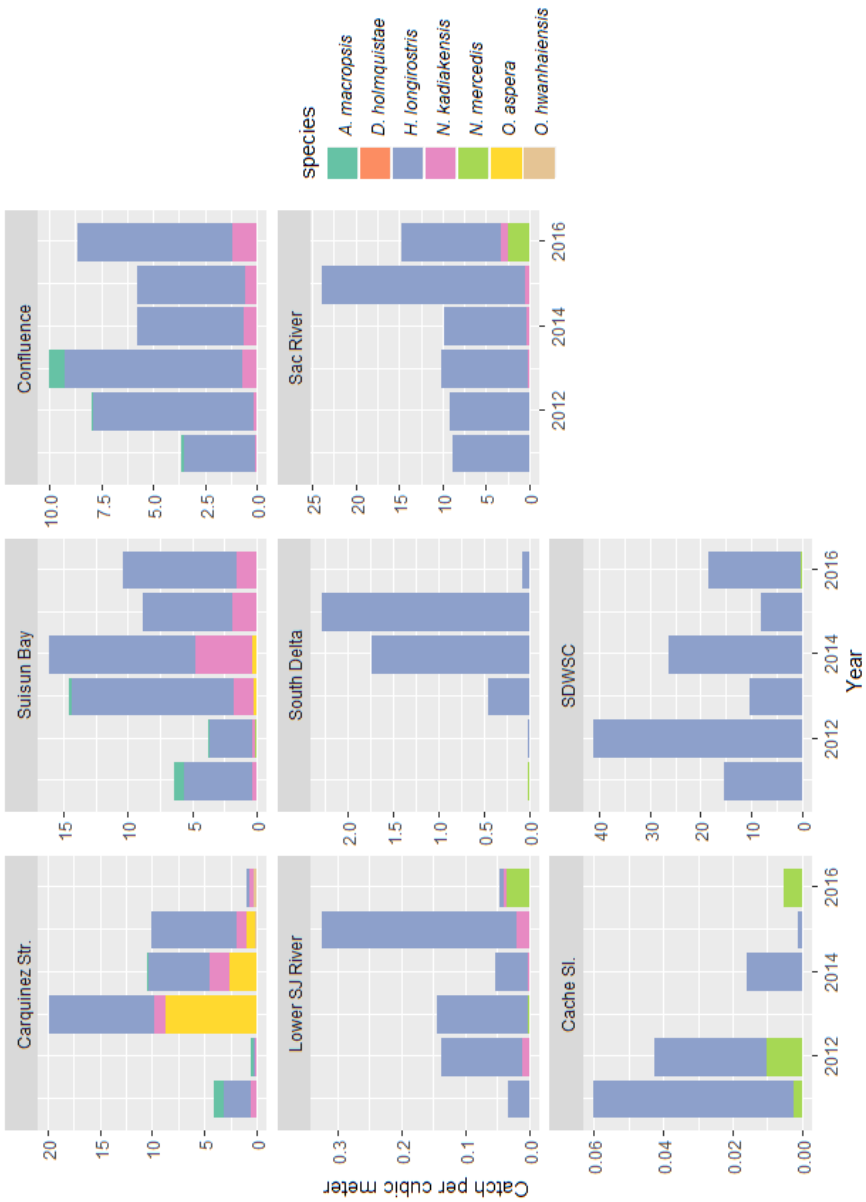

Figure 5. Regional mean CPUE (catch per cubic meter) of mysids collected by Fall Midwater Trawl mysid sampling, 2011–2016, with species differentiated by color. Note the differences in y-axes for the different regions.

Table 1. Count model coefficients (negative binomial with log link)

	N. mercedis				*H. longirostris*			
	Estimate	**SE**	**z-value**	**p-value**	**Estimate**	**SE**	**z-value**	**p-value**
(Intercept)	-2.020	0.123	-16.478	<0.0001*	2.133	0.066	32.104	<0.0001*
Temperature	-0.230	0.148	-1.551	0.121	0.386	0.065	5.963	<0.0001*
Turbidity	0.079	0.095	0.833	0.405	0.468	0.105	4.466	<0.0001*
Conductivity	-0.056	0.134	-0.419	0.675	-0.198	0.066	-2.996	0.0027*
Log(theta)	11.268	156.942	0.072	0.943	-0.776	0.059	-13.108	<0.0001*
Zero-inflation model coefficients (binomial with logit link)								
	N. mercedis				*H. longirostris*			
	Estimate	**SE**	**z-value**	**p-value**	**Estimate**	**SE**	**z-value**	**p-value**
(Intercept)	-7.223	3.936	-1.835	0.067	-22.685	5.956	-3.809	0.0001*
Temperature	-4.679	2.351	-1.990	0.047*	-0.492	0.206	-2.391	0.0170*
Turbidity	0.059	0.502	0.117	0.907	-4.115	1.214	-3.390	0.0007*
Conductivity	2.336	1.487	1.571	0.116	-26.858	8.107	-3.313	0.0009*

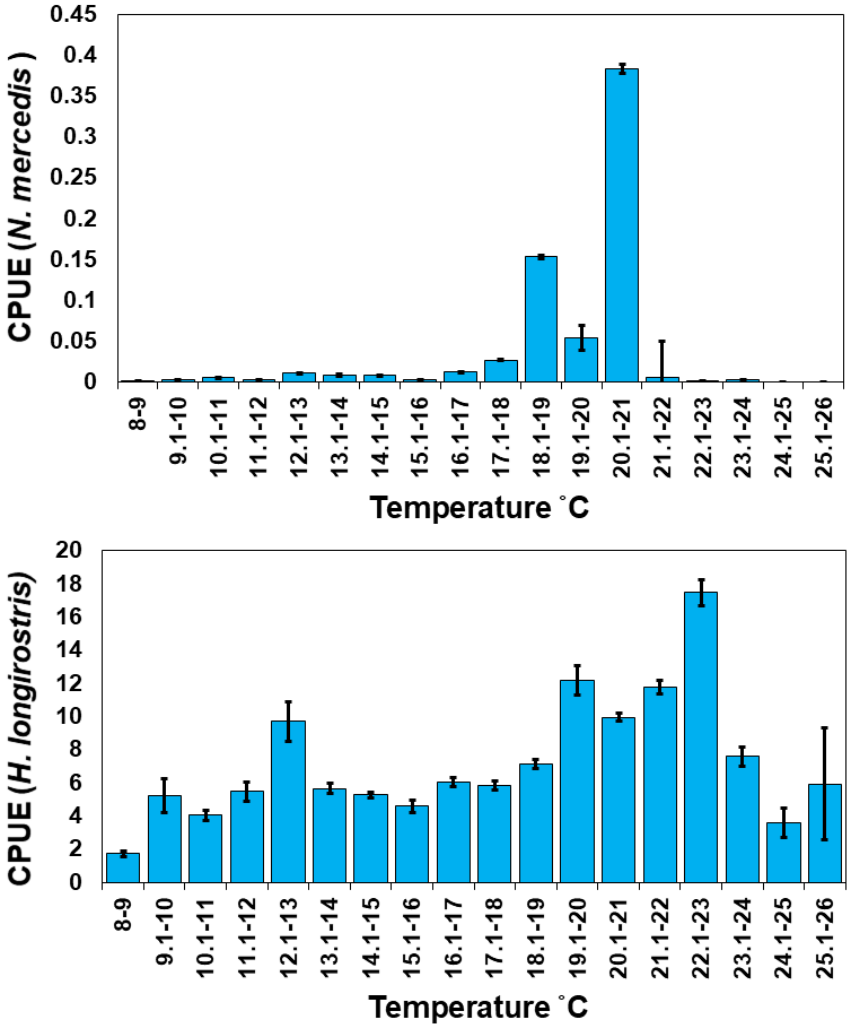

Figure 6. Mean CPUE (catch per cubic meter) (± 1 SE) for *N. mercedis* (top) and *H. longirostris* (bottom) by 1°C temperature intervals, from Fall Midwater Trawl mysid sampling, 2011–2016.

DISCUSSION

Among the mysid species, the invasive *H. longirostris* is by far the most abundant in the region of the upper estuary sampled by the FMWT. FMWT mysid data confirmed the dominance of *H. longirostris* both numerically and geographically over all other mysid species present. *H. longirostris* matured at a smaller size and possessed larger broods at size, which may result in shorter generation times and lower food requirements. *H. longirostris* was more common across a wider range of temperatures than *N. mercedis*. Some combina-

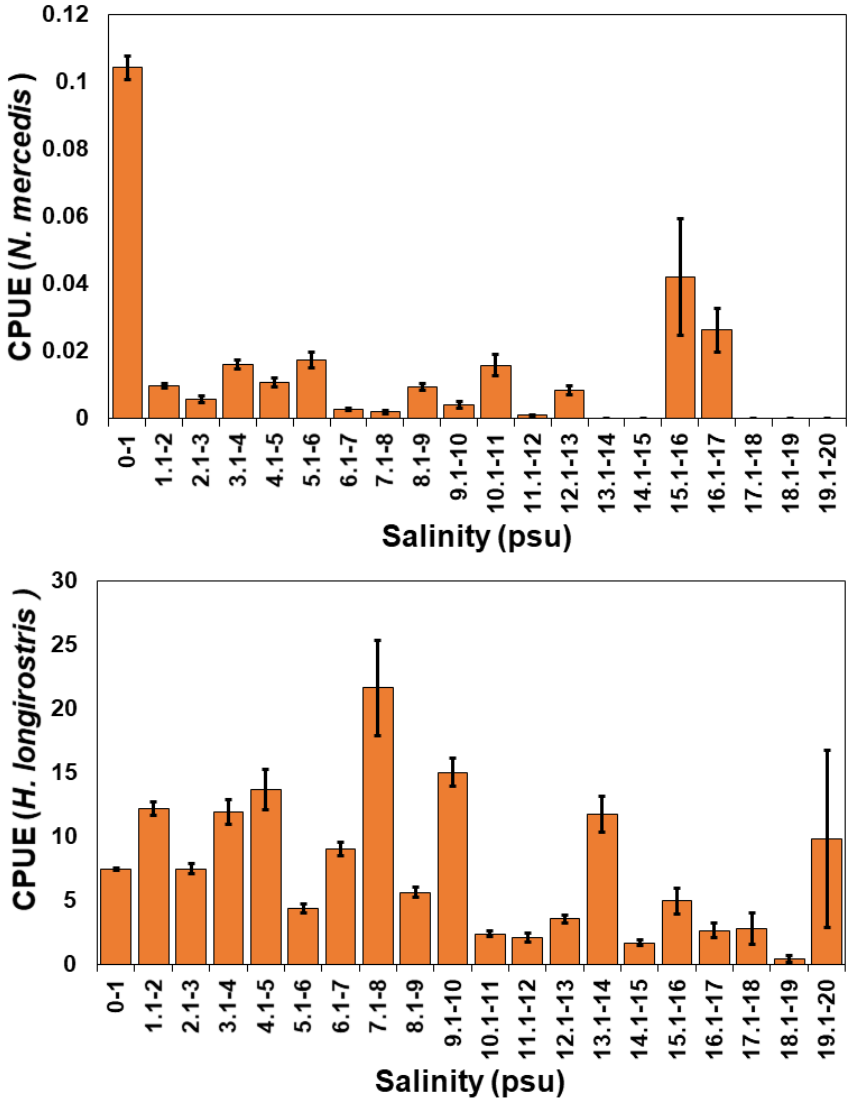

Figure 7. Mean CPUE (catch per cubic meter) (±1 SE) for *N. mercedis* (top) and *H. longirostris* (bottom) by 1 psu salinity intervals, from Fall Midwater Trawl mysid sampling, 2011–2016.

tion of these factors likely allows *H. longirostris* to out-compete *N. mercedis* in fall. The replacement of *N. mercedis* with *H. longirostris* may ultimately be detrimental to fish in the SFE, since work by Feyrer et al. (2003) suggests that *H. longirostris* may be a less favorable source of energy for fish due to its smaller size.

Given the continued low density of mysids caught in the FMWT, availability of *N. mercedis* as a food source for fish remains limited during the fall months (Figure 4). *H. longirostris* abundance was greater than all other species by several orders of magnitude (Figure 4). *N. kadiakensis*, a mysid similar in size to *N. mercedis*, was the second most

abundant collected after *H. longirostris*. Other mysid species were either found sporadically (*D. holmquistae)* or in low numbers (*O. aspera* and *O. hwanhaiensis*) and only collected in downstream regions suggesting that FMWT mysid stations sample a very limited portion of their geographic range in the SFE.

The collapse of mysid populations as a whole in the last few decades is likely related to food limitation (Orsi and Mecum 1996, Winder and Jassby 2011), but the FMWT mysid data may provide clues as to why *H. longirostris* dominates over the previously abundant *N. mercedis.* One possible factor is temperature tolerance, since our data show abundance of *H. longirostris* peaks at a higher temperature than *N. mercedis*. Laboratory experiments from the 1950s and 1970s showed a sharp decrease in *N. mercedis* survival at 22˚C (Hair 1971), with one study determining the upper lethal temperature as 24.2˚C to 25.5 ˚C for specimens caught in the SFE (Hair 1971) and another citing 23.9˚C for organisms from a British Columbia population (Wilson 1951). A laboratory rearing experiment using *N. mercedis* for toxicity testing employed an ideal temperature of 16-19˚C and documented a slight increase in mortality corresponding with higher temperatures (Brandt et al 1993). Heubach (1969) noted a sharp decline in *N. mercedis* abundance in September 1965 and August 1966 when temperatures exceeded 22 ˚C. Knutson and Orsi (1979) reported *N. mercedis* in the estuary at daytime temperatures as high as 25.6 ˚C as long as dissolved oxygen levels remained saturated, but admitted that this was likely outside the ideal range for the species. In the FMWT mysid results, *N. mercedis* CPUE peaked at 20-21˚C (Figure 6), although this may be driven by two specific tows in the lower Sacramento River in 2016. Without those two tows, the peak would be 18-19 ˚C, and *N. mercedis* was not collected in FMWT mysid sampling at temperatures above 23.7˚C.

There are no known laboratory temperature experiments on *H. longirostris*, so temperature data is limited to field observations. In FMWT mysid sampling, likelihood of *H. longirostris* presence increased with temperature, and CPUE was highest at 22-23˚C, at the upper end of the thermal tolerance for *N. mercedis*. Some individuals were caught at 25-26˚C (highest temperature range recorded during the sample period). One study of mysids in Suisun Marsh in the spring also noted *H. longirostris* peaking at warmer temperatures and hypothesized that their smaller size may give them a competitive advantage at high temperatures (Carlson and Matern 2000). From their native range, Suzuki et al (2009) found high densities of juvenile *H. longirostris* between 15-25˚C in the Chikugo River estuary, with organisms present in waters up to 30˚C. Further sampling at warmer temperatures, or controlled laboratory experiments on *H. longirostris* are needed to refine our knowledge of their temperature tolerances.

Water temperature data for FMWT was limited by the seasonality of the sampling period, declining from a median around 20℃ in September to 10℃ in December (Figure 26 in Brown et al. 2011). The Environmental Monitoring Program (EMP), which samples year-round, reported that mean CPUE for both *H. longirostris* and *N. mercedis* since the introduction of *Potamocorbula* is usually higher in spring (March-May) and summer (June-August), and extremely low in fall (September-November) (Hennessy and Enderlein 2013). Suzuki et al (2009) found a seasonal variation among life stages of *H. longirostris;* small juveniles (<1 mm carapace length) were almost completely absent during July and August, except in one case of high flows resulting in lower water temperature. EMP data also indicates a consistent food limitation in late summer and fall months (Hennessy and Enderlein 2013); abundance of copepods (a major food source for mysids) drops sharply

as grazing rates of *Potamocorbula* increase in the summer. With food limitation already present during warmer months, temperature may be a secondary detrimental factor for *N. mercedis* and allow the apparently more heat tolerant *H. longirostris* to flourish in its place (Figure 6). If higher temperature tolerance is the driving factor, as hypothesized here, then the predictions of increased temperature under most climate change scenarios may further favor this invasive species (Brown et al. 2016).

The FMWT mysid data can be used to examine the salinity range of *H. longirostris*, but it is limited by the geographic range and seasonality of estuarine conditions encountered in the study (i.e., seasonal location of the mixing zone and salinity gradient). *H. longirostris* was often collected at the most saline sampling locations (Figure 7, Suisun Bay and Carquinez Strait), and likelihood of presence increased with salinity (Table 1), so it is unlikely that FMWT data captures the upper salinity maximum of the species. The highest salinity recorded during the study for *H. longirostris* was 19.2 psu, though Mecum (2007) cites a salinity range of freshwater to 28 psu for the species. CPUE was highest between 0-10 psu, which is consistent with data from the Chikugo River estuary in Japan (Suzuki et al 2009).

N. mercedis was documented across a wide range of salinities (freshwater to 17 psu), with an upper salinity limit slightly lower than *H. longirostris*. Orsi (1997) reported that *H. longirostris* was slightly more euryhaline than *N. mercedis*. Previous laboratory work using *N. mercedis* demonstrated mortality in freshwater for specimens collected in areas of higher salinity (Wilson 1951). Field studies (Heubach 1969) hypothesized that reproduction may be reduced in freshwater due to lower percentages of gravid females compared with low salinity regions. The FMWT mysid data did not show reduced abundance in freshwater, however, *N. mercedis* catch was extremely low, so salinity values may not be an accurate representation of salinity habitat distribution within the estuary, or *N. mercedis* may be excluded from higher salinity water due to food limitation or competition with the more euryhaline *H. longirostris*.

The higher CPUE of mysids at turbidity values >10 ntu is likely related to negatively phototaxic behavior. Studies have documented the vertical migration of other mysid species following changes in light intensity (Beeton and Bowers 1982), with individuals moving towards the bottom of the water column as light intensity increases. Kimmerer et al. (1998) found *N. mercedis* vertically migrates at night, however the incidence of this behavior changed with environmental conditions, including turbidity. The FMWT mysid data found low CPUE values for both *H. longirostris* and *N. mercedis* at very low turbidity levels (<10 ntu; Figure 8) where light intensity is highest. Low CPUE associated with low turbidity could be due to vertical migration to deeper waters during daytime hours. FMWT mysids were sampled using oblique tows exclusively during the day, so the net only spent a portion of each tow near the bottom.

The FMWT mysid data indicated an upper turbidity limit of between 140-160 ntu for both *H. longirostris* and *N. mercedis*, but this is likely a sample size limitation resulting from few samples taken during extremely high flows. In the Chikugo River estuary, where *H. longirostris* is overwhelmingly dominant, turbidities often exceed 200 ntu during high flows (Suzuki et al. 2009). An upper limit for *H. longirostris* and *N. mercedis* could be determined with more mysid sampling, but the FMWT mysid data indicate that both species are common across a turbidity range of 10-80 ntu.

Due to small sample size, size-at-maturity statistics were not developed for *N. mercedis* from FMWT mysid data though there is some published information. It is already known that *H. longirostris* is smaller than *N. mercedis* (Feyrer et al. 2003; Hennessy 2011), with

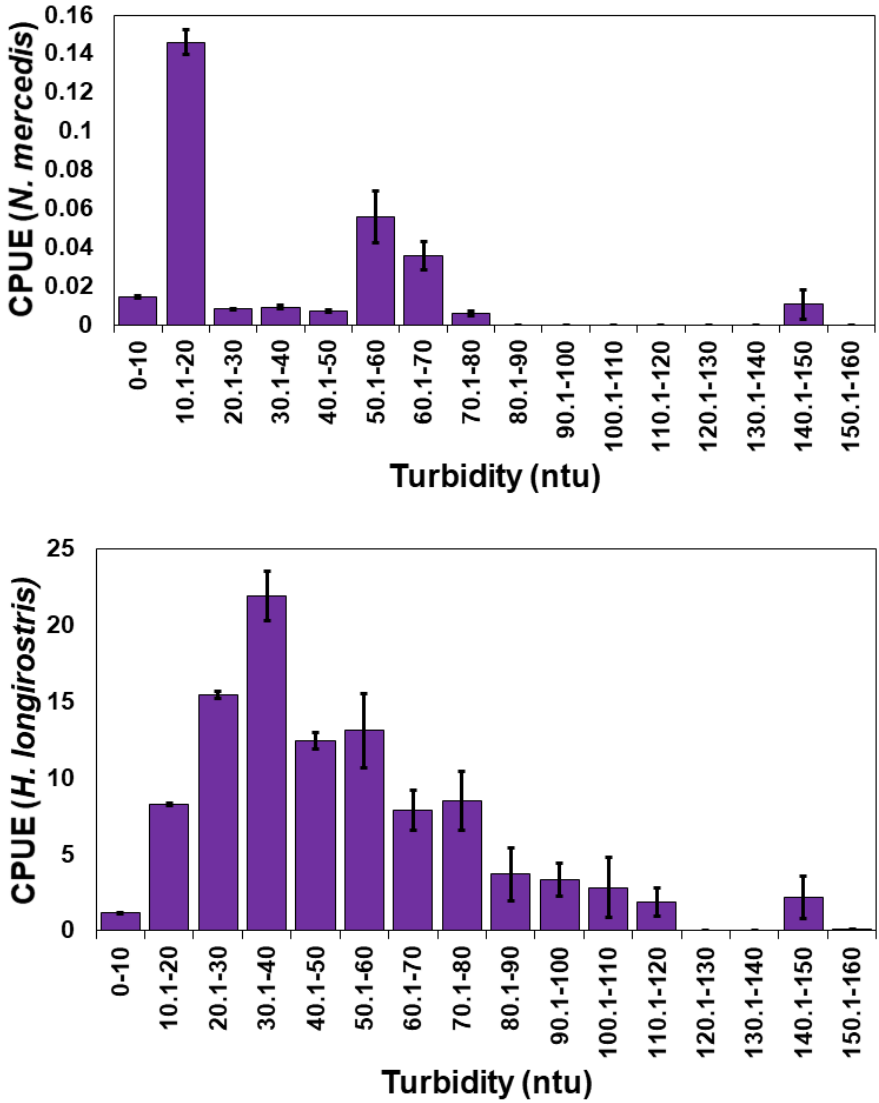

Figure 8. Mean CPUE (catch per cubic meter) (±1 SE) for *N. mercedis* (top) and *H. longirostris* (bottom) by 10 ntu intervals, from Fall Midwater Trawl mysid sampling, 2011–2016.

the latter maturing around 7 mm (Heubach 1969). In contrast, FMWT mysid data contained mature *H. longirostris* as small as 4-5 mm, and average size of adults being smaller overall (Figure 9). There is no known data on age-at-maturity for *H. longirostris.* If the smaller size at maturity of *H. longirostris* results in a younger age-at-maturity this shorter generation time may result in a competitive advantage over *N. mercedis*. Furthermore, smaller size may make *H. longirostris* less subject to food limitation, a chronic problem in the SFE (Orsi and Mecum 1996).

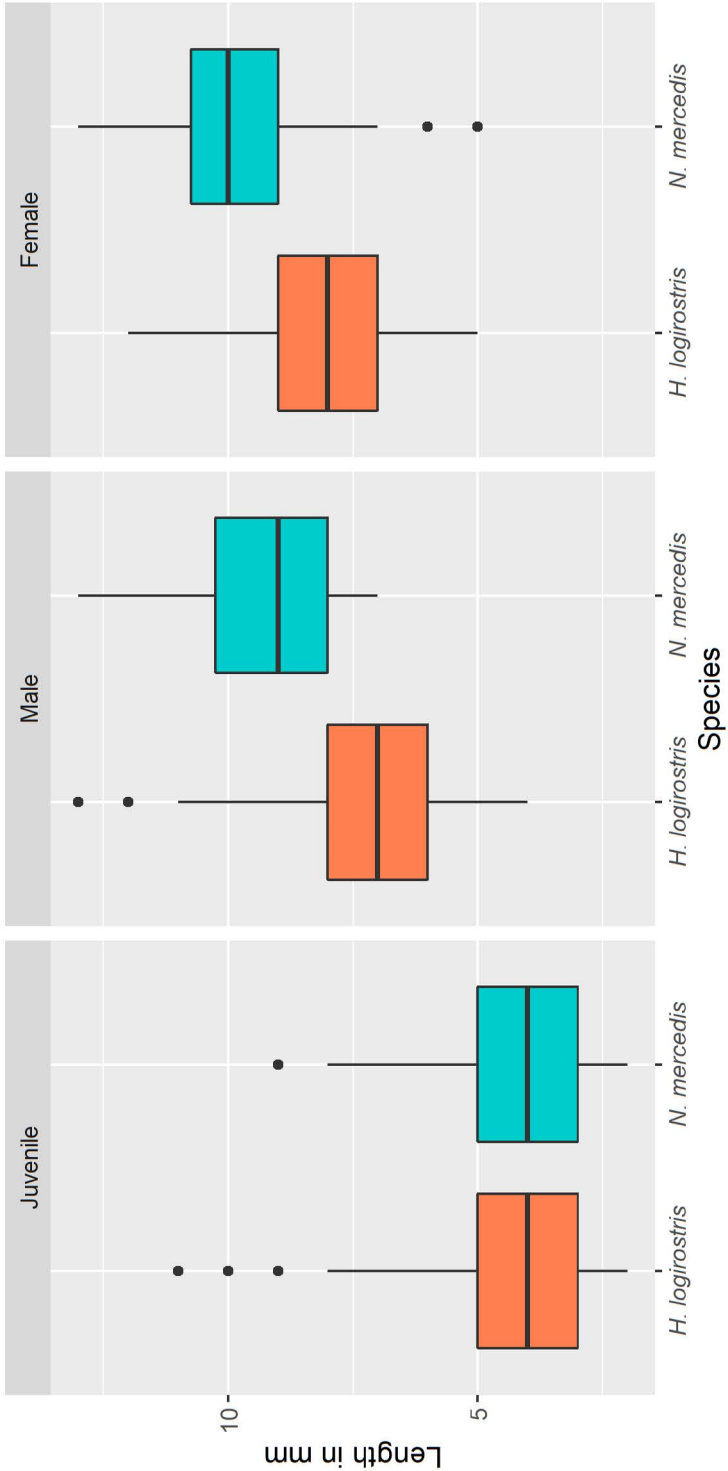

Figure 9. Length distribution of juveniles, adult males, and adult females for *N. mercedis* and *H. longirostris*.

As with size-at-maturity, sample size for gravid *N. mercedis* in FMWT was too small to directly compare fecundity with *H. longirostris.* Previously published information on *N. mercedis* (referred to as *Neomysis awatschensis* in the study) found that fecundity is based on size and time of year (Heubach 1969) with relatively high numbers of eggs produced by females of the same size during spring and summer, and lower numbers in fall and winter. Laboratory raised *N. mercedis* were found to have brood sizes ranging from 4 to 31, with an average of 15.1 (Bailey 1985) based on number of young successfully released from the brood pouch. This is higher than the mean brood size of *H. longirostris* found in the FMWT mysid data (7.7 for stage 3, the closest to being released), but the ideal laboratory conditions used in the study likely produced high values that would not be seen under normal field conditions. *H. longirostris* may follow the same trend as *N. mercedis*, with the highest reproduction in spring. If reproduction is normally reduced in fall, FMWT mysid data is inadequate for determining actual brood size ranges for either mysid species. An analysis of EMP data from 1993-1996 (Orsi 1997) found that *H. longirostris* at the same size had larger average brood sizes than *N. mercedis.* Future analysis of more recent EMP data compared with that of FMWT would improve our knowledge of mysid fecundity.

Further studies are necessary to document the overall abundance of mysid species across the full range of the SFE, characterize the life history of *H. longirostris*, and further understand why *H. longirostris* is the most abundant mysid in the upper SFE and the native *N. mercedis* is not.

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Author Contributions

Conceived and designed the study – MA
Collected the data – MA
Performed the analyses – MA & RH
Authored the MS – MA
Critical revisions - RH

LITERATURE CITED

Bailey, H. C. 1985. Brood size and growth of *Neomysis mercedis*. Report prepared for California State Water Resources Control Board, Sacramento, CA, USA.

Beeton A. M., and J. A. Bowers. 1982. Vertical migration of *Mysis relicta* Lovén, Hydrobiologia 93:53–61.

Brandt, O. M, R. W., Fujimura, and B. J. Finlayson. 1993. Use of *Neomysis mercedis* (Crustacea: Mysidacea) for estuarine toxicity tests. Transactions of the American Fisheries Society 122:279–288.

Brown, L. R., R. Baxter, G. Castillo, L. Conrad, S. Culberson, G. Erickson, F. Feyrer, S. Fong, K. Gehrts, L. Grimaldo, B. Herbold, J. Kirsch, A. Mueller-Solger, S. Slater, T. Sommer, K. Souza, and E. Van Nieuwenhuyse. 2014. Synthesis of studies in the fall low salinity zone of the San Francisco Estuary, September–December 2011. U.S. Department of the Interior, U.S. Geological Survey, Sacramento, CA, USA.

Brown, L. R., L. M. Komoroske, R. W. Wagner, T. Morgan-King, J. T. May, R. E. Connon, and N. A. Fangue. 2016. Coupled downscaled climate models and ecophysiological metrics forecast habitat compression for an endangered estuarine fish. PLOS ONE 11:e0146724.

Bryant M., and J. Arnold. 2007. Diets of age-0 Striped Bass in the San Francisco Estuary, 1973–2002. California Fish and Game 93:1–22.

Carlson, S. M., and S. A. Matern. 2000. Mysid shrimp in Suisun marsh. Interagency Ecological Program Newsletter 13:16–20.

Daniels, R. A., and P. B. Moyle. 1983. Life history of Splittail (Cyprinidae: *Pogonichthys Macrolepidotus*) in the Sacramento-San Joaquin Estuary. Fishery Bulletin 81(3): 647–654.

Department of Water Resources and Department of Fish and Wildlife. 2015. Fish Restoration Program Cache Slough Complex Conservation Assessment. Draft Volume 1: Characterization Report. Prepared by California Dept. of Water Resources and California Dept of Fish and Wildlife with assistance from Stillwater Sciences, Davis, CA. Contract No. 4200009291.

Feyrer, F., B. Herbold, S. Matern, and P. Moyle. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. Environmental Biology of Fishes 67: 277–288.

Hair, J. R. 1971. Upper lethal temperature and thermal shock tolerances of the opossum shrimp, *Neomysis awatschensis* from the Sacramento-San Joaquin Estuary, California. California Fish & Game 57:17–27.

Hennessy, A. 2011. Double whammy in the San Francisco Estuary: smaller mysids and less of them. Poster presented at the 2011 State of the Estuary Conference, Oakland, CA, USA. Available from: https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentId=44696

Hennessy, A., and T. Enderlein. 2013. Zooplankton Monitoring 2012. IEP Newsletter 26(4):16–23.

Heubach, W. 1969. *Neomysis awatschensis* in the Sacramento-San Joaquin River Estuary. Limnology and Oceanography 14:533–546.

Jackman, S., A. Tahk, A. Zeileis, C. Maimone, and J. Fearon. 2016. Package: pscl - Political Science Computational Laboratory. Stanford University, Stanford, CA, USA. Available from: http://pscl.stanford.edu/

Kayfetz, K., and W. Kimmerer. 2017. Abiotic and biotic controls on the copepod *Pseudodiaptomus forbesi* in the upper San Francisco Estuary. Marine Ecology Progress Series 581:85–101. Available from: http://www.int-res.com/abstracts/meps/v581/p85-101/

Kimmerer, W. J., J. R. Burau, and W. A. Bennett. 1998. Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. Limnology and Oceanography 43:1697–1709.

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

Knutson, Jr., A. C., and J. J. Orsi. 1983. Factors regulating abundance and distribution of the shrimp *Neomysis mercedis* in the Sacramento-San Joaquin Estuary. Transactions of the American Fisheries Society 112:476–485.

Mecum, W. L. 2007. A key to Mysidacea of the Upper San Francisco Estuary. IEP Technical Report 75. Interagency Ecological Program for the San Francisco Estuary. Available from: http://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=44693

Modlin, R. F., and J. J. Orsi. 1997. *Acanthomysis bowmani*, a new species, and *A. aspera Ii*, Mysidacea newly reported from the Sacramento-San Joaquin Estuary, California (Crustacea: Mysidae). Proceedings of the Biological Society of Washington, 1 10(3):439–446.

Moyle, P. B., B. Herbold, D. E. Stevens, and L. W. Miller. 1992. Life history and status of Delta Smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67–77.

Orsi, J. J. 1997. Relative abundance and some aspects of the biology of native and introduced mysid shrimp in Suisun Bay and the Delta. Interagency Ecological Program for the Sacramento-San Joaquin Estuary Newsletter 10 (3): 13–14.

Orsi, J. J., and A. C. Knutson, Jr. 1979. The role of mysid shrimp in the Sacramento-San Joaquin estuary and factors affecting their abundance and distribution. Pages 401–408 in T. J. Conomos, editor. San Francisco Bay: The Urbanized Estuary. Pacific Division of the American Association for the Advancement of Science, San Francisco, CA, USA.

Orsi, J. J., and W. L. Mecum. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento-San Joaquin Estuary. Pages 375–401 in J. T. Hollibaugh, editor. San Francisco Bay: The Ecosystem. Pacific Division of the American Association for the Advancement of Science, San Francisco, CA, USA.

Schemel, L. E. 2001. Simplified conversions between specific conductance and salinity units for use with data from monitoring stations. Interagency Ecological Program Newsletter 14(1):17–18. Available from: http://pubs.er.usgs.gov/publication/70174311

Slater, S. B., and R. D. Baxter. 2014. Diet, prey selection and body condition of age-0 Delta Smelt, *Hypomesus transpacificus*, in the upper San Francisco Estuary. San Francisco Estuary and Watershed Science 14.

Suzuki, K., K. Nakayama, and M. Tanaka. 2009. Horizontal distribution and population dynamics of the dominant mysid *Hyperacanthomysis longirostris* along a temperate macrotidal estuary (Chikugo River estuary, Japan). *Estuarine, Coastal and Shelf Science* 83(4):516–528

Wilson, R. R. 1951. Distribution, growth, feeding habits, abundance, thermal, and salinity relations of *Neomysis mercedis* (Holmes) from the Nicomekl and Serpentine Rivers, British Columbia (T). University of British Columbia, Vancouver, Canada. Available from: https://open.library.ubc.ca/cIRcle/collections/831/items/1.0106596

Winder, M., and A. Jassby. 2011. Shifts in zooplankton community structure: implications for food web processes in the Upper San Francisco Estuary. Estuaries and Coasts 34(4): 675–690.

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Occurrences of Steelhead Trout (*Oncorhynchus mykiss*) in southern California, 1994-2018

ROSI DAGIT[1*], MICHAEL T. BOOTH[2], MAURICIO GOMEZ[3], TIMOTHY HOVEY[4], STEVE HOWARD[5], SCOTT D. LEWIS[6], SANDRA JACOBSON[7], MARY LARSON[4], DANA MCCANNE[4], AND TIMOTHY H. ROBINSON[8]

[1] *Resource Conservation District of the Santa Monica Mountains, Topanga, CA 90290, USA*

[2] *United Water Conservation District, 106 N 8th St, Santa Paula, CA 93060, USA (Current affiliation: Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45220, USA)*

[3] *South Coast Habitat Restoration, P.O. Box 335, Carpinteria, CA 93014, USA*

[4] *California Department of Fish and Wildlife, Region 5, 3883 Ruffin Road, San Diego, CA 92123, USA*

[5] *United Water Conservation District, 106 N 8th St, Santa Paula, CA 93060, USA (Current affiliation: Rincon Consultants, Inc.)*

[6] *Casitas Municipal Water District, 1055 Ventura Ave, Oak View, CA 93022, USA*

[7] *California Trout - South Coast Region, 5425 Oberlin Drive, Suite 209, San Diego, CA 92121, USA*

[8] *Cachuma Operations Management Board, 3301 Laurel Canyon Rd., Santa Barbara, CA 93105, USA*

**Corresponding Author: rdagit@rcdsmm.org*

Observations of federally endangered Southern Steelhead Trout (*Oncorhynchus mykiss*) were compiled for the southern California Distinct Population

Segment (DPS) that extends approximately 500 kilometers from the Santa Maria River (Santa Barbara County) south to the Mexican border. Existing monitoring programs and anecdotal observations documented 177 adult Steelhead in the past 25 years. The level of monitoring effort and technology used varied by watershed and year. Thus, the low numbers of adult Steelhead observed during the past 25 years provides relative abundance and distribution documentation of occurrences but likely underestimates the abundance of adult Steelhead throughout the DPS. The patchy distribution observed suggests that fish are opportunistically entering creeks and river mouths based on available hydrologic passage opportunities associated with higher rainfall years. Given the extremely low numbers of anadromous adults, long recovery timeline, future uncertainty with respect to climate change, and a multitude of anthropogenic factors, additional conservation actions including state and federal protection of resident *O. mykiss* are recommended to increase the likelihood of the continued existence of the species within the DPS. Additional focused monitoring, research, and implementation of recovery actions are needed to expand our knowledge of southern California Steelhead distribution and abundance.

Key words: anadromous adults, Rainbow Trout, southern California, Southern Steelhead

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The Southern California Steelhead Trout (*Oncorhynchus mykiss*) Evolutionarily Significant Unit (ESU) populations located from the Santa Maria River in Santa Barbara County south to Malibu Creek in the Santa Monica Bay were listed as endangered in 1997 under the Endangered Species Act (NOAA 1997: 62 FR 43937). After recognizing that additional populations of Steelhead were found further south in Topanga Creek near Malibu, and San Mateo Creek near San Diego, the ESU was extended to the Mexican border in 2002 (NOAA 2002: 7 FR 21586). Subsequently, the National Marine Fisheries Service (NOAA) adopted the Distinct Population Segment (DPS) designation to replace the use of ESU in 2006 (NOAA 2006: 71 FR 5248). Based on these designations, all naturally spawned *O. mykiss* found in freshwater habitat below impassible natural and artificial barriers are protected by this listing. Additionally, any individuals spawned upstream of these barriers that migrate downstream into designated critical habitat are also protected.

When observed in rivers and streams, it is difficult to determine the life history phenotype of an individual *O. mykiss* without genetic (Pearse et al. 2014), morphological (Beeman et al. 1995; Haner et al. 1995), or physiological evaluations (Negus 2003). However, it is possible to identify anadromous adults when they return to rivers and streams from the ocean because they are typically larger (fork length > 400 mm), have greater girth, and are steel-gray in color (Moyle et al. 2017). Using these identifying characteristics to document adult occurrences in the DPS is critical to evaluate population viability and progress towards recovery goals (Boughton et al. 2006; Boughton 2010a, b; Adams et al. 2011; NOAA 2012). Resident *O. mykiss* in upper watershed areas outside the designated critical habitat are not protected by either state or federal endangered species acts, despite their documented link in maintaining maximum numbers of Steelhead (NOAA 2012).

The federal Recovery Plan (NOAA 2012) defines DPS-level and population-level criteria to lower the risk of extinction both for individual populations in a given river/creek system and the DPS as a whole (Boughton et al. 2007). Criteria listed include preventing extinction by protecting existing populations and all life history expressions, expanding distribution to historically occupied areas, restoring suitable habitat, conserving existing genetic diversity, and providing opportunities for genetic mixing between and within populations. Mean annual run size, which was estimated based on Lindley's (2003) "random walk with drift" model using field data from the Central Valley (Boughton et al. 2007; Williams et al. 2016), resulted in a run size estimate of 4,150 spawners per year (100% anadromous) and generated a 95% chance of species persistence over a 100-year time period. In southern California however, the number of spawners observed is far below this estimate.

The objective of this study was to compile and examine the occurrence and geographic distribution of adult Steelhead over the past 25 years throughout the southern California DPS that could serve as a baseline for future conservation efforts. This information will help assess the effectiveness of restoration and recovery actions. Individuals documented upstream of barriers to anadromous migration were considered resident *O. mykiss* and were not included in the enumeration of anadromous adults, although they are important components of Steelhead recovery. Due to uneven monitoring efforts and detection limitations, these observations provide only a limited snapshot, and they do not represent a census within any specific watershed or the DPS as a whole. They do, however, provide insight into relative abundance, distribution, and monitoring efforts over 25 years (1994 – 2018) since Southern Steelhead were federally listed as an endangered species.

METHODS

Study area

The study area spans the entire geographic region of the southern California Steelhead DPS identified in the recovery planning area (NMFS 2012; Figure 1). The southern DPS includes 50 creek/river systems and their tributaries covering approximately 500 kilometers of coastline, and it is further divided into five Biogeographical Population Groups (BPG). At the northern end of the DPS, the Monte Arido Highlands BPG includes the Santa Maria, Santa Ynez, Ventura, and Santa Clara rivers, which are large watersheds that extend well inland. Several smaller coastal creeks are also found throughout that region but were not included in the BPG such as the highly urbanized Conejo Creek, which is a tributary of Calleguas Creek. The Conception Coast BPG extends 80 km from Jalama Creek to Rincon Creek and includes: Arroyo Hondo, Mission, and Carpinteria creeks as well as the Goleta Slough complex, which includes Tecolotito, Los Carneros, San Pedro, Las Vegas, Maria Ygnacio, San Jose, and Atascadero creeks. The Santa Monica Mountains BPG extends approximately 52 km from Big Sycamore Creek south to Topanga Creek, including populations in Arroyo Sequit and Malibu Creeks. The Mojave Rim BPG encompasses the large watersheds and upper tributaries of the Los Angeles, San Gabriel, and Santa Ana Rivers, as well as Ballona Creek, which historically was an outlet of the Los Angeles River. The Santa Catalina Gulf Coast BPG extends from San Juan Creek at the north near Dana Point, south to the Mexican Border at the Tijuana River. This BPG includes coastal rivers such as San Mateo, San Onofre, Santa Margarita, San Luis Rey, and San Dieguito Rivers, as well as the larger San Diego Bay estuary, which is the terminus of the Sweetwater and Otay Rivers.

Survey methodology

We compiled and reviewed a variety of gray literature reports and technical memos in addition to published records for Steelhead occurrence data throughout the DPS (M. Gomez (South Coast Habitat Restoration), D. Hyatt (Bureau of Reclamation), K. McLaughlin (CDFW), C. Swift, personal communication; Hovey 2004; Capelli 2000 - 2017, CDFG 2007; CMWD 2009 – 2017; Downie and Kajtaniak 2010; Barabe 2013; COMB 2013, 2015; Allen 2014; Booth 2016; FOLAR 2016; COMB 2018; Dagit et al. 2018a, b). Surveys for adult Steelhead varied widely both in level of effort and timing throughout the DPS, but covered the majority of publicly accessible portions of the designated critical habitat, which extends from the ocean upstream to the limits of anadromy in numerous priority watersheds. Some reaches on private property were not surveyed. Upstream migration barriers were either natural, such as waterfalls, or, more commonly, anthropogenic barriers such as dams, bridges, and culverts. Detailed descriptions of these watersheds and barriers are found in the Southern California Steelhead Recovery Plan (NOAA 2012).

Documenting presence and abundance of adult Steelhead varied from opportunistic observations to more standardized observation methods consistent with protocols developed by the California Department of Fish and Wildlife (CDFW) Coastal Monitoring Program. These methods included snorkel/redd/carcass surveys, fish passage facilities, weir traps, video surveillance systems, Vaki Riverwatchers (VAKI Aquaculture Systems LTD, Iceland), in-stream Passive Integrated Transponder (PIT) antennas, and Dual-Frequency Identification Sonar (DIDSON: Sound Metrics, Washington, USA) cameras. Table 1 summarizes the location of all in-stream monitoring stations and devices. The time of equipment deployment within any year varied, depending on flow.

Table 1. Summary of fish passage/weir traps, video surveillance systems, in-stream antenna, and DIDSON deployments (UWCD = United Water Conservation District, CMWD = Casitas Municipal Water District, COMB = Cachuma Operation and Maintenance Board, RCDSMM = Resource Conservation District of the Santa Monica Mountains, CDFW = California Department of Fish and Wildlife).

Device	Deployment Location/River	Deployment Time Frame	Operators
Fish Passage	Vern Freeman Diversion Dam, Santa Clara River	1994–2018	UWCD
	Robles Fish Passage Facility, Ventura River	2006–2018	CMWD
Traps	Salsipuedes Creek, Santa Ynez River	1995–2018	COMB
	Hilton Creek, Santa Ynez River	1994–2018	COMB
	Lower Santa Ynez River	2005–2018	COMB
	Topanga Creek	2008–2014	RCDSMM
In-stream PIT antenna	Topanga Creek	2008–2016	RCDSMM
DIDSON camera	Salsipuedes Creek, Santa Ynez River	2013–2018	CDFW
	Carpinteria Creek	2014–2017	CDFW
	Ventura River	2014–2018	CDFW
	Topanga Creek	2012–2018	RCDSMM

Due to a variety of limitations, the level of monitoring effort was not consistent through time and geographic areas. Adult Steelhead were typically observed in traps, weirs, or by in-steam PIT antenna, video surveillance, and DIDSON cameras, or at fish passage facilities following storm events when flows could support migration. During spring and summer visual and snorkel surveys Steelhead were observed when detection in lower flows was possible. Stream flows in this region are flashy and inconsistent, making it difficult to effectively monitor the patchy spatial and temporal distribution of adult Steelhead throughout the DPS, particularly under turbid conditions. High turbidity is a distinctive feature of high flows in this region and depending on the drainage, can last days or weeks after significant rainfall with associated stormflow. Turbid conditions made it difficult to detect adult Steelhead at monitoring stations due to operational challenges and dangerous conditions at high flows when conditions might be favorable for migration. In addition, opportunistic observations were contributed by a variety of sources, including local conservation groups, governmental agency staff, and the general public. Opportunistic observations were verified by state, federal, or other experienced fisheries biologists based on photos, carcasses, or on-site visual confirmation.

Geographic observation details proceeding north to south

Cachuma Maintenance Operations Board (COMB) Fisheries Division staff have conducted migrant trapping from January to June since 1994 using weir traps at several locations within the lower Santa Ynez River (LSYR), Salsipuedes Creek, and Hilton Creek. During the migration season, COMB staff routinely conducted spawner/redd surveys according to National Marine Fisheries Service (NMFS) protocols throughout the LSYR basin in those reaches that historically provided spawning opportunities (AMC 2009). Monitoring was conducted to prepare biological assessments and for compliance measures set forth in the Cachuma Project Biological Opinion (NOAA 2000). In addition, COMB staff conducted snorkel surveys during spring, summer, and fall from 1994 to the present. Most reaches that hold over-summering *O. mykiss* were surveyed annually, and additional estuary monitoring was also conducted opportunistically during the study period in association with migrant trapping to track population abundance and distribution.

Snorkel and spawner/redd surveys were conducted at specific reaches within the Ventura River and upper tributaries. The Casitas Municipal Water District conducted redd and snorkel surveys since 2009 at index sites throughout the Ventura Basin (CMWD 2009 - 2017). Allen (2014) conducted snorkel surveys and electrofishing surveys in a subset of index reaches throughout the upper Ventura River from 2006 to 2012. The Robles Fish Passage Facility (23 km upstream from the ocean) was constructed in 2005 and is operated by Casitas Municipal Water District. Fish passage monitoring through the Robles facility was conducted with a VAKI Riverwatcher.

The Vern Freeman Diversion Dam (16 km upstream from the ocean) on the Santa Clara River is operated by United Water Conservation District and has monitored upstream migration since 1994. Prior to 1997, fish were captured in an upstream migrant trap at the facility's Denil fish ladder. From 1998 to 2003 fish were incidentally encountered through periodic dewatering of the fish ladder facility. In 2003 this facility was retrofitted to include

a false weir with a passive, video-based migrant surveillance system and was updated in 2010. This system was thought to potentially undercount adult Steelhead based on collection of several downstream migrating kelts observed in the facility's downstream migrant trap through 2014 that did not match observed upstream migrants. Due to permitting restrictions, the downstream migrant trap was not operated after 2015 and no upstream migrants were observed in the video surveillance system in this period (Booth 2016) although the system continues to be updated as technology improves. Stoecker and Kelley (2005) and Kelley (2008) conducted surveys throughout the Santa Clara River.

The Resource Conservation District of the Santa Monica Mountains (RCDSMM) in Arroyo Sequit and Malibu Creeks conducted monthly snorkel surveys in the Santa Monica Mountains BPG from 2005 through 2019, and in Topanga Creek from 2001 through 2019. Presence/absence surveys and lagoon monitoring were also conducted in Big Sycamore, Las Flores, Solstice, Trancas, and Zuma Creeks annually 2013 through 2018. DIDSON cameras have been used in several locations (Table 1) to augment storm event monitoring, but limitations due to high turbidity, bedload, fine sediment fouling, and extremely low flows resulted in fewer than 10 confirmed observations. The RCDSMM conducted five seining and angling efforts in the lower Los Angeles River from May 2014 to August 2015.

In 2016, the South Coast Steelhead Coalition initiated post-rain reconnaissance surveys in the four high-priority Steelhead recovery rivers in San Diego and Orange Counties including: San Juan/Arroyo Trabuco Creek, San Mateo Creek, Santa Margarita River, and the San Luis Rey River. These river mouths have seasonally accessible estuaries where adult Steelhead have occasionally been observed. Prior to the more organized surveys, opportunistic monitoring and incidental observations by CDFW, Caltrout, local conservation groups, and Trout Unlimited members documented adult Steelhead on several occasions.

Finally, we attempted to fit regression models to test for relationships between precipitation and associated stormflow with adult Steelhead abundance. However, due to the variable sampling methods, efforts and locations, the models fit the data poorly and had low explanatory ability, so the results were not reported.

RESULTS

In the 25 years from 1994 through 2018, we observed a total of 177 adult Steelhead throughout the southern California DPS. Annual Steelhead observations ranged from 1 fish (1997, 2016, and 2018) to 49 fish (2008), with a mean of 7 fish (SD = 10). Three or fewer fish were observed in 11 years. Most noteworthy were the Santa Ynez River (n = 16) and Mission Creek (n = 13) (Capelli 2008; USBR 2011).

Records of adult Steelhead observed are presented in Table 2 and were compiled from various sources. Observations are grouped based on the BPG location and 34 of the 50 river/creek systems within the DPS were surveyed. Of these, annual monitoring occurred for 25 years at the Freeman Diversion on the Santa Clara River, 24 years on the Santa Ynez River, 18 years in Topanga Creek, and 14 years in both Arroyo Sequit and Malibu Creeks. Monitoring in all other systems was more erratic and limited due to private property access issues, although seven more systems (Ventura River, San Antonio, Big Sycamore, Las Flores, Solstice, Trancas, and Zuma Creeks) were annually monitored from 2013 through 2018.

Table 2. Summary of adult steelhead observations for locations in the southern California Distinct Population Segment Biogeographical Population Groups (BPG) from 1994 through 2018 listed from north to south. Blank spaces indicate that no formal visual or snorkel survey results were available, and opportunistic observations noted in bold. A zero indicates that surveys were conducted but no anadromous *O. mykiss* observed.

BPG	Location	DPS Core Ranking	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	Total
Monte Arido Highlands	Santa Maria River	1	1	0	0	0	0	0						3	0	1	0	0	0									5
	Santa Ynez River	1		0	0	2	1	3	0	4	0	1	0	1	1	0	16	1	1	9	0	0	0	0	0	0	0	40
	Robles Diversion	1													4	0	6	0	1	0	0	0	0	0	0	0	0	11
	Ventura River	1														4						0	0	0	0	0	0	4
	San Antonio Creek	1																				0	0	0	0	1	0	1
	Santa Clara Freeman Diversion	1	1	1	2	0	0	1	2	2	0	0	0	0	0	0	2	2	0	0	3	0	0	0	0	0	0	16
Conception Coast	Arroyo Hondo	3																								**2**		2
	Goleta Slough Maria Ygnacio Creek	1							**1**								**1**	**1**								**1**		4
	Goleta Slough Atascadero Creek	1																	**2**			**2**						4
	Goleta Slough San Pedro Creek	1		1													**1**											2
	Mission Creek	1							**2**		**2**		**1**	**2**	**1**	**5**	**13**							**1**				27
	Carpinteria Creek	1															**3**											3
Santa Monica Mountains	Conejo Creek	Not listed																				**1**						1
	Big Sycamore Creek	3																				0	0	0	0	0	0	0
	Arroyo Sequit Creek	2												0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
	Las Flores Creek																					0	0	0	0	0	0	0
	Solstice Creek	3																				0	0	0	0	0	0	0
	Malibu Creek	1												0	1	2	4	1	2	2	3	3	5	1	0	1	0	25
	Topanga Creek	1								2	0	0	0	0	1	2	2	1	1	0	1	0	0	0	0	2	0	12
	Trancas Creek	Not listed																					0	0	0	0	0	0
	Zuma Creek	Not listed																					0	0	0	0	0	0

Table 2 continued.

BPG	Location	DPS Core Ranking	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	Total
Mohave Rim	Ballona Creek	Not listed														**2**												2
	Los Angeles River	3																						0				0
	San Gabriel River	1																							**1**			1
	Santa Ana River	2																										0
Santa Catalina Gulf Coast	San Juan Creek	1												**2**		**1**	**1**				**1**					0	1	6
	San Mateo Creek	1								**2**		**1**														1	0	4
	Santa Margarita River	1																**3**								0	0	3
	San Luis Rey River	1														**1**										0	0	1
	Los Penasquitos Creek	Not listed																			**1**							1
	TOTAL DPS		2	2	2	2	1	4	5	10	2	2	1	8	8	18	49	9	7	11	9	6	5	2	1	10	1	177

DISCUSSION

Survey results

The level of monitoring effort and efficiency varied throughout the DPS, and as a result, the low numbers of adult Steelhead observed during the past 25 years provides documentation of abundance and distribution. Anadromous Steelhead are difficult to detect, especially when numbers are low, because they typically migrate following peak flows when visibility is usually compromised and accessibility to river sites is dangerous for monitoring. Levels of effort to observe adult Steelhead increased over time using a variety of methods. Absence of documented sightings does not necessarily mean that adult Steelhead were not present, just that they were not observed, or that no surveys were conducted. We recognize that the occurrence numbers reported here likely underestimate the abundance of adult Steelhead across the DPS. As reported by Williams et al. (2016) and confirmed by our observations, at no point since Steelhead were listed as endangered in 1997 was the preliminary provisional viable population goal of 4,150 annual anadromous spawners observed in any individual watershed, nor throughout the DPS as a whole.

No geographic distribution pattern was observed, but larger systems with more hydrologically persistent estuaries and flow regimes (Santa Ynez River watershed) reported more adult Steelhead than smaller, more intermittently connected systems. Adult Steelhead were typically observed in traps, or by in-stream PIT antenna, video surveillance, and DIDSON cameras following storm events when flows could support migration. They were also observed during spring/summer visual and snorkel surveys when detectability was increased in lower flows and fish were trapped in the freshwater system and concentrated in refugia habitats. The large rainfall events in 2005 and 2008 provided good upstream migration, spawning, and rearing opportunities throughout the DPS and the potential for out-migrating smolts, which resulted in a substantial increase in adult anadromous Steelhead returns observed in 2008 and 2011, when there was also enough rainfall and associated flows to support migration. Having a close sequence of wet years provided the opportunity for previous cohorts to return in subsequent years as adults (e.g., the 2005 cohort returned in 2008). However, even though we logically expect these results the overall low abundance, variable sampling methods, inconsistent levels of effort, and differences in monitoring protocols used at each location made it difficult to identify clear correlations between adult abundance and rainfall/flows.

The limited and inconsistent monitoring for all life stages occurring in southern California makes it challenging to answer key questions regarding smolt production and adult returns, although the extreme drought from 2012 to 2016 was known to play a role in the lower Santa Ynez River (COMB 2015) and in Topanga Creek by reducing connectivity and limiting available rearing space (Dagit et al. 2017) and the overall population. Further monitoring and research are needed to determine what combinations of factors are resulting in such low numbers of adults (Boydstun and McDonald 2005; Adams et al. 2011; NOAA 2016). Although more Steelhead of all life stages were observed in locations with more consistent monitoring programs, differences still existed when considering passage limitations and system size. For instance, even though the monitoring effort and detection potential were higher in Topanga Creek than in Malibu Creek, passage restrictions at Topanga lagoon and drought-related low flow conditions resulted in fewer Steelhead accessing that system

as compared to Malibu Creek (Dagit et al. 2018a).

Given the limitations of the data available, it was not possible to examine the potential role of other variables on adult Steelhead migration such as lagoon breaching dynamics, timing of wet years needed for sufficient flow for adult migration, basin size, passage barriers, and smolt production, survival and emigration conditions. The fact that adult Steelhead were observed in some locations more frequently than others could reflect migration access, suitable habitat, level and type of monitoring effort and detection efficiency and ocean conditions.

Lack of a discernible distribution pattern of adult Steelhead is inconclusive given the monitoring limitations, overall low population densities, limited passage opportunities, and persistent drought conditions. All these systems were highly impacted by drought, especially from 2012 through 2016, resulting in little if any connection to the ocean, both intermittent and interrupted stream flow, and fragmented habitat upstream (COMB 2015; Dagit et al. 2017). Genetic data from southern California indicates that although many adults return to their natal stream to spawn, others stray (Clemento et al. 2009; Pearse et al. 2014). Due to the limited genetic information available it was not possible to assess the percentage of strays from the monitoring data evaluated during this study.

Influences of anadromy and residency

Factors influencing residency versus anadromy have been explored by Kendall et al. (2015), and their findings suggest that environmental conditions such as those occurring in southern California play an important role in determining propensity for anadromy, in addition to an individual's genotype (Hendry et al. 2004). The genetic potential for anadromy appears to persist in upper watershed locations throughout the southern California DPS below and in some instance above barriers (Thrower et al. 2004; Pearse et al. 2009; COMB 2013; Abadia-Cardoso et al. 2016; RCDSMM, unpublished data) and when opportunity arises, resident fish can smolt and emigrate to the ocean (McPhee et al. 2007; Holecek at al. 2012; Corter et al. 2013; Kendall et al. 2015). However, given the limited opportunity for passage due to low flows, there may not be sufficient numbers of smolts making it to the ocean, resulting in low numbers of adults returning. The snorkel/redd survey data, various fish passage/traps, and DIDSON camera data available from a few systems (Arroyo Sequit, Malibu, and Topanga Creeks (Dagit et al. 2018a, b); lower Santa Ynez River (COMB 2013; COMB 2018); Santa Clara River (Booth 2016); and Ventura River (CDFW, unpublished data), have documented low numbers of smolts throughout the DPS. Additionally, the effects of ocean conditions on smolts is another important factor. Michel (2018) found that flow levels during outmigration explained survival patterns for Chinook salmon more than marine conditions, and Kendall et al. (2015) suggest that there is a wide range of environmental and individual fitness variables that might influence marine survival. Analysis of the smolt-to-adult survival ratio in Southern Steelhead needs further study.

If the number of anadromous *O. mykiss* continues to decline, there will be increased dependence on resident Rainbow Trout for smolt production to maintain or re-establish the Steelhead life history. Resident *O. mykiss* currently play a key role in smolt production. Ultimately reproduction by both resident and anadromous life histories contributes to the overall abundance of *O. mykiss* (NOAA 2012). However, these resident populations are at risk from negative anthropogenic impacts, environmental effects, and other population-

level threats. Decreased expression of and/or retention of genetic markers associated with anadromy, coupled with low population numbers and barriers to migration, could exacerbate the issue of inbreeding in small isolated populations (Pearse et al. 2009). Sharp declines in local population numbers can cause inbreeding depression and lower fitness (Pearse et al. 2014; Abadia-Cardoso et al. 2016; Leitwein et al. 2016). Recent genetic studies of Southern California Steelhead populations indicate that these populations have low allelic diversity (Clemento et al. 2009; Pearse et al. 2009; Jacobson et al. 2014; Abadia-Cardosa et al. 2016; Apgar et al. 2017). Strays may be important for re-establishing populations once extirpated (Bell et al. 2011) and provide additional genetic diversity (Garza et al. 2014). Many of these populations retain alleles associated with anadromy (Pearse et al. 2009; Abadia-Cardosa et al. 2016), suggesting that despite their primarily freshwater resident life history pattern, the genetic potential for anadromy is still present. Importantly, the potential for resident *O. mykiss* to establish anadromous populations (Nielsen 1999; Courter et al. 2013; Phillis et al. 2016; Apgar et al. 2017) further supports their importance in promoting Steelhead recovery. Given recent occurrence of multiple large-scale catastrophic events in this region (e.g., wildfires and drought), genetically informed conservation actions must happen expediently to avoid further loss of genetic diversity potentially present in these isolated populations while other Steelhead recovery efforts continue.

Recovery planning and future needs

How should monitoring approaches be adjusted to accommodate challenges in assessing DPS status and trends? There are numerous identified factors contributing to the decline of this species within the southern California DPS both in its freshwater and ocean environments. The federal Recovery Plan (NOAA 2012) provides a thorough assessment of the threats to southern California DPS Steelhead and prioritizes recovery actions specific to each watershed that could help mitigate these threats. Increased and consistent monitoring efforts are needed, especially in the smaller systems and tributaries, to further understand distribution and abundance patterns and assess the effectiveness of restoration and recovery actions to increase populations over time. Further monitoring and research are needed to assess what combinations of factors are resulting in such low numbers of adults, although the extreme drought from 2012 to 2016 played a large role in population reduction in Topanga Creek (Dagit et al. 2017) and the lower Santa Ynez River (COMB 2015). Additional threats such as barriers to fish passage and migration, impacts to freshwater habitat quality, degradation of estuarine habitat, water quality and quantity, increased development, prolonged and intensive drought, loss of habitat due to wildfires, and increased number of both aquatic and terrestrial invasive species are well documented within the southern California DPS and have cumulatively taken a toll (NOAA 2012).

Numerous barrier removal and habitat restoration projects have been implemented in the past 25 years to address some of these threats throughout the DPS (NOAA 2016), but recent wildfires, floods, and persistent drought have seriously reduced the effectiveness of those efforts (Smith et al. 2018). These events, especially wildfires, have further reduced the number of small, isolated remnant populations found mostly in upper tributaries (Smith et al. 2018; CDFW, unpublished data). Restoring dependable flow through a natural flow regime despite drought and anthropogenic impacts are long-term efforts key to promoting Steelhead recovery. Advancements in surface and groundwater management to address the

competing needs of providing potable water supply as well as maintain stream baseflow during the dry season may provide opportunities to ensure more reliable stream flows. The Thomas Fire (2017) impacted many drainages throughout Santa Barbara and Ventura Counties; the Whittier Fire (2017) impacted the Santa Ynez watershed in Santa Barbara County, and the Woolsey Fire (2018) impacted all creeks in the Santa Monica Mountains except Topanga Creek. Subsequent fire related floods and debris flows continue to impact these areas and caused local extirpation (CDFW, unpublished data). Evidence from previous wildfires suggests that when local populations are extirpated, intervention may be needed for re-establishment (Rinne 1996; Cooper et al. 2015).

To identify the proximate causes limiting the DPS from meeting population level recovery criteria proposed for viable populations in core watersheds (NOAA 2012), continued and consistent monitoring efforts are needed. Building quantitative models that consider both anadromous and resident fish in the production of smolts, in addition to watershed-specific carrying capacities would be a valuable effort towards refining population goals. Removal of fish passage barriers, habitat improvement, invasive species removal, and adequate river flow are essential components, but may not be sufficient to restore populations.

Novel approaches are needed to protect and increase the resiliency of resident and anadromous *O. mykiss.* Such approaches may include one or more of the following as part of a carefully considered regional conservation strategy for the DPS: 1) removal of invasive aquatic species (in particular predatory species such as bass and sunfish) to create additional suitable habitat; 2) translocation and assisted migration of *O. mykiss* into vacant refugia habitat both above and below dams to increase geographic distribution; 3) conservation hatcheries to increase abundance and genetic diversity; and, 4) cryopreservation to preserve genetic material of high-risk populations (Labbe et al. 2001). Policies that afford further protection to resident Rainbow Trout should also be considered, such as the Similarity of Appearance clause in the ESA (Fejtek 2017). Additional genetic work is needed to better understand factors that regulate anadromy.

Projected impacts of climate changes (Sun et al. 2015) suggest that protecting the more resilient, and warm water tolerant (Matthews and Berg 1997; Myrick and Check 2005; Spina 2007; Sloat and Osterback 2013) Steelhead populations found in southern California would be prudent. Southern Steelhead Trout are incredibly resilient (Boughton et al. 2010; NOAA 2012; Moyle et al. 2017), but despite 25 years of protection under the federal Endangered Species Act, have not been able to overcome the many threats to their survival. The future of this species at the southern extent of its range will depend on a suite of carefully planned and expeditiously implemented recovery actions but most importantly, recognition that protecting both resident and anadromous *O. mykiss* together is beneficial for the recovery of the species as a whole.

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Author Contributions

Conceived and designed the study - RD, ML, DMCC, THR
Collected the data - all
Performed the analysis of the data - RD, MTB, SH, SDL, SJ, THR
Authored the manuscript - RD, MTB, SH, SDL, SJ, THR
Provided critical revision of the manuscript - RD, MTB, TH, SH, SDL,ML, SJ, THE

LITERATURE CITED

Adams, P. B., L. B. Boydstun, S. P. Gallagher, M. K. Lacy, T. McDonald, and K. E. Shaffer. 2011. California Coastal Salmonid Population Monitoring: Strategy, Design and Methods. Fish Bulletin 180. California Department of Fish and Game, Sacramento, CA, USA. Available from: https://pdfs.semanticscholar.org/ d725/649665 dbbd038fade2590f47d72bb2f320a3.pdf

Abadia-Cardoso, A., D. E. Pearse, S. Jacobson, J. Marshall, D. Dalrymple, F. Kawasaki, G. Ruiz-Campos, and J. C. Garza. 2016. Population genetic structure and ancestry of Steelhead/Rainbow Trout (*Oncorhynchus mykiss*) at the extreme southern edge of their range in North America. Conservation Genetics 17:675–689.

Allen, M. 2014. Steelhead population and habitat assessment in the Ventura River/ Matilija Creek Basin 2006–2012. Normandeau Associates, Inc., Arcata, CA, USA. Available from: http://www.matilijadam.org/documents/ Steelhead_Surveys/Ventura%20Steelhead%20Assessment%202012%20FINAL.pdf

Santa Ynez River Adaptive Management Committee (AMC). 2009. Summary and analysis of annual fishery monitoring in the Lower Santa Ynez River, 1993–2004. Prepared for the National Marine Fisheries Service by the Santa Ynez River Adaptive Management Committee. Santa Barbara, CA, USA. Available from: https://www.cachuma-board.org/files/ 12c4b6d73/Addendum+NOD+2008-07-22.pdf

Apgar, T. M., D. E. Pearse, and E. P. Palkovacs. 2017. Evolutionary restoration potential evaluated through the use of a trait linked genetic marker. Evolutionary Applications 2017:10:485–497.

Barabe, R. 2013. Population estimate for Pauma Creek. Technical Report, California Department of Fish and Wildlife, CA, USA. Available upon request from: www.rcdsmm.org

Beeman, J. W., D. W. Rondorf, M. E. Tilson, and D. A. Venditti. 1995. A nonlethal measure of smolt status of juvenile Steelhead based on body morphology. Transactions of the American Fisheries Society 124:764–769.

Bell, E., R. Dagit, and F. Lignon. 2011. Environmental factors controlling a persistent population of southern California Steelhead (*Oncorhynchus mykiss).* Bulletin of the Southern California Academy of Sciences 110:1–16.

Booth, M. T. 2016. Fish passage monitoring at the Freeman 1993–2014. United Water

Conservation District, Santa Paula, CA, USA. Available from: https://www.unitedwater.org/images/stories/Resource-Conservation/Freeman-Diversion/Monitoring-Reports/Booth_2016-focal_spp_report.pdf

Boughton, D. A., P. B. Adams, E. Anderson, C. Fusaro, E. Keller, E. Kelley, L. Lentsch, J. Nielson, K. Perry, H. Regan, J. Smith, C. Swift, L. Thompson, and F. Watson. 2006. Steelhead of the south-central/southern California coast: population characterization for recovery planning. NOAA Technical Memorandum National Marine Fisheries Service. Southwest Regional Office, Long Beach, CA, USA. Available from: http://swfsc.noaa.gov/ publications/TM/SWFSC/NOAA-TM-NMFS-SWFSC-407.PDF

Boughton, D. A., P. B. Adams, E. Anderson, C. Fusaro, E. Keller, E. Kelley, L. Lentsch, J. Nielsen, K. Perry, H. Regan, J. Smith, C. Swift, L. Thompson, and F. Watson. 2007. Viability criteria for Steelhead of the south-central and southern California coast. NOAA Technical Memorandum NMFS- SWFSC-407, CA, USA. Available from: https://swfsc.noaa.gov/publications/TM/ SWFSC/NOAA-TM-NMFS-SWFSC-407.PDF

Boughton, D. A. 2010a. A forward-looking frame of reference for Steelhead recovery on the South-Central and southern California Coast. NOAA Technical Memorandum NMFS- SWFSC-466. California, USA. Available from: https:// swfsc.noaa.gov/ publications/FED/00009.pdf

Boughton, D. A. 2010b. Some research questions on recovery of Steelhead on the South-Central and Southern California Coast. NOAA Technical Memorandum NMFS-SWFSC-467. California, USA. Available from: https:// repository.library.noaa.gov/view/noaa/3821

Boydstun, L. B., and T. McDonald. 2005. Action plan for monitoring California's coastal salmonids. WASC-#-1925. Final report to NOAA Fisheries, Santa Cruz, CA, USA. Available from: https://swfsc.noaa.gov/publications/FED/ 00856.pdf

Capelli, M. 2000. Report adult Steelhead lower Mission Creek (Santa Barbara County). Technical Memo, March 17, 2000. Available upon request from: www.rcdsmm.org

Capelli, M. 2001. Adult Steelhead recovered from San Pedro Creek (tributary to the Goleta Slough), Santa Barbara County. Technical Memo, March 15, 2001. Available upon request from: www.rcdsmm.org

Capelli, M. 2004. Report adult Steelhead lower Mission Creek (Santa Barbara County). Technical Memo, January 20, 2005. Available upon request from: www.rcdsmm.org

Capelli, M. 2005. Report adult Steelhead lower Mission Creek (Santa Barbara County). Technical Memo, October 15, 2005. Available upon request from: www.rcdsmm.org

Capelli, M. 2006. Report adult Steelhead lower Mission Creek (Santa Barbara County). Technical Memo, October 20, 2006. Available upon request from: www.rcdsmm.org

Capelli, M. 2007. Report deceased adult Steelhead lower Mission Creek (Santa Barbara County). Technical Memo, March 21, 2007. Available upon request from: www.rcdsmm.org

Capelli, M. 2007. Report adult Steelhead lower Mission Creek (Santa Barbara County).

Technical Memo, March 31, 2007. Available upon request from: www.rcdsmm.org

Capelli, M. 2007. Report adult Steelhead lower San Juan Creek (Orange County). Technical Memo, March 31, 2007. Available upon request from: www.rcdsmm.org

Capelli, M. 2007. Report Steelhead spawning in lower Mission Creek (Santa Barbara County). Technical Memo, April 30, 2007. Available upon request from: www.rcdsmm.org

Capelli, M. 2007. Report Steelhead spawning in lower Mission Creek (Santa Barbara County). Technical Memo, June 30, 2007. Available upon request from: www.rcdsmm.org

Capelli, M. 2007. Recent Ventura River Steelhead (*Oncorhynchus mykiss*) sightings. Technical Memo, August 27, 2007. Available upon request from: www.rcdsmm.org

Capelli, M. 2008. Observation of Steelhead, lower Mission Creek (Santa Barbara County). Technical Memo, February 21, 2008. Available upon request from: www.rcdsmm.org

Capelli, M. 2008. Report adult Steelhead, lower Mission Creek (Santa Barbara County). Technical Memo, March 30, 2008. Available upon request from: www.rcdsmm.org

Capelli, M. 2008. Observation of Steelhead, lower Mission Creek (Santa Barbara County). Technical Memo, March 30, 2008. Available upon request from: www.rcdsmm.org

Capelli, M. 2008. Adult Steelhead observations in lower San Pedro Creek (February 28-March 21, 2008). Technical Memo, March 30, 2008. Available upon request from: www.rcdsmm.org

Capelli, M. 2008. Report adult Steelhead, lower San Juan Creek (Orange County). Technical Memo, March 31, 2008. Available upon request from: www.rcdsmm.org

Capelli, M. 2008. Report of deceased adult Steelhead, Maria Ygnacio Creek. Technical Memo, April 2, 2008. Available upon request from: www.rcdsmm.org

Capelli, M. 2008. Observation of Steelhead in Carpinteria Creek (Santa Barbara County). Technical Memo, April 15, 2008. Available upon request from: www.rcdsmm.org

Capelli, M. 2008. Observation of Steelhead, lower Mission Creek (Santa Barbara County). Technical Memo, May 30, 2008. Available upon request from: www.rcdsmm.org

Capelli, M. 2009. Report Steelhead kelt, Maria Ygnacio Creek. Technical Memo, May 15, 2009. Available upon request from: www.rcdsmm.org

Capelli, M. 2012. Report adult Steelhead, lower San Juan Creek (Orange County). Technical Memo, April 30, 2012. Available upon request from: www.rcdsmm.org

Capelli, M. 2013. Atascadero Creek Steelhead observation, Santa Barbara, California (March 18-19, 2013). Technical Memo, April 9, 2013. Available upon request from: www.rcdsmm.org

Capelli, M. 2016. Report adult Steelhead, lower Mission Creek (Santa Barbara County). Technical Memo, January 30, 2016. Available upon request from: www.rcdsmm.org

Capelli, M. 2017. Observation of Steelhead redds, Arroyo Hondo (Santa Barbara County). Technical Memo, March 21, 2017. Available upon request from: www.rcdsmm.org

Capelli, M. 2017. Adult Steelhead observation, Maria Ygnacio Creek (Santa Barbara

County). Technical Memo, May 30, 2017. Available upon request from: www.rcdsmm.org

California Department of Fish and Game (CDFG). 2007. Field survey report: Steelhead sighting in the San Luis Rey River. CDFG South Coast Region, 2 May 2007. Available from: https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID =75573

Casitas Municipal Water District (CMWD). 2009. Annual Robles Fish Passage Facility Progress Report. Casitas Municipal Water District, Oak View, CA, USA. Available from: https://www.casitaswater.org/home/show document?id=10

Casitas Municipal Water District (CMWD). 2010. Annual Robles Fish Passage Facility Progress Report. Casitas Municipal Water District, Oak View, CA, USA. Available from: https://www.casitaswater.org/home/show document?id=10

Casitas Municipal Water District (CMWD). 2011. Annual Robles Fish Passage Facility Progress Report. Casitas Municipal Water District, Oak View, CA, USA. Available from: https://www.casitaswater.org/home/show document?id=10

Casitas Municipal Water District (CMWD). 2012. Annual Robles Fish Passage Facility Progress Report. Casitas Municipal Water District, Oak View, CA, USA. Available from: https://www.casitaswater.org/home/show document?id=10

Casitas Municipal Water District (CMWD). 2013. Annual Robles Fish Passage Facility Progress Report. Casitas Municipal Water District, Oak View, CA, USA. Available from: https://www.casitaswater.org/home/show document?id=10

Casitas Municipal Water District (CMWD). 2014. Annual Robles Fish Passage Facility Progress Report. Casitas Municipal Water District, Oak View, CA, USA. Available from: https://www.casitaswater.org/home/show document?id=10

Casitas Municipal Water District (CMWD). 2015. Annual Robles Fish Passage Facility Progress Report. Casitas Municipal Water District, Oak View, CA, USA. Available from: https://www.casitaswater.org/home/show document?id=10

Casitas Municipal Water District (CMWD). 2016. Annual Robles Fish Passage Facility Progress Report. Casitas Municipal Water District, Oak View, CA, USA. Available from: https://www.casitaswater.org/home/show document?id=10

Casitas Municipal Water District (CMWD). 2017. Annual Robles Fish Passage Facility Progress Report. Casitas Municipal Water District, Oak View, CA, USA. Available from: https://www.casitaswater.org/home/show document?id=10

Cachuma Operation and Maintenance Board (COMB). 2013. 2011 Annual Monitoring Summary and Trend Analysis. Prepared for the Bureau of Reclamation and the National Marine Fisheries Service, Cachuma Operation and Maintenance Board (COMB), Fisheries Division. Cachuma Operations and Maintenance Board, Santa Barbara, CA, USA. Available from: https:// www.cachuma-board.org/files/79687fbc3/2011+Annual+Monitoring+Summary. pdf

Cachuma Operation and Maintenance Board (COMB). 2015. 2014 Annual Monitoring Summary and Trend Analysis. Prepared for the Bureau of Reclamation and the National Marine Fisheries Service, Cachuma Operation and Maintenance Board (COMB), Fisheries Division. Cachuma Operations and Maintenance Board, Santa Barbara, CA, USA. Available from: https://www.cachumaboard.org/files/5d3cb4d9c/2014+Annual+Monitoring+Summary.pdf

Cachuma Operation and Maintenance Board (COMB). 2018. WY2017 Annual Monitoring Summary. Prepared by the Cachuma Operation and Maintenance Board (COMB),

Fisheries Division. Cachuma Operations and Maintenance Board, Santa Barbara, CA, USA. Available from: https://www.cachuma-board.org/files/9caad22f0/WY2017-AMS-all-final-072219-1.pdf

Clemento, A. J., E. C. Anderson, D. Boughton, D. Girman, and J. C. Garza. 2009. Population genetic structure and ancestry of *Oncorhynchus mykiss* populations above and below dams in south-central California. Conservation Genetics 10:1321–1336.

Cooper, S. D., H. M. Page, S. W. Wiseman, K. Klose, D. Bennett, T. Even, S. Sadro, C.E. Nelson and T. L. Dudley. 2015. Physiochemical and biological responses of streams to wildfire severity in riparian zones. Freshwater Biology 60:2600–2619.

Courter I. I., D. B. Child, J. A. Hobbs, T. M. Garrison, J. J. G. Glessner, and S. Duery. 2013. Resident rainbow trout produce anadromous offspring in a large interior watershed. Canadian Journal of Fisheries and Aquatic Science 70:701–710.

Dagit, R., D. Alvarez, R. Dauksis, B. Demirci, H. Nuetzel, Stillwater Sciences, and J. C. Garza. 2018a. Comprehensive lifecycle monitoring report for *O. mykiss* in Topanga Creek, California. Final Report 2008–2018. Prepared for California Department of Fish and Game Contract No. P1550012, RCD of the Santa Monica Mountains, Topanga, CA, USA. Available from: https://www.rcdsmm.org/wp-content/uploads/2016/04/P1550012-Lifecycle-Final-Report-May-2018.pdf

Dagit, R., D. Alvarez, S. Contrares, and R. Dauksis. 2018b. Santa Monica Bay anadromous adults and juvenile Steelhead monitoring. Final Report 2013–2018. Prepared for CDFW Contract No. P1250013. Prepared by Resource Conservation District of the Santa Monica Mountains, Topanga, CA, USA. Available upon request from: www.rcdsmm.org

Dagit, R., E. Bell, K. Adamek, J. Mongolo, E. Montgomery, N. Trusso, and P. Baker. 2017a. The effects of a prolonged drought on southern Steelhead Trout (*Oncorhynchus mykiss*) in a coastal creek, Los Angeles County, California. Bulletin Southern California Academy of Sciences 116:162–172.

Downie, S., and D. Kajtaniak. 2010. San Luis Rey River Assessment. Coastal Watershed Planning and Assessment Program. California Department of Fish and Game. CA, USA. Available upon request from: www.rcdsmm.org

Fejteck, S. M. 2017. The implications of current restoration practices and regulatory Policy for recovery of federally endangered southern California Steelhead. Dissertation, University of California, Los Angeles, CA, USA. Available from: https://escholarship.org/uc/item/4nq5n311

Friends of the Los Angeles River (FOLAR). 2016. State of the River: The Long Beach Fish Study. Published by Friends of the Los Angeles River. Available from: https://www.watershedhealth.org/single-post/2016/06/10/Long-Beach-Fish-Study

Garza, J. C., E. A. Gilbert-Horvath, B. C. Spence, T.H. Williams, H. Fish, S. A. Gough, J. H. Anderson, D. Hamm, and E. C. Anderson. 2014. Population structure of Steelhead in coastal California. Transactions of the American Fisheries Society 143:134–152.

Haner, P. V., J. C. Faler, R. M. Schrock, D. W. Rodndorf, and A. G. Maule. 1995. Skin reflectance as a nonlethal measure of smoltification for juvenile salmonids. North American Journal of Fisheries Management 15:814–822.

Hendry, A. P., T. Bohlin, B. Jonsson, and O. K. Berg. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. Pages 27-32 in A. P. Hendry and A. C. Stea-

rns, editors. Evolution Illuminated, Salmon and Their Relatives. Oxford University Press, Oxford, UK.

Holecek, D. E., D. L. Scarnecchia, and S. E. Miller. 2012. Smoltification in an impounded, adfluvial Redband Trout Population upstream from an impassable dam: Does it persist? Transactions of the American Fisheries Society 141:68–75.

Hovey, T. E. 2004. Current status of southern Steelhead rainbow trout in San Mateo Creek, California. California Fish and Game 90:140–154.

Jacobson, S., J. Marshall, D. Dalrymple, F. Kawasaki, D. Pearse, A. Abadia-Cardoso, and J. C. Garza. 2014. Genetic analysis of trout (*Oncorhynchus mykiss*) in southern California coastal rivers and streams. Final Report for California Department of Fish and Wildlife Fisheries Restoration Grant Program; Project No. 0950015, CA, USA. Available from: https:// californiatroutinc.app.box.com/s/ zk05my3n-noxphhyo4kdd1telkbnnrbc5/folder/49630781777

Kelley, E. 2008. Steelhead trout smolt survival in the Santa Clara and Santa Ynez River estuaries. Prepared by University of California, Santa Barbara, for California Department of Fish and Game, Fisheries Restoration Grant Program. Santa Barbara, CA, USA. Available from: https://www.westcoast. fisheries.noaa.gov/ publications/recovery_planning/salmon_Steelhead/domains/south_central_ southern_california/kelley._Steelhead_smolt_survival_in_the_santa_clara_and_ santa_ynes_river_esturies__california_2008.pdf

Kendall, N. W., J. R. McMillan, M. R. Sloat, T. W. Buehrens, T. P. Quinn, G. R. Pess, K. V. Kuzishchin, M. M. McClure, and R. W. Zabel. 2015. Anadromy and residency in Steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and patterns. Canadian Journal of Fisheries and Aquatic Science 72:319–342.

Labbe, C., A. Martoriati, A. Devaux, and G. Maisse. 2001. Effect of sperm cryopreservation on sperm DNA stability and progeny development in rainbow trout. Molecular Reproduction and Development 60:397–404.

Leitwein, M., J. C. Garza, and D. E. Pearse. 2016. Ancestry and adaptive evolution of anadromous, resident, and adfluvial rainbow trout (*Oncorhynchus mykiss*) in the San Francisco bay area: application of adaptive genomic variation to conservation in a highly impacted landscape. Evolutionary Applications 10:56–67.

Lindley, S. T. 2003. Estimation of population growth and extrication parameters from noisy data. Ecological Applications 13:806–813.

Mattews, K. R., and N. H. Berg. 1997. Rainbow Trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. Journal of Fish Biology 50:50–67.

McPhee, M. V., F. Utter, J. A. Stanford, K. V. Kuzishchin, K. A. Savvaitova, D. S. Pavlov, and F. W. Allendorf. 2007. Population structure and partial anadromy in *Onchorhynchus mykiss* from Kamchatka: relevance for conservation strategies around the Pacific Rim. Ecology of Freshwater Fisheries 16:539–547.

Michel, C. J. 2018. Decoupling outmigration from marine survival indices outsized influence of streamflow on cohort success for California's Chinook salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 76:1398–1410.

Moyle, P., R. Lusardi, P. Samuel, and J. Katz. 2017. State of the Salmonids: Status of California's emblematic fishes 2017. Center for Watershed Sciences, University of California, Davis and California Trout, San Francisco, CA, USA. Available from:

https://watershed.ucdavis.edu/files/content/news/SOS% 20II Final.pdf

Myrick, C. A., and J. J. Cech, Jr. 2005. Effects of temperature on the growth, food consumption, and thermal tolerance of age-0 Nimbus-strain Steelhead. North American Journal of Aquaculture 67:324–30.

National Marine Fisheries Service (NOAA). 1997. Federal Register 43937.

National Marine Fisheries Service (NOAA). 2000. Cachuma Project Biological Opinion, U.S. Bureau of Reclamation operation and maintenance of the Cachuma Project on the Santa Ynez River in Santa Barbara, California. National Marine Fisheries Service, Southwest Region, Long Beach, CA, USA.

National Marine Fisheries Service (NOAA). 2002. Federal Register 21586.

National Marine Fisheries Service (NOAA). 2006. Federal Register 5248.

National Marine Fisheries Service (NOAA). 2012. Southern California Steelhead Recovery Plan. NOAA Fisheries. South West Coast Region, California Coastal Office, Long Beach, CA, USA. Available from: https://www. westcoast.fisheries.noaa.gov/publications/recovery_planning/salmonSteelhead/domains/south_central_southern_california/2013_scccs_recoveryplan final.pdf

National Marine Fisheries Service (NOAA). 2016. 5-Year Review: summary and evaluation of southern California Coast Steelhead Distinct Population Segment. National Marine Fisheries Service. West Coast Region, California Coastal Office, Long Beach, CA, USA. Available from: https://www.westcoast. fisheries.noaa.gov/publications/status_reviews/salmon_Steelhead/2016/2016_cc-chinook_nc-steelhd.pdf

Negus, M. T. 2003. Determination of smoltification status in juvenile migratory rainbow trout and Chinook salmon in Minnesota. North American Journal of Fisheries Management 23:913–927.

Nielsen, J. L. 1999. The evolutionary history of Steelhead (*Oncorhynchus mykiss*) along the US Pacific Coast: Developing a conservation strategy using genetic diversity. Journal of Marine Science 56:449–458.

Pearse, D. E., S. A. Hayes, M. H. Bond, C. V. Hanson, E. C. Anderson, R. B. MacFarlane, and J. C. Garza. 2009. Over the falls? Rapid evolution of ecotypic differentiation in Steelhead/rainbow trout (*Oncorhynchus mykiss*). Journal of Heredity 100:515–525.

Pearse, D. E., M. R. Miller, A. Abadía-Cardoso, and J. C. Garza. 2014. Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in Steelhead/rainbow trout. Proceedings Biological Sciences/The Royal Society 281:20140012.

Phillis, C. C., J. W. Moore, M. Buoro, S. A. Hayes, J. C. Garza, and D. E. Pearse. 2016. Shifting thresholds: rapid evolution of migratory life histories in Steelhead/rainbow trout, *Oncorhynchus mykiss*. Journal of Heredity Symposium Article 51–60.

Rinne, J. N. 1996. Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. North American Journal of Fisheries Management 16:653–658.

Smith, S. F., M. Gomez, J. White, and L. Boyd. 2018. Fire and flow forum strategic plan. Published by South Coast Habitat Restoration. Available from: http:// schabitatrestoration.org/projects/fire-and-flow

Sloat, M. R. and A. K. Osterback. 2013. Maximum stream temperature and the occurrence,

abundance, and behavior of Steelhead Trout (*Oncorhynchus Mykiss*) in a Southern California stream. Canadian Journal of Fisheries and Aquatic Sciences 70:64–73.

Spina, A. P. 2007. Thermal ecology of juvenile Steelhead in a warm-water environment. Environmental Biology of Fishes 80:23–24.

Stoecker, M., and E. Kelley. 2005. Santa Clara River Steelhead trout: assessment and recovery opportunities. Prepared for The Nature Conservancy and The Santa Clara River Trust Council, Santa Clara, CA, USA. Available from: http://www.stoeckerecological.com/reports/SantaClaraReport.pdf

Sun, F., D. B. Walton, and A. Hall. 2015. A hybrid dynamical-statistical downscaling technique. Part II: End of century warming projections predict a new climate state in the Los Angeles region. Journal of Climate 28:4618–4636.

Thrower, F. P., J. J. Hard, and J. E. Joyce. 2004. Genetic architecture of growth and early life-history transitions in anadromous and derived freshwater populations of Steelhead. Journal of Fisheries Biology 65:286–307.

U.S. Bureau of Reclamation (USBR). 2011. 2008 Annual monitoring report and trend analysis for 2005-2008. Prepared for the National Marine Fisheries Service by the Cachuma Operation and Maintenance Board for USBR, Santa Barbara, CA, USA. Available from: https://www.cachuma-board.org/ files/12c4b6d73/Addendum+NOD+2008-07-22.pdf

Williams, T. H., B. C. Spence, D. A. Boughton, R. C. Johnson, L. Crozier, N. J. Mantua, M. O'Farrell, and S. T. Lindley. 2016. Viability assessment for Pacific salmon and Steelhead listed under the Endangered Species Act: Southwest. 2 February 2016 Report to National Marine Fisheries Service – West Coast Region from Southwest Fisheries Science Center, Fisheries Ecology Division, USA. Available from: https://watershed.ucdavis.edu/files/biblio/NOAA-TM-NMFS-SWFSC-564_0.pdf

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Reported vessel strike as a source of mortality of White Sturgeon in San Francisco Bay

NICHOLAS J. DEMETRAS*, BRENNAN A. HELWIG, AND ALEXANDER S. MCHURON

University of California, Santa Cruz, Cooperative Institute for Marine Ecosystems and Climate (CIMEC), Affiliated with: Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060, USA

**Corresponding Author: nicholas.demetras@noaa.gov*

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Ship strikes are a source of injury and mortality for many aquatic species worldwide (Holland 1986; Laist and Shaw 2006; Hazel et al. 2007). Over the past few years, the impact of vessel strikes involving large cetaceans has received significant attention (Laist et al. 2001; Peel et al. 2018). However, the impact of vessel strikes on large adult fishes has received considerably less attention worldwide. Currently, the knowledge base of vessel strikes and their potential impact on fishes in the scientific literature is limited to a few studies involving large, long-lived fishes such as sturgeon (Gutreuter et al. 2003; Simpson and Fox 2009; Brown and Murphy 2010; Balazik et al. 2012; Watanabe et al. 2013). Recently, both Simpson and Fox (2009) and Brown and Murphy (2010) reported vessel strike mortalities of the ESA listed Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the Delaware River estuary, while Balazik et al. (2012) reported vessel strike mortalities of Atlantic sturgeon in the tidal freshwater portion of the James River, Virginia. Using an-egg-per-recruit analysis, Brown and Murphy (2010) demonstrated that vessel strike mortalities could be detrimental to the population if more than 2.5% of the female Atlantic Sturgeon are killed annually in the Delaware Estuary.

Despite the potential importance of vessel strike mortalities in limiting Atlantic Sturgeon recovery on the US East Coast (Brown and Murphy 2010), very little is known about White Sturgeon (*A. transmontanus*) vessel interactions on the US West Coast, especially in the heavily trafficked waters of the San Francisco Estuary (SFE). Though anecdotal evidence and personal observations (with no supporting information) abound, we were unable to find any direct evidence of confirmed White Sturgeon vessel interactions in the scientific literature. In this short article, we report on a vessel strike that we observed which resulted in the decapitation of a White Sturgeon in the SFE.

All observations and specimen collections were made from the National Oceanic & Atmospheric Administration's R/V Heron near the Port of Benicia, California USA. Due to the incomplete and decapitated nature of the specimen encountered, we used a head to body length of 4.5:1 as reported by Ruiz-Campos et al. (2011) to estimate its total length. Using this estimate of size we applied the length at age equation, l_t=230.59[1–$e^{-0.0533(t+2.9176)}$])] developed by Brennan & Cailliet (1989) for White Sturgeon in the SFE, where l_t is the length at age t (years) to estimate a minimum age. We used ArcGIS v10.5 to visualize the location of the observed vessel strike with an added bathymetry layer of the surrounding area.

On 24 April 2018 at approximately 1000 (PDT), we observed a crude oil tanker depart from the Port of Benicia on the north shore of the Carquinez Strait, directly downstream of the Interstate 680 Bridge, in approximately 20 m of water (Figure 1). The tanker measured approximately 250 m in length with a beam of 44 m and a maximum draught of 14.8 m. Immediately after its departure, we saw what appeared to be a live White Sturgeon struggling at the surface in an area the tanker had previously occupied. Upon closer inspection, it was determined to be a recently decapitated adult White Sturgeon measuring 92 cm total length without the head (Figures 2, 3). A significant amount of blood was still present in the body, which immediately drained upon removal from the water. Several strong tail beats and a general thrashing of the body suggested that the removal of the head occurred immediately prior to our observation of the fish struggling at the surface. No marine mammals, anglers, or other potential perpetrators were observed in the immediate vicinity prior to, during or after the fish was brought on board. The clean nature of the decapitation wounds (Figure 2) suggest they were caused by something quite sharp and powerful, and are not consistent

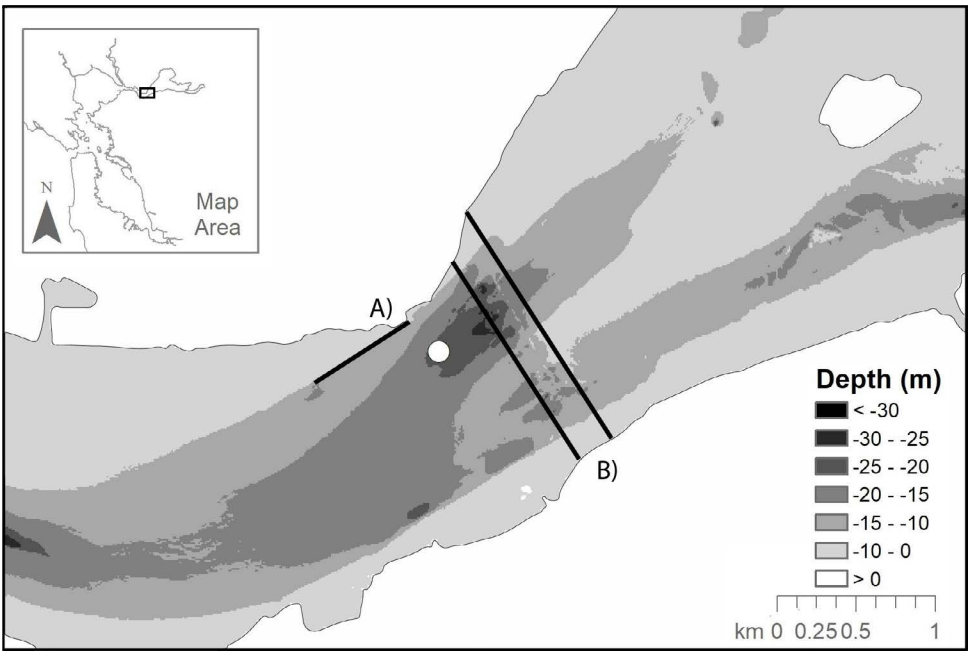

Figure 1. Location of Carquinez Strait in relation to the greater San Francisco Estuary, CA, USA (upper left). A) Port of Benicia with black line representing wharf structure. B) Parallel black lines indicate the location of the east and west spans of the I-680 Bridge. White circle denotes approximate location of observed vessel strike of White Sturgeon overlaid with the surrounding bathymetry.

Figure 2. Close up of wound with noticeable slice marks presumably caused by the vessel's propeller.

Figure 3. Lateral view of the white sturgeon with noticeable lacerations and trauma to the head region.

with the dentition of the California sea lion (*Zalophus californianus*), the dominant marine mammal predator in the area (Sinai et al. 2014).

The size of the fish and presence of male gonads suggest that the fish may have been at least 10 to 12 years old and possibly of breeding age (Moyle 2002). Using the measured body length of 92 cm and a head to body length ratio of 4.5:1, as reported by Ruiz-Campos et al. (2011), we estimated the total length *including* the head, at approximately 112 cm. The length at age equation, developed by Brennan and Cailliet (1989) for White Sturgeon in the SFE supports the minimum age estimate of our specimen at approximately 10 years old. This length at age equation relies in large part upon age data inferred from annual rings laid down in the cross section of White Sturgeon pectoral fins. However, this method may underestimate the true age of White Sturgeon by as much as 30-60% in some cases (Paragamian and Beamesderfer 2003).

Though we are aware of anecdotal and speculative reports of vessel strikes involving San Francisco Bay-Delta White Sturgeon in the scientific literature (Hildebrand et al. 2016), we are unaware of any previously published eyewitness accounts. The Carquinez Strait, within the greater SFE complex, is a heavily trafficked passageway that connects San Pablo Bay to Suisun Bay and the interior Sacramento-San Joaquin Delta. Both San Pablo and Suisun Bay are the primary, non-spawning habitat of adult White Sturgeon in the SFE and they move regularly between the two (Israel et al. 2011). This effectively acts as a bottleneck through which all fishes must pass and results in a deep channel with increased tidal flow suitable for the navigation of large vessels.

The characteristic bathymetry and tidal flow of the Carquinez Strait may increase the spatial overlap of White Sturgeon and large vessels in shipping channels as observed by Hondrop et al. (2017) in Lake Sturgeon (*A. fulvescens*) from the Detroit River. In addition, a growing body of research has shown that many Sturgeon species may not be as benthic oriented as once believed (Kelly and Klimley 2012; Watanabe et al. 2013; Beardsall et al. 2016; Taylor et al. 2016; Breece et al. 2018). Using vector analysis, Kelly and Klimley (2012) found that Green sturgeon spent the majority of their time in the upper water column, often at the surface, while undergoing rapid long-distance movements in deep, high-current areas such as the Carquinez Strait. To compound matters, Dijohnson (2019) found that Atlantic Sturgeon did not exhibit a behavioral avoidance response in the presence of vessel traffic. While similar vector analysis data is lacking for White Sturgeon, and behavioral data in the presence of vessel traffic is lacking for both Green and White Sturgeon, it may be reasonable to suggest that they behave similarly. Taken together these factors may lead to an increased risk of vessel strikes for both species in the Carquinez Strait.

While the impact of vessel strikes in the SFE on the White Sturgeon population may currently be of minor importance on its own, the cumulative impact when taken into consideration along with other stressors may present significant future challenges (Moyle et al. 2015). At this time, vessel strikes may have a greater impact on the population persistence of the ESA listed southern distinct population segment (sDPS) of Green Sturgeon (*A. medirostris*) due to their smaller population sizes. Southern DPS Green Sturgeon regularly pass through the SFE and the Carquinez Strait from late winter to spring in route to spawning grounds in the Sacramento and Feather Rivers (Mora et al. 2017; Seesholtz et al. 2015). However, we were unable to find any reports (anecdotal or otherwise) of vessel strikes involving Green Sturgeon in the SFE. This lack of observed vessel strikes may reflect upon the much smaller population size of Green Sturgeon in comparison to White Sturgeon in the SFE (Heublein et

al. 2017). The apparent use of the Carquinez Strait primarily as a migration corridor by adult Green Sturgeon, as opposed to White Sturgeon that regularly transit the Carquinez Strait between feeding grounds, may limit the vessel strike susceptibility of adult Green Sturgeon to specific periods of migration (Heublein et al. 2009). However, sub-adult Green Sturgeon, similar to the size of our specimen, have been recorded in and around the Carquinez Strait, and may be vulnerable to vessel strikes as well (NMFS 2009).

It is apparent through both anecdotal reports and now eyewitness accounts that vessel strikes pose a risk of both injury and mortality to White Sturgeon in the Carquinez Strait, the SFE, and possibly elsewhere. However, the magnitude and extent of the threat, not only in the SFE but also throughout its entire range, is not fully understood. As a first step, a registry to report Sturgeon vessel strikes would provide a centralized repository of data that is currently lacking, similar to NOAA Fisheries National Marine Mammal Stranding Network (https://www.westcoast.fisheries.noaa.gov/protected_species/marine_mammals/national_stranding_network.html) or that of the International Whaling Commission's Ship Strikes database (https://iwc.int/ship-strikes). Such a database could assist fishery managers in making future decisions in regard to White Sturgeon, a long-lived fish that faces significant threats throughout its native range.

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Author Contributions

Collected the data: ND, BH, AM
Authored the manuscript: ND
Provided critical revision of the manuscript: BH, AM

LITERATURE CITED

Balazik, M. T., K. J. Reine, A. J. Spells, C. A. Fredrickson, M. L. Fine, G. C. Garman, and S. P. McIninch. 2012. The potential for vessel interactions with adult Atlantic Sturgeon in the James River, Virginia. North American Journal of Fisheries Management 32:1062–1069.

Beardsall, J. W., M. J. W. Stokesbury, L. M. Logan-Chesney, and M. J. Dadswell. 2016. Atlantic Sturgeon *Acipenser oxyrinchus* Mitchell, 1815 seasonal marine depth and temperature occupancy and movement in the Bay of Fundy. Journal of Applied Ichthyology 142:1202–1214.

Breece, M. W., D. W. Fox, and M. J. Oliver. 2018. Environmental drivers of adult Atlantic Sturgeon movement and residency in the Delaware Bay. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 10:269–280.

Brennan, J. S., and G. M. Cailliet. 1989. Comparative age-determination techniques for White Sturgeon in California. Transactions of the American Fisheries Society 118:296–310.

Brown, J. J., and G. W. Murphy. 2010. Atlantic Sturgeon vessel-strike mortalities in the Delaware estuary. Fisheries 35:72–83.

Dijohnson, A. M. 2019 Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) behavioral responses to vessel traffic and habitat use in the Delaware River, USA. Thesis, Delaware State University, Dover, USA.

Gutreuter, S., J. M. Dettmers, and D. H. Wahl. 2003. Estimating mortality rates of adult fish from entrainment through propellers of river towboats. Transactions of the American Fisheries Society 132:646–661.

Hazel, J., I. R. Lawler, H. Marsh, and S. Robson. 2007. Vessel speed increases collision risk for the Green turtle *Chelonia mydas.* Endangered Species Research 3:105–113.

Heublein, J. C., J. T. Kelly, C. E. Crocker, A. P. Klimley, and S. T. Lindley. 2009. Migration of Green Sturgeon, *Acipenser medirostris*, in the Sacramento River. Environmental Biology of Fishes 84:245–258.

Heublein, J., R. Bellmer, R. D. Chase, P. Doukakis, M. Gingras, D. Hampton, J.A. Israel, Z. J. Jackson, R. C. Johnson, O. P. Langness, S. Luis, E. Mora, M. L. Moser, L. Rohrbach, A. M. Seesholtz, T. Sommer, and J. S. Stuart. 2017. Life history and current monitoring inventory of San Francisco Estuary Sturgeon. USDOC National Oceanic & Atmospheric Administration, National Marine Fisheries Service, Southwest Fishery Science Center, Fisheries Ecology Division, Santa Cruz, CA, USA.

Hildebrand, L. R., A. D. Schreier, K. Lepla, S. O. McAdam, J. McLellan, M. J. Parsley, V. L. Paragamian, and S. P. Young. 2016. Status of White Sturgeon (*Acipenser transmontanus* Richardson, 1863) throughout the species range, threats to survival, and prognosis for the future. Journal of Applied Ichthyology 32:261–312.

Holland, L. E. 1986 Effects of barge traffic on distribution and survival of ichthyoplankton and small fishes in the Upper Mississippi River. Transactions of the American Fisheries Society 115:152–165.

Hondrop, D. W., D. H. Bennion, E. F. Roseman, C. M. Holbrook, J. C. Boase, J. A. Chiotti, M. V. Thomas, T. C. Wills, R. G. Drouin, S. T. Kessel, and C. C. Krueger. 2017. Use of navigation channels by Lake Sturgeon: does channelization increase vulnerability of fish to ship strikes? PLOS ONE 12(7): e0179791.

Israel, J., A. Drauch, and M. Gingras. 2011. Life history conceptual model for White Sturgeon (*Acipenser transmontanus*). Delta Conceptual Model. California Department Fish and Wildlife, Sacramento, CA, USA.

Kelly, J. T. and A. P. Klimley. 2012. Relating the swimming movements of Green Sturgeon to the movement of water currents. Environmental Biology of Fishes 93(2):151–167.

Laist, D. W., and C. Shaw. 2006. Preliminary evidence that boat speed restrictions reduce deaths of Florida Manatees. Marine Mammal Science 22:472–479.

Laist, D. W., A. R. Knowlton, J. G. Mead, A. S. Collet, and M. Podesta. 2001. Collisions between ships and whales. Marine Mammal Science 17(1):35–37.

Mora, E. A., R. D. Battleson, S. T. Lindley, M. J. Thomas, R. Bellmer, L. J. Zari, and A. P. Klimley. 2017. Estimating the annual spawning run size and population size of the Southern Distinct Population Segment of the Green Sturgeon. Transactions of the American Fisheries Society 147:195–203.

Moyle, P. B. 2002. Inland Fishes of California. University of California Press, Berkeley and Los Angeles, CA, USA.

Moyle, P. B., R. M Quiñones, and J. V. Katz, and J. Weaver. 2015. Fish species of special concern in California. California Department of Fish and Wildlife, Sacramento, CA, USA.

National Marine Fisheries Service (NMFS), Southwest Region Protected Resources Division. 2009. Designation of critical habitat for the threatened southern Distinct Population Segment of North American Green Sturgeon: Final Biological Report Available from: https://www.westcoast.fisheries.noaa.gov/publications/protected_species/other/green_sturgeon/g_s_critical_habitat/gschd_finalbiologicalrpt.pdf

Paragamian, V. L., and R. C. Beamesderfer. 2003. Growth estimates from tagged White Sturgeon suggest that ages from fin rays underestimate true age in the Kootenai River, USA and Canada. Transactions of the American Fisheries Society 132:895–903.

Peel, D., J. N. Smith, and S. Childerhouse. 2018. Vessel strike of whales in Australia: the challenges of analysis of historical data. Frontiers in Marine Science 5(69):1–14.

Ruiz-Campos, G., J. L. Castro-Aguirre, and F. J. Garcia-De Leon. 2011. First specimen of the White Sturgeon (*Acipenser transmontanus*, Richardson, 1863) in coastal waters of Mexico with data on its genetic identity. California Fish and Game 97:36–42.

Seesholtz, A. M., M. J. Manuel, and J. P. Van Eenennaam. 2014. First documented spawning and associated habitat conditions for Green Sturgeon in the Feather River, California. Environmental Biology of Fishes 98:905–912.

Simpson, P. C., and D. A. Fox. 2009. A contemporary understanding of the Delaware River Atlantic Sturgeon: survival in a highly impacted aquatic ecosystem. Pages 1–4 in A. Haro, K. L. Smith, R. A. Rulifson, C. M. Moffitt, R. J. Klauda, M. J. Dadswell, R. A. Cunjak, J. E. Cooper, K. L. Beal, and T. S. Aver, editors. Challenges for diadromous fishes in a dynamic global environment. American Fisheries Society, Symposium 69, Bethesda, MD, USA.

Sinai, N. L., R. H. Dadaian, P. H. Kass, and F. J. M. Verstraete. 2014. Dental pathology of the California sea lion (*Zalophus californianus*). Journal of Comparative Pathology 151:113–121.

Taylor, D. A., K. Ohashi, J. Sheng, M. K. Litvak. 2016. Oceanic distribution, behaviour, and winter aggregation area of adult Atlantic Sturgeon, *Acipenser oxyrinchus oxyrinchus*, in the Bay of Fundy, Canada. PLOS ONE 11(4):e0152470.

Watanabe, Y. Y., Q. Wei, H. Du, L. Li, and N. Myazaki. 2013. Swimming behavior of Chinese Sturgeon in natural habitat as compared to that in a deep reservoir: preliminary evidence for anthropogenic impacts. Environmental Biology of Fishes 96:123–130.

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A retrospective look at mountain lion populations in California (1906-2018)

JUSTIN A. DELLINGER* AND STEVEN G. TORRES[†]

California Department of Fish and Wildlife, Wildlife Investigations Lab, 1701 Nimbus Rd, Suite D, Rancho Cordova, CA 95670, USA

[†]*Retired*

**Corresponding Author: justin.dellinger@wildlife.ca.gov*

Mountain lion (*Puma concolor*) population management in California has varied widely over the past 100 plus years, ranging from a bounty system (1906-1963) to specially-protected status (1972-present). To elucidate how these different management approaches have influenced California's mountain lion populations, we estimated historical population trends by combining purposeful (i.e., bounty and depredation) and incidental (i.e., vehicle strike) mortality statistics with estimates of annual growth and mortality rates derived from the literature. We used a backwards population projection method to estimate annual abundance and population trends, starting with population sizes drawn randomly from a uniform distribution ranging from 1,000-5,000. These back-calculations suggest that the bounty was effective at reducing mountain lion populations, as all simulations indicated a statewide population decline during this period. Specially-protected status was also likely effective, as mountain lion populations appear to have increased statewide following cessation of the bounty period. These analyses demonstrate the effectiveness of various management approaches to influence mountain lion population trends for the intended results, and provide context for understanding historical aspects of mountain lion populations in California, which is unique from other areas given the species' specially-protected status here.

Key words: bounty, depredation, mortality, *Puma concolor*, vehicle strike

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Mountain lion (*Puma concolor*) population management in California has gone through many changes (Table 1), resulting from changing attitudes of public stakeholders, policy makers, and elected officials (Bruskotter and Shelby 2010; Davenport et al. 2010). Mountain lions were subject to a bounty system in California from 1906-1963 (Mansfield and Weaver 1989), with the amount paid per mountain lion varying over time and with sex

Table 1. Management status of mountain lions (*Puma concolor*) through time in California, USA.

Years	Status	per Male	per Female
1906–1916	Bounty	$20	$20
1917–1944	Bounty	$20	$30
1945–1963	Bounty	$50	$60
1964–1969	Vermin	NA	NA
1970–1971	Game	$1[a]	$1
1972–1986	Protected	NA	NA
1987–1990	Game	NA[b]	NA
1991–2018	Protected	NA	NA

[a]Price per hunting tag

[b]No hunting season occurred

(Table 1). In 1919, the California Department of Fish and Game (Department) employed the first full-time statewide lion hunter (McLean 1954), and the number of individuals employed for this purpose grew to a maximum of five in 1948. The Department employed at least one individual through 1959, prior to terminating the bounty program in 1963 (Nowak 1974). Records show that bounty hunters took 224 mountain lions on average each year, totaling 12,580 over the duration of the bounty system (Mansfield and Weaver 1989). After the bounty system ended in 1963, hunters could take mountain lions year-round without a bag limit or hunting license. In 1970 the Fish and Game Commission designated mountain lions as a game species, wherein a hunting license and tag were required for the 1970 and 1971 hunting seasons. In 1972, the state legislature enacted a moratorium on the hunting of mountain lions due to growing public concern over the status of the species in California (Fitzhugh and Gorenzel 1986). The moratorium expired in 1986 and ungulate conservation groups successfully lobbied to re-designate mountain lions as a game species. As a result, the Department began to develop regulations for harvest quotas and management zones, and to assess environmental impacts in compliance with the California Endangered Species Act (Mansfield and Weaver 1989). However, a majority vote by the citizens of California passed Proposition 117 (Fish & Game Code §4800-4809) in 1990, which classified mountain lions as a specially-protected mammal species. This unique status was a political designation, and not based on biological information regarding population abundance or trend. Thus, from 1990 to present, human-caused mountain lion mortalities have been limited to vehicle strikes, targeted removal under the authority of a depredation permit, poaching, public safety concerns, and take of mountain lions negatively impacting California bighorn sheep (Torres et al. 1996; Fish & G. Code §4801).

Mountain lions' specially-protected status has resulted in a spectrum of concerns from interested parties. On one end of the spectrum are ungulate conservation groups who have expressed concern that the mountain lion population may be increasing and thus negatively impacting deer (*Odocoileus hemionus*) herds due to high rates of predation (Proposition 197 [1996]; Walgamuth 2017). Conversely, predator conservation groups have suggested that a combination of mortality factors (e.g., habitat loss, degradation, and fragmentation; vehicle

strikes; depredation take; disease; etc.) may be causing the state's mountain lion population to decline in numbers and genetic diversity to a level that may threaten the species' viability (Proposition 117 [1990]; Walter 2015). To address these concerns, wildlife managers and biologists must gain insight into historical trends and the contemporary abundance of mountain lion populations to make effective management decisions.

In light of the controversies regarding mountain lion status in California, the Department seeks to clarify the effects of historical management on mountain lion populations. For this purpose, we proposed the following hypotheses: 1) the statewide mountain lion population in California declined during the bounty period (1906-1963); and 2) the statewide mountain lion population in California increased during the period of increasing legal protections (1972-2018). We tested these hypotheses by analyzing historical statewide data on mountain lion mortalities within a discrete growth equation to estimate historical population trends. Our objectives were to estimate statewide population trends during and after the bounty period, and to elucidate how historical and current management policies have affected the statewide mountain lion population.

METHODS

Study area

We collected mortality data from California county courthouses; California Departments of Fish and Wildlife (Department), and Transportation (Caltrans); California Highway Patrol (CHP); and United States Department of Agriculture, Wildlife Services (USDA Wildlife Services). County courthouse and Department records supplied data on mountain lions removed during the bounty period, and included data from all counties except Imperial, Sacramento, San Francisco, Solano, and Sutter, from which no bounty records were available. CHP and Caltrans supplied statewide data on mountain lions killed due to vehicle strikes. Department and USDA Wildlife Services supplied statewide data on mountain lions removed due to depredation.

Data collection

We collected statewide data on mountain lions purposefully killed due to bounties, hunting, and depredations from 1906-2018 (McLean 1954; Fitzhugh and Gorenzel 1986; Mansfield and Weaver 1989), and on mountain lions incidentally killed due to vehicle strikes from 2009-2018 (Table 2). There were no data available on purposeful removals between the conclusion of the bounty system in 1963 and establishment of a hunting season in 1970, nor were accurate data available on sex and age of individuals for any animals (bountied, hunted, depredated, vehicle-killed) but the most recent depredations (2015-2017).

For all these data, we made a number of assumptions described here, which may variously have contributed to over- or under-estimates of the number of lions removed from the population. Throughout the time period of interest, mountain lions undoubtedly died due to additional human-related incidents (e.g., poaching). Because of a scarcity of accurate data on such incidents, we assumed that our bounty, hunting, depredation, and vehicle strike data represented the majority of human-caused mountain lion mortalities. This assumption may underestimate the number of individuals removed. In addition, bounty systems encourage

Table 2. Data on mountain lions (*Puma concolor*) purposefully (i.e., bounty, hunting, and depredation) and incidentally (i.e., vehicle strike) removed through time in California. Incidental removals 2015–2018 are raw data while incidental removals prior to that are derived based on the assumption of decreasing traffic volume backward through time.

Status	Year	# Purposefully Removed	# Incidentally Removed
Depredation	2018	100	56
	2017	87	70
	2016	120	47
	2015	101	49
	2014	90	52
	2013	68	51
	2012	77	61
	2011	105	55
	2010	108	50
	2009	103	57
	2008	123	61
	2007	137	51
	2006	128	56
	2005	125	59
	2004	133	56
	2003	111	57
	2002	124	51
	2001	121	57
	2000	151	56
	1999	120	48
	1998	123	52
	1997	104	47
	1996	110	48
	1995	117	52
	1994	124	45
	1993	76	46
	1992	83	52
	1991	74	47
	1990	76	51
	1989	76	45
	1988	61	44
	1987	50	48
	1986	45	40
	1985	58	47
	1984	37	44

Table 2 continued

Status	Year	# Purposefully Removed	# Incidentally Removed
	1983	26	42
	1982	18	48
	1981	12	46
	1980	12	48
	1979	21	40
	1978	8	36
	1977	7	36
	1976	6	44
	1975	2	44
	1974	3	37
	1973	4	40
	1972	6	42
Hunting	1971	35	41
	1970	83	36
Bounty	1963	99	33
	1962	115	38
	1961	144	36
	1960	127	39
	1959	112	37
	1958	136	35
	1957	157	39
	1956	165	33
	1955	188	34
	1954	155	36
	1953	188	35
	1952	167	31
	1951	140	33
	1950	202	35
	1949	228	29
	1948	188	35
	1947	199	35
	1946	213	34
	1945	152	34
	1944	177	29
	1943	155	29
	1942	159	30

Table 2 continued

Status	Year	# Purposefully Removed	# Incidentally Removed
	1941	236	29
	1940	224	28
	1939	291	28
	1938	252	27
	1937	221	29
	1936	185	31
	1935	249	27
	1934	225	32
	1933	268	23
	1932	313	27
	1931	292	26
	1930	293	24
	1929	297	23
	1928	339	26
	1927	247	24
	1926	253	26
	1925	240	27
	1924	279	28
	1923	230	23
	1922	302	21
	1921	252	25
	1920	238	22
	1919	263	22
	1918	192	23
	1917	171	24
	1916	181	25
	1915	170	23
	1914	196	23
	1913	232	22
	1912	253	21
	1911	270	21
	1910	322	20
	1909	360	22
	1908	443	20
	1907	117	23
	1906	118	23

inflated reporting (i.e., submitting animals for bounty in California while they were actually taken in a neighboring state), so bounty data may overestimate the number of individuals removed (Fitzhugh and Gorenzel 1986). However, it should be noted that the majority (>50%) of the bounty records submitted were by agency employees. Further, none of the border counties had high numbers of bounties paid relative to interior counties. As such, we assumed that these records are accurately reported and represent animals taken within California. There is also a likelihood that vehicle strike data are underreported. We assumed that the proportion of missing records is similar from year-to-year and does not account for a significant number of records in a given year. To account for potentially missing depredation reports, we compared Department records and USDA Wildlife Services records for 1998-2018. Discrepancies between the two sets of records were generally within ±10 individuals statewide, and occurred for a variety of reasons (e.g., lost paperwork, position vacancies, etc.). Where discrepancies existed between the two datasets, we used the higher of the two reported numbers to represent number of animals removed via depredation in the given year.

Population simulations

Using a back-calculation method to estimate the historical population of mountain lions in California, we began with a discrete growth equation, modified to include rates of human-caused mortality:

$$N_{t+1} = N_t\lambda_t - d_t - N_t\lambda_t m_t, \quad (1)$$

where λ is the annual intrinsic growth rate, *d* is the combined number of individuals taken purposefully and incidentally per year, and *m* is the coefficient of additional mortality (e.g., intraspecific strife, poaching, and disease) per year (Mykra and Pohja-Mykra 2015). Estimating the trend of a population from one year to the next requires an estimate of potential annual growth and mortality. Based on results reported by Beausoleil et al. (2013), we established the mean intrinsic growth (λ) at 1.14 (14% annual increase) with a standard deviation of 0.03 to allow for annual stochasticity (Robinson et al. 2008; Cooley et al. 2009; Robinson and DeSimone 2011; Beausoleil et al. 2013). We estimated the number of mountain lions killed annually by vehicle strike from 2000-2014 (prior to available data) by using the mean number killed annually by vehicle strike from 2015-2018, with a standard deviation of ±10% to account for annual stochasticity. For every decade prior to this (e.g., 1990-1999, 1980-1989), we decreased the mean by 10% from the next most recent timespan (i.e., mean for 1990-1999 was 10% less than mean for 2000-2014), but held standard deviation at ±10%. We decreased the mean from current to past to simulate decreased vehicle traffic in the past, and thus decreasing likelihood of vehicle strike. We established the coefficient of additional mortality per year (*m*) at a mean of 0.10 with a standard deviation of 0.03 to allow for annual stochasticity in additional mortality factors (Robinson et al. 2008; Cooley et al. 2009; Robinson and DeSimone 2011; Beausoleil et al. 2013). For the years in which there were no take data (1964-1969), *d* is the average removal rate during the two hunting seasons (59 mountain lions/year), and we allowed annual population parameters to vary stochastically as with all other iterations. Thus, for each year that we simulated population abundance, we randomly drew values for λ and *m* from a normal distribution with a mean of 0.14 and 0.10, respectively, and a standard deviation of 0.03. To assess impacts of missing data on population trends, we estimated sensitivity of population simulations to changes in mean values of *λ* and *m* (see Supplementary Material).

For estimating population sizes via back-calculation, we transformed Equation 1:

$$N_{t-1} = (N_t + d_t)/[(1 - m_t)\lambda_t]. \quad (2)$$

We considered N_{t-1} to be the population size at the end of the year after accounting for annual growth, additional mortality, and individuals taken that year. We iterated the backwards equation annually starting with 2018 and ending with 1906. We randomly drew the initial population abundance at 2018 from a uniform distribution ranging from 1,000-5,000 individuals. We selected the upper limit of the uniform distribution from potential mountain lion densities previously identified within high, medium, and low suitability habitats across California (Torres et al. 1996; Table 3). These upper threshold values are within reported confidence intervals derived in other areas of the western United States (Cougar Management Guidelines Working Group 2005). We selected the lower limit of the uniform distribution from recently published results on effective population size (N_e) in regional mountain lion populations (Gustafson et al. 2018) and ratios between N_e/N (Frankham 1995). Together, the upper and lower thresholds likely contain the actual statewide abundance of mountain lions in California, particularly considering the estimated average adult mountain lion density across the western United States (1.6/100 km^2; Quigley and Hornocker 2010; Beausoleil et al. 2013), and the amount of mountain lion habitat in California (186,000 km^2; Torres et al. 1996). We also assessed sensitivity of population simulations to changes in starting values (see Supplementary Material).

After deriving initial abundance, we iterated back-calculations according to Equation 2 for 112 years (timespan from 1906-2018) with 1,000 replications, and values of λ and m varying stochastically according to mean and standard deviation values detailed above. We also generated minimum and maximum population trajectories with our simulations to illustrate the extreme limits within which California mountain lion populations may grow or decline. For the minimum population trajectory, we kept the annual growth rate constant at one standard deviation above the mean λ for a value of 1.17, and the additional annual mortality rate constant at one standard deviation below the mean of m for a value of 0.07. For the maximum population trajectory, we kept the annual growth rate constant at one standard deviation below the mean of λ for a value of 1.11, and the additional annual mortality rate constant at one standard deviation above the mean of m for a value of 0.13.

Table 3. Demonstration of systematically adjusted density values for each habitat suitability class and derived range of initial mountain lion population values for back calculation of mountain lion (*Puma concolor*) population projections.

Suitability	Habitat Suitability Score[a]	Size	Mountain Lion Density (animals/100km^2)[b]
High	>0.60	170,486 km^2	2.20
Medium	0.41–0.60	63,085 km^2	1.60
Low	0.20–0.40	24,641 km^2	1.00
None	<0.20	165,759 km^2	0.00

[a]Habitat suitability thresholds were on a scale of 0–1

[b]Densities of mountain lions (animals/100km^2) for each habitat suitability.

Sensitivity testing

Because each replicate began with a randomly drawn value, we estimated the sensitivity of population trend estimates to variation in input values. We thus derived the upper and lower 10% population values for each decade (beginning in 1910 and concluding in 2010) for all 1,000 replicates. Next, we estimated slopes of values between decades (e.g., 1910 to 1920) for those upper and lower 10% values, and tested for significant differences between them. For example, we estimated the slope between the upper 10% values for 1910 and 1920 to represent population trend between the two periods. We did the same for the lower 10% values in the same timeframe, and then statistically compared the two slopes using a Student's t-test (Mykra and Pohja-Mykra 2015). We elected to use conservatively high and low initial values, to maximize the possibility that the actual mountain lion population would be represented within these estimates. All non-significant ($\alpha > 0.05$) p-values thus provided increased confidence in the given range for mountain lion abundance for the given time period. We used Program R, version 3.1.2 (R Core Team 2014) for all statistical analyses.

Hypothesis testing

To test our two hypotheses, we determined the proportion of years among all simulations in which removal was above or below 14% of N_t. Removals from the simulated populations above this level would lead to a decline that presumably corresponds with a removal threshold for mountain lions in California above which populations would have declined (Cougar Management Guidelines Working Group 2005, Beausoleil et al. 2013). Removals from the simulated populations below 14% would lead to an increase that presumably corresponds with a removal threshold for mountain lions in California below which populations would have increased.

Results

Results of 1,000 replicates of back-calculations on mountain lion removal data consistently suggest a steady decline occurred in mountain lion populations from 1906 to the mid-1960s, followed by an increase until the mid-1990s, after which the population appears to have stabilized until about 2000. However, after 2000, our results diverged (Figure 1). Replicates with starting values in the low 1,000s exhibited a second population decline occurring in the early 2000s that continues until present. Replicates with starting values ranging from approximately 1,500 to 5,000 exhibited a slowing or stabilizing population growth rate from the late 1990s to mid-2000s, and a stable or increasing population growth rate, with population values comparable to the input values.

We found no significant differences between the slopes of the upper and lower 10-year population trends (the sensitivity analysis) from 1910 to 1980 (Table 4). However, after 1980 we detected significant differences in those slopes in the simulated data. This divergence began several decades after the conclusion of the bounty period, and was likely a result of the large range in starting values which itself was due to uncertainty about the current status of the mountain lion population across California. The closer the date a given annual population simulation was to the initial starting value, the greater influence that initial starting value had on the associated numeric value of that simulation. Thus, all simulations

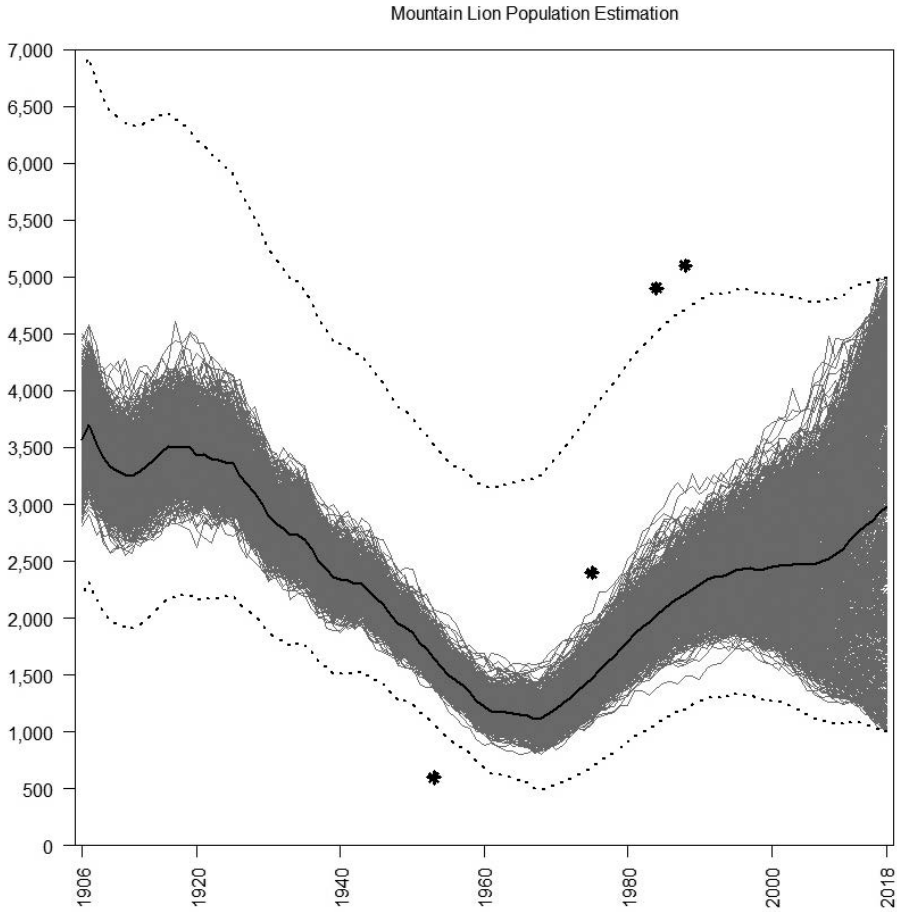

Figure 1. Mountain lion (*Puma concolor*) population simulation results for California from 1906-2018. Simulation results were yielded by running 1,000 iterations wherein a random number between 1,000-5,000 was selected as a starting population estimate. Back calculation of yearly population size to 1906 was then done using mountain lion demographic estimates derived from literature searches and mountain lion removal data from California. Previous mountain lion population abundance estimates reported by California Department of Fish and Game are represented by asterisks (*) symbols. Individual simulations are represented by gray lines. The mean for all simulations is represented by the bold black line. The maximum and minimum population simulations are represented by the dotted black lines. The upper dotted line was created by holding annual population growth constant at 1.17 (one standard deviation above the mean of 1.14) and additional annual mortality constant at 0.07 (one standard deviation below the mean of 0.10). The lower dotted line was created by holding annual population growth constant at 1.11 (one standard deviation below the mean of 1.14) and additional annual mortality constant at 0.13 (one standard deviation above the mean of 0.10).

Table 4. Statistical comparisons of slopes of simulated population trends over 10-year periods for the lower and upper 10% starting population values, respectively, using a Student's t-test. The first mean lower 10% value represents the mean of the lowest 10% of the simulated population estimates for the first year in the comparison. For example, the value 2,898 represents the mean value of the lower 10% of simulated population estimates for 1910, while the value 3,094 represents the mean value of the lower 10% of simulated population estimates for 1920. The same associations apply for the upper 10% column.

Years compared	Mean lower 10%	Mean upper 10%	t-score[a]	p-value
1910 & 1920	2,898; 3,094	3,816; 3,996	-0.34	0.74
1920 & 1930	3,094; 2,749	3,996; 3,527	-1.69	0.09
1930 & 1940	2,749; 2,139	3,527; 2,749	1.48	0.14
1940 & 1950	2,139; 1,729	2,749; 2,210	1.64	0.10
1950 & 1960	1,729; 1,177	2,210; 1,549	1.11	0.27
1960 & 1970	1,177; 927	1,549; 1,364	-1.68	0.09
1970 & 1980	927; 1,389	1,364; 1,984	-176	0.08
1980 & 1990	1,389; 1,840	1,984; 2,676	-2.48	0.01
1990 & 2000	1,840; 1,897	2,676; 3,103	-6.15	<0.01
2000 & 2010	1,897; 1,524	3,103; 3,685	-10.75	<0.01

[a]Degrees of Freedom = 3,996

support that the statewide mountain lion population experienced a decline during the bounty period and a subsequent increase (Table 4) after the bounty was ended.

DISCUSSION

The type of modeling we report here is not inherently tied to mountain lion populations, nor are such analyses new (Elton and Nicholson 1942; Jedrzejewski et al. 1996; Kojola 2005; Mykra and Pohja-Mykra 2015). This simple approach to using purposeful and incidental mortality data to infer historical population trends is an important tool for managers who lack adequate population information. However, the approach does have limitations, and its results cannot be assumed to represent precise population figures. In addition to the assumptions described previously, the data and our population modeling approach present limitations which preclude such precision. Neither the size and ecological diversity of California, nor the magnitude of anthropogenic changes to habitat that have occurred therein during the period of interest (Torres et al. 1996) are accounted for in our results. For example, although we did adjust for decreasing vehicle density going back in time, our estimates were limited by lack of accurate data. Nor did our estimates account for changes in road densities and other developments that may have affected lion densities and removal rates. Further, our model did not account for density dependent factors, including prey abundance, that may have affected our results. Our model treated all mountain lion removals as additive, which was likely not the case with the actual removals, at least not for all lion subpopulations (Lambert et al. 2006; Robinson et al. 2008; Cooley et al. 2009). Consequently, the actual rates of decline and subsequent increase were likely somewhat different than those we detected with our model. We suspect that density dependence was

likely marginally important under intense removal during the bounty period but became more so as carrying capacity changed due to human-caused habitat conversion (Cougar Management Guidelines Working Group 2005). Finally, our model did not account for the disproportionate impact that mortalities of different sex and age classes have on population dynamics. However, detecting these fine-scale population effects were beyond the scope of this study, and despite the limitations discussed herein, our model provides important insight into the overall effects of historical policies and laws on the statewide mountain lion population in California.

To our knowledge, no population estimates were conducted on mountain lions in California during most of the bounty period. The first known estimate by McLean (1954) of 600 mountain lions in California was made 10 years prior to the end of the bounty period. The next estimate of approximately 2,400 was published nearly 10 years after the bounty period ended (Sitton et al. 1976). We were unable to determine how these two estimates were derived. Subsequent researchers reported the number of mountain lions in California at 4,100 - 5,700 individuals (California Department of Fish and Game 1984), in which Department staff averaged adult densities from various studies across suitable mountain lion habitat statewide. The minimum population estimate (5,100) reported in Mansfield and Weaver (1989) did not distinguish between high, medium, and low habitat suitability, and thus identified almost 25% more highly suitable habitat for mountain lions than Torres et al. (1996), and used a density estimate 1.8 times greater than our highest estimate (Table 3). Given the differences in how these various estimates were derived, we were unable to use our findings to support or dispute any of these previous estimates.

A simple calculation of average adult mountain lion density (1.6/100 km^2; Quigley and Hornocker 2010; Beausoleil et al. 2013) in the western United States, and a recent estimate of mountain lion habitat in California (165,350-170,085 km^2; Dellinger et al. in press) suggests that the statewide mountain lion population in California occurs within the 1,500-5,000 range. Recent work estimating the effective population size (that portion of the total population likely to contribute to the next generation – essentially the breeding individuals in a population) of mountain lions in California is approximately 400 (Gustafson et al. 2018) also suggests that California's statewide mountain lion population is most likely in the 1,500-5,000 range (Frankham 1995). However, none of the population estimates discussed here are based on systematic assessments of mountain lions. In the absence of such robust data, we present our simulations based on the data available to us.

The general agreement among the results of our simulations with respect to mountain lion population trends during the bounty period regardless of input value (Figure 1), and low variation in trend slopes (see Supplementary Material), suggests that our model is a reasonable estimation of mountain lion population trends for that period. Some researchers have suggested that the bounty had little to no impact on the statewide mountain lion population (Fitzhugh and Gorenzel 1986), likely because previous research suggested it could sustain 25-30% removal rates. However, our analyses suggest that removal rates in many years during the bounty period regularly exceeded the removal threshold of 14% from our simulated populations (Figure 2). A plot of the take data for which removals exceeded the estimated removal threshold of 14% suggests that during the bounty period the number of mountain lions taken exceeded the population's ability to replace itself (Figure 2).

Our simulations also suggest that mountain lion populations increased following the bounty period (Figure 1), and that removal was below the replacement threshold of 14%

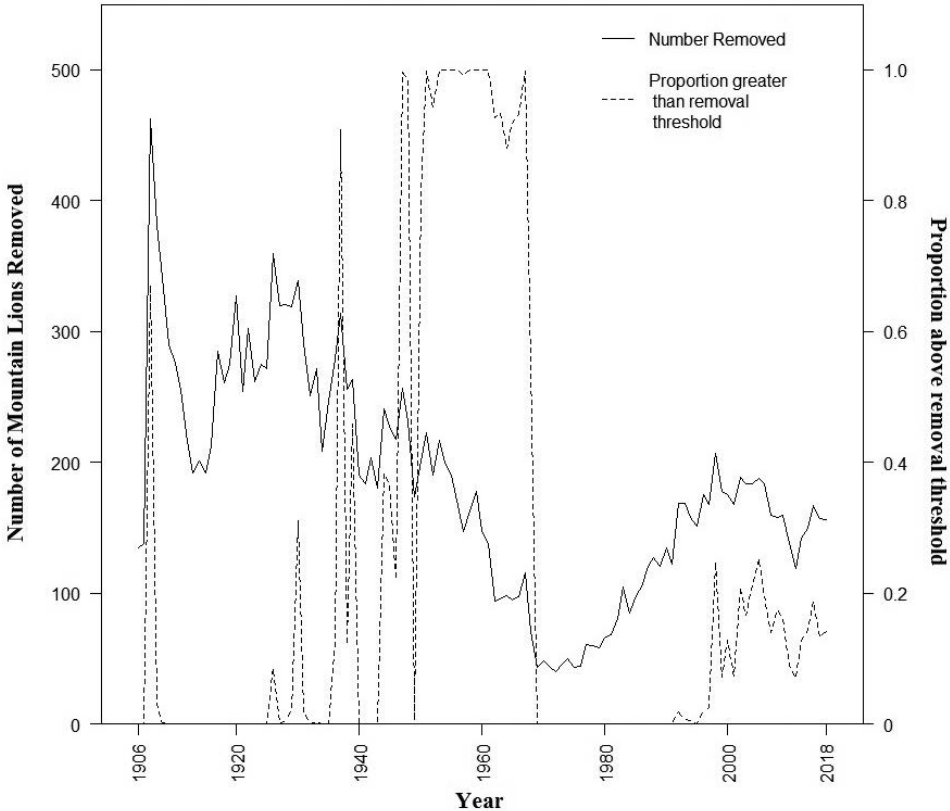

Figure 2. Mountain lion (*Puma concolor*) removal in California from 1906-2018 in relation to population simulation removal thresholds. Removal thresholds were determined from literature searches and set at 0.14 or 14% of the population. Likelihood of whether number of mountain lions removed in a given year (solid line) surpassed the removal threshold of 14% of the population was done by assessing proportion of all 1,000 simulations where removal > 0.14 x Nt (dotted line). The greater the proportion of instances where actual removal was greater than simulations for a given year, the greater the support for mountain lion populations having decreased during that given year (e.g., 1950-1970 in the figure).

(Figure 2), allowing the population to recover. Though our trend estimates began to diverge in the 1980s, the upward trend remained consistent until the 1990s (Table 4), after which our results were inconsistent, again likely due to the range in initial starting values. Further support for a rapid increase in the mountain lion population in the few decades following the end of the bounty period was an increase in distribution and number of mountain lions taken via depredation permit in California over the same time period (Torres et al. 1996). For example, mountain lions may have been extirpated from or severely reduced in the Santa Cruz Mountains based on the fact that only five animals were bountied in the Santa

Cruz Mountains, with the last one taken in 1923 (McLean 1954). Then it appears mountain lions subsequently recolonized the area following the bounty period based on the fact that there have been ≥12 mountain lion depredation events per year in the Santa Cruz Mountains in the last 10 years (CDFW 2019). This example demonstrates the ability of mountain lion populations to recover quickly following intense removal (Cougar Management Guidelines Working Group 2005; Quigley and Hornocker 2010). Release from incentivized and widespread intensive removal likely decreased overall anthropogenic mortality of mountain lions, increased their survival rates, and allowed the population to grow. This increase in number of mountain lions taken via depredation permit could have arisen in part due to increased human density, land-use changes, and an increase in development; however, increased human-carnivore conflict has been shown to increase with increasing carnivore population size (Torres et al. 1996; Thompson 2009; Vickers et al. 2015; Poudyal et al. 2016; Teichman et al. 2016). Further, Torres et al. (1996) demonstrated that most mountain lion depredations in California from 1972-1995 were not in counties with high human densities or development. This suggests that increases in mountain lion depredations could be the result of an overall increase in mountain lion populations. Additional research into how local mountain lion abundance relates to local depredation incidents and human density and development is needed to tease apart how these factors interact in California.

A logical explanation of our results is that California's mountain lion population was unable to withstand the high rates of removal under the bounty, causing their numbers to decline significantly from the early 1900s until well into the 1960s; after which they were released into an overabundant prey base, allowing their numbers to increase rapidly into the 1990s. During the 1960s, as the bounty on mountain lions ended, deer populations in California had peaked (Longhurst et al. 1976). During the decades following the 1960s, deer were declining due to a number of factors (Chapel and Rempel 1981; Neal et al. 1987; Loft and Bleich 2014), while the mountain lion population initially increased rapidly, and eventually came into equilibrium with its much-declined prey base after 2000.

We attribute the variability in our results for the most recent period (e.g., 2000-2018) to the broad range of input values (Tables 3, 4). Efforts to effectively assess mountain lion populations are lacking (Sitton et al. 1976; Weaver 1982; CDFG 1984; Fitzhugh and Gorenzel 1986; Mansfield and Weaver 1989), and that lack of effort is especially notable since the 1970s. Wildlife policies and laws are most effective when based on scientifically rigorous data. Given the diversity of stakeholder interests and agency issues related to managing and conserving mountain lions in California (Bruskotter and Shelby 2010; Davenport et al. 2010), our results highlight the need to remedy the knowledge deficit by significantly increasing our assessment efforts. This would give the Department the information they need to accurately assess the implications of the specially-protected status of mountain lions in California.

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This work was supported by the California Department of Fish and Wildlife. We recognize and appreciate the efforts of past employees who carefully compiled and maintained the important historical and current databases used to carry out these analyses. We thank M. Kenyon Jr., D. Weaver, L. Sitton, C. Del Signore, H. Keough.

Author Contributions:

Conceived and designed the study – JD & ST
Collected the data – ST
Performed the analyses – JD
Authored the MS – JD & ST
Critical revisions – JD

LITERATURE CITED

Beausoleil, R. A., G. M. Koehler, B. T. Maletzke, B. N. Kertson, and R. B. Wielgus. 2013. Research to regulation: cougar social behavior as a guide for management. Wildlife Society Bulletin 37:680–688.

Bruskotter, J. T., and L. B. Shelby. 2010. Human dimensions of large carnivore conservation and management: Introduction to the special issue. Human Dimensions of Wildlife 15:311–314.

California Department of Fish and Game (CDFG). 1984. Computer simulation model for mountain lions. California Department of Fish and Game, Sacramento, CA, USA.

California Department of Fish and Wildlife (CDFW). 2019. Table of mountain lion depredation permits issued by CDFW and number of mountain lions reported taken by permittees in California by county (2001–2018). Available from: http://nrm.dfg.ca.gov/ FileHandler.ashx?DocumentID=171192&inline

Chapel, M., and R. Rempel. 1981. Management plan for the North Kings deer herd. U.S. Forest Service, Fresno, CA, USA.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cougar Management Guidelines Working Group. 2005. Cougar management guidelines. Opal Creek Press, Salem, OR, USA.

Davenport, M. A., C. K. Nielsen, and J. C. Mangun. 2010. Attitudes toward mountain lion management in the Midwest: implications for a potentially recolonizing large predator. Human Dimensions of Wildlife 15:373–388.

Dellinger, J. A., B. Cristescu, J. Ewanyk, D. J. Gammons, D. Garcelon, P. Johnston, Q. Martins, C. Thompson, T. W. Vickers, C. C. Wilmers, H. U. Wittmer, and S. G. Torres. *in press.* Using mountain lion habitat selection in management. Journal of Wildlife Management.

Elton, C., and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. The Journal of Animal Ecology 11:215–244.

Fitzhugh, E. L., and W. P. Gorenzel. 1986. The biological status of the California mountain lion. Vertebrate Pest Conference 12:336–346.

Frankham, R. 1995. Effective population size/adult population size ratios in wildlife: a review. Genetic Research 66:95–107.

Gustafson, K. D., R. B. Gagne, T. W. Vickers, S. P. Riley, C. C. Wilmers, V. C. Bleich, B. M. Pierce, M. Kenyon, T. L. Drazenovich, J.A. Sikich, and W. M. Boyce. 2019. Genetic source-sink dynamics among naturally structured and anthropogenically fragmented puma populations. Conservation Genetics 20: 215–227.

Jedrzejewski, W., B. Jedrzejewska, H. Okarma, K. Schmidt, A. N. Bunevich, and L. Milkowski. 1996. Population dynamics (1869–1994), demography, and home ranges of the lynx in Bialowieza Primeval Forest (Poland and Belarus). Ecography 19:122–138.

Kojola, I. 2005. The biology of the wolf and the viability of the wolf population. Pages 8–5 in Management Plan for the Wolf Population in Finland. Ministry of Agriculture and Forestry, Helsinki, Finland.

Lambert, C. M. S., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

Loft, E. R., and V. C. Bleich. 2014. History of the conservation of critical deer ranges in California: concepts and terminology. California Fish and Game 100:451–472.

Longhurst, W. M., E. O. Garton, N. F. Heady, and G. E. Connolly. 1976. The California deer decline and possibilities for restoration. Transactions of the Western Section of the Wildlife Society 16:74–101.

Mansfield, T., and R. Weaver. 1989. The status of mountain lions in California. Transactions of the Western Section of the Wildlife Society 25:72–76.

McLean, D. D. 1954. Mountain lions in California. California Fish and Game 40:147–166.

Mykra, S., and M. Pohja-Mykra. 2015. Back-calculation of large carnivore populations in Finland in 1865–1915. Annales Zoologici Fennici 52:285–300.

Neal, D. L., G. N. Stegar, and R. C. Bertram. 1987. Mountain lions: preliminary findings on home-range use and density in the central Sierra Nevada. Pacific Southwest Forest and Range Experimental Station, Research Note PSW-392, CA, USA.

Nowak. R. M. 1974. The cougar in the United States and Canada. United States Fish and Wildlife Service, Office of Endangered Species, Washington D.C., USA.

Poudyal, N., N. Baral, and S. T. Asah. 2016. Wolf lethal control and livestock depredations: counter-evidence from respecified models. PLOS ONE 11:e0148743.

Quigley, H., and M. Hornocker. 2010. Cougar population dynamics. Pages 59–75 in M.G. Hornockerand, and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, IL, USA.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.R-project.org

Robinson, H. S., and R. M. DeSimone. 2011. The Garnet Range mountain lion study: characteristics of a hunted population in West-central Montana. Final report, Montana Department of Fish, Wildlife, and Parks, Wildlife Bureau, Helena, MT, USA.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Sitton, L. W., S. Wallen, R. A. Weaver, and W. G. MacGregor. 1976. California mountain lion study. California Department of Fish and Game, Sacramento, CA, USA.

Teichman, K. J., B. Critescu, and C. T. Darimont. 2016. Hunting as a management tool? Cougar-human conflict is positively related to trophy hunting. BMC Ecology 16:44.

Thompson, D. J. 2009. Population demographics of cougars in the black hills: survival, dispersal, morphometry, genetic structure, and associated interactions with density

dependence. Dissertation. South Dakota State University, Brookings, SD, USA.

Torres, S. G., T. M. Mansfield, J. E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. Wildlife Society Bulletin 24:451–460.

Vickers, T. W., J. N. Sanchez, C. K. Johnson, S. A. Morrison, R. Botta, T. Smith, B. S. Cohen, P. R. Huber, H. B. Ernest, and W. M. Boyce. 2015. Survival and mortality of pumas (*Puma concolor*) in a fragmented, urbanizing landscape. PLOS ONE 9:e0131490.

Walgamuth, D. 2017. California Deer Summer 2017: deer first. California Deer Association. Sacramento, CA, USA.

Walter, R. 2015. Cats in a cage. Sierra: the national magazine of the Sierra Club. Sierra Club, Oakland, CA, USA.

Weaver, R. A. 1982. Status of the mountain lion in California with recommendations for management. California Department of Fish and Game, Sacramento, CA, USA.

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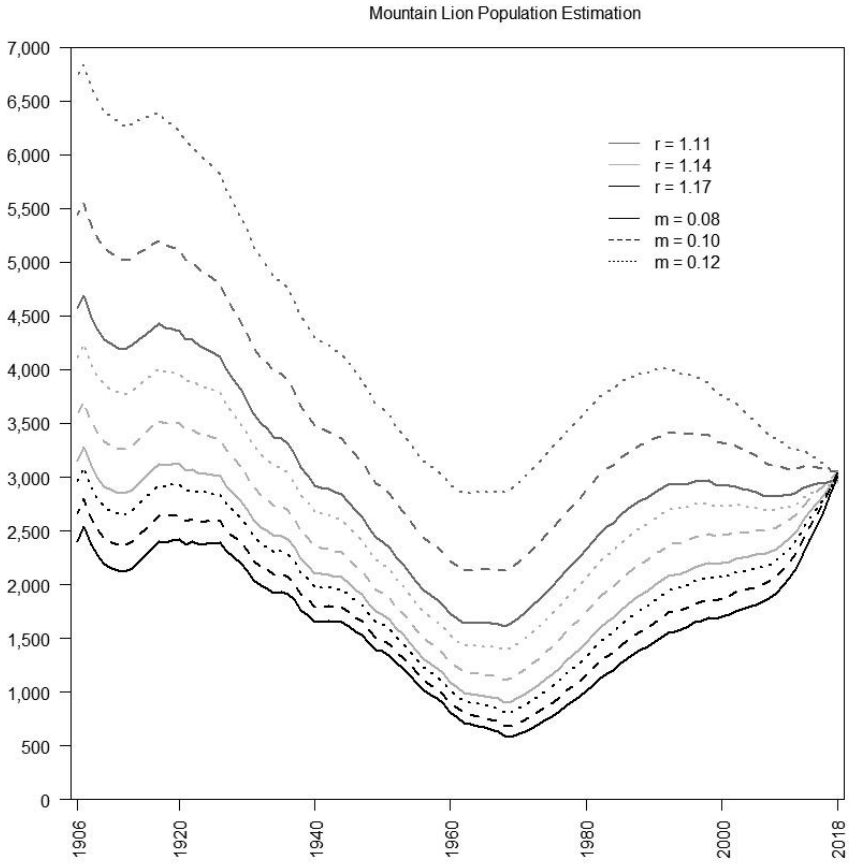
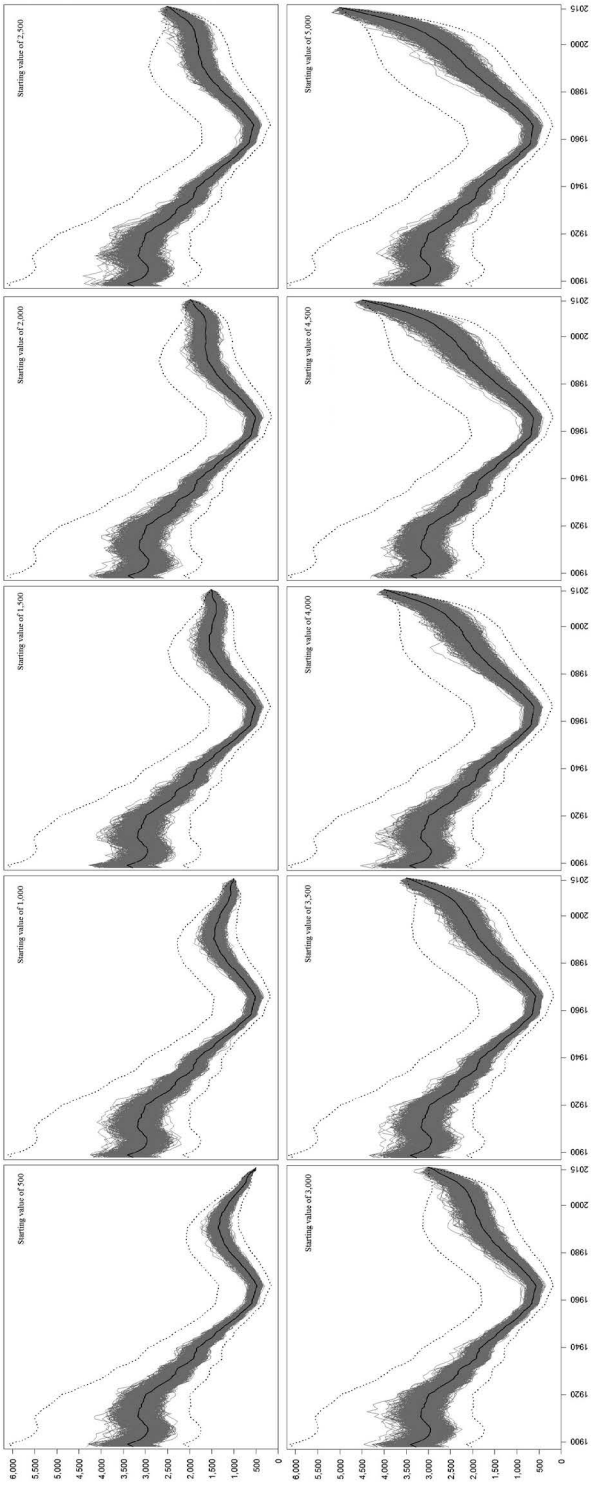
SUPPLEMENTARY MATERIAL

We estimated the sensitivity of population simulations to changes in annual population growth (λ) and additional annual mortality (m) rates. We allowed the input value to vary in a uniform distribution between 500 and 5,000 while changing the mean λ and m values. We set the mean value of λ variously at 1.11, 1.14 (used in main analyses), and 1.17, and that of m at 0.08, 0.10 (used in the main analyses), and 0.12. We conducted 1,000 simulations for each λ and m value, which resulted in 9 different groupings of 1,000 simulations. For example, one set of 1,000 simulations had a mean λ value of 1.11 and a mean m value of 0.08. Visual examination of the results demonstrated that changes to mean λ and m values, respectively, did change the results of our population simulations, but the population trends (i.e., overall decreasing during the bounty period and overall increasing post-bounty) were unchanged (Supplementary Figure 1).

We also estimated the sensitivity of our simulations to input population values. We used the parameterizations described in the manuscript but held the input value constant for 1,000 simulations. We did this for different input population values in intervals of 500. For example, we conducted 1,000 simulations wherein we held the input population value constant at 500. We then conducted another 1,000 simulations wherein we held the input population constant at 1,000. We did this at intervals of 500 up to a starting population value of 5,000. Visual examination of the results demonstrated that influence of starting value on simulated population trends decreased around the year 2000 (Supplementary Figure 2). Furthermore, starting population value did not change the overall trends of simulated populations during the bounty (i.e., decreasing mountain lion population size) or post-bounty up to the mid-1990s (i.e., increasing mountain lion population size).



Supplementary Figure 1.



Supplementary Figure 2.

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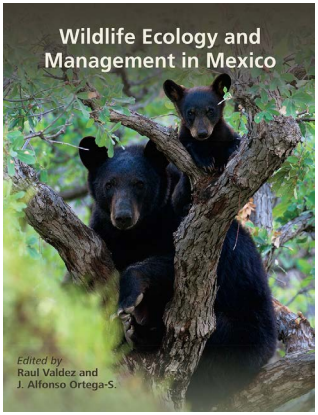
BOOK REVIEW

Wildlife Ecology and Management in Mexico

Edited by Raul Valdez and J. Alfonso Ortega-S. 2019. Texas A&M University Press, College Station, Texas, USA. 402 pages (hard cover). $60.00. ISBN:978-1-62349-723-1



This book is the English-language translation of an earlier work that was published in Spanish. In 2014, Drs. Valdez and Ortega-S. co-edited the volume *Ecologia y Manejo de Fauna Silvestre en Mexico*, published by Editorial Colegio de Postgraduados in Mexico. That work (hereafter, *Ecologia y Manejo*) was the most complete volume on wildlife and conservation in that country since publication of A. Starker Leopold's 1959 classic, *Wildlife of Mexico: The Game Birds and Mammals*. Leopold's work was translated into Spanish, and was a seminal contribution that stimulated many students and professionals in Mexico to pursue interests in wildlife research and conservation in that country. Sixty years following publication of Leopold's tome, Valdez and Ortega's *Wildlife Ecology and Management in Mexico* has made the tremendous amount of information in their Spanish-language volume, *Ecologia y Manejo*, readily available to a vast, English-speaking readership.

The editors brought together a team of 46 experts to contribute to this work. It is especially noteworthy that the majority of contributors are scientists representing Mexican universities or agencies and that are, or previously have been, actively involved in research on or management of birds or mammals in their country. Most of the other contributors also have worked for many years in Mexico, either through affiliations with academic institutions or agencies in that country, or through American universities. Thus, familiarity with the history, policies, and challenges to wildlife conservation, or knowledge of the biology of the taxa discussed in this work largely was gained first-hand.

The book consists of 22 chapters, 5 of which address historical, social, political, or economic aspects of wildlife conservation in Mexico, and the remainder of which are dedicated to various species or groups that represent the primary game birds and large mammals occurring there. Mexico ranks fifth in biodiversity on a world-wide scale. The country is inhabited by 1,107 species of birds and 544 mammals; thus, the current work concerns but a tiny fraction of the avian and mammalian fauna found there. Nevertheless, the taxa addressed are, in many ways, those most apt to require attention from a management or conservation perspective. To that end, Valdez, Ortega-S., and the contributors have produced a volume that not only will have a long-term influence on wildlife management in Mexico, but will be a lasting reference for English-speaking scientists not familiar with conservation and management issues in that country. I believe it will also stimulate more English-speaking scientists to initiate collaborative work with Mexican researchers or managers and, thereby, lead to enhanced efforts on behalf of conservation.

An unfortunate, albeit unavoidable, consequence of the 4-year process involved in producing the English-language edition of *Ecologia y Manejo* was the inability to include references to the most recent ongoing work. The literature is complete, however, up to publication of *Ecologia y Manejo* and many of the chapters include references published as recently as 2013. From my perspective, this is not an issue that should be of concern to interested readers, and it does not detract from the utility or value of this work. Indeed, among the extremely valuable material included was that dedicated to enhancing the reader's understanding of the historical and conservation perspectives of wildlife (Chapter 1); natural and human landscapes (Chapter 2), wildlife as a public and economic resource (Chapter 3); evolution of wildlife laws and policies (Chapter 21); and challenges to wildlife conservation strategies (Chapter 22) in Mexico. These are topics with which many wildlife biologists—me included—likely would not be familiar, but also are topics central to issues of wildlife conservation, whether game, 'non-game', or endangered species.

Valdez and Ortega-S. are to be commended for producing this book, which will be of value to those working on management and conservation issues in Mexico, as well as those seeking a better understanding of the complexities of conservation in that country. There is much to be learned, and the material included has important implications for the management of wildlife in Mexico and will be a "go-to" source for many years to come. As the first major contribution of this type since Leopold's 1959 effort, publication in English is timely, welcomed, and appreciated.

VERNON C. BLEICH, *Department of Natural Resources and Environmental Science, University of Nevada Reno and Eastern Sierra Center for Applied Population Ecology, Bismarck, ND, USA*

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INFORMATION FOR AUTHORS

The California Fish and Wildlife Journal (CFWJ) is a peer-reviewed, scientific journal focused on the biology, ecology, and conservation of the flora and fauna of California and surrounding areas, and the northeastern Pacific Ocean.

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Front. One-and--half-inch long young of the year Giant Seabass. Photo © Michael Couffer.

Back. Mountain lion (*Puma concolor*). Photo by Gerald and Buff Corsi © California Academy of Science

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